Title
Systematic Research on the Millipede Assassin Bugs (Hemiptera: Reduviidae: Ectrichodiinae)

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Publication Date
2016

UNIVERSITY OF CALIFORNIA
RIVERSIDE

Systematic Research on the Millipede Assassin Bugs (Hemiptera: Reduviidae: Ectrichodiinae)

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

Doctor of Philosophy

in

Entomology

by

Michael Forthman

March 2016

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Acknowledgments

Attaining a doctorate in science is by no means an easy feat. I could not have achieved this dream had it not been for the support, encouragement, and love from so many people during my graduate career. First and foremost, I want to express my gratitude to my dissertation advisor, Christiane Weirauch, who offered substantial guidance with my research projects and professional development with grant proposals, scientific writing, presentations, and organizational involvement. I also want to thank all the members of my dissertation committee (John Heraty, Mark Springer, and Bradley Mullens), all of whom provided valuable support and guidance on my dissertation, as well as amazing encouragement, throughout my time at UCR. I also thank a good friend and collaborator, Dominik Chłond, who contributed to a massive monograph of Madagascan Ectrichodiinae.

There are many colleagues from the Weirauch and Heraty labs that I consider as family. All of them have provided a lot of perspective on grad school, project design, data analysis, the plethora of phylogenetic programs in existence, and life in general: Austin Baker, Lily Berniker, Roger Burks, Dimitri Forero, Sarah Frankenberg, Eric Gordon, John Hash, Judith Herreid, Rochelle Hoey-Chamberlain, Wei Song Hwang, Alexandr Knyshov, Sunghoon Jung, Stephanie Leon, Paul Masonick, Jason Mottern, Elizabeth Murray, Ryan Perry, Guanyang Zhang, and Junxia Zhang.

I would like to extend my appreciation to the following individuals who donated or loaned specimens for the purpose of this dissertation: Jean-Michel Berenger, Dominik Chłond, Eliane de Coninck, Jason Cryan, David Grimaldi, Eric Guilbert, Tom Henry, Michael Ivie, John Longino, Rudolf Meier, Joshua Oyelade, Norm Penny, Dávid Rédei, Ruth Salas, Toby Schuh, Michael Sharkey, David Wagner, Mick Webb, and the students and instructors of the 2010 Organization for Tropical Studies field-course in Costa Rica. I want to thank Claudia Alvarez, Nick Duncan, Rochelle Hoey-Chamberlain, and Sarah Frankenberg for assisting me with specimen curation for a ridiculously large amount of material. Rochelle Hoey-Chamberlain also willingly assisted with some molecular benchwork for the last chapter. I extend my appreciation to Petra Sierwald for providing references on millipede taxonomy and to Wanzhi Cai for verifying the identifications of some Asian Ectrichodiinae. Ted Garland, Jr. was very helpful with running PLogReg.m.

I am lucky to have a very close, loving, and supportive group of friends and family. Unfortunately, many of my family members that supported my decision to get a Ph.D. in entomology are no longer here to see my achievements. Regardless, I owe everything I have and everything I am to living and deceased family members and all my friends. In particular, my late mother, Carol Forthman, always taught me to love who I am, pursue what I love, and always be humble and compassionate along the way. She sacrificed a lot in life for my education and career goals. I am also very appreciative of my great-uncle, Thomas Bruce, who passed away 11 days before my defense after a long fight with cancer. He was very encouraging and financially supportive in my endeavor to become a professional academic. Lastly, I must thank two very important people in my life, John Nelson and Steve Weber for their love, support in life, and sacrifices so that I could pursue my love of entomology and systematics. Both also put in a lot of effort on the final aspects of my dissertation: Steve literally made thousands of pie charts for the last chapter, and John helped to curate specimens.

This dissertation was supported by the National Science Foundation PEET DEB 093333853 grant (awarded to Christiane Weirauch); Entomological Society of America Systematic, Evolution, and Biodiversity Travel Award; Earle C. Anthony Graduate Student Travel Award; Graduate Dean's Dissertation Research Grant; Department of Entomology at the University of California – Riverside; and the University of California – Riverside Graduate Division

Dissertation Year Program Award. Some specimens loaned for this research were acquired under NSF DEB 0542864 (awarded to Michael Sharkey and Brian Brown), NSF BSI 0072713 (awarded to Brian Fisher and Charles Griswold), and NSF DEB 1354739 (awarded to John Longino).

The text of this dissertation, in part, is a modified reprint of the material as is appears in Forthman & Weirauch (2012; *European Journal of Entomology* 109: 147–153), Forthman et al. (in press; *Bulletin of the American Museum of Natural History*), and Forthman & Weirauch (in press; *Molecular Phylogenetics and Evolution*). The co-author Christiane Weirauch directed and supervised the research that forms the basis of this dissertation. The co-author Dominik Chłond contributed to the taxonomic descriptions for some of the new species, including images and drawings.

Dedication

This dissertation is dedicated to

all of my family, even those who rest eternally.

ABSTRACT OF THE DISSERTATION

Systematic Research on the Millipede Assassin Bugs (Hemiptera: Reduviidae: Ectrichodiinae)

by

Michael Forthman

Doctor of Philosophy, Graduate Program in Entomology
University of California, Riverside, March 2016
Dr. Christiane Weirauch, Chairperson

The predominantly circumtropical millipede assassin bugs (Ectrichodiinae) comprise the fifth largest subfamily of Reduviidae with 736 described species in 121 genera. Ectrichodiinae appear to be specialized millipede predators and stand out among other Reduviidae in the high proportions of aposematically colored and sexually dimorphic species. These phenomena make Ectrichodiinae an attractive group for ecological, behavioral, and evolutionary research, but is hindered by a lack of thorough taxonomic treatments and phylogenetic hypotheses. This dissertation improves our knowledge of Ectrichodiinae life history, diversity, and phylogeny by: 1) reviewing Ectrichodiinae predatory behaviors and supplementing this with field observations; 2) revising the Madagascan fauna; 3) investigating historical biogeographic patterns of Madagascan Ectrichodiinae; and 4) constructing the most comprehensive Ectrichodiinae+ Tribelocephalinae phylogeny to study the evolution of aposematic coloration and sexual dimorphism. (1) About 2% of Ectrichodiinae species are documented to prey on juliform and, to a lesser extent, polydesmid millipedes. The majority of observations suggest that immatures typically exhibit communal predation, while adults usually engage in solitary predation. (2) The taxonomic monograph includes description of 63 new species and three new genera of endemic Madagascan Ectrichodiinae, as well as redescriptions and synonymies of previously described taxa. (3) Madagascan Ectrichodiinae do not form a monophyletic group, with lineages exhibiting close relationships with Oriental or Afrotropical taxa. Ectrichodiinae colonized Madagascar in the last 68 my via transoceanic dispersal at least twice from the Oriental region and once from the Afrotropical region; a single out-of-Madagascar dispersal event to the Afrotropical region is recovered in some analyses. Dispersal between these regions were likely facilitated by islands and/or ocean currents. (4) Ectrichodiinae are not monophyletic with respect to Tribelocephalinae. Aposematic coloration evolved from a cryptic ancestor early in the evolutionary history of Ectrichodiinae+Tribelocephalinae, with subsequent reversals and regains. A positive association between the prevalence of aposematic coloration and body length is recovered when phylogenetic logistic regressions are conducted on ultrametric trees, but is not supported when phylograms are used. Extreme sexual dimorphism is shown to evolve multiple times from a more limited condition. Based on phylogenetic results, a new Ectrichodiinae classification is proposed.

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Introduction

Assassin bugs, or Reduviidae, are the largest hemimetabolous clade of predatory insects (>7,000 spp.) and the second most speciose family of Heteroptera (Hemiptera). While most species are generalist predators, there is a striking range of prey specialization in several subfamilies (e.g., termite-feeding Salyavatinae [Gordon & Weirauch, 2016]; araneophagic Emesinae [Wignall & Taylor, 2011]). Reduviidae also include the notorious vertebrate-blood feeding Triatominae that vector Chagas disease (Lent & Wygodzinsky, 1979). Species in some clades have evolved morphological adaptations for prey-capture, e.g., sticky-trap predation (Harpactorinae; Weirauch, 2006; Zhang & Weirauch, 2013), subchelate and chelate forelegs (Phymatinae; Weirauch et al., 2011), and tibial attachment structures in several subfamilies (Weirauch, 2007). A number of studies have advanced our understanding of Reduviidae phylogenetics (e.g., Weirauch, 2008; Weirauch & Munro, 2009; Hwang & Weirauch, 2012; Zhang et al., 2016), but the relationships and monophyly of several subfamilies remain uncertain.

The predominantly circumtropical millipede assassin bugs, or Ectrichodiinae, comprise the fifth largest Reduviidae subfamily (736 described species, 121 genera; Gil-Santana, 2015; Forthman et al., in press and references within). Ectrichodiinae are the most evolutionarily successful, in in terms of extant diversity, clade of millipede specialists, a group of prey organisms few arthropods exploit (Forthman & Weirauch, 2012). They further stand out among other Reduviidae in the high proportions of species with aposematic coloration and metallic features. A number of species also exhibit drastic sexual dimorphism, which poses significant difficulty in associating sexes when using morphology alone. These phenomena make Ectrichodiinae an attractive group for ecological, behavioral, and evolutionary research, which is hindered by a lack of thorough taxonomic treatments and phylogenetic hypotheses. Prior to this dissertation, relationships between genera had not been cladistically tested beyond a genus-level phylogeny of New World taxa (Dougherty, 1995). Faunistic checklists and descriptions of taxa based on few specimens of a single sex predominate the taxonomic literature, which is characterized by a lack of illustrations, identification keys, and synthetic revisions. Few Ectrichodiinae have been incorporated in recent Reduviidae phylogenetic analyses based on morphological or molecular datasets (Weirauch, 2008; Weirauch & Munro, 2009; Weirauch, 2010; Hwang & Weirauch, 2012; Zhang et al., 2016). Based on these studies, Ectrichodiinae monophyly is not firmly established and remains to be investigated using morphological and molecular data for a larger sample of taxa. My dissertation research integrates natural history, revisionary taxonomy, and morphological and molecular phylogenetics to improve our knowledge of Reduviidae phylogenetics, specifically the subfamily Ectrichodiinae.

Chapter 1: Predatory behaviors of Ectrichodiinae: Several species are known to feed on chemically defended millipedes (e.g., Green, 1925; Haridass & Ananthakrishnan, 1980; Haridass, 1985). However, details on the ectrichodiine-millipede relationship are scarce, and documentation is mostly based on anecdotal evidence. To investigate predatory behaviors in Ectrichodiinae, natural history observations in the field and laboratory are made and supplemented with published literature and online images to investigate prey specificity, communal predation, and insertion of mouthparts into millipedes.

Chapter 2: Taxonomic monograph of the Madagascan Ectrichodiinae: Madagascar is one of the world's premier biodiversity hotspots (Myers et al., 2000), and the island's terrestrial arthropods are in danger of extinction due to anthropogenic influences (Sussman et al., 1996; Myers et al., 2000). An impediment to identifying areas for conservation is the incomplete knowledge of the island's pattern of species richness, turnover, and endemism (Schatz, 2002; Smith et al., 2005). The California Academy of Sciences' Terrestrial Arthropod Inventory of Madagascar Project addressed the need for taxonomic exploration of the arthropod fauna and has yielded >2,000 Ectrichodiinae specimens, revealing a dramatic undescribed species-level diversity. Thus, the Madagascan Ectrichodiinae is documented and revised.

Chapter 3: Biogeography of the Madagascan Ectrichodiinae: Despite Madagascar's proximity to Africa, a large proportion of the known biota is closely related to Oriental lineages (Vences, 2004; Yoder & Nowak, 2006). Although Gondwanan vicariance is thought to be responsible for the presence of some Madagascan lineages, most colonized the island via transoceanic dispersal after the island separated from Africa (~160 mya) and India (80–90 mya) (Vences 2004; Yoder & Nowak, 2006). A recent divergence dating analysis of Reduviidae suggests that Ectrichodiinae arose after the Madagascar-India split (Hwang & Weirauch, 2012). Thus, dispersal is likely responsible for the endemic Madagascan Ectrichodiinae fauna, but the origin and timing of colonization remains unknown. Morphological and molecular phylogenies are constructed and used for divergence dating and biogeographic analyses to investigate geographic and oceanic factors that may have facilitated long-distance dispersal between Madagascar and other regions.

Evolution of aposematic coloration and sexual dimorphism: A few comparative phylogenetic studies support a positive correlation between aposematic coloration and body size (e.g., Hagman & Forsman, 2003; Rudh, 2013), while others support a negative or no correlation (Nilsson & Forsman, 2003; Cheney et al., 2014). Few insect phylogenetic studies investigating the relationship between these two traits are restricted to the Lepidoptera (Tullberg & Hunter, 1996; Nilsson & Forsman, 2003), but larval gregariousness may confound results (Nilsson & Forsman, 2003). Ectrichodiinae exhibit a diversity of color patterns across all body sizes, are generally solitary, and are thus an excellent model for investigating the coloration-body size relationship. Some species also exhibit drastic sexual dimorphism with major changes in female morphology, and this remains to be explored in a phylogenetic context. A comprehensive

phylogeny is constructed for Ectrichodiinae and Tribelocephalinae using morphology and molecular data, ancestral state reconstructions on coloration and sexual dimorphism are performed, and a phylogenetic comparative method is employed to test for a coloration-body size association. Phylogenetic results are used to revise the Ectrichodiinae classification.

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Chapter 1: Toxic associations: natural history observations and review of the predatory behaviors of millipede assassin bugs (Hemiptera: Reduviidae: Ectrichodiinae)

Abstract

Ectrichodiinae (Hemiptera: Reduviidae), the millipede assassin bugs, are a speciose group (>660 species) of assassin bugs that appear to be specialist predators on Diplopoda, or millipedes. Apparently capable of coping with the noxious defensive compounds produced by many millipedes, Ectrichodiinae are engaged in a predator-prey relationship with millipedes realized only by few other arthropods. Unfortunately, feeding behaviors of Ectrichodiinae are inadequately documented, rendering this exciting phenomenon largely inaccessible. We here present a literature review on ectrichodiine prey selection and feeding behaviors, with supplemental original observations on *Rhiginia cinctiventris* (Stål), 1872, in Costa Rica. Thirteen species in 12 genera have been observed to feed on millipedes. The majority of diplopod prey species were reported from the orders Spirostreptida and Spirobolida, whereas Polydesmida are rarely attacked. Ectrichodiinae insert their stylets at the millipede's intersegmental membranes on the ventral and ventrolateral trunk area or between the head and collum. Communal predation was observed among conspecific nymphs, among groups of nymphs with a conspecific adult, and more rarely among adults. Immature ectrichodiines were rarely observed to engage in solitary predation. Observations on *R. cinctiventris* indicate that this species preys on spirobolid and polydesmid millipedes and are in agreement with behaviors described for other Ectrichodiinae.

Introduction

Millipedes (Diplopoda) are a diverse group of arthropods that include 16 orders represented by approximately 12,000 species in 145 families (Sierwald & Bond, 2007). In 11 of these orders, millipedes are protected from predators by chemical defenses produced in glands that vary in number among orders and are located laterally or mid-dorsally in the diplosegments (Eisner et al., 1978; Hopkin & Read, 1992). The major defense components of these secretions seem to exhibit a phylogenetic pattern: Julida, Spirostreptida, and Spirobolida (Superorder Juliformia) produce benzoquinones; Callipodida and Chordeumatida produce phenols; Glomerida and Polyzoniida produce alkaloids and quinazolinones; Polydesmida produce cyanogenic compounds; and Platydesmida, Siphonocryptida, and Siphonophorida produce terpenoids (Eisner et al., 1978; Hopkin & Read, 1992; Sierwald & Bond, 2007). Despite such defenses, many vertebrates prey on millipedes (Sierwald & Bond, 2007). In addition, some invertebrates are specialized predators or parasitoids on juliform millipedes (Banks, 1911; Picard, 1930; Lawrence, 1984; Eisner et al., 1998; Dejean et al., 2001; Brunke et al., 2009; Larsen et al., 2009). None of these groups of millipede specialists are particularly speciose. This is dramatically different in the Ectrichodiinae, the fifth largest subfamily of Reduviidae (Hemiptera: Heteroptera), or assassin bugs, that appears to be specialized on millipedes (Green, 1925; Haridass & Ananthakrishnan, 1980; Haridass, 1985).

The circumtropical millipede assassin bugs comprise >660 species in 123 genera (Maldonado, 1990; Dougherty, 1995; Carpintero & Maldonado, 1996; Weirauch et al., 2009; Chłond, 2010). Species have been collected while feeding on millipedes, but details on the predator-prey relationships, including prey specificity and point of mouthpart insertion are largely undocumented. Thus, it is unknown if Ectrichodiinae target the millipede’s nervous system to maximize the impact of their toxic saliva. It is also unknown if Ectrichodiinae target the body regions that possess defensive glands to sequester their own defensive compounds, or if they avoid the millipedes’ defense glands. In addition, predation in Ectrichodiinae may be a communal activity (Haridass & Ananthakrishnan, 1980; Haridass, 1985) rather than a solitary behavior as usually observed in Reduviidae (Readio, 1927; McMahan, 1983; Li et al., 2010), but details on this unusual subsocial behavior are scarce.

Here, we compile published data and evaluate images available on the Internet for prey specificity, point of stylet insertion, and communal predation. In addition, data for *Rhiginia cinctiventris* (Stål), 1872, are presented based on observations in the field and laboratory at one site in Costa Rica; feeding observations have never been reported for this genus before. Literature and original data were analyzed in response to three questions: (1) Does the literature data suggest a pattern of Ectrichodiinae prey preference for species in particular millipedes orders? (2) Assuming that Ectrichodiinae either target or circumvent the millipede's defense glands, where do they insert their mandibular and maxillary stylets to inject toxic saliva and digestive enzymes? (3) Are communal predation strategies commonly observed in nymphs and adults?

Literature Review and Analysis of Online Image Material

Publications and online images containing information on Ectrichodiinae feeding behavior were evaluated for information regarding ectrichodiine and millipede taxa, ectrichodiine developmental stage, stylet insertion, and communal predation (Table 1.1). Even though some references identified millipedes to genus or species (Cachan, 1952; Miller, 1953; Haridass & Ananthakrishnan, 1980; Lawrence, 1984; Giliomee, 1985; Ambrose, 1999), the validity of these names have changed over the years and identification without voucher material is tentative. Thus, We focus on establishing a pattern based on the prey order level instead. Victor Cheah (http://www.clubsnap.com/ forums/threads/861603-Assassin-feed-on-millipede; accessed 20 Jun. 2011), Jonker Fourie (http://fireflyafrica. blogspot.com/2009/01/shongololo-millipede.html; accessed 13 Jun. 2011), Helcio Gil-Santana (http://www. nadiplochilo.com/fpseudonannolenidae.html; accessed 18 Aug. 2011), Joce Gordon (http://www.

marlothparkhonoraryrangers.co.za/?page_id=976; accessed 18 Oct. 2011), Zichen Wang (http://www.flickr. com/photos/biozcw/5247453267/; accessed 18 Aug. 2011), Eddy Lee (http://www.flickr.com/photos/ lonesomecrow/5750042813/; accessed 18 Aug. 2011), Ted MacRae (http://beetlesinthebush.wordpress.com/ 2009/02/18/millipede-assassin-bug/; accessed 18 Aug. 2011), Alan Weaving (http://imagepro.photography.com/ weaving; accessed 18 Aug. 2011), and Arend van de Wetering (http://www.whatsthatbug.com/2008/08/22/ millipede-assassin-bugs-from-south-africa/; accessed 18 Oct. 2011) took images used in the analysis and gave permission to publish the data and images (Fig. 1.1). Two images did not specify the photographer or provide contact information; these images were found on the following websites: http://www.flickr.com/photos/ 12639178@N07/5631578778/ (accessed 18 Oct. 2011) and http://www.whatsthatbug.com/2008/08/22/millipedeassassin-bugs-from-south-africa/ (accessed 18 Oct. 2011).

Field and Laboratory Procedures

Specimens of *Rhiginia cinctiventris* were collected at La Selva Biological Research Station, Costa Rica (10.430862°N 84.006467°W) from August 9–15, 2010. Ectrichodiinae and millipedes were placed individually into petri dishes or larger containers with moist tissue. Immature ectrichodiines were determined to be the same species as adults based on coloration and proximity to adults. Sex and developmental stages were determined prior to feeding observations. Individual specimens or groups of individuals were exposed to millipedes representing the orders Spirobolida and Polydesmida, resulting in 25 trials. For each trial, specimens were removed after 20 min if the ectrichodiine(s) did not approach, grip, or probe the millipede. If individuals interacted with the millipede, observations continued until the individual(s) had ceased these interactions for more than 15 min or until after feeding. All ectrichodiine specimens and one representative of each millipede species were preserved in 100% ethanol, barcode labeled, databased, and deposited at the Entomological Research Museum at the University of California, Riverside (UCR).

Ectrichodiinae Prey Specificity

Representatives of 12 Ectrichodiinae genera have been documented in the literature to feed on millipedes in 42 separate observations (Table 1.1). Seventeen observations involved millipedes in the order Spirostreptida, six in Spirobolida, and one in Polydesmida. Six additional observations included millipedes that could only be identified to the superorder Juliformia, based on identifications made by Rowland Shelley (some online images) and identification keys (Loomis, 1968; Sierwald, http://archive. fieldmuseum.org/millipeet/milli_key.html; accessed 18 Oct. 2011). Two of the 25 laboratory observations and one field observation made by the senior author indicate that *Rhiginia cinctiventris* preys on Spirobolida and Polydesmida. Although feeding was not observed directly in the field, observation of an adult female and two late instar (3–5) nymphs with swollen abdomens in close proximity to a dead spirobolid millipede (Fig. 1.2A) indicate a recent meal.

The observation that only three of the 16 millipede orders have been reported as prey of Ectrichodiinae may be, in part, due to a lack of data or may be based on the fact that these orders have high species diversity (Sierwald & Bond, 2007). However, this observation may also hint to a potential prey preference for the benzoquinone-producing Juliformia over cyanogenic Polydesmida. The relative toxicity of benzoquinones and cyanogenic compounds to ectrichodiines is unknown. Based on material safety data sheets, benzoquinone has an LD_{50} of 25 mg/kg (mouse; oral), whereas hydrogen cyanide has an LD_{50} of 3.7 mg/kg (mouse; oral). The degree of toxicity between the two compounds may be relatively similar for ectrichodiines.

Point of Stylet Insertion

From the literature, only 18 observations made reference to the millipede's body region attacked by ectrichodiines, all of which were on the trunk. Fourteen of these stated that the ventral or ventrolateral area was targeted (Figs. 1.1C, D, F, J), with 8 of these attacks at intersegmental membranes (Fig. 1.1I). Four less specific observations by Miller (1953) indicated that ectrichodiines targeted trunk intersegmental membranes, and Lawrence (1984) mentioned intersegmental membranes without reference to body region. Haridass (1985) stated that ectrichodiines also insert stylets at the head-collum intersegmental membrane. In our two laboratory trials, specimens of *R. cinctiventris* inserted stylets at the head-collum intersegmental membrane and/or at intersegmental membranes along the ventral, ventrolateral, and/or dorsal trunk (Figs. 1.2B). Overall, the data suggest Ectrichodiinae primarily target the millipede's ventral or ventrolateral trunk, with some exceptions.

There are several possible explanations for this behavior. These areas may be more penetrable than others, making a more suitable entry point for the typically smooth, unarmored stylets (Weirauch, 2003, 2008). Unfortunately, little is known about diplopod cuticular ultrastructure and chemical composition to further support this claim (Subramoniam, 1974; Walker & Crawford, 1980; Ansenne et al., 1990). Alternatively, Ectrichodiinae may initially target the millipede's ventral ganglia or the supra-esophageal ganglion to expose the nervous system to toxic salivary secretions. The millipede's ventral or head-collum region may be selected to avoid inserting stylets into laterally or dorsally located defensive glands along the trunk during millipede immobilization and consumption. It remains to be shown if, once immobilized, the millipede's defense gland reservoirs are targeted by ectrichodiines to sequester toxic secondary metabolites. At least half of the genera of Ectrichodiinae exhibit aposematic coloration to a larger extent than seen in most other reduviid subfamilies. Although ectrichodiines are presumably well protected from vertebrate predation due to their generally powerful bites and defensive secretions (Louis, 1974; Ambrose, 1999), a millipede diet may provide ectrichodiines with additional defensive benefits in the form of toxic secondary metabolites. Secondary defense metabolites have been investigated in other insects, such as aposematically colored Lepidoptera that sequester many chemicals from their host plants and biochemically alter them for defense purposes (Bowers, 1990; Nishida, 2002). Ectrichodiinae may potentially employ a similar strategy by targeting the defense gland reservoirs.

Communal Predatory Strategies

Evidence for communal predation comprises 13 observations. Of these, two involved groups of conspecific nymphs in the presence of a conspecific adult, whereas eight involved groups of conspecific nymphs. Conspecific adults engaging in communal behaviors have only been documented in *Cleptria cinctiventris* Stål, 1855 (Lawrence, 1984). Evidence of immatures engaging in solitary predation has only been documented for a *Haematorrhophus* species (Green, 1925). Communal predation was observed in only one of our laboratory trials with *R. cinctiventris* (Fig. 1.2C): early instar (1–2) nymphs, in the presence of an adult female and two later instar nymphs, frequently attempted predation on a millipede without immobilizing it. Overall, the data may indicate that communal, conspecific feeding among immatures or immatures and adults is the rule but rather an exception among adults. One potential explanation is that the salivary secretions produced by a single nymph may not be sufficiently toxic to immobilize and kill a millipede. Thus, the attack of multiple individuals may be necessary to increase the toxic effects, especially to subdue large-bodied prey items.

Conclusion

The predator-prey association between Ectrichodiinae and millipedes was first documented almost a century ago (Green, 1925), but has since received little attention. Judging from published data, it is obvious that the feeding behavior of Ectrichodiinae is still poorly understood. About 2% of ectrichodiine species have been documented to prey on millipedes, leaving ample room to further test the claim that Ectrichodiinae, as a group, specialize on millipedes. Based on our analysis, Ectrichodiinae may be exclusive millipede specialists, with a potential preference for the benzoquinone-producing Juliformia. Millipedes were usually not identified below the order level in the literature and online images. Thus, future investigations should attempt accurate genus or species determination of millipedes. Furthermore, the millipede's ventral trunk area and intersegmental membranes, including between the head and collum, are typically targeted. Whether these areas are attacked in relation to the location of the millipede nervous system or defense glands remains to be investigated. Lastly, immature and adult Ectrichodiinae exhibit both solitary and communal predation. The majority of observations suggest that immatures typically exhibit communal predation, whereas adults usually predate solitarily. Given that these conclusions are general and preliminary, it is imperative that future studies provide detailed documentation regarding these aspects of ectrichodiine predation. Other relevant investigations that will contribute to understanding this phenomenon include examining the chemical composition of ectrichodiine salivary secretions and the ability of ectrichodiines to sequester secondary metabolites from diplopods for defense.

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Figure 1.1. Internet images used for analysis of Ectrichodiinae predatory behavior. A. An adult *Brontostoma trux* feeding on a spirostreptid millipede (Gil-Santana). Millipede identified by R. Shelley and ectrichodiine identified by H. Gil-Santana. B. *Ectrichodia* sp. nymphs communally feed on a spirostreptid millipede (Fourie). C. *Ectrichodia* sp. nymphs feeding on the venter of a millipede (Weaving). D. An adult *Neozirta eidmanni* feeding on a juliform millipede carcass (Wang). W. Cai identified the ectrichodiine. E. *Ectrichodia* sp. nymphs communally feed on a juliform millipede (van de Wetering). F. An adult and three immature *Ectrichodia crux* share a juliform millipede carcass (MacRae). T. MacRae identified the ectrichodiine. G. An adult *Ectrichodia crux* consumes a juliform millipede (http://www.flickr.com). H. *Ectrichodia crux* nymphs communally feed on a spirostreptid millipede (http://www.whatsthatbug.com). R. Shelley identified the millipede. I. An adult *Schottus* sp. feeds on a spirobolid millipede (Cheah). J. An adult *Schottus* sp. feeds on a juliform millipede (Lee).


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Figure 1.2. Field and laboratory images of *Rhiginia cinctiventris* predation on millipedes at La Selva Biological Station, Costa Rica. A. Field image of an adult and two immature *Rhiginia cinctiventris* near a spirobolid millipede carcass at La Selva Biological Station, Costa Rica. B. An adult female feeds on a small polydesmid millipede. C. An adult female, two early instar nymphs, and two later instar nymphs in the presence of a spirobolid millipede.


A
B
C

Table 1.1. Data extracted from published literature and Internet images for analysis of Ectrichodiinae predatory behavior.

Ectrichodiinae taxon	**Stage**	**Prey millipede taxa**	**Stylet insertion**	**Communal predation**	**Reference**
Brontostoma notatum (Stål), 1859	Adult	Diplopoda		Solitary	McGavin (1993)
Brontostoma trux (Stål), 1859	Adult	Spirostreptida		Solitary	Gil-Santana (image)
Cleptria cinctiventris Stål, 1855	Adults	Spirostreptida	Intersegmental membrane	Conspecific adults	Lawrence (1984)
Ectrichodia spp.		Spirostreptida	Intersegmental membrane on trunk		Miller (1953)
Ectrichodia spp.		Spirostreptida			Miller (1971)
Ectrichodia sp.	Nymphs	Juliformia		Conspecific nymphs	van de Wetering (image)
Ectrichodia sp.	Nymphs	Spirostreptida		Conspecific nymphs	Fourie (image)
Ectrichodia sp.	Nymphs	Diplopoda	Ventral trunk	Conspecific nymphs	Weaving (image)
Ectrichodia barbicornis (Fabricius), 1775		Diplopoda			Louis (1974)
Ectrichodia crux (Thunberg), 1783	Nymphs	Juliformia		Conspecific nymphs	Gordon (image)
Ectrichodia crux (Thunberg), 1783		Spirostreptida	Intersegmental membrane on ventral trunk	Solitary	Giliomee (1985)
Ectrichodia crux (Thunberg), 1783		Diplopoda	Intersegmental membrane on ventral trunk	Solitary	Giliomee (1985)
Ectrichodia crux (Thunberg), 1783	Adult & Nymphs	Juliformia	Ventral trunk	Conspecific nymphs with adult	MacRae (image)
Ectrichodia crux (Thunberg), 1783	Adults	Spirostreptida	Intersegmental membrane on ventral trunk	Solitary	Miller (1953)
Ectrichodia crux (Thunberg), 1783		Diplopoda			Paulian (1948)

Table 1.1. (Continued).

Ectrichodiinae taxon	**Stage**	**Prey millipede taxa**	**Stylet insertion**	**Communal predation**	**Reference**
Ectrichodia crux (Thunberg), 1783	Adult	Juliformia		Solitary	http://www.flickr.com (image)
Ectrichodia crux (Thunberg), 1783	Nymphs	Spirostreptida		Conspecific nymphs	http://www.whatsthatbug.com (image)
Ectrichodia gigas (Herrich-Schaeffer), 1848	Adult & Nymphs	Spirostreptida	Intersegmental membrane on ventral trunk	Conspecific nymphs; nymphs with adult	Cachan (1952)
Ectrychotes pilicornis (Fabricius), 1794		Diplopoda			Haridass (1978)
Glymmatophora spp.		Spirostreptida	Intersegmental membrane on trunk		Miller (1953)
Glymmatophora sp.	Nymphs	Spirostreptida	Intersegmental membrane	Conspecific nymphs	Lawrence (1984)
Guionius nigripennis (Fabricius), 1794		Diplopoda			Haridass (1978)
Haematorrhophus sp.		Diplopoda			Livingstone & Ambrose (1984)
Haematorrhophus sp.		Spirobolida			Ambrose (1999)
Haematorrhophus sp.		Spirobolida			Ambrose (1999)
Haematorrhophus sp.		Spirobolida			Ambrose (1999)
Haematorrhophus sp.	Nymph	Diplopoda	Ventral posterior trunk	Solitary	Green (1925)
Haematorrhophus linnaei (Stål), 1859	Adult	Diplopoda			Green (1925)
Haematorrhophus linnaei (Stål), 1859	Adult	Diplopoda	Ventral posterior trunk		Sahayaraj (2006)
Haematorrhophus nigroviolaceus (Reuter), 1873	Adult & Nymphs	Spirobolida	Intersegmental membrane on ventral posterior trunk	"Nymphs as well as adults"	Haridass & Ananthakrishnan (1980)
Haematorrhophus nigroviolaceus (Reuter), 1873	Adult & Nymphs	Spirobolida	Intersegmental membrane on ventral posterior trunk	"Nymphs as well as adults"	Haridass & Ananthakrishnan (1980)

Table 1.1. (Continued).

Ectrichodiinae taxon	**Stage**	**Prey millipede taxa**	**Stylet insertion**	**Communal predation**	**Reference**
Haematorrhophus nigroviolaceus (Reuter), 1873	Adult & Nymphs	Polydesmida	Intersegmental membrane on ventral posterior trunk	“Nymphs as well as adults”	Haridass & Ananthakrishnan (1980)
Haematorrhophus nigroviolaceus (Reuter), 1873		Spirostreptida			Haridass & Ananthakrishnan (1980)
Maraenaspis spp.		Spirostreptida			Miller (1953)
Maraenaspis spp.		Spirostreptida			Miller (1971)
Maraenaspis problematica (Gerstaecker), 1892	Nymphs	Spirostreptida	Intersegmental membrane on trunk	Conspecific nymphs	Miller (1953)
Neozirta eidmanni (Taueber), 1930	Adult	Juliformia	Ventral posterior trunk	Solitary	Wang (image)
Nularda nobilitata Stål, 1859		Diplopoda			Louis (1974)
Scadra spp.		Spirostreptida	Intersegmental membrane on trunk		Miller (1953)
Scadra spp.		Spirostreptida			Miller (1971)
Schottus sp.	Adult	Spirobolida	Intersegmental membrane on ventrolateral trunk	Solitary	Cheah (image)
Schottus sp.	Adult	Juliformia	Ventral or ventrolateral trunk	Solitary	Lee (image)

Chapter 2: Taxonomic monograph of the endemic millipede assassin bug fauna of Madagascar (Hemiptera: Reduviidae: Ectrichodiinae)

Abstract

Madagascar is one of the world's most recognized biodiversity hotspots and has a diverse assassin bug (Reduviidae) fauna that is still incompletely known, especially for the Ectrichodiinae, or millipede assassin bugs. Ectrichodiinae are a speciose (673 described species, 118 genera), worldwide group of assassin bugs that is most diverse in the Old and New World tropics, but so far only six genera and 10 species have been described from Madagascar. Based on examination of 1,981 ectrichodiine specimens mostly from the California Academy of Sciences, as well as a few other collections, dramatic undescribed species-level diversity is revealed. The island's Ectrichodiinae fauna is taxonomically revised with the description of three new genera (*Marojejycoris, Tanindrazanus*, and *Toliarus*) and 63 new species: *Gibbosella andasibe*, *Gibbosella betampona*, *Gibbosella brunalvus*, *Gibbosella conisimilis*, *Gibbosella fulva*, *Gibbosella mantella*, *Gibbosella megafrons*, *Gibbosella nitida*, *Gibbosella notoconica*, *Gibbosella pallidacorium*, *Gibbosella pallidalata*, *Gibbosella planiscutum*, *Gibbosella quadocris*, *Gibbosella vangocris*, *Glymmatophora (Glymmatophora) carolae*, *Marojejycoris auranticorium*, *Marojejycoris brevifrons*, *Marojejycoris francais*, *Marojejycoris notadichroa*, *Marojejycoris ranomafana*, *Tanindrazanus amboasaricus*, *Tanindrazanus andohahela*, *Tanindrazanus anjozorobeus*, *Tanindrazanus antananarivo*, *Tanindrazanus bemaraha*, *Tanindrazanus brunneus*, *Tanindrazanus hannajagodae*, *Tanindrazanus harinhali*, *Tanindrazanus irwini*, *Tanindrazanus joffrevillus*, *Tanindrazanus kathrynae*, *Tanindrazanus mahafaly*, *Tanindrazanus marginatus*, *Tanindrazanus marojejy*, *Tanindrazanus nigripes*, *Tanindrazanus notatus*, *Tanindrazanus simulans*, *Tanindrazanus tenebricus*, *Tanindrazanus varicolor*, *Tanindrazanus vohiparara*, *Toliarus karinae*, *Toliarus trichrous*, *Toxopus ambohitantely*, *Toxopus ampitavananima*, *Toxopus antsiranana*, *Toxopus basalis*, *Toxopus brucei*, *Toxopus farafangana*, *Toxopus fisheri*, *Toxopus griswoldi*, *Toxopus insignis*, *Toxopus italaviana*, *Toxopus melobrunneus*, *Toxopus miandritsara*, *Toxopus namoroka*, *Toxopus pallidus*, *Toxopus parkeri*, *Toxopus simulans*, *Toxopus steineri*, *Toxopus tibialis*, *Toxopus toamasina*, *Toxopus toliara*, and *Toxopus vazimba*. *Toxopus* Bergroth, 1905, is redescribed, with the first description of males in the genus, and *Cleptria signoretii* Reuter, 1887, is transferred to *Toxopus*. *Gibbosella* Chłond, 2010, is also redescribed and includes description of males for the first time. *Gibbosella elongata* Chłond, 2010, *Glymmatophora crassipes* Horváth, 1914, and *Maraenaspis bidens* (Reuter), 1887, are redescribed, with the first description of males for each species. Habitus images, documentation of male and female genitalic features, identification keys, and distribution maps are provided. Males and females are associated based on morphology, geographic information, and, when available, molecular data. The newly discovered species diversity constitutes a sixfold increase over the previously documented millipede assassin bug fauna in Madagascar.

Introduction

Madagascar, often referred to as "the island continent" due to its wide range of ecosystems and size (Scales, 2014), is one of the most biologically diverse places in the world. More than 13,000 species of plants, 900 of vertebrates, and 5,800 of invertebrates are known to occur on the island (Goodman & Benstead, 2005; Phillipson et al., 2006), although, for invertebrates at least, these numbers are probably gross underestimates of true diversity. Among noninvasive species, about 50% of birds, 95% of reptiles, 100% of amphibians and mammals, 86% of invertebrates, and more than 90% of vascular plants are endemic to the approximately 600,000 km^2 island (Goodman & Benstead, 2005; Yoder & Nowak, 2006; Phillipson et al., 2006; Buerki et al., 2013).

Such diversity and endemicity is extraordinary when compared to islands of relatively similar size, e.g., Sumatra (~473,500 km^2: 201 mammals, 4% endemic; 580 birds, 3% endemic) (Whitten et al., 2000) or Borneo (~748,000 km^2: 1,500 vertebrates, 30% endemic) (Quek, 2009). The remarkable Madagascan biodiversity is under threat from a variety of anthropogenic influences, such as introduction of invasive species (Myers et al., 2000) and poaching of endangered species (Rakotomanana et al., 2013), although the greatest threat comes from habitat loss and fragmentation (Myers et al., 2000). Given the immense threat to its largely endemic biota, Madagascar has been deemed the world's "hottest" biodiversity hotspot and its flora and fauna is of critical conservation priority (Myers et al., 2000; Ganzhorn et al., 2001; Scales, 2014).

Nevertheless, knowledge of the island's patterns of species richness, turnover, and endemism is still incomplete (Schatz, 2002; Smith et al., 2005). This gap impedes the ability to identify and prioritize critical areas of endemism for conservation efforts (Schatz, 2002; Smith et al., 2005). Thus, taxonomic surveys of the Madagascan biota are severely needed. The California Academy of Sciences' (CAS) Terrestrial Arthropod Inventory of Madagascar Project (2000–2009) was conducted to address the need for taxonomic exploration of the arthropod fauna. This project has yielded a plethora of arthropod specimens for many taxonomic studies (e.g., Mugrabi & Azevedo, 2010; Krishnankutty & Dietrich, 2011; Álvarez-Padilla et al., 2012), and has yielded more than 3,000 specimens of Reduviidae, or assassin bugs.

The morphologically and ecologically diverse Reduviidae is the second largest family of true bugs (Hemiptera: Heteroptera) that comprises 7,000 described species worldwide (Putshkov & Putshkov, 1986–1989; Maldonado, 1990; Weirauch et al., 2014). Prior to the turn of the 21st century, 253 species were known to occur on Madagascar (Maldonado, 1990), ~85% of which were described by André Villiers in 30 papers published between 1948–1979 (e.g., Villiers, 1948; Villiers, 1968a; Villiers, 1979; see Maldonado, 1990, for other references). A number of small taxonomic studies (i.e., no monographs) have since focused on Madagascan assassin bugs and the described diversity has increased by 24 species (Labina & Kerzhner, 2001; Weirauch, 2008a; Chłond, 2010a, 2010b, 2010c, 2011a, 2011b, 2014; Chłond & Junkiert, 2010, 2011; Hwang & Weirauch, 2010; Zhang & Weirauch, 2011; Chłond & Guilbert, 2012; Chłond & Baňař, 2013). Of these 277 species, only 10 currently classified in six genera belong to the fifth largest reduviid subfamily Ectrichodiinae, the millipede assassin bugs (673 species, 118 genera) (Carpintero & Maldonado, 1990, 1991; Maldonado, 1990, 1995; Dougherty, 1995; Murugan & Livingstone, 1995; Kerzhner & Günther, 2003; Gil-Santana & Costa, 2005; Gil-Santana et al., 2004; Gil-Santana et al., 2005; Gil-Santana & Baena, 2009; Weirauch et al., 2009; Chłond, 2010a; Rédei & Tsai, 2012; Rédei et al., 2012; Gil-Santana et al., 2013; Gil-Santana, 2014, 2015). All described Madagascan ectrichodiine species and three of the six genera (*Distirogaster* Horváth, 1914; *Gibbosella* Chłond, 2010; *Toxopus* Bergroth, 1905) are endemic to the island. The 1,819 ectrichodiine specimens collected by CAS's taxonomic inventory, together with 162 specimens loaned from various European and American museums and colleagues, has provided a unique opportunity to examine, document, and revise the dramatic undescribed species-level ectrichodiine diversity in Madagascar. We here describe three new genera and 63 new species, revise the existing genera *Toxopus* and *Gibbosella* and describe the males of both genera for the first time. We also transfer *Cleptria signoretii* Reuter, 1887, to *Toxopus*. The species *Gibbosella elongata* Chłond, 2010, *Glymmatophora crassipes* Horváth, 1914, and *Maraenaspis bidens* (Reuter), 1887, are redescribed, including, for the first time, descriptions of males for each species. The genus *Distirogaster* will be treated in a separate revision (Chłond et al., in prep.) due to the limited CAS material, the abundant material from European collections available to the second author (Chłond; taking the lead on the revision of *Distirogaster*), and timely finalization of the monograph; however, the taxon is included in the key to Madagascan genera and several specimens are sequenced for molecular data. Our taxonomic approach is largely focused on male specimens, since ~90% of the material collected by CAS are males (likely due to collecting methods). Sexual dimorphism, where males are typically macropterous and females are apterous, is widespread among Ectrichodiinae and poses a significant problem for associating male and female specimens. Wherever feasible, males are associated with females (and immatures) based on a combination of morphology and geographic information and, where successfully amplified, molecular data. Cladistic methods are utilized in formulating generic concepts and informing diagnostic features of Madagascan genera and species, but results of these analyses are being published in a companion paper (Forthman & Weirauch, in press).

Material and methods

Specimens and databasing

A total of 1,981 specimens were examined for this taxonomic revision, of which 1,661 are males, 48 females, and 272 immatures; five additional specimens classified as *Distirogaster* were included in the molecular approach to associating dimorphic sexes. The skewed abundance of males compared to females and immatures is likely a result of collecting techniques employed by the CAS taxonomic survey: a significant proportion of the material (~80%) was collected in Malaise traps that typically favor the capture of winged insects, and thus in the case of Ectrichodiinae, male specimens. Leaf litter sifting, pitfall traps, light traps, and hand collecting resulted in a small sample (~12% of total material indicating collecting method from CAS material) of apterous female and immature specimens. Only 10 immatures were collected in Malaise traps.

Unique specimen identifier (USI) labels were affixed to specimens. All USI labels are comprised of the prefix UCR_ENT followed by an eight-digit number. USI codes are provided in the material examined section of each species description, but the prefix (UCR_ENT) is omitted to save space. Specimen information was databased using the American Museum of Natural History's Planetary Biodiversity Inventory (PBI) Arthropod Easy Capture Software database (http://www.research.amnh.org/pbi/locality/index.php) and are available through the Heteroptera Species Pages (http://research.amnh.org/pbi/heteropteraspeciespage/). Specimens with locality data including GPS coordinates were databased verbatim. For some older specimens deposited in European collections, locality records were georeferenced using Google Earth v7.1.2.2041 and GeoLocate (http://www.museum.tulane.edu/geolocate/) to determine geographic coordinates and elevation; locality data from these specimens were databased using current geopolitical names. In several cases, locality records on older specimens could not be successfully georeferenced.

Morphological methods

External morphology and genitalic characters were examined using Nikon NiU (University of Silesia [SU]; Chłond), Nikon SMZ1000 (University of California-Riverside [UCR]; Forthman and Weirauch), Nikon SMZ1500 (SU and UCR), and Olympus SZH 10 (SU) dissecting microscopes. For males, genitalia (abdominal segment 8, pygophore, and phallus) were dissected from the body, cleared in heated 10% potassium hydroxide (KOH) for 3–8 minutes, washed in distilled water and 100% ethanol (EtOH), examined in glycerol, and permanently stored in genitalic capsules pinned to the specimen. For females, genitalia were dissected from the body using a similar protocol with the exception that the entire abdomen was detached from the thorax, heated in KOH initially, opened to expose internal structures, and subsequently cleared in heated KOH for 5–10 minutes. Female internal genitalia were permanently stored in genitalic capsules pinned to the specimen, while external abdominal structures were mounted to card stock pinned to the specimen. Genitalic structures were stained with Chlorazol Black E in 70% EtOH solution to provide contrast to membranous areas. Morphological characters were coded in the Descriptive Language for Taxonomy (DELTA) program. Natural language taxonomic descriptions were subsequently generated.

Imaging, distribution maps, and measurements

Dorsal (Figs. 2.1–2.4), lateral (Figs. 2.5–2.7), and ventral (Figs. 2.8–2.11) habitus images were produced for representatives of species and types of some described species (except *Glymmatophora crassipes* provided by Dávid Rédei) (Fig. 2.12) using Microptics-USA or Leica Z16 APO imaging systems LAS v4.3 (UCR) or a Nikon D300 on Fomei CS-920 copy stand (SU). Images of select morphological features (head: Fig. 2.13; antenna: Fig. 2.14; thorax: Fig. 2.15; metathoracic gland evaporatorium and leg armature: Fig. 2.16; wings: Fig. 2.17; abdomen: Fig. 2.18; male and female genitalia: Fig. 2.19–23) were produced using a Leica Z16 APO imaging system. For genitalic images, genitalia were mounted on top of hand sanitizer and immersed in 70% EtOH. All images were stacked using LAS v4.3 and Zerene Stacker v1.04 (UCR). Distribution maps were created using SimpleMappr (http://www.simplemappr.net) based on GPS coordinates (Maps 2.1–2.13). Measurements (in mm) were made using an Olympus SZX9 stereoscopic microscope with a micrometer (SU) and a Lomo MBC-10 stereoscopic microscope with a two-axes movable stage and two digital micrometers connected to a Microcode II RS-232 readout (UCR) (Table 2.1). Because the hemelytron is often distorted in mounted specimens, body length is reported as the length from the clypeal apex to the posterior margin of the abdomen for the holotype in species descriptions, followed by a range where multiple specimens are available. In cases where the hemelytron obscured the posterior abdominal margin in dorsal view, a light source was positioned under the specimen and illuminated the outline of the abdomen under the hemelytron in dorsal view.

Identification keys

An identification key is provided for genera found in Madagascar. Keys to species are given for each genus with more than one Madagascan species known. For genera having more than one extremely sexually dimorphic species, separate male and female identification keys are given. No specimens were examined for *Toxopus politus* Bergroth, 1905, which is known only from the female holotype, which may be lost (Jansson & Coscarón, 1989; Larry Huldén, personal commun.). This species is included in the key to females of this genus, but diagnostic features are based on the original description.

Molecular data and pairwise genetic distance analysis

To associate males and females, sequencing and pairwise genetic distance analysis of part of the mitochondrial cytochrome oxidase I (COI) gene was performed following Zhang & Weirauch (2011) for 61 male specimens representing 39 species (including representatives of *Distirogaster*) and 10 female specimens representing 10 putative female-based species; sequence-quality specimens were not available for 35 male- and 17 putative female-based species. A hind leg was removed from each specimen for DNA extraction using QIAGEN DNeasy Blood and Tissue Kit. Amplification of partial COI was performed using COI primers C1-J-2183 (5′-CAACATTTATTTTGATTTTTTGG-3′, forward) (Simon et al., 1994) and C1-N-2609 (5′-CGAATACTGCTCCTATTGATA-3’′ reverse) (Damgaard et al., 2000), GE Healthcare Life Sciences PuReTaq Ready-To-Go PCR Beads, and a Fisher Scientific Thermocycler with the following settings: denaturation 94° C (30 s), annealing 48° C (30 s), and extension 72° C (45 s) for 35 cycles, with an initial denaturation at 94° C (2 min) and a final extension at 72° C (7 min). PCR products were cleaned using Bioline SureClean. Sequencing was performed on an Applied Biosystems 3730xl DNA Sequencher at UCR’s Institute for Integrative Genome Biology.

Sequences were assembled and beginning and ending nucleotides with unresolved chromatograms were deleted in Sequencher v4.8. Sequences are available at GenBank under the accession numbers listed in Table 2.2. Sequence alignment was performed with the online version of MAFFT (Katoh et al., 2005; Katoh et al., 2008; http://mafft.cbrc.jp/alignment/server/index.html) using the E-INS-i algorithm, which produced the shortest aligned dataset without internal gaps. TaxonDNA/SpeciesIdentifier 1.5alpha10 (Meier et al., 2006) was used to compute uncorrected pairwise genetic distances. The smallest distance between female and male sequences were determined and compared to intra- and interspecific distances. Following Zhang & Weirauch (2011), putative matches were then investigated further to assess morphological similarities and geographic proximity (DeSalle et al., 2005).

Terminology, specimen depositories, and abbreviations

Terminology generally follows a subset of terms used by Dougherty (1995), Weirauch (2008b), and Forero & Weirauch (2012). Terminology for wing venation follows Hill (2014) and Weirauch (2008b), although homology concepts across Paraneoptera are currently being reviewed (Dávid Rédei, personal commun.). Abbreviations used in plates and/or text (capitalized abbreviations used within generic and species descriptions with the exception of standard wing venation abbreviations): **1A,** first anal vein; **aa,** articulatory apparatus (basal plate and basal plate extension); **ad,** aedeagus; **afsp,** anterior femoral subapical protuberance; **alp,** anterolateral pronotal projection; **ana,** antennal articulation; **anf,** antennifer; **aoc,** anteocular area; **ap,** antennal pseudoarticulation; **apl,** anterior pronotal lobe; **as,** antennal shield; **asp8,** abdominal spiracle 8; **bc,** bursa copulatrix; **bcl,** bursa copulatrix lateral lobe; **BFLA,** basiflagellomere; **bp,** basal plate; **BPE,** basal plate extension; **ca,** clypeal apex; **cl,** collar; **cly,** clypeus; **co,** corium; **cp,** corial pterostigma; **Cu,** cubitus; **DFLA,** distiflagellomere; **dl,** dorsal laterotergite; **dlp,** dorsal laterotergite protuberance; **dpes,** dorsal phallothecal sclerite-endosomal struts fusion; **dps,** dorsal phallothecal sclerite; **en,** endosoma; **es,** endosomal struts; **exM,** extension of M beyond M+Cu distal junction; **fmp,** femoral medial protuberance; **ft,** femoral tubercle; **gl,** gula; **is,** interocular sulcus; **L2,** labial segment II (first visible segment); **L3,** labial segment III (second visible segment); **L4,** labial segment IV (third visible segment); **lb,** labrum; **M,** media; **MGE,** metathoracic gland evaporatorium; **mms,** transverse suture between meso- and metasterna; **mo,** median oviduct; **mpp,** medial pygophore process; **mss,** mesosternum; **mtc,** metacoxa; **mts,** metasternum; **mxp,** maxillary plate; **nk,** neck; **oc,** ocelli; **ot,** ocellar tubercle; **p,** pedicel; **pa,** paramere; **pap,** trochanter and/or femoral papillae; **pc,** sternal paramedian carinae; **pcd,** postclypeal depression; **pfsp,** posterior femoral subapical protuberance; **pltf,** lateral furrow of posterior pronotal lobe; **pls,** pronotal longitudinal sulcus; **poc,** postocular; **ppl,** posterior pronotal lobe; **pts,** pronotal transverse suture; **R,** radius; **s,** scape; **S2,** sternite 2; **S3,** sternite 3; **sc,** scutellum; **sis,** sternal intersegmental suture; **sl,** synthlipsis; **sld,** sternal medial longitudinal depression; **T8,** tergite 8; **T9,** tergite 9; **T10,** tergite 10; **V1,** valvula 1; **V3,** valvula 3; **vap,** ventral anterior process of endosomal struts; **vf1,** valvifer 1; **vpp,** ventral posterior process of endosomal struts.

Abbreviations for depositories: **AMNH,** American Museum of Natural History, New York; **BMNH,** Natural History Museum, London, United Kingdom; **CAS,** California Academy of Sciences, California; **HNHM,** Hungarian Natural History Museum, Budapest, Hungary; **MMBC,** Moravské Museum, Brno, Czech Republic; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France; **MRAC,** Musée Royal de l'Afrique Centrale, Tervuren, Belgium; **MTEC,** Montana State University, Montana; **NMW,** Naturhistorisches Museum, Vienna, Austria; **SU**, Department of Zoology, University of Silesia, Poland; **TLMF,** Tiroler Landesmuseum Ferdinandeum, Innsbruck, Austria; **UCR,** University of California, Riverside Entomological Research Museum, California; **USNM,** National Museum of Natural History, Washington D.C.

Results of the molecular association of males and females

Pairwise genetic distances of COI between intraspecific males were less than 3.75%. Between interspecific males within a genus or between genera, COI pairwise genetic distances were greater than 7.10%. Of the 10 females that were sequenced for COI, two had pairwise genetic distances with two male-based species that were less than 0.80% (*Toxopus griswoldi*: 0.76% [Figs. 2.3, 2.4, 2.7, 2.10]; an undescribed species of *Distirogaster*: 0.75%). These two results were corroborated by examination of geographic distance between male and female specimens (*Toxopus griswoldi*: same locality; *Distirogaster* sp.: 2.28 km), as well as morphology (see taxonomic descriptions and discussions). For the remaining eight females (Fig. 2.24) sequenced, female-to-male pairwise distances exceeded 9.5%, and therefore, COI sequences did not offer a way of associating these females with conspecific males. In addition, these females were collected at localities that were near those of males belonging to several species, such that geographic proximity could not be used as a line of evidence. Generic and species diagnoses based on males heavily rely on structural differences on the head, thorax, and wings, among other features. However, all eight females have drastically reduced morphological features (e.g., head structures, scutellum, wings, etc.), and three of these females could not be unambiguously associated with any of the male-based genera treated in this monograph. The remaining five females could be associated with the genus *Gibbosella* based on morphology (see generic discussion) but could not be unambiguously associated to any male-based species within this genus.

Taxonomy

Identification key to Ectrichodiinae genera of Madagascar

1. Abdominal spiracles circular; body small (<10 mm); dull colored 2

- Abdominal spiracles ovoid to elliptical; body medium to large (≥10 mm); color variable 3

2. Male: Metathoracic gland evaporatorium (MGE) not visible in lateral view (Fig. 2.16B, C); scutellar processes dorsally directed in lateral view (except in *Gibbosella planiscutum*) (Fig. 2.15C); hemelytron with distal part of M and Cu fused basally (Fig. 2.17A); dorsal laterotergites with posterior protuberances (Fig. 2.18A). Female: apterous; 6- or 8-segmented antenna with short vestiture; dorsal laterotergites with posterior protuberances reduced to absent. Bicolored, dark brown and pale in both sexes .... *Gibbosella* Chłond

- Males only known. MGE visible in lateral view (Fig. 2.16A); scutellar processes horizontally directed (i.e., parallel to dorsal abdominal surface) in lateral view (Fig. 2.15D); hemelytron with distal part of M and Cu separate basally (Fig. 2.17B, C); dorsal laterotergites unarmed (Fig. 2.18B); coloration generally uniform, orange-brown ....*Marojejycoris*, new genus

3. Distiflagellomere (DFLA) (Fig. 2.14A, C) divided into four pseudosegments; antenna thus appearing 8-segmented; very pronounced anterolateral protuberances on anterior pronotal lobe (Fig. 2.15A); metallic coloration 4

- DFLA divided into two or three pseudosegments; antenna thus appearing 6- or 7-segmented; anterolateral protuberances on anterior pronotal lobe much smaller or absent; coloration not metallic...5

4. Dorsal laterotergites with posterior protuberances (Fig. 2.18A); abdominal sternites with paramedian, longitudinal carinae and shallow medial longitudinal depression (Fig. 2.18C). Male: macropterous; subquadrate head in lateral view; relatively slender abdomen. Female: apterous; more ovate head shape; abdomen wider .... *Distirogaster* Horváth

- Dorsal laterotergites without posterior protuberances; abdominal sternites without paramedian longitudinal carinae and shallow medial longitudinal depression; head ovoid (Fig. 2.13E); abdomen wide; males and females of the only Madagascan species apterous ....*Maraenaspis* Karsch

5. Forefemur with anterior subapical and medial protuberances and mid and hind femora with anterior and posterior subapical and medial protuberances in both sexes (Fig. 2.16E); body glabrous except on antenna and tibiae; DFLA divided into two pseudosegments, thus, antenna appearing 6-segmented .... *Glymmatophora* Stål

- Femora unarmed in males, with small papillae (Fig. 2.16D) in females; body with dense vestiture; DFLA divided into two or three pseudosegments, thus, antenna appearing 6- or 7-segmented 6

6. Males only known; meso- and metasterna completely divided by a transverse suture (Fig. 2.15F); dorsal laterotergite II not distinctly expanded; head subtriangular in lateral view (Fig. 2.13G–I)..7

- Male: meso- and metasterna not completely divided by a transverse suture (Fig. 2.15E); dorsal laterotergite II distinctly expanded; head short and subquadrate (Fig. 2.13K) to subovate or elongate cylindrical (Fig. 2.13J). Female: apterous; shiny blackish coloration, sometimes with pale yellow markings; 7-segmented antenna with short vestiture; fore and mid trochanters with small papillae (Fig. 2.16D) .... *Toxopus* Bergroth

7. DFLA divided into three pseudosegments; antenna thus appearing 7-segmented (except 6-segmented in some specimens of *Tanindrazanus harinhali*); posterior pronotal lobe smooth or transversely striated .... *Tanindrazanus*, new genus

- DFLA divided into two pseudosegments; antenna thus appearing 6-segmented; posterior pronotal lobe punctate.. *Toliarus*, new genus

Gibbosella Chłond, 2010

Figs. 2.1, 2.5, 2.8, 2.12, 2.13C, 2.15C, 2.16D, 2.17A, 2.18A, 2.19A, 2.19B, 2.20A–C, 2.21A, 2.21B, 2.22A, 2.23A, 2.23B, 2.24; Maps 2.1–2.3

Gibbosella Chłond, 2010: 62.

TYPE SPECIES: *Gibbosella mirabilis* Chłond, 2010

REVISED DIAGNOSIS: Males recognized by the small body size, shallow anteromedial depression on the ventral head surface, large antennal shield that does not conceal the antennal insertion in lateral view, depressed postclypeus, 8-segmented antenna (6-segmented in *G. pallidalata*), dorsally oriented long and slender scutellar processes (short, stout, and horizontally oriented in *G. planiscutum*), basally fused distal part of M and Cu, dorsal laterotergites transversely bicolored pale yellow and brown and with posterolateral protuberances, and apex of abdomen with very long setae. Females recognized by the apterous condition, reduced pale markings, head about as wide as anterior margin of pronotum, 6- or 8-segmented antenna with short vestiture, scape (Fig. 2.14A) longer than distance between anterior margin of eye and apex of head, anterior pronotal lobe much longer than posterior lobe, scutellar processes reduced and dorsally directed, and dorsal laterotergites with posterior protuberances reduced or absent. Males are similar to males of the monotypic Afrotropical genus *Synavecoris* Villiers, 1968b (Fig. 2.12), but the presence of the antennal shield, lack of femoral armature, separation of the proximal part of M and Cu (Fig. 2.17A), and armature of the dorsal laterotergites differentiate males of *Gibbosella* from *Synavecoris*. and armature of the dorsal laterotergites differentiate males of *Gibbosella* from *Synavecoris*. Due to reduced morphological features in both genera, females of *Gibbosella* appear very similar to females of *Synavecoris* but may be distinguished by the apterous condition, dorsally directed scutellar processes, and the pronotum lacking lateral carinae.

REDESCRIPTION: **MALE:** Macropterous, small body size. COLORATION: Pale to dark brown color patterns. VESTITURE: Sparse to dense, semierect to erect, long pale to brown setae on head, thorax, legs, corium of hemelytra, and abdomen; setae longer on apex of abdomen compared to rest of vestiture on body; setae on tibiae stouter and denser near apex. STRUCTURE: HEAD (Fig. 2.13C): Circular, ovoid, or cylindrical; shorter than pronotum; ventrally with shallow anteromedial depression; clypeal apex not dorsally elevated relative to labrum; maxillary plate not reaching dorsal clypeal surface (Fig. 2.13E, I); postocular (hind eye margin to posterior constriction; Fig. 2.13J) broad in dorsal view (Fig. 2.13B ocelli present, separated by less than diameter of ocellus; distinct constriction between postocular and neck; antennal shield not concealing antennal insertion in lateral view; scape surpassing clypeal apex; pedicel (Fig. 2.14A) slightly curved; slightly curved; flagellum subdivided into BFLA (Fig. 2.14A, B) and DFLA (Fig. 2.14A, C); BFLA divided into two pseudosegments; DFLA divided into two or four pseudosegments; antenna thus appearing 6- or 8-segmented. THORAX (Fig. 2.15C): Pronotum wider than long, anterior margin distinctly concave, smooth, collar distinct (Fig. 2.15B); anterior pronotal lobe shorter than posterior lobe, more than half as wide as posterior lobe; pronotal longitudinal furrow reaching anterior but not posterior margin of pronotum, foveate posteriorly (Fig. 2.15B); pronotal transverse furrow distinct; lateral depressions on posterior pronotal lobe distinct; scutellum with two moderately separated apical processes, directed dorsally in most species (horizontally directed in *G. planiscutum*), disc medially depressed; MGE with shallow meshlike cuticle that does not extend dorsally in lateral view (Fig. 2.16B, C); fossula spongiosa on foretibia, absent on mid tibia in some species; hemelytron (Fig. 2.17A) with corium restricted to areas adjacent to basal wing veins, with pterostigmalike appearance on anterodistal margin; proximal parts of M and Cu veins separate; distal parts of M and Cu fused basally; distal part of M extending beyond apical junction of

M+Cu. ABDOMEN (Fig. 2.18A): Dorsal laterotergites II-VI with posterolateral protuberances; sternal intersegmental sutures (Fig. 2.18B, C) carinulate; spiracles circular; pygophore process directed dorsoposteriad, not surpassing posterior margin of pygophore; DPS apex rounded (Fig. 2.21A, B); endosomal struts with anterior ventral process (Fig. 2.22G); endosoma weakly to strongly sclerotized medially (Fig. 2.21A, B). **FEMALE:** Differs from males in the following characteristics: apterous; reduced pale markings; head about as wide as anterior pronotal margin; in some species, head ventrally with small tubercles; postclypeus not depressed; antennal shield not expanded; ocelli absent; eye small; antennal vestiture much shorter; scape longer than distance between anterior margin of eye and apex of head; collar not distinct; anterior pronotal lobe much longer than and as wide as or wider than posterior lobe (Fig. 2.15A), sometimes elevated dorsally; pronotal longitudinal furrow reduced to deep medial depression near posterior margin of anterior pronotal lobe (Fig. 2.15A) and present or obsolete on posterior lobe; lateral depressions on posterior pronotal lobe present or obsolete; scutellum processes weakly developed, dorsally directed; meso- and metasterna convex; in some species, fore- and mid trochanters and base of forefemur with ventral patches of small papillae (Fig. 2.16D) and femora ventrally with small tubercles (Fig. 2.16D); hind femur slightly curved in dorsal view; fossula spongiosa larger; dorsal laterotergites with posterior protuberances reduced or absent; external genitalia short, platelike (Fig. 2.23A, B).

DISTRIBUTION: Species are known from all provinces and occur in habitats between 9–1,600 m elevation. Macrohabitats are described as spiny forests, tropical forests, mixed tropical forests, low and high altitude rainforests, tropical dry forests, montane rainforest, sclerophyl forests, dwarf littoral forests, and secondary tropical forests.

DISCUSSION: Chłond (2010a) recently described this genus and two species, *G. mirabilis* and *G. elongata*, from single female representatives with no males or immatures known. One male specimen from undetermined material showed some morphological features similar to the described females, e.g., an elongate cylindrical head, a slightly dorsally pronounced anterior pronotal lobe, dorsally directed scutellar processes, general color pattern, and body size. Given the morphological similarities, we assign this male specimen to the genus and to the species *G. elongata* (see species redescription for discussion on species-level assignment). Examination of other undetermined male specimens revealed similar morphology to the previously mentioned male: general coloration, body size, dorsally directed scutellar processes, slightly to very distinctly dorsally pronounced anterior pronotal lobe, and wing venation pattern, among many other features. Given the morphological similarities between these males and the male of *G. elongata*, we assign these males to *Gibbosella* despite the fact that head shapes in these males are not elongated but rather spherical or short and ovoid.

Nineteen female specimens have been identified as representatives of this genus based on morphological features mentioned in the generic redescription, e.g., small body sizes, antennal segmentation, slightly dorsally projecting scutellar processes, and dark coloration. Despite availability of morphological, molecular, and geographic data, we were unable to associate 16 of them with male-based species. The remaining three female specimens were associated with two male-based species (*G. brunalvus* and *G. planiscutum*) using morphology and geographic data (see species discussions).

There is scutellar and antennal variation among species in this genus: the short, stout scutellar processes in *G. planiscutum* are horizontally oriented (Fig. 2.15D) and the antenna 6-segmented in *G. pallidalata*. As previously mentioned, head shape is also variable among *Gibbosella* species, ranging from spherical or ovoid in most species to elongate and cylindrical in two previously described species.

This genus is very similar to *Synavecoris* by the small size, general dull coloration, ventral head depression restricted to the anteocular (apex of clypeus to anterior eye margin; Fig. 2.13K) region, moderately separated scutellar processes, shallowly depressed MGE that does not extend dorsally in lateral view, basally fused M and Cu in the distal part of the hemelytron, and circular spiracles, but is distinguished by the characters mentioned in the diagnosis. Maldonado (1990) incorrectly listed 1953 as the year *Synavecoris* was described and indicated that the description was based on "nymphs, probably of *Ectrichodia*." Villiers (1968b) described *Synavecoris* based on one macropterous adult male (Fig. 2.12) and two micropterous adult females; nymphs of *Synavecoris* were not described by Villiers. The small size of *Synavecoris*, relatively slender legs, pronotal structure, and wing venation patterns distinguish *Synavecoris* from *Ectrichodia* Lepeletier & Serville, 1825, and thus, we considered *Synavecoris* a valid genus.

Identification key to the males of species of Gibbosella

1. Scutellar processes slender, long, and dorsally directed (Fig. 2.15C) 2
- Scutellar processes short, stout, and horizontally directed (Fig. 2.15D) ....
....*planiscutum*, new species
2. Head circular or ovoid in lateral view, not distinctly elongate and cylindrical 3
- Head very elongate, cylindrical in lateral view .... *elongata* Chłond
3. DFLA divided into four pseudosegments; antenna thus appearing 8-segmented........................4
- DFLA divided into two pseudosegments; antenna thus appearing 6-segmented ....
.... *pallidalata*, new species
4. Head as long as wide..5
- Head longer than wide 9

5. Head ovoid to subpentagonal; labial segment II longer than III; anterior pronotal lobe not laterally carinate..6

- Head nearly circular in lateral view (Fig. 2.13C); labial segments II and III subequal in length; anterior pronotal lobe slightly carinate laterally ....*pallidacorium*, new species

6. Synthlipsis about two times width of eye 7

- Synthlipsis less than two times width of eye 8

7. Head subpentagonal; eye not reaching dorsal and ventral head surfaces; fossula spongiosa absent on mid tibia; body length <7 mm .... *nitida*, new species

- Head ovoid; eye almost reaching dorsal and ventral head surfaces; fossula spongiosa present on mid tibia; body length >7 mm.. *fulva*, new species

8. Synthlipsis about width of eye; fossula spongiosa absent on mid tibia ....*betampona*, new species

- Synthlipsis less than width of eye; fossula spongiosa present on mid tibia .... *mantella*, new species

9. Anteocular region shorter than postocular 10

- Anteocular region as long as postocular (Fig. 2.13C) 11

10. Postclypeus not medially depressed (Fig. 2.13A); synthlipsis width about 2.5 times width of eye; sternal intersegmental sutures carinulate between II–IV .... *andasibe*, new species

- Postclypeus medially depressed (Fig. 2.13B); synthlipsis width about 3.5 times width of eye; sternal intersegmental sutures carinulate between II–VI ....*megafrons*, new species

11. Ventral margin of labial segment III convex (Fig. 2.13C); anterior pronotal lobe not dorsally projecting (Fig. 2.15D); mesosternum with medial and lateral depressions................................. 12

- Ventral margin of labial segment III straight (Fig. 2.13G–I, K); anterior pronotal lobe dorsally projecting above pronotal disc (Fig. 2.15C); mesosternum with one large, shallow medial depression 14

12. Postclypeus distinctly depressed (Fig. 2.13B); synthlipsis width 1.5 times width of eye; pronotal transverse suture complete, not divided by paramedian ridges; vestiture sparse 13

- Postclypeus not distinctly depressed (Fig. 2.13A); synthlipsis width two times width of eye; pronotal transverse suture incomplete, divided by paramedian ridges (Fig. 2.15B); vestiture dense ....*brunalvus*, new species

13. Labial segment II longer than III; abdominal sternites convex, keellike; median pygophore process spadelike in caudal view (Fig. 2.19B) .... *vangocris*, new species

- Labial segment II and III subequal in length; abdominal sternites with shallow medial longitudinal depression (Fig. 2.18C); median pygophore process subquadrate in caudal view (Fig. 2.19A) ....*quadocris*, new species

14. Synthlipsis width about 1.5 times width of eye; eye not reaching dorsal and ventral head surfaces; sternal intersegmental sutures carinulate between II and III and laterally between III–VI .... *conisimilis*, new species

- Synthlipsis width about width of eye; eye reaching dorsal and ventral head surfaces; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI .... *notoconica*, new species

Identification key to the females of species of Gibbosella

1. Head elongate, cylindrical (Fig. 2.12); anterior pronotal lobe strongly elevated dorsally in lateral view; body length >8 mm 2

- Head shorter, ovate (Fig. 2.13F); anterior pronotal lobe slightly to moderately elevated dorsally in lateral view; body length <8 mm 3

2. Scutellar processes convergent; hind tibia with dark apical half....................... *mirabilis* Chłond

- Scutellar processes not convergent; hind tibia yellowish with dark annulus in basal part.............. .... *elongata* Chłond

3. Synthlipsis width three times width of eye; generally brown to dark brown with scutellar apical projections whitish to pale .... *planiscutum*, new species

- Synthlipsis width two times width of eye; generally brown to dark brown with scutellar apical projections brown to dark brown .... *brunalvus*, new species

Gibbosella andasibe, new species

Figs. 2.1, 2.5, 2.8; Map 2.2

DIAGNOSIS: Males recognized among other species in this genus by the very small body size, coloration, anteocular region shorter than the postocular, postclypeus not depressed, synthlipsis width about 2.5 times the width of an eye, and fossula spongiosa absent on mid tibia. This species is similar to *G. megafrons*, from which it differs by the light brown anterior pronotal lobe, brown posterolateral margin of pronotum, pale posterior half of scutellum, the flat postclypeus, smaller synthlipsis width, lack of a fossula spongiosa on the mid tibia, and intersegmental sutures carinulate between sternites II–IV.

DESCRIPTION: **MALE:** Body length: 3.64 mm (holotype). COLORATION: Dark brown with antennal segments VII and VIII, posterolateral margin of pronotum, pleura dorsad of coxae, spot on dorsoposterior margin of mesopleuron, posterior half of scutellum, corium basally, coxae, trochanters, femora basally, laterotergites, except posterior half of VII, and sternites medially and anterolaterally pale. Wing membrane, remainder of antenna, legs, and corium brown. Labium, neck dorsally, and anterior pronotal lobe light brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region shorter than postocular; gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus flat (Fig. 2.13A); synthlipsis about 2.5 times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I);); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel as long as scape; antenna 8-segmented; labium stout; labial segment III subequal to II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections slightly dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum slightly medially longitudinally depressed posteriorly; legs slender; fossula spongiosa absent on mid tibia; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex; distal part of R absent. ABDOMEN: Apex medially notched; sternites medially convex, intersegmental sutures carinulate between II–IV; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate.

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Andasibe National Park, Madagascar.

DISTRIBUTION: The single known specimen was collected southeast of Andasibe National Park headquarters in the Toamasina province (Map 2.2).

HOLOTYPE: Male: **Madagascar: Toamasina:** 7 km SE of Andasibe National Park headquarters, 18.96266°S 48.45266°E, 1050 m, 07 Jan 2001–22 Jan 2001, M. Irwin, R. Harin'Hala (00044816) (CAS).

Gibbosella betampona, new species

Figs. 2.1, 2.5, 2.8; Map 2.3

DIAGNOSIS: Males recognized among other species in *Gibbosella* by the circular head shape in lateral view that is as long as it is wide in dorsal view, large ocelli, eyes reaching dorsal and ventral head margin, labial segment II longer than III, mesosternum with large medial depression, absence of the fossula spongiosa on the mid tibia, and BPE shorter than the basal plate. This species is similar to *G. mantella*, but the pale posterior margin of the pronotum and lateral spots on the meso- and metasterna, the brown corium, larger synthlipsis width, meso- and metasterna not completely separated by a distinct suture, absence of the fossula spongiosa on the mid tibia, and shorter BPE relative to the basal plate distinguish this species from *G. mantella*.

DESCRIPTION: **MALE:** Body length: 6.40 mm (holotype). COLORATION: Dark brown with pale labial segment IV, antennal segment V apically, antennal segments VI–VIII, lateral spots on meso- and metasterna, coxae, trochanters, forefemur basally, mid and hind femora basally and subapically, foretibia except medially, mid and hind tibiae, tarsi, anterior half of laterotergites, paramedian spots on sternites III–V, and lateral margin of sternite VII. Remainder of labium, corium, and basal wing veins brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13C); as long as wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large, located on distinct median tubercle (Fig. 2.13C); eye about half of head length, not reaching dorsal head surface, reaching ventral head surface; antenna inserted dorsally on head; pedicel about as long as scape; antenna 8-segmented; labium stout; labial segment III shorter than II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna not completely or weakly separated by distinct transverse suture (Fig. 2.15E); mesosternum with large medial depression; metasternum slightly medially longitudinally depressed; forefemur slightly incrassate; fossula spongiosa absent on mid tibia; tarsomeres I and II combined shorter than III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex medially notched; sternites flat, intersegmental sutures carinulate between II–IV and laterally between IV–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G); area of endosomal struts–DPS fusion ovate (Fig. 2.21A).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the locality in which the two known specimens were collected, Reserve Betampona, Madagascar.

DISTRIBUTION: Betampona Reserve in the Toamasina province (Map 2.3).

HOLOTYPE: Male: **Madagascar: Toamasina:** Reserve Betampona, Camp Vohitsivalana, 37.1 km 338 Toamasina, 17.88666°S 49.2025°E, 520 m, 01 Dec 2005–03 Dec 2005, Fisher et al. (00006143) (CAS).

PARATYPE: **Madagascar: Toamasina**: Reserve Betampona, Camp Vohitsivalana, 37.1 km 338 Toamasina, 17.88666°S 49.2025°E, 520 m, 01 Dec 2005–03 Dec 2005, Fisher et al., 1♂ (00007255) (CAS).

Gibbosella brunalvus, new species

Figs. 2.1, 2.5, 2.8, 2.23A; Map 2.1

DIAGNOSIS: Males are recognized among others in *Gibbosella* by a combination of the following characters: the coloration, dense vestiture, postclypeus not depressed, pronotal transverse suture divided by paramedian ridges, and scutellar processes dorsally directed. Females are recognized by the coloration and synthlipsis about two times the width of an eye. Males are very similar to *G. fulva*, from which *G. brunalvus* differs by the more abundant pale markings on the pronotum, scutellum, corium, and sternites, smaller body size, dense vestiture, head longer than wide, flat postclypeus, and divided pronotal transverse furrow, among several other features. Females are similar to *G. planiscutum* based on the features mention in the generic description, but are distinguished by the dark brown antennal segment VIII and scutellum, femora basally and tibiae apically and basally pale to light brown, and smaller synthlipsis width.

DESCRIPTION: **MALE:** Body length: 4.89 mm (holotype), 4.79–5.13 mm. COLORATION: Dark brown with pale color on posterolateral margin of pronotum, scutellar processes, basal half of corium, coxae ventrally, trochanters, femora and tibiae basally, tarsi, anterior half of laterotergites, and sternites anterolaterally pale. Antennal segment V apically and segments VI-VIII white. Dorsal head surface, except synthlipsis and ocellar tubercle, markings throughout anterior pronotal lobe, labium, and antenna brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin (Fig. 2.13E, G–K); postclypeus flat (Fig. 2.13A); synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about as long as scape; antenna 8-segmented; labium stout; labial segment III shorter than II, ventrally convex. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; forefemur incrassate; fossula spongiosa on mid tibia; tarsomeres I and II combined subequal to III; hemelytron reaching or surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex rounded; sternites convex, shallowly depressed between paramedian ridges on sternites II–V, intersegmental sutures carinulate between II–IV and laterally between IV–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G), fused anterior to fusion with DPS; area of endosomal struts–DPS fusion circular. **FEMALE:** Body length: 4.54 mm. Similar to males, but differ in the following characters: COLORATION: Dark brown with pale to light brown scape, pedicel, antennal segments III-IV and basal half of V, labium, femora except basal, and tibiae except apical and basal parts. Remaining antennal segments, coxae, trochanters, femora basally, tibiae apically and basally, and tarsi whitish to pale brown. STRUCTURE: In addition to characters mentioned in the generic description: HEAD: Synthlipsis about two times width of eye. THORAX:

Pronotal longitudinal furrow restricted to anterior lobe; lateral depressions on posterior pronotal lobe obsolete; forefemur with small ventral tubercles (Fig. 2.16D). ABDOMEN: Intersegmental sutures carinulate between sternites II–VI; external genitalia as in Fig. 2.23A; bursa copulatrix membranous, with lateral lobes (Fig. 2.23F); vermiform gland and lateral spermathecae damaged.

ETYMOLOGY: The species epithet is a noun in the nominative case and is named after the nearly uniform dark brown venter.

DISTRIBUTION: Tsingy de Bemaraha National Park in Mahajanga province (Map 2.1).

DISCUSSION: The coloration is entirely dark brown on the head and anterior pronotal lobe, pale to brown medial stripes on the abdominal sternites in some male specimens. A female specimen was associated with males based on morphology and the same collection event as one other male.

HOLOTYPE: Male: **Madagascar: Mahajanga:** Parc National Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Vazimba, 19.14194°S 44.82805°E, 50 m, 06 Nov 2001–10 Nov 2001, Fisher et al. (00006317) (CAS).

PARATYPES: **Madagascar: Mahajanga:** Parc National Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Vazimba, 19.14194°S 44.82805°E, 50 m, 06 Nov 2001–10 Nov 2001, Fisher et al., 3♂ (00006122, 00006318, 00099043) (UCR), 3♂ (00006319, 00006321, 00099044) (SU), 5♂ (00006322–00006326) (CAS), 2♂ (00006327, 00006328) (BMNH), 2♂ (00006329, 00006455) (USNM). Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 19.70944°S 44.71806°E, 150 m, 16 Nov 2001–20 Nov 2001, Fisher et al., 1♂ (00045686), 1♀ (00048066) (CAS). **Unknown:** 2♂ (00007154, 00044944) (CAS).

Gibbosella conisimilis, new species

Figs. 2.1, 2.5, 2.8, 2.15C, 2.18A; Map 2.1

DIAGNOSIS: Males are recognized among other species in *Gibbosella* by the larger body size, synthlipsis width 1.5 times the width of an eye, labial segment III ventrally straight, conically elevated anterior pronotal paramedian lobes in lateral view, anterior pronotal lobe without anterolateral protuberances, continuous pronotal transverse suture, and mesosternum with large medial depression. This species is similar to *G. notoconica*, but the slightly smaller body size, pale apex of antennal segment V, dark brown pronotum (except anterior and posterolateral margins and disc) and mesosternum (except anterolaterally and posteriorly), larger synthlipsis width, interocular sulcus posterior to the hind margin of the eye, smaller ocelli, eye size relative to the head length and height, and intersegmental sutures carinulate between II and III and laterally between III–VI distinguish this species from *G. notoconica*. The conical anterior pronotal paramedian lobes are also not as distinct as in *G. notoconica*.

DESCRIPTION: **MALE:** Body length: 7.92 mm (holotype), 7.86–8.44 mm. COLORATION: Dark brown with pale dorsal head surface (except clypeal apex, mandibular plates, antennifers, anterior of interocular sulcus, interocular sulcus, and dorsal surface of ocellar tubercle), scape basally, antennal segment V apically, and segments VI-VIII, anterior and posterolateral margins of pronotum, pronotal disc, lateral longitudinal depressions of posterior pronotal lobe, stridulatory groove, mesosternum anterolaterally and posteriorly, metasternum, scutellum medially, corium basally, coxae, trochanters, femora basally and ventrally, mid and hind tibiae medially, tarsi, anterior margin of laterotergites, and sternites medially and anterolaterally. VESTITURE: Very sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.5 times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-third longer than scape; antenna 8-segmented; labium slender; labial segment III subequal to II, ventrally straight (Fig. 2.13G, H, K). THORAX (Fig. 2.15C): Anterior pronotal lobe slightly conical in lateral view, without distinct anterolateral projections; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed; meso- and metasterna not completely or weakly separated by distinct transverse suture (Fig. 2.15E); mesosternum with large medial depression; metasternum slightly medially longitudinally depressed; legs slender; fossula spongiosa on mid tibia; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN (Fig. 2.18A): Apex medially notched or sinuate; sternites medially convex, intersegmental sutures carinulate between II and III and laterally between III–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS, ventrally obscured by semiextended endosoma; area of endosomal struts–DPS fusion ovate (Fig. 2.21A).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the similar pronotal appearance of the pronotum in *G. notoconica*.

DISTRIBUTION: Marojejy Nature Reserve in Antsiranana province (Map 2.1).

DISCUSSION: Coloration is variable with the dark brown area around the ocellar tubercle and interocular sulcus variable in size. The anterior pronotal lobe may be dorsally pale, and the pronotal transverse sulcus entirely or nearly entirely pale.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 26 Sep 2005–04 Oct 2005, M. Irwin, R. Harin'Hala (00044850) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 15 Dec 2004–20 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00007113) (CAS), 1♂ (00045329) (SU); 25 Dec 2004–30 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00007260) (UCR); 10 Jan 2005–15 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00045259) (CAS); 25 Feb 2005–04 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00007066) (CAS); 25 Mar 2005–04 Apr 2005, M. Irwin, R. Harin'Hala, 1♂ (00045427) (CAS); 04 Apr 2005–16 Apr 2005, M. Irwin, R. Harin'Hala, 2♂ (00007079, 00007083) (CAS), 2♂ (00007150, 00007199) (BMNH); 18 May 2005–30 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00044819) (CAS); 30 May 2005–11 Jun 2005, M. Irwin, R. Harin'Hala, 1♂ (00045317) (SU); 11 Jun 2005–28 Jun 2005, M. Irwin, R. Harin'Hala, 1♂ (00045495) (UCR); 14 Oct 2005–22 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00007054) (AMNH). R.N.I. de Marojejy, 8.0 km NW Manantenina, 14.43667°S 49.775°E, 450 m, 05 Oct 1996–13 Oct 1996, E. Quinter and T. Nguyen, 1♂ (00078363) (AMNH). **Unknown:** 1♂ (00007064) (CAS).

Gibbosella elongata, Chłond, 2010

Figs. 2.1, 2.5, 2.12; Map 2.2

Gibbosella elongata Chłond, 2010: 64.

REVISED DIAGNOSIS: Males recognized among other species in this genus by the larger body size, synthlipsis width same as width of an eye, labial segment III ventrally convex, elevated anterior pronotal paramedian lobes in lateral view, anterior pronotal lobe with small anterolateral projections. Females are recognized by the cylindrical head, scape surpassing apex of the head, and very gibbous anterior pronotal lobe with small anterolateral projections. This species can be easily distinguished from *G. mirabilis* by the enlarged, elongated, and much more elevated anterior pronotal lobe and lack of a depression in the posterior part of anterior pronotal lobe.

REDESCRIPTION: **MALE:** Body length: 9.90 mm. COLORATION: Dark brown with pale basal part of scape, coxa, trochanters, basal part of forefemur, basal and apical part of mid and hind femur, apical and middle part of mid tibiae, hind tibiae except small subapical ring, anterior part of laterotergites III-VII and middle part of abdominal tergites III-VII. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Elongate ovoid to cylindrical in lateral view; longer than wide in dorsal view; anteocular region longer than postocular; gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large sized, located on distinct median tubercle; eye about one-third of head length, reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel slightly longer than scape; labium stout; labial segment III shorter than II, ventrally convex. THORAX: Anterior pronotal lobe gibbous (Fig. 2.5) with small anterolateral projections; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe striated transversely; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); forefemur incrassate; fossula spongiosa on mid tibia; tarsomeres I and II combined same length as III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Sternites medially convex, intersegmental sutures carinulate between II–IV; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; area of endosomal struts–DPS subquadrate. **FEMALE:** Body length: 9.40 mm (holotype). Similar to males, but differ in the following characters:

COLORATION: Shining, dark brown with pale labrum, DFLA, small spots on pronotum and thorax, coxae, trochanters, basal half of forefemur and two-thirds of mid and hind femora, as well as apical part of all femora, tibiae and anterior part of laterotergites. STRUCTURE: In addition to characters mentioned in the generic description: HEAD (damaged): Slightly convex gula. THORAX: Anterior pronotal lobe gibbous with small anterolateral projections (Fig. 2.12); visible medial longitudinal sutures on both pronotal lobes; lateral depressions on posterior pronotal lobe striated transversely. ABDOMEN: Tergites laterally and laterotergites striated transversely; tergites posterior distinctly rounded, except tergite III; sternites with distinct visible fold near lateral margin; intersegmental sutures carinulate between sternites II-VII; valvifer I triangular with flat dorsal part and one long setae; valvula I small with long hairs placed on small fold visible in middle part; valvula III elongate, convolute in apical part with distinct dome-shaped elevation.

DISTRIBUTION: The type specimen was collected in the Anjanaharibe-Sud Reserve, west of Andapa, which is located in the southern part of Antsiranana province (Map 2.2). The only known male specimen was collected in Maroantsetra near the Toamasina-Antsiranana border, which is in close proximity to the type locality.

DISCUSSION: Chłond (2010a) recently described this species from a single female representative. An undetermined male specimen was observed to have morphological similarities to *G. elongata* and *G. mirabilis*: elongate, cylindrical head shape; dorsally protruding anterior pronotal lobe; dorsally oriented scutellar processes; and general dark brown to blackish and pale coloration. Although extreme sexual dimorphism exists in *Gibbosella*, we assign the male to *G. elongata* based on the small basal dark brown band on the hind tibia and broader pale bands on the dorsal laterotergites; in *G. mirabilis*, the hind tibia is dark brown on the apical one-third to one-half and the dorsal laterotergites have more narrow pale bands. Furthermore, the male was collected near the border of Toamasina and Antsiranana provinces, in close proximity to the type locality of *G. elongata*; *G. mirabilis* has been collected from the southwestern region of Toamasina, near the Antananarivo-Toamasina border.

HOLOTYPE: Female: **Madagascar: Antsiranana:** Andapa District, Anjanaharibe-Sud Reserve, 14.69889°S 49.45483°E, 1600 m, 1960, P. Soga (MNHN).

OTHER MATERIAL EXAMINED: **Madagascar: Toamasina:** Maroantsetra/Ambodivoangy, 15.43231°S 49.74013°E, 9 m, no date provided, 1♂ (MNHN).

Gibbosella fulva, new species

Figs. 2.1, 2.5; Map 2.2

DIAGNOSIS: Males are recognized among other species in this genus by the shiny brown color of the body, the head about as long as wide in dorsal view, synthlipsis two times the width of an eye, medium sized ocelli, eyes almost reaching dorsal and ventral head margin, labial segment II longer than III, anterior pronotal lobe without anterolateral projections, mesosternum with large medial depression, and fossula spongiosa on the mid tibia. This species is similar to *G. brunalvus*, but can be distinguished by the dark brown pronotum, scutellum, and corium, larger body size, sparse vestiture, head about as long as wide, depressed postclypeus, and pronotal transverse furrow continuous, among several other features.

DESCRIPTION: **MALE:** Body length: 7.40 mm (holotype), 7.37–7.40 mm. COLORATION: Dark brown with labial segments III and IV, antennal segments V–VIII, and anterior part of laterotergites pale. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); about as long as wide in dorsal view; anteocular region as long as postocular (Fig. 2.13E); gula flat, conforming to rounded shape of head (Fig. 2.13E); postclypeus with deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B);

ocelli medium sized, located on shallow median tubercle (Fig. 2.13I); eye about one-third of head length, almost reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel as long as scape; antenna 8-segmented; labium stout; labial segment III shorter than II, ventrally convex (Fig. 2.13E). THORAX: Anterior pronotal lobe without anterolateral projections; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections slightly dorsally directed (Fig. 2.15C); ventrally obscured by card mount; forefemur incrassate; fossula spongiosa on mid tibia; tarsomeres I and II combined shorter than III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex medially notched, sternites medially obscured by card mount, but intersegmental sutures carinulate at least laterally between II–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; area of endosomal struts–DPS fusion basally narrow but distally wider and ovate.

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named after the shiny brown color of the body.

DISTRIBUTION: Antanambe and Seranambe in the Mananara District of Toamasina (Map 2.2).

HOLOTYPE: Male: **Madagascar: Toamasina:** Mananara-Nord District, Seranambe, 16.24683°S 49.83916°E, 16 m, Jul 1965, J. Vadon and A. Peyrieras (MNHN).

PARATYPE: **Madagascar: Toamasina:** Mananara-Nord District, Antanambe, 16.43333°S 49.85°E, 8 m, no date provided, J. Vadon and A. Peyrieras, 1♂ (MNHN).

Gibbosella mantella, new species

Figs. 2.1, 2.5, 2.8, 2.13C; Map 2.3

DIAGNOSIS: Males recognized among other species in *Gibbosella* by the circular head shape in lateral view that is as long as it is wide in dorsal view, synthlipsis less than the width of an eye, large ocelli, eyes reaching dorsal and ventral head margin, labial segment II longer than III, mesosternum with large medial depression, fossula spongiosa on the mid tibia, and BPE as long as the basal plate. This species is similar to *G. betampona*, but the slightly darker pronotum, pale meso- and metasterna and corium, smaller synthlipsis width, meso- and metasterna separated by a distinct suture, presence of the fossula spongiosa on the mid tibia, and longer BPE relative to the basal plate distinguish this species from *G. betampona*.

DESCRIPTION: **MALE:** Body length: 5.42 mm (holotype). COLORATION: Dark brown with pale labial segment IV, apical half of antennal segment V, antennal segments VI–VIII, posterior margin of pronotum, stridulatory groove, meso- and metasterna, corium and basal wing veins, coxae, trochanters, femora basally, mid and hind tibiae medially, tarsi, laterotergites except posterior margin, and sternites medially and laterally. Remainder of antenna and labium, dorsal surface of pronotum, and legs brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD (Fig. 2.13C): Ovoid in lateral view; as long as wide in dorsal view; anteocular region as long as postocular; gula flat, conforming to rounded shape of head; postclypeus with deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis less than width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large, located on distinct median tubercle; eye about half of head length, reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel as long as scape; antenna 8-segmented; labium stout; labial segment III shorter than II, ventrally convex. THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with large medial depression; metasternum slightly medially longitudinally depressed; forefemur incrassate; fossula spongiosa on mid tibia; tarsomeres I and II combined shorter than III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex medially notched; sternites medially convex, intersegmental sutures carinulate between II–IV and laterally between IV–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G); endosomal struts–DPS fusion basally narrow, distally wider and ovate (Fig. 2.21A).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Camp Mantella, Marojejy National Park, Madagascar.

DISTRIBUTION: Marojejy Nature Reserve in Antsiranana province (Map 2.3).

HOLOTYPE: Male: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 11 Feb 2005–18 Feb 2005, M. Irwin, R. Harin'Hala (00006458) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 28 Apr 2005–07 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00006460) (CAS); 14 Oct 2005–22 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00007038) (UCR). R.N.I. de Marojejy, 10.0 km NW Manantenina, 14.43333°S 49.76167°E, 750 m, 15 Oct 1996–22 Oct 1996, E. Quinter and T. Nguyen, 1♂ (00078367) (AMNH).

Gibbosella megafrons, new species

Figs. 2.1, 2.5, 2.8; Map 2.1

DIAGNOSIS: Males recognized among other species in *Gibbosella* by the very small body size, coloration, anteocular region shorter than the postocular, postclypeus depressed, synthlipsis width about 3.5 times the width of an eye, and distal part of R absent. This species is similar to *G.*

andasibe, from which it differs by the entirely dark brown pronotum and scutellum, depressed postclypeus, larger synthlipsis width, presence of a fossula spongiosa on the mid tibia, and intersegmental sutures carinulate between II–VI.

DESCRIPTION: **MALE:** Body length: 3.78 mm (holotype), 3.78–5.05 mm. COLORATION: Dark brown with pale antennal segments VI and VII, posterodorsal spot on mesopleuron, spots on pleura dorsad of coxae, corium basally, coxae, trochanters, femora basally, anterior half of laterotergites, sternites III–VI medially, and anterolateral margins of sternites pale. Antennal segments IV and V, labium, scutellar processes, remainder of corium, basal wing veins, and remainder of legs brown. Wing membrane light brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region shorter than postocular; gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 3.5 times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel as long as scape; antenna 8-segmented; labium stout; labial segment III subequal to II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); separation of meso- and metasterna obscured; mesosternum with medial and paramedial longitudinal depressions; metasternum slightly medially longitudinally depressed; forefemur slightly incrassate; presence of fossula spongiosa on mid tibia cannot be determined due to tibial apex obscured; tarsomeres I and II combined shorter than III; hemelytron surpassing abdominal apex; distal part of R absent. ABDOMEN: Apex medially notched; sternites medially convex, intersegmental sutures carinulate between II–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; basal plate and BPE damaged; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate.

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the very large synthlipsis width.

DISTRIBUTION: Ranomafana National Park and Midongy du Sud National Park in the Fianarantsoa province (Map 2.1).

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1110 m, 28 Nov 2001–06 Dec 2001, M. Irwin, R. Harin'Hala (00007168) (CAS).

PARATYPE: **Madagascar: Fianarantsoa:** Sud-Est Midongy, Sud Mont Papango (sud-ouest Befotaka), 23.85000°S 46.98333°E, 1200 m, Mar 1959, Andria Robinson, 1♂ (MNHN).

Gibbosella mirabilis Chłond, 2010

Fig. 2.12; Map 2.1

Gibbosella mirabilis Chłond, 2010: 63.

DISTRIBUTION: The only known specimen was collected from "Périnet" (currently known as Andasibe-Mantadia National Park) in the Toamasina province (Map 2.1).

DISCUSSION: This species was recently described by Chłond (2010a) from a single female representative. No other female or male specimens have been examined, and, thus, this species is not redescribed. This species is very similar to *G. elongata,* but is distinguished by the more strongly dorsally elevated anterior pronotal lobe, convergent scutellar processes, and hind tibiae with dark coloration on the apical half.

HOLOTYPE: Female: **Madagascar: Toamasina:** Périnet (Andasibe), 18.82666°S 48.44778°E, 1119 m, Oct 1972, A. Peyrieras (MNHN).

Gibbosella nitida, new species

Figs. 2.1, 2.5; Map 2.2

DIAGNOSIS: Males are recognized among other species in this genus by the small body size, synthlipsis two times the width of an eye, eye one-fourth of head length, fossula spongiosa absent on the mid tibia, and corium with relatively large shiny granulations not covered by setae, as well as small granulations with very short, erected, flattened setae. This species is similar to *G. megafrons*, but is distinguished by the smaller body size, more subpentagonal head that is as long as it is wide, anteocular length subequal to postocular, smaller synthlipsis width, longer labial segment II relative to III, and appearance of the corium.

DESCRIPTION: **MALE:** Body length: 4.75 mm (holotype). COLORATION: Dark brown with labial segment III and IV brown. Labial segment II apically and III basally, basal two-thirds of scape, coxae, trochanters, femora ventrally, and sternites II–VI medially and laterally pale. Corium with shiny areas due to relatively large shiny granulations not covered by setae, as well as dull areas due to very small granulations with very short, erect, flattened setae. VESTITURE: Dense; corium with shorter, flattened setae; other features as in generic description. Hemelytra covered by very dense, small granulations with very short and flattened setae, as well as sparse relatively large granulations without setae. STRUCTURE: HEAD: Ovate, almost pentagonal in lateral view; about as long as wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula slightly swollen ventrolaterally, not distinctly produced beyond ventral head margin (Fig. 2.13F–K); postclypeus with deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis two times width of eye; interocular sulcus near hind margin of eye

(Fig. 2.13B); ocelli large, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel slightly longer than scape; antenna 8-segmented; labium stout; labial segment III shorter than II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe without anterolateral projections; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); ventrally obscured by card mount; forefemur incrassate; fossula spongiosa absent on mid tibia; tarsomeres I and II combined shorter than III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; sternites medially obscured by card mount, but intersegmental sutures carinulate at least laterally between II–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; area of endosomal struts–DPS fusion basally narrow but distally wider and ovate subquadrate.

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the shiny hemelytra.

DISTRIBUTION: The only known specimen was collected in the Marojejy Nature Reserve in that Antsiranana province (Map 2.2).

HOLOTYPE: Male: **Madagascar: Antsiranana:** Sambava District, Marojejy, Ambinanitelo, 14.44133°S 49.73908°E, 500 m, Dec 1958, Raharizonina (MNHN).

Gibbosella notoconica, new species

Figs. 2.1, 2.5, 2.8, 2.20A, 2.21A; Map 2.2

DIAGNOSIS: Males are recognized among other species in this genus by a combination of the following characters: the larger body size, synthlipsis as wide as an eye, large ocelli, eyes reaching the dorsal and ventral head margins in lateral view, labial segment III ventrally straight, conically elevated anterior pronotal paramedian lobes in lateral view, anterior pronotal lobe without anterolateral protuberances, continuous pronotal transverse suture, and mesosternum with large medial depression. This species is similar to *G. conisimilis*, but the slightly larger body size, pale antennal segment V, dark brown pronotum with pale lateral spots extending from posterior half of anterior lobe to anterior half of posterior lobe, pale meso- and metasterna, smaller synthlipsis width, interocular sulcus near the hind margin of the eye, larger ocelli, eye size relative to the head length and height, the more distinctive conical anterior pronotal paramedian lobes with a dorsal protuberance, and intersegmental sutures carinulate between II–IV and laterally between IV–VI distinguish this species from *G. conisimilis*.

DESCRIPTION: **MALE:** Body length: 9.48 mm (holotype), 8.53–9.48 mm. COLORATION: Dark brown with pale synthlipsis laterally, postocular dorsally except ocellar tubercle, neck dorsally, scape basally, antennal segments V–VIII, anterior and posterolateral margins of pronotum, lateral spots extending from posterior half of anterior pronotal lobe to anterior half of posterior lobe, stridulatory groove, meso- and metasterna, coxae, trochanters, forefemur basally and ventrally, mid and hind femora basally and subapically, tibiae medially, anterior area of laterotergites, lateral margins of sternites, and sternites medially. Labium and remainder of antenna brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large, located on distinct median tubercle (Fig. 2.13C); eye about half of head length, reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-fourth longer than scape; antenna 8-segmented; labium slender; labial segment III subequal to II, ventrally straight (Fig. 2.13G–I, K). THORAX: Anterior pronotal lobe conical in lateral view (Fig. 2.15C), without distinct anterolateral projections; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe transversely striated; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with large medial depression; metasternum slightly medially longitudinally depressed; legs slender; fossula spongiosa on mid tibia; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex medially notched or sinuate; sternites medially convex, intersegmental sutures carinulate between II–IV and laterally between IV–VI; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G); area of endosomal struts–DPS fusion ovate (Fig. 2.21A).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the conical anterior pronotal paramedian lobes.

DISTRIBUTION: Marojejy Nature Reserve in Antsiranana province (Map 2.2).

DISCUSSION: The coloration is slightly variable with the postclypeus entirely dark brown, the pronotum less pale, and the brown ventrolateral longitudinal band on the sternites varying in size in some specimens.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 30 May 2005–11 Jun 2005, M. Irwin, R. Harin'Hala (00045367) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 25 Dec 2004–30 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00007240) (CAS); 18 Feb 2005–25 Feb 2005, M. Irwin, R. Harin'Hala, 1♂

(00045655) (CAS); 11 Mar 2005–18 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00044813) (SU); 28 Apr 2005–07 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00007174) (UCR); 14 Oct 2005–22 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00045558) (UCR). **Unknown:** 1♂ (00006144) (CAS).

Gibbosella pallidacorium, new species

Figs. 2.1, 2.5, 2.8; Map 2.1

DIAGNOSIS: Males are recognized among other species of *Gibbosella* by a combination of the following characters: the coloration, circular head shape in lateral view that is as long as it is wide in dorsal view, large ocelli, anterior pronotal lobe laterally carinate, meso- and metasterna not completely separated by a distinct suture, and intersegmental sutures carinulate between II–IV and laterally between IV and V. This species is similar to *G. betampona*, but differs by the pale postocular and neck, pale markings on the pronotum, pale corium, pale ventral abdominal surface with dark brown longitudinal stripe laterally, circular head shape, relatively deeper postclypeal depression, eye not reaching ventral head margin, labial segment II and III subequal, anterior pronotal lobe laterally carinate, mesosternum with three longitudinal depressions, fossula spongiosa on the mid tibia, and intersegmental sutures carinulate between II–IV and laterally between IV and V.

DESCRIPTION: **MALE:** Body length: 5.78 mm (holotype). COLORATION: Dark brown with pale postocular and neck dorsally, scape basally, apical half of antennal segment V and segments VI and VII, labial segment IV, anterior pronotal lobe anteromedially, pronotal disc, posterior pronotal lobe anterolaterally and posterolateral margin, stridulatory groove, meso- and metasterna, corium except apical margin, basal wing veins, coxae, trochanters, mid and hind femora basally and medially (forelegs missing), mid tibia medially and apically, hind tibia except basally, dorsal laterotergites except posterior margin, ventral laterotergites, and sternites except pygophore and laterally. Labial segment III and wing membrane brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Circular in lateral view (Fig. 2.13C); as long as wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large, located on shallow median tubercle (Fig. 2.13I); eye about half of head length, nearly reaching dorsal and ventral head surface; antenna inserted dorsally on head; pedicel about one-fourth longer than scape; antenna 8-segmented; labium slender; labial segment III subequal to II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B), slightly carinate laterally; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe transversely striated; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna not completely separated by distinct transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum slightly medially longitudinally depressed; forelegs missing, mid and hind legs slender; fossula spongiosa on mid tibia; tarsi missing; hemelytron surpassing abdominal apex; distal part of R absent. ABDOMEN: Apex sinuate; sternites medially convex, intersegmental sutures carinulate between II–IV and laterally between IV and V; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS, posteriorly obscured by semiextended endosoma; area of endosomal struts–DPS fusion circular.

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the pale corium.

DISTRIBUTION: The only known specimen was collected in Marojejy Nature Reserve in Antsiranana province (Map 2.1).

HOLOTYPE: Male: **Madagascar: Antsiranana:** R.N.I. de Marojejy, 11.0 km NW Manantenina, 14.43667°S 49.74167°E, 1225 m, 25 Oct 1996–03 Nov 1996, Eric L. Quinter (00078364) (AMNH).

Gibbosella pallidalata, new species

Figs. 2.1, 2.5, 2.8; Map 2.1

DIAGNOSIS: Males recognized among other species in *Gibbosella* by the coloration, 6-segmented antenna, anterior pronotal lobe without distinct anterolateral protuberances, and fossula spongiosa absent on the mid tibia. This species is similar to *G. planiscutum*, but, in addition to the diagnostic features, it differs by the continuous pronotal transverse suture, separation of the meso- and metasterna, and intersegmental sutures carinulate between II–VI.

DESCRIPTION: **MALE:** Body length: 5.23 mm (holotype), 4.88–5.34 mm. COLORATION: Pale with dark brown head, propleuron medially, mesopleuron and metapleuron except dorsad of coxae, thoracic sterna, sternites ventrolaterally, and pygophore medially. Antenna, labium, posterior pronotal lobe medially, scutellum, distal half of corium, legs except femora basally and ventrally and mid and hind tibiae medially, and posterior half of laterotergites II–VI brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin (Fig. 2.13F–K); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about as long as scape; antenna 6-segmented; labium stout; labial segment III shorter than II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe without distinct anterolateral projections; pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum slightly medially longitudinally depressed; forefemur slightly incrassate; fossula spongiosa absent on mid tibia; tarsomeres I and II combined subequal to III on forelegs, longer on mid and hind legs; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex rounded or sinuate; sternites medially convex, intersegmental sutures carinulate between II–VI; pygophore process flattened in lateral view (Fig. 2.20F), subtriangular in caudal view (Fig. 2.19G, I), apex rounded; BPE shorter than basal plate; endosomal struts not reaching posterior margin of DPS, posteriorly obscured by semiextended endosoma; area of endosomal struts–DPS fusion elongate subquadrate.

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the pale wing membrane.

DISTRIBUTION: Fianarantsoa and Toliara provinces (Map 2.1).

DISCUSSION: Some specimens have small paramedian brown spots on the anterior pronotal lobe.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 14 Apr 2002–23 Apr 2002, M. Irwin, R. Harin'Hala (00044983) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 16 Oct 2001–08 Nov 2001, M. Irwin, R. Harin'Hala, 2♂ (00007237, 00007245) (CAS); 08 Nov 2001–15 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00007159) (SU); 22 Nov 2001–28 Nov 2001, M. Irwin, R. Harin'Hala, 2♂ (00045117, 00045624) (BMNH); 04 Feb 2002–12 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007206) (CAS); 26 Feb 2002–04 Mar 2002, M. Irwin, R. Harin'Hala, 1♂ (00007130) (AMNH); 31 Mar 2002–07 Apr 2002, M. Irwin, R. Harin'Hala, 2♂ (00045535, 00045541) (USNM); 07 Apr 2002–14 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00044918) (CAS); 14 Apr 2002–23 Apr 2002, M. Irwin, R. Harin'Hala, 2♂ (00007074, 00044825) (MNHN), 2♂ (00044914, 00045473) (BMNH); 28 Apr 2002–05 May 2002, M. Irwin, R. Harin'Hala, 2♂ (00005356, 00007215) (SU); 05 May 2002–13 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00007232) (CAS); 04 Jul 2002–14 Jul 2002, M. Irwin, R. Harin'Hala, 3♂ (00007205, 00007222, 00007243) (CAS); 14 Jul 2002–24 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00007246) (UCR). Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1110 m, 28 Nov 2001–06 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00044934) (CAS), 1♂ (00045471) (MNHN); 15 Dec 2001–21 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00099046) (CAS); 28 Jan 2002–04 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00044827) (SU); 04 Feb 2002–12 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007235) (CAS); 06 May 2002–15 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00007194) (CAS); 04 Jun 2002–14 Jun 2002, M. Irwin, R. Harin'Hala, 2♂ (00007262, 00007267) (USNM); 15 Jul 2002–25 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00045533) (UCR). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 28 Nov 2001–06 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00045580) (CAS); 31 Mar 2002–09 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00007132) (CAS); 09 Apr 2002–16 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00007228) (AMNH); 15 Jul 2002–25 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00005358) (USNM); 07 Sep

2003–18 Sep 2003, M. Irwin, R. Harin'Hala, 2♂ (00007108, 00044902) (CAS) ; 21 Mar 2004–02 Apr 2004, M. Irwin, R. Harin'Hala, 1♂ (00007036) (SU); 18 Mar 2006–30 Mar 2006, M. Irwin, R. Harin'Hala, 1♂ (00007145) (CAS); 17 Oct 2006–01 Nov 2006, M. Irwin, R. Harin'Hala, 1♂ (00045653) (UCR). Ranomafana JIRAMA water works, 21.2485°S 47.45216°E, 690 m, 22 Nov 2001–28 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00007210) (CAS), 1♂ (00007227) (UCR). Ranomafana National Park, Talatakely, 21.25°S 47.41667°E, 900 m, 09 Jan 2001–19 Jan 2001, D.H. and K.M. Kavanaugh, R.L. Brett, E. Elsom, and F. Vargas, 2♂ (00007110, 00044853) (CAS), 2♂ (00044979, 00044996) (AMNH). **Toliara:** Berenty Special Reserve, 8 km NW Amboasary, 25.021°S 46.3055°E, 35 m, 29 Aug 2004–08 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044876) (CAS). Parc National d'Andohahela, Col du Sedro, 3.8 km 113° ESE Mahamavo, 37.6 km 341° NNW Tolagnaro, 24.76388°S 46.75166°E, 900 m, 21 Jan 2002–25 Jan 2002, Fisher et al., 1♂ (00006463) (UCR), 1♂ (00007085) (CAS), 1♂ (00007247) (MNHN). **Unknown:** 6♂ (00007076, 00007125, 00007204, 00007216, 00007249, 00007264) (CAS).

Gibbosella planiscutum, new species

Figs. 2.1, 2.5, 2.8, 2.17A, 2.23B; Map 2.3

DIAGNOSIS: Males are recognized among other species in this genus by a combination of the following characters: the coloration, dense vestiture, pronotal transverse suture divided by paramedian ridges, scutellar processes horizontally directed, meso- and metasterna not entirely separated by a distinct suture, and intersegmental sutures carinulate between II–VI and laterally between VI and VII. Females are recognized by the coloration and synthlipsis about three times the width of an eye. Males are similar to *G. brunalvus*, from which it differs by the pale markings on the head (e.g., mandibular and maxillary plates, antennifers, ventral and lateral anteocular and postocular surface), pale pronotum with dark brown paramedian spots on the anterior lobe and margins of posterior lobe, depressed postclypeus, orientation of the scutellar processes, lack of a distinct separation between the meso- and metasterna, and intersegmental sutures carinulate between II–VI and laterally between VI and VII. Females are very similar to *G. brunalvus*, but are distinguished by the nearly black body, pale apex of antennal segment VIII and apex of scutellum, and larger synthlipsis width.

DESCRIPTION: **MALE:** Body length: 5.08 mm (holotype), 4.91–5.90 mm. COLORATION: Dark brown with pale mandibular and maxillary plates, antennifers, ventral and lateral anteocular and postocular surface, except at posterior margin, scape basally, antennal segments VI–VIII, anterior pronotal lobe except paramedian spots and pronotal longitudinal furrow, posterior pronotal lobe except medially, anterior propleural lobe except medially, posterior propleural lobe dorsally, mesopleuron and metapleuron dorsad of coxae, apical half of scutellum, basal half of corium, coxae, trochanters, forefemur basally and ventrally, mid and hind femora basally, tibiae basally, anterior half of laterotergites, and sternites medially and anterolaterally. Remainder of antenna, labium, remainder of legs, apical half of corium, and basal wing veins brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin (Fig. 2.13F–K); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about as long as scape; antenna 8-segmented; labium stout; labial segment III shorter than II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions on posterior pronotal lobe transversely striated; scutellar apical projections horizontally directed (Fig. 2.15D); meso- and metasterna not completely separated by distinct transverse suture (Fig. 2.15E); mesosternum with medial and paramedial longitudinal depressions; metasternum slightly medially longitudinally depressed; fore- and mid femora incrassate; fossula spongiosa on mid tibia; tarsomeres I and II combined shorter than III; hemelytron reaching or surpassing abdominal apex; distal part of R vein present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex rounded; sternites with shallow medial depression (Fig. 2.18C), intersegmental sutures carinulate between II–VI and laterally between VI and VII; pygophore process subtriangular in lateral (Fig. 2.20A) and caudal (Fig. 2.19G, I) views, apex rounded; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G), fused anterior to fusion with DPS; area of endosomal struts–DPS fusion ovate (Fig. 2.21A). **FEMALE:** Body length: 4.78–5.06 mm. Similar to males, but differ in the following characters: COLORATION: Dark brown with brown scape, pedicel, antennal segments III–IV, base of segment V, apex of segment VIII, labium, and legs except trochanter and tarsi. Remainder of antennal segments, scutellar processes, trochanters, and tarsi whitish to pale brown. STRUCTURE: In addition to characters mentioned in the generic description: HEAD: Synthlipsis about three times width of eye. THORAX: Pronotal longitudinal furrow restricted to anterior lobe; lateral depressions on posterior pronotal lobe obsolete; forefemur with small ventral tubercles (Fig. 2.16D). ABDOMEN: Intersegmental sutures carinulate between sternites II–VI; external genitalia as in Fig. 2.23B; bursa copulatrix membranous, with lateral lobes (Fig. 2.23F); vermiform gland elongate, much longer than bursa copulatrix; lateral spermathecae inserted on median oviduct with slender, fragile duct and large ovoid pouch.

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the horizontally-oriented scutellar apices.

DISTRIBUTION: Antananarivo and Mahajanga provinces (Map 2.3).

DISCUSSION: In some specimens**,** the entire postocular is dark brown, the brown spots on the paramedian anterior pronotal lobes are absent, and the scutellum is entirely pale. Females were associated to males based on morphology and the same collection event as another male.

HOLOTYPE: Male: **Madagascar: Mahajanga:** Analamanitra Forest, 14 km NE of Misinjo, 16.13333°S 45.7°E, 20 m, 20 Nov 2007–04 Dec 2007, M. Irwin, R. Harin'Hala (00044849) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 10 Jan 2004–20 Jan 2004, M. Irwin, R. Harin'Hala, 1♂ (00006461) (CAS), 1♂ (00007266) (SU); 20 Jan 2004–01 Feb 2004, M. Irwin, R. Harin'Hala, 1♂ (00007058) (UCR). **Mahajanga:** 160 km N of Maevatanana on RN 04, Ampijoroa National Park, 16.31933°S 46.81333°E, 43 m, 07 Feb 2005–19 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00045216) (USNM). Namoroka, 53 km from Soalala, 3 km N Vilanandro Village, 16.47333°S 45.39133°E, 122 m, 30 Nov 2007–09 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00045296) (USNM). Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 16.40666°S 45.31°E, 100 m, 12 Nov 2002–16 Nov 2002, Fisher et al., 1♂ (00006320), 1♀ (00045373) (CAS), 1♀ (00045711) (UCR). Parc National de Namoroka, 17.8 km 329° WNW Vilanandro, 16.37666°S 45.32666°E, 100 m, 08 Nov 2002–12 Nov 2002, Fisher et al., 1♂ (00007209) (CAS). Réserve forestière Beanka, 50.2 km E Maintirano, 18.02638°S 44.05055°E, 250 m, 19 Oct 2009–26 Oct 2009, B.L. Fisher et al., 1♂ (00006464) (CAS). Réserve Spéciale de Bemarivo, 23.8 km 223° SW Besalampy, 16.925°S 44.36833°E, 30 m, 19 Nov 2002–23 Nov 2002, Fisher et al., 1♂ (00045515) (SU). **Unknown:** 1♂ (00007149) (CAS).

Gibbosella quadocris, new species

Figs. 2.1, 2.5, 2.8, 2.19A, 2.20B; Map 2.2

DIAGNOSIS: Males are recognized among other species in *Gibbosella* by the small body size, ovoid head shape in lateral view that is longer than it is wide in dorsal view, synthlipsis 1.5 times the width of an eye, labial segments II and III subequal, subquadrate median pygophore process with truncated apex in caudal view, and BPE as long as the basal plate. This species is very similar to *G*. *vangocris*, but is distinguished by the smaller body size, slightly shorter head, more narrowly depressed postclypeus, relative lengths of the labial segments, meso- and metasterna not distinctly or weakly separated by a distinct transverse suture, and shape of the pygophore process in caudal view.

DESCRIPTION: **MALE:** Body length: 5.39 mm (holotype), 5.33–5.78 mm. COLORATION: Dark brown with pale interocular sulcus, anterior pronotal lobe except interspersed brown markings posterolateral margin of pronotum, metasternum, corium basally, coxae, trochanters, femora basally and ventrally, mid and hind tibiae basally, laterotergites except posterior margin, and sternites (except medial pygophore and lateral and posterolateral margins of sternites II–VI). Antennal segment V (except basally) and VI–VIII white. Remainder of antenna, labium, parts of anterior pronotal lobe, posterior pronotal lobe, and rest of corium and basal wing veins brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about as long as scape;

antenna 8-segmented; labium stout; labial segment III subequal to II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna not completely or weakly separated by distinct transverse suture (Fig. 2.15E); mesosternum with medial and paramedial depressions; metasternum slightly medially longitudinally depressed; forefemur incrassate; fossula spongiosa on mid tibia; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex rounded or sinuate; sternites longitudinally depressed medially (Fig. 2.18C), intersegmental sutures carinulate between II–VI; pygophore (Figs. 2.19A, 2.20B) process subtriangular in lateral view, subquadrate in caudal view, apex truncated; BPE as long as basal plate; endosomal struts not reaching posterior margin, posteriorly obscured by semiextended endosoma; fused anterior to fusion with DPS; area of endosomal struts–DPS fusion elongate ovoid.

ETYMOLOGY: The species epithet is a noun in apposition and is named for the subquadrate median pygophore process.

DISTRIBUTION: Ranomafana National Park, Fianarantsoa province (Map 2.2).

DISCUSSION: In some specimens, the posterior pronotal lobe is dark brown, the anterior pronotal lobe have reduced pale coloration and appear almost uniformly brown, and the corium and basal wing veins range from pale to brown.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 08 Nov 2001–15 Nov 2001, M. Irwin, R. Harin’Hala (00007072) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 08 Nov 2001–15 Nov 2001, M. Irwin, R. Harin'Hala, 2♂ (00006457, 00007128) (CAS), 1♂ (00007258) (UCR); 28 Nov 2001–06 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00007200) (SU); 02 Jan 2002–10 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00007153) (CAS); 10 Jan 2002–14 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00007172) (CAS); 12 Feb 2002–19 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007236) (CAS); 31 Mar 2002–07 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00045552) (CAS); 07 Apr 2002–14 Apr 2002, M. Irwin, R. Harin'Hala, 2♂ (00044888, 00045425) (AMNH); 14 Apr 2002–23 Apr 2002, M. Irwin, R. Harin'Hala, 3♂ (00044909, 00044949, 00044951) (USNM), 2♂ (00044954, 00045166) (MNHN); 28 Apr 2002–05 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00007184) (CAS); 05 May 2002–13 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00007186) (CAS); 13 Jun 2002–23 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (00044802) (CAS); 04 Jul 2002–14 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00044895) (CAS); 24 Jul 2002–04 Aug 2002, M. Irwin, R. Harin'Hala, 1♂ (00007219) (BMNH). Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1100 m, 02 Jan 2002–10 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00007188) (CAS); 19 Feb 2002–26 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007257) (SU); 04 Jun 2002–14 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (00044860) (UCR). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 14 Jan 2002–21 Jan 2002, M. Irwin, R. Harin'Hala, 2♂ (00044882, 00045572) (BMNH); 21 Jan 2002–28 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00045651) (SU). Parc National Ranomafana, radio tower at forest edge, 21.25083°S 47.40716°E, 1130 m, 18 Mar 2006–30 Mar 2006, M. Irwin, R. Harin'Hala, 1♂ (00007224) (CAS). Ranomafana JIRAMA water works, 21.2485°S 47.45216°E, 690 m, 06 Dec 2001–15 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00007166) (CAS), 1♂ (00007203) (AMNH); 21 Dec 2001–24 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00006465) (UCR); 21 Jan 2002–28 Jan 2002, M.

Irwin, R. Harin'Hala, 1♂ (00045348) (CAS). **Unknown:** 4♂ (00007117, 00007180, 00007181, 00007261) (CAS).

Gibbosella vangocris, new species

Figs. 2.1, 2.5, 2.8, 2.19B, 2.20C, 2.21B, 2.22A; Map 2.3

DIAGNOSIS: Males recognized among other *Gibbosella* species by the relatively larger body size, slightly broader postclypeal depression, synthlipsis 1.5 times the width of an eye, labial segment III shorter than II, intersegmental sutures carinulate between II–VI, and spadelike median pygophore process in caudal view. This species is very similar to *G. quadocris*, but is distinguished from *G. quadocris* by the larger body size, slightly more elongate head, more broadly depressed postclypeus, labial segment II longer than III, meso- and metasterna distinctly separated by a distinct transverse suture, and shape of the pygophore process in caudal view.

DESCRIPTION: **MALE:** Body length: 7.17 mm (holotype), 6.80–7.61 mm. COLORATION: Dark brown with antennal segment V apically; antennal segments VI–VIII; posterior margin of pronotum; corium basally; coxae; trochanters; basal half of femora; anterior areas of laterotergites; sternites medially, except pygophore; and anterolaterally on sternites II–VI pale. Remainder of corium and basal wing veins brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; anteocular region as long as postocular (Fig. 2.13C); gula flat, conforming to rounded shape of head (Fig. 2.13C); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.5 times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small, located on shallow median tubercle (Fig. 2.13I); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about as long as scape; antenna 8-

segmented; labium stout; labial segment III shorter than II, ventrally convex (Fig. 2.13C). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe smooth; scutellar apical projections dorsally directed (Fig. 2.15C); meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; legs slender; fossula spongiosa on mid tibia; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Apex rounded; sternites medially convex, with shallow medial depression on posterior half of segment VI, intersegmental sutures carinulate between II–VI; pygophore (Figs. 2.19B, 2.20C) process subtriangular basally and apically flattened and curved in lateral view, spadelike in caudal view, apex rounded; BPE as long as basal plate (Fig. 2.22A); endosomal struts reaching posterior margin of DPS, with posterior ventral process (Fig. 2.22G), fused anterior to fusion with DPS; area of endosomal struts–DPS fusion ovate (Fig. 2.21B).

ETYMOLOGY: The species epithet is a noun in apposition and is named for the spadelike median pygophore process.

DISTRIBUTION: Marojejy National Park in the Antsiranana province, Ranomafana National Park in the Fianarantsoa province, and Berenty Special Reserve in the Toliara province (Map 2.3).

DISCUSSION: The coloration is slightly variable with the posterior pronotal lobe, corium, and basal wing veins ranging from pale to brown.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 16 Oct 2001–08 Nov 2001, M. Irwin, R. Harin'Hala (00006995) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 25 Feb 2005–04 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00007275) (CAS). **Fianarantsoa:** Parc National Ranomafana, Bevaohazo-Ranomana, 21.2°S 47.48333°E, 970 m, Nov 2000, M. Irwin, R. Harin'Hala, 1♂ (00044919) (CAS). Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 16 Oct 2001–08 Nov 2001, M. Irwin, R. Harin'Hala, 3♂ (00006984, 00007000, 00007001) (USNM), 13♂ (00007005, 00007014, 00007022, 00007029, 00007030, 00007033, 00007055, 00007057, 00007063, 00007070, 00007071, 00007077, 00007092) (CAS), 4♂ (00007111, 00007114, 00007126, 00007254) (MNHN), 3♂ (00007268, 00007270, 00048227) (AMNH); 08 Nov 2001–15 Nov 2001, M. Irwin, R. Harin'Hala, 3♂ (00006085, 00007006, 00007017) (MNHN), 4♂ (00007018, 00007044, 00007144, 00007274) (BMNH); 15 Nov 2001–22 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00045570) (UCR); 22 Nov 2001–28 Nov 2001, M. Irwin, R. Harin'Hala, 6♂ (00048028–00048033) (CAS); 15 Dec 2001–21 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00045586) (SU); 24 Dec 2001–02 Jan 2002, M. Irwin, R. Harin'Hala, 3♂ (00007093, 00044929, 00045720) (USNM); 19 Feb 2002–26 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007016) (UCR); 31 Mar 2002–07 Apr 2002, M. Irwin, R. Harin'Hala, 5♂ (00048052–00048056) (CAS); 07 Apr 2002–14 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00048034) (SU), 6♂ (00048036–00048041) (CAS); 14 Apr 2002–23 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00045342) (CAS); 05 May 2002–13 May 2002, M. Irwin, R. Harin'Hala, 2♂ (00006985, 00007013) (AMNH); 13 May 2002–23 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00007027) (CAS); 13 Jun 2002–23 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (00045716) (CAS); 04 Jul 2002–14 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00007273) (BMNH); 14 Jul 2002–24 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00045172) (BMNH); 24 Jul 2002–04 Aug 2002, M. Irwin, R. Harin'Hala, 2♂ (00007032, 00007280) (USNM) ; 15 May 2003–28 May 2003, M. Irwin, R.

Harin'Hala, 1♂ (00006993) (UCR). Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1100 m, 28 Nov 2001–06 Dec 2001, M. Irwin, R. Harin'Hala, 4♂ (00044845, 00044870, 00045020, 00045230) (BMNH), 3♂ (00045406, 00045409, 00045676) (CAS), 1♂ (00045688) (UCR); 02 Jan 2002–10 Jan 2002, M. Irwin, R. Harin'Hala, 2♂ (00006999, 00007023) (AMNH); 28 Jan 2002–04 Feb 2002, M. Irwin, R. Harin'Hala, 4♂ (00048042–00048045) (MNHN), 6♂ (00048046–00048051) (CAS); 19 Mar 2002–26 Mar 2002, M. Irwin, R. Harin'Hala, 2♂ (00045199, 00045384) (SU); 26 Mar 2002–31 Mar 2002, M. Irwin, R. Harin'Hala, 1♂ (00007040) (CAS); 08 Apr 2002–15 Apr 2002, M. Irwin, R. Harin'Hala, 2♂ (00007042, 00007097) (CAS); 22 Apr 2002–29 Apr 2002, M. Irwin, R. Harin'Hala, 2♂ (00007272, 00007278) (CAS); 06 May 2002–15 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00007015) (UCR); 04 Jun 2002–14 Jun 2002, M. Irwin, R. Harin'Hala, 2♂ (00007116, 00007119) (USNM); 15 Jul 2002–25 Jul 2002, M. Irwin, R. Harin'Hala, 2♂ (00045313, 00045578) (AMNH). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 06 Dec 2001–15 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00007011) (MNHN), 1♂ (00007213) (CAS); 15 Dec 2001–21 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00045588) (UCR); 21 Dec 2001–24 Dec 2001, M. Irwin, R. Harin'Hala, 2♂ (00007019, 00045037) (SU); 14 Jan 2002–21 Jan 2002, M. Irwin, R. Harin'Hala, 2♂ (00045516, 00045554) (AMNH); 19 Feb 2002–26 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007008) (CAS); 12 Mar 2002–19 Mar 2002, M. Irwin, R. Harin'Hala, 1♂ (00006994) (CAS); 23 Apr 2002–30 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00007187) (SU); 14 Jun 2002–24 Jun 2002, M. Irwin, R. Harin'Hala, 2♂ (00006997, 00007007) (BMNH); 24 Jun 2002–05 Jul 2002, M. Irwin, R. Harin'Hala, 1♂ (00007105) (UCR); 15 Jul 2002–25 Jul 2002, M. Irwin, R. Harin'Hala, 2♂ (00007004, 00007025) (USNM); 18 Feb 2003–27 Feb 2003, M. Irwin, R. Harin'Hala, 1♂ (00045078) (AMNH); 20 Mar 2003–03 Apr 2003, M. Irwin, R. Harin'Hala, 1♂ (00007121) (SU);

06 Jul 2003–17 Jul 2003, M. Irwin, R. Harin'Hala, 1♂ (00007269) (CAS); 27 Aug 2003–07 Sep 2003, M. Irwin, R. Harin'Hala, 1♂ (00007021) (UCR); 28 Sep 2003–08 Oct 2003, M. Irwin, R. Harin'Hala, 2♂ (00007002, 00007233) (CAS); 02 Apr 2004–15 Apr 2004, M. Irwin, R. Harin'Hala, 1♂ (00007003) (USNM); 11 Jun 2004–24 Jun 2004, M. Irwin, R. Harin'Hala, 1♂ (00045507) (CAS); 24 Jun 2004–08 Jul 2004, M. Irwin, R. Harin'Hala, 1♂ (00007169) (AMNH); 23 Sep 2004–07 Oct 2004, M. Irwin, R. Harin'Hala, 1♂ (00045660) (SU); 11 Dec 2004–18 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00045625) (UCR); 02 Feb 2005–17 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00045563) (CAS); 27 Feb 2005–13 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00007069) (UCR); 25 Jul 2006–09 Aug 2006, M. Irwin, R. Harin'Hala, 1♂ (00045371) (CAS). Ranomafana JIRAMA water works, 21.2485°S 47.45216°E, 690 m, 22 Nov 2001–28 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00006124) (UCR); 06 Dec 2001–15 Dec 2001, M. Irwin, R. Harin'Hala, 4♂ (00006982, 00006988, 00006991, 00006996) (CAS), 2♂ (00007020, 00007031) (SU); 21 Dec 2001–24 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00007276) (CAS); 24 Dec 2001–02 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00006986) (UCR); 21 Jan 2002–28 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00044847) (SU), 1♂ (00045687) (CAS). **Toliara:** Berenty Special Reserve, 8 km NW Amboasary, 25.021°S 46.3055°E, 35 m, 29 Aug 2004–08 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00007197) (UCR), 1♂ (00007248) (CAS), 1♂ (00007250) (SU). **Unknown:** 12♂ (00006983, 00006987, 00006989, 00006990, 00006992, 00007010, 00007024, 00007026, 00007221, 00007271, 00007277, 00007279) (CAS).

Glymmatophora Stål, 1853

Figs. 2.1, 2.2, 2.5, 2.8, 2.12, 2.13A, 2.13D, 2.15E, 2.16B, 2.16C, 2.16E, 2.17B, 2.19C, 2.20D, 2.21C, 2.21D, 2.22B, 2.23C, 2.23D, 2.23F; Map 2.4

Glymmatophora Stål, 1853: 261.

TYPE SPECIES: *Glymmatophora submetallica* Stål, 1853

DISTRIBUTION: Thirty-five described species of *Glymmatophora* occur throughout Africa (Maldonado, 1990). Within Madagascar, the two species of *Glymmatophora* are known from the Toliara and Fianarantsoa provinces. Specimens have been collected in spiny forest thicket, degraded grassland, and in the Antsarongaza dry forest between 18–825 m elevation.

DISCUSSION: The largely Afrotropical genus *Glymmatophora* was described by Carl Stål in 1853. In 1914, Géza Horváth described three subgenera: (*Cyclosandalus*), (*Glymmatophora*), and (*Haematorrhophus*), the last of which is currently treated as a distinct genus. The former two subgenera were primarily diagnosed based on the presence (subgenus *Glymmatophora*) or absence (subgenus *Cyclosandalus*) of ocelli in the female and the size and shape of the fossula spongiosa (large and oblong in subgenus *Glymmatophora*; small and round in subgenus *Cyclosandalus*). Prior to this monograph, one species of *Glymmatophora* was known from Madagascar, *G.* (*Cyclosandalus*) *crassipes*. A new Madagascan species of *Glymmatophora* is here described, *G.* (*Glymmatophora*) *carolae*.

Identification key to the males and females of Madagascan species of Glymmatophora

1. Males only known; macropterous; ocelli present .... (*Glymmatophora*) *carolae*, new species
- Males and females apterous; ocelli absent (Fig. 2.13D) .... (*Cyclosandalus*) *crassipes* Horváth

Glymmatophora (*Glymmatophora*) *carolae*, new species

Figs. 2.1, 2.5, 2.8, 2.16C, 2.17B, 2.20D, 2.21C; Map 2.4

DIAGNOSIS: Males are recognized among other *Glymmatophora* species by the very distinctive coloration (mostly red with some black markings), anteriorly concave postclypeus, forefemur with anterior subapical and medial protuberances and macropterous condition. This species is very similar to the Afrotropical *G. lothei* Villiers, 1948, from which it differs by the slightly smaller body size, black antenna, red abdomen with black markings (i.e., anterior band on laterotergites IV and V, laterotergite VI except posterolaterally, anterior half of laterotergite VII, lateral margin of abdominal sternite VI, and anterolateral margin of sternite VII), more medially concaved anterior pronotal margin, and forefemur with only two protuberances.

DESCRIPTION: **MALE:** Macropterous, medium body size (length: 16.91 mm, holotype; 14.90–16.91 mm). COLORATION: Red with antenna, hemelytron except corium basally and anteriorly, anterior band on laterotergites IV and V, laterotergite VI except posterolaterally, anterior half of laterotergite VII, lateral margin of abdominal sternite VI, and anterolateral margin of sternite VII black. VESTITURE: Glabrous, except antenna with long, erect brown setae and tibiae with stout pale brown setae that are denser near apex. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13D); wider than long in dorsal view; ventrally flat; anteocular region as long as postocular; gula swollen ventrolaterally, slightly produced beyond ventral margin of head (Fig. 2.13E); maxillary plate not reaching dorsal clypeal surface (Fig. 2.13E, I); postclypeus concave anteriorly with shallow, very narrow medial longitudinal depression to middle of interocular area; synthlipsis (Fig. 2.13A) about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli small, located on distinct median tubercle (Fig. 2.13H), separated by more than diameter of ocellus; eye about one-third head length, not reaching dorsal and ventral head surfaces; antennal shield concealing antennal insertion in lateral view (Fig. 2.13D); antenna inserted sublaterally on head; pedicel about one-fourth longer than scape, slightly curved. THORAX: Pronotum wider than long, anterior margin moderately concave, smooth; anterior pronotal lobe shorter than posterior lobe (Fig. 2.15B), more than half as wide as posterior lobe, without distinct anterolateral projections; pronotal longitudinal furrow reaching anterior but not posterior margin, weakly foveate posteriorly (Fig. 2.15B); pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15A, B); lateral depressions of posterior pronotal lobe distinct (Fig. 2.15B), weakly transversely striated; meso- and metasterna not completely separated by transverse suture (Fig. 2.15E); mesosternum with medial and paramedial longitudinal depressions (Fig. 2.15F); metasternum medially longitudinally depressed (Fig. 2.15F); MGE with shallow meshlike cuticle that does not extend dorsally in lateral view (Fig. 2.16B, C); forefemur with anterior subapical and medial protuberances (Fig. 2.16E), base ventrally carinate; mid and hind femora with anterior and posterior subapical and medial protuberances; foretibia with ventral spine basal to fossula spongiosa; hemelytron (Fig. 2.17B) surpassing abdominal tergite VII but not reaching apex; corium well developed; distal part of R present but not forming R+M cell; proximal parts of M and Cu fused; distal part of M extending beyond apical junction of M+Cu; base of M+Cu cell shorter than or as wide as Cu+1A cell. ABDOMEN: Apex rounded; dorsal laterotergite II expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; sternites shallowly depressed medially (Fig. 2.18C); spiracles ovoid; pygophore process dorsally knoblike in lateral view (Fig. 2.20D), subtriangular in caudal view (Fig. 2.19C), directed dorsoposteriad, not surpassing posterior margin of pygophore, apex rounded; BPE shorter than basal plate; DPS apex concave medially (Fig. 2.21C); endosomal struts reaching posterior margin of DPS (Fig. 2.21C), ventrally obscured by semiextend endosoma; area of endosomal struts–DPS fusion elongate subquadrate; endosoma medially sclerotized posteriorly and sclerotization extending anterolaterally (Fig. 2.21C).

ETYMOLOGY: This species epithet is a noun in the genitive case and is named in memoriam of the senior author's mother, Carol Forthman.

DISTRIBUTION: Antsarongaza dry forest in the Toliara province (Map 2.4).

DISCUSSION: Female specimens are unknown. We assign this species to the subgenus *Glymmatophora* based on the features mentioned in the generic discussion.

HOLOTYPE: Male: **Madagascar: Toliara:** Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 17 Nov 2008–25 Nov 2008, M. Irwin, R. Harin'Hala (00044889) (CAS).

PARATYPES: **Madagascar: Toliara:** Bekily, 24.22802°S 45.30858°E, 388 m, Oct 1936, A. Seyrig, 2♂ (MNHN); Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 05 Feb 2009–13 Feb 2009, M. Irwin, R. Harin'Hala, 1♂ (00045479) (CAS).

Glymmatophora (*Cyclosandalus*) *crassipes* Horváth, 1914

Figs. 2.1, 2.2, 2.5, 2.8, 2.12, 2.13A, 2.13D, 2.15E, 2.16B, 2.16E, 2.19C, 2.21D, 2.22B, 2.23C, 2.23D, 2.23F; Map 2.4

Glymmatophora (*Cyclosandalus*) *crassipes* Horváth, 1914: 128.

REVISED DIAGNOSIS: Males and females are recognized among other species in this genus by the apterous condition, lack of ocelli in both sexes, and fossula spongiosa on foretibia small and round. This species is similar to apterous forms of *G. lothei*, but the presence of two protuberances on the forefemur distinguishes *G. crassipes* from *G. lothei*.

REDESCRIPTION: **MALE:** Apterous, medium body size (length: 15.52–19.60 mm). COLORATION: Black with head, labium, scape, pedicel basally, pronotum except pronotal longitudinal furrow, propleuron except dorsal spot and stripe on anterior lobe, meso- and metapleura dorsad of coxae, meso- and metasterna laterally, legs, laterotergite II, laterotergite III and IV posteriorly, sternites II–VI transversely basally, sternite VII posteriorly, and pygophore red. VESTITURE: Glabrous, except antenna with short, semierect to erect brown setae and tibiae with stout, pale brown setae that are denser near apex. STRUCTURE: HEAD (Fig. 2.13A, D): Subquadrate in lateral view; longer than wide in dorsal view; ventrally flat; anteocular region longer than postocular; gula swollen ventrolaterally, not produced beyond ventral margin of head, carinate; maxillary plate not reaching dorsal clypeal surface (Fig. 2.13E, I); postclypeus flat; synthlipsis about 2.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antennal shield concealing antennal insertion in lateral view; antenna inserted sublaterally on head; pedicel slightly longer than scape, slightly curved. THORAX (Fig. 2.15E): Pronotum as long as wide, anterior margin slightly concave, smooth; anterior pronotal lobe longer than and as wide as posterior lobe (Fig. 2.15A), without distinct anterolateral projections; pronotal longitudinal furrow not reaching anterior and posterior margins, reduced to deep medial depression near posterior margin of anterior lobe (Fig. 2.15A); pronotal transverse furrow weakly to strongly divided by paramedian longitudinal ridges (Fig. 2.15A); lateral depressions of posterior pronotal lobe obsolete; meso- and metasterna not completely separated by transverse suture; mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; MGE with shallow meshlike cuticle that does not extend dorsally in lateral view (Fig. 2.16B, C); trochanters and fore- and mid femora basally with patches of small papillae (Fig. 2.16E); forefemur with anterior subapical and medial protuberances (Fig. 2.16E); mid and hind femora with anterior and posterior subapical and medial protuberances; foretibia with ventral spine basal to fossula spongiosa. ABDOMEN: Apex rounded; dorsal laterotergite II slightly expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; sternites medially flat; spiracles ovoid; pygophore (Figs. 2.19C, 2.20D) process dorsally knoblike in lateral view, subtriangular in caudal view, directed dorsoposteriad, not surpassing posterior margin of pygophore, apex rounded; BPE about as long as basal plate (Fig. 2.22B); DPS apex rounded (Fig. 2.21D); endosomal struts reaching posterior margin of DPS, with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21D); endosoma medially sclerotized posteriorly and extends anterolaterally

(Fig. 2.21D). **FEMALE:** Body length: 16.50 mm (holotype; from original description), 16.50–23.90 mm. Similar to males, but differ in the following characters: COLORATION: Red on prothorax, mesopleuron, metapleuron dorsad of coxa, lateral metanotal spots, scutellum laterally, meso- and metasterna, laterotergite II, posterolateral margin of laterotergites III–VII, and sternite VII posteromedially. STRUCTURE: THORAX: Fossula spongiosa larger. ABDOMEN: External genitalia as in plate Fig. 2.23C, D; bursa copulatrix membranous, with lateral lobes (Fig. 2.23F); vermiform gland and lateral spermathecae missing.

DISTRIBUTION: Most specimens were collected in the Fianarantsoa and Toliara provinces and were successfully georeferenced (map 4). Some could not be georeferenced beyond province based on locality data, with most of them collected in the Toliara province. One specimen was associated with historical locality data that could not be georeferenced (i.e., "Amboasary [Imerina]"). Imerina refers to a kingdom that once existed and likely is part of modern-day Antananarivo province. A second specimen could not be georeferenced but was collected from "P. Majanga" in the Mahajanga province. It is not clear if "P. Majanga" is referring to a park within the Mahajanga province or the town Mahajanga.

DISCUSSION: A few specimens without or with reduced red coloration on the scutellum, laterotergites, and sternites were examined and are treated as conspecific with *G. crassipes* based on corresponding external and internal morphology. Specimens of both color morphs were collected in close proximity.

HOLOTYPE: Female: **Madagascar: Toliara:** Tsivory, 24.0684°S 46.07471°E, 431 m, 1906 Fauchère (HNHM).

OTHER MATERIAL EXAMINED: **Madagascar: Antananarivo:** Amboasary (Imerina), 1899, G. Grandidier, 1♀ (MNHN). **Fianarantsoa:** Ikongo, 21.99483°S 47.37065°E, 536 m, 1902, G. Grandidier, 1♂ (MNHN). **Mahajanga:** P. Majanga, Nov 1965, Malzy 1♂ (MNHN). **Toliara:** 18

km NW Betroka, 23.16333°S 45.96861°E, 825 m, 04 Dec 1994–09 Dec 1994, M.A. Ivie and D.A. Pollock, 1♂ (00120258) (MTEC). Ankazoabo, 21.50348°S 45.20956°E, 278 m, 1902, J. Bastard, 1♀ (MNHN); 1920, G. Le Barbier, 1♂ (MNHN); no date provided, 1♀ (MNHN). Antaloba, no date provided, 1♀ (MNHN). Bas Mangoky, Agriculture Station, no date provided, 1♂, 1♀ (MNHN). Behara, 24.95347°S 46.38593°E, 49 m, 10 Aug 1918–11 Aug 1918, A.R., 1♀ (MNHN). Bekily, 24.22802°S 45.30858°E, 388 m, Mar 1936, A. Seyrig, 1♂ (MNHN). Berenty Reserve, W of Fort Dauphin, 25.00564°S 46.30278°E, 09 Nov 2008–24 Nov 2008, J.R. Cryan and G. Svenson, 2♂ (00088087, 00088088) (UCR). Betroka, Andalamby, 23.26833°S 46.10444°E, 822 m, Jan 1958, J. Elie, 1♀ (MNHN). Country Mahafaly, 1906, J. Bastard, 1♂ (MNHN). Lambomakandro, 22.69831°S 44.70099°E, 526 m, 1936, R. Catala 1♀ (MNHN). Mahafaly Plateau, 6.2 km 74° ENE Itampolo, 24.65361°S 43.99666°E, 80 m, 21 Feb 2002–25 Feb 2002, Fisher et al., 1♀ (00007050) (CAS). Mahafaly Plateau, Ankalirano, 25.45°S 45.71667°E, 18 m, 17 Jan 1974, P. Viette & A. Peyrieras, 1♀ (MNHN). On plateau, 23.00283°S 43.70366°E, 30 m, 26 Feb 2003–08 May 2003, Frontier Wilderness Project, CAS, 1♀ (00006372) (CAS). Onilahy River, 1922, G. Petit, 1♀ (MNHN). Ranobe, 23.00943°S 43.60934°E, 20 m, 1905, F. Geay, 2♀ (MNHN). Réserve Spéciale de Cap Sainte Marie, 12.3 km 262° W Marovato, 25.58166°S 45.16833°E, 200 m, 11 Feb 2002–15 Feb 2002, Fisher et al., 1♂ (00044857) (CAS). Zombitse-Vohibasia National Park, Eastern Sakaraha, Matsabory, 22.8417°S 44.68184°E, 640 m, 13 Feb 1974, P. Viette and A. Peyrieras, 1♂ (MNHN).

Maraenaspis Karsch, 1892

Figs. 2.2, 2.5, 2.8, 2.13E, 2.15A, 2.19D, 2.20E, 2.21E, 2.22C; Map 2.4

Maraenaspis Karsch, 1892: 134.

TYPE SPECIES: *Maraenaspis typhlops* Karsch, 1892

DISTRIBUTION: Thirty-eight described species of *Maraenaspis* occur throughout the Afrotropics (Maldonado, 1990). Specimens of the only known Madagascan species *Maraenaspis* have been collected from Nosy Be Island off the northwest coast, as well as the Antsiranana, Mahajanga, and Toamasina provinces. Records are from tropical dry forest between 8–135 m elevation.

DISCUSSION: *Maraenaspis* was described by Ferdinand Karsch in 1892. *Maraenaspis bidens* (Reuter), which was originally described from an apterous female, is the only species of *Maraenaspis* known from Madagascar. The male of *M. bidens* is described here for the first time.

Maraenaspis bidens (Reuter), 1887

Figs. 2.2, 2.5, 2.8, 2.13E, 2.15A, 2.19D, 2.20E, 2.21E, 2.22C; Map 2.4

Cleptria bidens Reuter, 1887: 108.

Maraenaspis bidens: Villiers, 1945: 199.

REVISED DIAGNOSIS: Males and females are recognized among other species of *Maraenaspis* by a combination of the following characters: the large body size, coloration, anterior pronotal lobe with very large anterolateral projections, apterous condition, ovoid abdomen that is apically notched, and sternites convex. This species is similar to *M. neglecta* Villiers, 1948, but is distinguished by the slightly larger body size, bluish-black coloration on the head and legs, and very strong anterolateral protuberances on the anterior pronotal lobe.

REDESCRIPTION: **MALE:** Apterous; large body size (length: 21.63–22.08 mm). COLORATION: Bluish-black suffused with violet sheen on abdominal tergites. Antennal segments III, IV, base of V, and apex of VIII brown and antennal segments V apically, VI, VII, and VIII basally pale to light brown. VESTITURE: Glabrous, except antenna with short, semierect to erect pale to brown setae and tibiae with stout pale orange-brown setae that are denser near apex. STRUCTURE: HEAD (Fig. 2.13E): Ovoid in lateral view; longer than wide in dorsal view; ventrally flat; anteocular region longer than postocular; gula swollen ventrolaterally, produced beyond ventral margin of head, carinate; maxillary plate not reaching dorsal clypeal surface; postclypeus flat; antennal shield not concealing antennal insertion in lateral view; synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-fourth longer than scape, slightly curved. THORAX (Fig. 2.15A): Pronotum as long as wide, smooth; anterior pronotal lobe with large anterolateral projections; pronotal longitudinal furrow reaching anterior but not posterior margins, deeply depressed near posterior margin of anterior lobe; pronotal transverse furrow divided by paramedian longitudinal ridges; lateral depressions of posterior pronotal lobe obsolete; meso- and metasterna not completely separated by transverse suture (Fig. 2.15E); mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; MGE with shallowly depressed meshlike cuticle that does not extend dorsally in lateral view (Fig. 2.16B, C); trochanters and fore- and mid femora basally with small papillae (Fig. 2.16E). ABDOMEN: Apex medially notched; dorsal laterotergite II expanded; intersegmental sutures carinulate between sternites II and III and laterally between III–VII; sternites medially flat; spiracles elliptical; pygophore (Figs. 2.19D, 2.20E) process hooklike in lateral view, subtriangular in caudal view, directed dorsoposteriad, not surpassing posterior margin of pygophore, apex rounded; BPE shorter than basal plate; DPS apex rounded (Fig. 2.21E); endosomal struts reaching posterior margin of DPS, ventrally obscured by semiextended endosoma; area of endosomal struts–DPS fusion circular (Fig. 2.21E); endosoma with platelike sclerite on posterior margin (Fig. 2.21E). **FEMALE:** Body length: 21.5 mm (holotype; original description), 21.30–23.00 mm; coloration and structure same as the male.

DISTRIBUTION: Natural Reserve of Lokobe on Nosy Be Island, and the Antsiranana, Mahajanga, and Toamasina provinces (Map 2.4).

DISCUSSION: This species was described from a single female specimen collected (coll. Stumpff) in "Loucoubé," which is currently known as the Natural Reserve of Lokobe on Nosy Be Island. Putshkov & Putschkov's (1986) Ectrichodiinae catalog indicates that the holotype for *M. bidens* is deposited in the National Museum of Natural History, Paris, France, but the type could not be located (Eric Guilbert, personal commun.). Correspondence with other major European collections did not offer any further leads, and we conclude that the type may be lost or placed within undetermined material. Given the potential that the holotype may be located among undetermined material that we have not examined, we refrain from designating a neotype.

The male and female specimens examined match Reuter's original description of the species, except the antennal coloration. The original description states the last four antennal segments in the female as "straminous" with the "base of the fifth yellowish." In the females examined, distal antennal segments were missing; in the males, antennal segments III, IV, base of V, and apex of VIII are brown, while segments V apically, VI, VII, and VIII basally are pale to light brown. This slight difference is considered to be variation within the species or between the sexes.

HOLOTYPE: Female: **Madagascar: Toliara:** Nosy Be, Lokobe Natural Reserve, 13.39917°S 48.31833°E, 204 m (see Discussion regarding depository).

OTHER MATERIAL EXAMINED: **Madagascar: Antsiranana:** Forêt d'Anabohazo, 21.6 km 247° WSW Maromandia, 14.30888°S 47.91444°E, 120 m, 11 Mar 2001–16 Mar 2001, Fisher et al., (00044913) (CAS). **Mahajanga:** Parc National d'Ankarafantsika, Forêt de Tsimaloto, 18.3 km 46° NE de Tsaramandroso, 16.22805°S 46.14361°E, 135 m, 02 Apr 2001–08 Apr 2001, Fisher et al., 1♂ (00045017) (CAS). **Toamasina:** Alahakato Forest, 1888, Edouard Perrot, 1♀ (MNHN). Antanambe, 16.43333°S 49.85°E, 8 m, 1898, A. Mocquerys, 1♀ (MNHN).

Marojejycoris, new genus

Figs. 2.2, 2.5, 2.6, 2.9, 2.13F, 2.19E, 2.20F, 2.21F, 2.22D; Map 2.5

TYPE SPECIES: *Marojejycoris notadichroa*, new species

DIAGNOSIS: Males are recognized by the small body size, dull coloration, dense vestiture, broadly depressed postclypeus, ocelli located on a shallow medial ocellar tubercle, large antennal shield that does not conceal the antennal insertion in lateral view, continuous transverse suture on the pronotum, MGE with deeply depressed meshlike cuticle the extends dorsally in lateral view, distal part of M not extending beyond apical junction of M+Cu, dorsal laterotergite II not expanded, and circular spiracles. *Marojejycoris* species are similar to the Afrotropical genus *Synavecoris*, but are distinguished by the denser vestiture, head longer than wide in dorsal view, depressed postclypeus, presence of the antennal shield, more medially excavated anterior margin of the pronotum, anterior pronotal lobe lacking carinae laterally, continuous transverse suture, meso- and metasterna separated by a distinct transverse suture, MGE extending dorsally in lateral view, unarmed legs, proximal part of M and Cu veins not fused, distal parts of M and Cu not fused, and dorsal laterotergites uniform in color and not expanded.

DESCRIPTION: **MALE:** Macropterous, small body size. COLORATION: Orange-brownish or brown with pale markings. VESTITURE: Dense, semierect to erect, long pale to brown setae on head, thorax, legs, corium of hemelytra, and abdomen; setae on tibiae stouter and denser near apex. STRUCTURE: HEAD (Fig. 2.13F): Ovoid or subtriangular, longer than wide in dorsal view, shorter than pronotum; anteocular region as long as postocular; ventrally with shallow anteromedial depression; clypeal apex not elevated relative to labrum; maxillary plate not reaching dorsal surface of clypeus (Fig. 2.13E, I); postclypeus broadly depressed (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli present, located on shallow medial tubercle, separated by less than diameter of ocellus; distinct constriction between postocular and neck; gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin; antennal shield not concealing antennal insertion in lateral view; antenna inserted dorsally on head; scape surpassing clypeal apex; pedicel slightly curved; flagellum subdivided into BFLA and DFLA; BFLA divided into two pseudosegments; DFLA divided into two or three pseudosegments; antenna thus appearing 6- or 7-segmented; labium relatively slender; labial segment III shorter than II, ventrally convex (appears dorsal when reposed). THORAX: Pronotum wider than long, anterior margin distinctly concave, collar distinct (Fig. 2.15B); anterior pronotal lobe shorter than posterior lobe (Fig. 2.15B), more than half as wide as posterior lobe, without distinct anterolateral projections, relatively smooth; pronotal longitudinal furrow reaching anterior but not posterior margin of pronotum, weakly to strongly foveate posteriorly (Fig. 2.15B); pronotal transverse furrow continuous; lateral depressions on posterior pronotal lobe distinct (Fig. 2.15B), transversely striated; scutellum with two moderately separated apical processes, disc medially depressed; meso- and metasterna separated by distinct transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; MGE with deeply depressed meshlike cuticle that extends dorsally in lateral view (Fig. 2.16A); fossula spongiosa on foretibia, absent on mid tibia in some species; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex; corium restricted to areas adjacent to basal wing veins, with pterostigmalike appearance on anterodistal margin (pl. 17A, C); proximal parts of M and Cu separate (Fig. 2.17A, C); proximal parts of M and Cu separate (Fig. 2.17A, C); distal part of M not extending beyond apical junction of M+Cu; base of M+Cu cell shorter than or as wide as Cu+1A cell (Fig. 2.17B, C). ABDOMEN: Apex rounded; dorsal laterotergites not expanded; sternites longitudinally depressed medially (Fig. 2.18C), intersegmental sutures carinulate; spiracles circular; pygophore (Figs. 2.19E, 2.20F) process flattened in lateral view, broadly rodlike in caudal view, directed dorsoposteriad, not surpassing posterior margin of pygophore, apex rounded; DPS apex rounded (Fig. 2.21F); endosomal struts reaching posterior margin of DPS, with anterior and posterior ventral processes (Fig. 2.22G); endosoma sclerotized medially (Fig. 2.21F).

ETYMOLOGY: The genus is a named after the type locality of the type species, Marojejy National Park, Madagascar. The gender is feminine.

DISTRIBUTION: Species are known from the Antsiranana, Fianarantsoa, and Toamasina provinces and in habitats between 10–1,130 m elevation. Macrohabitats are described as mixed tropical forests, low altitude rainforests and dense humid forests, and forested limestone ridge.

DISCUSSION: Female specimens are unknown for all species in this genus.

Identification key to the males of species of Marojejycoris

1. DFLA divided into two pseudosegments; antenna thus appearing 6-segmented 2

- DFLA divided into three pseudosegments; antenna thus appearing 7-segmented 3

2. Postclypeal depression extending to middle of interocular area (Fig. 2.13B); eye about one-fourth head length in lateral view; scape, pedicel, and antennal segments III–IV and base of V dark brown, nearly black; corium orange .... *auranticorium*, new species

- Postclypeal depression extending to interocular sulcus; eye about one-third head length in lateral view; scape apically, antennal segments II–IV, and base of V brown; corium brown.. *notadichroa*, new species

3. Fossula spongiosa absent or reduced on the mid tibia..4

- Fossula spongiosa distinctly present on the mid tibia .... *ranomafana*, new species

4. Synthlipsis about two times width of eye; eye not reaching dorsal and ventral head margins..*francais*, new species

- Synthlipsis about width of eye; eye reaching dorsal and ventral head margins (Fig. 2.13F)..*brevifrons*, new species

Marojejycoris auranticorium, new species

Figs. 2.2, 2.5, 2.9, 2.19E, 2.20F; Map 2.5

DIAGNOSIS: Males are recognized among other *Marojejycoris* species by the larger body size, coloration of antenna and corium, subtriangular head shape in lateral view, relatively small ocelli, and 6-segmented antenna. This species is similar to *M. notadichroa*, but differs by the uniform dull orange pronotum, orange corium, slightly more shallow postclypeal depression that extends to middle of interocular area, slightly smaller ocelli, and eye about one-fourth of the head length in lateral view.

DESCRIPTION: Body length: 9.10 mm (holotype), 8.54–9.18 mm. COLORATION: Dull orange with thorax, coxae, trochanters, and hemelytron basally light orange-brown. Scape, pedicel, antennal segments III–IV and base of V, posterior margin of pronotum, and wing membrane dark brown. Antennal segment V apically and VI white. VESTITURE: As in generic description. STRUCTURE: HEAD: Subtriangular in lateral view (Fig. 2.13G–I); postclypeus with very shallow medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna 6-segmented, pedicel about one-fourth longer than scape. THORAX: Posterior pronotal lobe smooth; forefemur slightly incrassate; fossula spongiosa present on mid tibia; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; BPE shorter than basal plate (Fig. 2.22D); area of endosomal struts–DPS fusion ovate (Fig. 2.21F).

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the orange corium.

DISTRIBUTION: Antsiranana and Toamasina provinces (Map 2.5).

DISCUSSION: The coloration varies throughout the body of some specimens from light orange-brown to dull orange.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Montagne Français, 12.325°S 49.33333°E, 150 m, 30 Jan 2001–15 Feb 2001, M. Irwin, R. Harin'Hala (00045023) (CAS).

PARATYPES: **Madagascar: Antsiranana:** 7 km N of Joffreville, 12.33333°S 49.25°E, 360 m, 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00045331) (CAS). Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 15 Jan 2005–26 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00044906) (CAS); 18 May 2005–30 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00045555) (UCR). Montagne Français, 12.325°S 49.33333°E, 150 m, 30 Jan 2001–15 Feb 2001, M. Irwin, R. Harin'Hala, 1♂ (00007120) (USNM); 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 2♂ (00007163, 00044966) (SU). Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 19 Mar 2001–05 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00044916) (CAS). Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 04 Mar 2001–19 Mar 2011, M. Irwin, R. Harin'Hala, 1♂ (00045016) (USNM); 19 Mar 2001–05 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006474) (UCR). **Toamasina:** Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 21 May 2001–04 Jun 2001, M. Irwin, R. Harin'Hala, 1♂ (00006125) (CAS). **Unknown:** 2♂ (00007103, 00044988) (CAS).

Marojejycoris brevifrons, new species

Figs. 2.2, 2.5, 2.9, 2.13F, 2.21F; Map 2.5

DIAGNOSIS: Males are recognized among other species in this genus by the small body size, coloration, ovoid head shape, 7-segmented antenna, synthlipsis width about the width of an eye, eye reaching dorsal and ventral head margins, and fossula spongiosa absent on mid tibia. This species is similar to *M. ranomafana*, but is differentiated by the slightly larger body size, dark brown head and corium, lateral areas of anterior pronotal lobe dark brown with medial area pale to light brown, abdomen uniformly light brown to dull orange-brown, smaller synthlipsis width, interocular sulcus near the hind margin of the eye, smooth posterior pronotal lobe, distal part of R present, intersegmental sutures carinulate between sternites II–V (sometimes VI) and laterally between V–VII, and BPE shorter than the basal plate.

DESCRIPTION: Body length: 7.13 mm (holotype), 5.63–7.13 mm. COLORATION: Pale brown with dark brown head (except ventral anteocular surface), scape except basally, pedicel except basally, anterior pronotal lobe laterally, dorsal half of pro- and mesopleura, scutellum except apical processes, wing membrane, femora distally, and tibiae. Postocular ventrolaterally, labium, and antennal segments III and IV orange-brown. Disc of pronotum, posterior pronotal lobe, corium (except basally), and basal wing veins brown. Antennal segments V and VI white. VESTITURE: As in generic description. STRUCTURE: HEAD (Fig. 2.13F): Ovoid in lateral view; postclypeus with very shallow medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large; eye about one-third of head length, reaching dorsal and ventral head surfaces; antenna 7-segmented, pedicel about as long as scape. THORAX: Posterior pronotal lobe smooth; forefemur slightly incrassate; fossula spongiosa absent on mid tibia; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Intersegmental sutures carinulate between sternites II–V (sometimes VI) and laterally between V–VII; BPE shorter than basal plate (Fig. 2.22D); area of endosomal struts–DPS fusion ovate (Fig. 2.21F).

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the short length of the anteocular.

DISTRIBUTION: Antsiranana, Fianarantsoa, and Toamasina provinces (Map 2.5).

DISCUSSION: In some specimens, the intersegmental suture between sternites V and VI is entirely carinulate rather than being restricted to the lateral area.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 09 Apr 2002–16 Apr 2002, M. Irwin, R. Harin'Hala (00006479) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 10 Jan 2005–15 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00044981) (CAS); 26 Jan 2005–04 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00007167) (SU); 04 Apr 2005–16 Apr 2005, M. Irwin, R. Harin'Hala, 1♂ (00007146) (UCR). R.N.I. de Marojejy, 8.0 km NW Manantenina, 14.43667°S 49.775°E, 450 m, 05 Oct 1996–13 Oct 1996, E. Quinter and T. Nguyen, 1♂ (00078365) (AMNH). R.N.I. de Marojejy, 10.0 km NW Manantenina, 14.43333°S 49.76167°E, 750 m, 15 Oct 1996–22 Oct 1996, E. Quinter and T. Nguyen, 1♂ (00078366) (AMNH). **Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 10 Jan 2002–14 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00006142) (CAS); 12 Feb 2002–19 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00007049) (UCR). Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1100 m, 04 Jun 2002–14 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (00007051) (CAS). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 28 Nov 2001–06 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00007122) (CAS); 09 Mar 2003–20 Mar 2003, M. Irwin, R.

Harin'Hala, 1♂ (00007198) (CAS); 17 Dec 2003–30 Dec 2003, M. Irwin, R. Harin'Hala, 1♂ (00007241) (BMNH); 08 Jul 2004–22 Jul 2004, M. Irwin, R. Harin'Hala, 1♂ (00045538) (BMNH); 09 Aug 2005–25 Aug 2005, M. Irwin, R. Harin'Hala, 2♂ (00044830, 00045518) (USNM); 27 Nov 2006–02 Dec 2006, M. Irwin, R. Harin'Hala, 1♂ (00006123) (SU). **Toamasina:** Forêt d'Analava Mandrisy, 5.9 km 195° Antanambe, 16.48555°S 49.84694°E, 10 m, 12 Nov 2005–13 Nov 2005, Brian L. Fisher et al., 1♂ (00045579) (CAS). Mobot Site, Analalava 7 km SW of Foulpointe, 17.69333°S 49.46027°E, 18 m, 30 Nov 2007–07 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00006480) (CAS). Parc National Mananara-Nord, 7.1 km 261° Antanambe, 16.455°S 49.7875°E, 225 m, 14 Nov 2005, Brian L. Fisher et al., 1♂ (00006471) (CAS). **Unknown:** 3♂ (00007157, 00007234, 00007239) (CAS).

Marojejycoris francais, new species

Figs. 2.2, 2.5, 2.9, 2.22D; Map 2.5

DIAGNOSIS: Males are recognized among other species in *Marojejycoris* by the small body size, ovoid head shape, 7-segmented antenna, fossula spongiosa absent on the mid tibia, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI. This species is similar to *M. notadichroa*, from which it differs by the small body size, less elongated and more ovoid head, slightly more shallow postclypeal depression, interocular sulcus near hind margin of the eye, 7-segmented antenna, fossula spongiosa absent on mid tibia, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI.

DESCRIPTION: Body length: 6.18 mm (holotype), 6.18–6.82 mm. COLORATION: Dull orange with labial segments III and IV, thoracic sterna, scutellum, corium basally, coxae, trochanters, femora basally, and abdomen pale. Scape apically, pedicel, and antennal segments III–VI dark brown. Wing membrane brown and antennal segment VII white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13D); postclypeus with very shallow medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna 7-segmented; pedicel about one-third longer than scape. THORAX: Posterior pronotal lobe smooth; forefemur incrassate; fossula spongiosa absent on mid tibia; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; BPE shorter than basal plate (Fig. 2.22D); area of endosomal struts–DPS fusion ovate (Fig. 2.21F).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Montagne Français, Madagascar.

DISTRIBUTION: Montagne des Français Reserve and Amber Mountain National Park in the Antsiranana province (Map 2.5).

HOLOTYPE: Male: **Madagascar: Antsiranana:** Montagne Français, 12.325°S 49.33333°E, 150 m, 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala (00006470) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Parc National Montagne d'Ambre, 12.51666°S 49.18333°E, 975 m, 25 Jan 2001–11 Feb 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 1♂ (00044900) (UCR). Parc National Montagne d'Ambre, 12.52027°S 49.17916°E, 1125 m, 04 Mar 2001–19 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006129) (CAS).

Marojejycoris notadichroa, new species

Figs. 2.2, 2.6, 2.9; Map 2.5

DIAGNOSIS: Males recognized among other species in this genus by a combination of the following characters: the larger body size, more deeply depressed postclypeus, postclypeal depression extending to the interocular sulcus, and 6-segmented antenna. This species is similar to *M. auranticorium*, from which it differs by the general brown color of the antenna, bicolored pronotum (anterior lobe orange-brown and posterior lobe dark brown), dark brown corium (except basally pale), deeper postclypeal depression that extends to the interocular sulcus, and eye about one-third of the head length in lateral view.

DESCRIPTION: Body length: 8.18 mm (holotype), 7.40–8.73 mm. VESTITURE: As in generic description. COLORATION: Orange with thoracic pleura and sterna, corium basally, and abdomen pale. Scape apically, pedicel, antennal segments III–IV and basal half of V, posterior pronotal lobe, and remainder of hemelytron brown. Apical half of antennal segment V and segment VI entirely white. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13D); postclypeus with relatively deep medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; ocelli large; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna 6-segmented, pedicel about as long as scape. THORAX: Posterior pronotal lobe smooth; forefemur incrassate; fossula spongiosa present on mid tibia; distal part of R present but not forming R+M cell (Fig. 2.17B, C). ABDOMEN: Intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; BPE shorter than basal plate (Fig. 2.22D); area of endosomal struts–DPS fusion ovate (Fig. 2.21F).

ETYMOLOGY: The species epithet is a noun in the nominative case and is named for the bicolored pronotum.

DISTRIBUTION: Antsiranana and Toamasina provinces (Map 2.5).

HOLOTYPE: Male: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 10 Jan 2005–15 Jan 2005, M. Irwin, R. Harin'Hala (00045019) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 09 Dec 2004–15 Dec 2004, M. Irwin, R. Harin'Hala, 2♂ (00045521, 00045672) (CAS); 15 Dec 2004–20 Dec 2004, M. Irwin, R. Harin'Hala, 2♂ (00044980, 00045013) (USNM); 25 Dec 2004–30 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00044940) (CAS); 26 Jan 2005–04 Feb 2005, M. Irwin, R. Harin'Hala, 2♂ (00007124, 00045532) (UCR); 16 Apr 2005–28 Apr 2005, M. Irwin, R. Harin'Hala, 1♂ (00044910) (SU); 18 May 2005–30 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00007115) (SU); 13 Jul 2005–28 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00044969) (UCR). Montaigne Français, 12.325°S 49.33333°E, 150 m, 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006475) (CAS). R.N.I. de Marojejy, 10.0 km NW Manantenina, 14.43333°S 49.76167°E, 750 m, 15 Oct 1996–22 Oct 1996, E. Quinter and T. Nguyen, 1♂ (00078361) (AMNH). **Toamasina:** Forêt d'Analava Mandrisy, 5.9 km 195° Antanambe, 16.48555°S 49.84694°E, 10 m, 12 Nov 2005–13 Nov 2005, Brian L. Fisher et al., 1♂ (00007179) (CAS). **Unknown:** 3♂ (00044991, 00044993, 00045015) (CAS).

Marojejycoris ranomafana, new species

Figs. 2.2, 2.6, 2.9; Map 2.5

DIAGNOSIS: Males are recognized among other *Marojejycoris* species by the small body size, bicolored head and thorax in lateral view, ovoid head shape, 7-segmented antenna, striated posterior pronotal lobe, distal part of R absent, intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI, and BPE as long as the basal plate. This species is similar to *M. brevifrons*, but differs by the slightly smaller body size, pale to light brown dorsal and dark brown ventral surfaces of the head and pronotum, pale corium and membrane, wider synthlipsis, interocular sulcus posterior to hind margin of the eye, striated posterior pronotal lobe, fossula spongiosa on mid tibiae, distal part of R absent, intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI, and BPE as long as the basal plate.

DESCRIPTION: Body length: 5.41 mm (holotype), 5.41–5.50 mm. COLORATION: Brown with head laterally and ventrally, pedicel apically, antennal segments III and IV, dorsal half of thoracic pleura, thoracic sterna, coxae, abdominal sternites II–VI laterally, and small lateral spot on sternite VII dark brown. Antennal segment VII, ventral half of thoracic pleura, scutellum except apical processes, corium, trochanters, femora basally, and remainder of abdomen pale. VESTITURE: As in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13D); postclypeus with very shallow medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; ocelli small; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna 7-segmented; pedicel about as long as scape. THORAX: Posterior pronotal lobe transversely striated; legs slender; fossula spongiosa present on mid tibia; distal part of R absent. ABDOMEN: Intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; BPE as long as basal plate; area of endosomal struts–DPS fusion elongate subquadrate; endosoma damaged.

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Ranomafana National Park, Madagascar.

DISTRIBUTION: Ranomafana National Park in the Fianarantsoa province (Map 2.5).

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 09 Mar 2003–20 Mar 2003, M. Irwin, R. Harin'Hala (00045464) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1100 m, 04 Feb 2002–12 Feb 2002, M. Irwin, R.

Harin'Hala, 1♂ (00007155) (CAS). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 21 Dec 2001–24 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00007137) (CAS); 26 Nov 2003–06 Dec 2003, M. Irwin, R. Harin'Hala, 1♂ (00048057) (UCR); 07 Oct 2005–16 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00048058) (UCR).

Tanindrazanus, new genus

Figs. 2.2, 2.3, 2.6, 2.7, 2.9, 2.10, 2.13G, 2.13H, 2.15D, 2.15F, 2.16A, 2.17C, 2.18B, 2.19F, 2.20G–I, 2.21G, 2.21H, 2.22E; Maps 2.6–2.9

TYPE SPECIES: *Tanindrazanus irwini*, new species

DIAGNOSIS: Male recognized by the subtriangular head in lateral view, maxillary plate reaching or nearly reaching dorsal clypeal surface, 7-segmented antenna (6-segmented in some specimens of *T. harinhali*), and slender labium with labial segment III ventrally (appears dorsal when folded under head) straight. *Tanindrazanus* is most similar to *Toliarus*, but can be differentiated by the the medium to large body size, maxillary plate reaching or nearly reaching the dorsal clypeal surface, 7-segmented antenna (except some *T. harinhali*), smooth or striated posterior pronotal lobe, and distinct transverse suture separating the meso- and metasterna.

DESCRIPTION: **MALE:** Macropterous, body size medium to large. COLORATION: Uniformly orange-brownish, brown, or black; red and black; orange and black; red and brown; or dark orange, brown, and black. VESTITURE: Dense, semierect to erect, long pale, orange, brown, and dark brown setae on head, thorax, legs, corium of hemelytra, and abdomen; setae on tibiae stouter and denser near apex. STRUCTURE: HEAD (Fig. 2.13G, H): Subtriangular in lateral view, longer than wide in dorsal view, shorter than pronotum; anteocular region longer than postocular; distinct constriction between postocular and neck; gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin; maxillary plate reaching or nearly reaching dorsal surface of clypeus; postclypeus depressed (Fig. 2.13B); ocelli present; antennal shield not concealing antennal insertion in lateral view; antenna inserted dorsally on head; scape surpassing clypeal apex; pedicel slightly curved; flagellum subdivided into BFLA and DFLA; BFLA divided into two pseudosegments; DFLA divided into three pseudosegments (may be two in some specimens of *T. harinhali*); antenna thus appearing 7-segmented (6-segmented in some specimens of *T. harinhali*); labium slender; labial segment III ventrally straight. THORAX (Fig. 2.15D, F): Pronotum wider than long, anterior margin distinctly concave, collar distinct (Fig. 2.15B); anterior pronotal lobe shorter than posterior lobe, more than half as wide as posterior lobe, relatively smooth; pronotal longitudinal furrow reaching anterior but not posterior margin of pronotum, foveate posteriorly (Fig. 2.15B); pronotal transverse furrow distinct (Fig. 2.15B); lateral depressions on posterior pronotal lobe distinct (Fig. 2.15B), transversely striated; scutellum with two broadly separated apical processes, disc medially depressed; meso- and metasterna separated by distinct transverse suture; mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; MGE with deeply depressed meshlike cuticle that extends dorsally in lateral view (Fig. 2.16A); fossula spongiosa on fore- and mid tibiae; hemelytron (Fig. 2.17C) with corium restricted to areas adjacent to basal wing veins, with pterostigmalike appearance on anterodistal margin; distal part of R present but not forming cell with M; proximal parts of M and Cu separate; distal part of M extending beyond apical junction of M+Cu; base of M+Cu cell shorter than or as wide as Cu+1A cell. ABDOMEN (Fig. 2.18B): Dorsal laterotergite II not distinctly expanded; sternites longitudinally depressed medially (Fig. 2.18C), intersegmental sutures carinulate; spiracles ovoid; pygophore process subtriangular caudal view (Fig. 2.19F, G, I), directed dorsoposteriad, not surpassing posterior margin of pygophore, apex rounded; DPS apex rounded (Fig. 2.20G, H); endosomal struts reaching posterior margin of DPS, with anterior and posterior ventral processes

(Fig. 2.22G); endosoma weakly to heavily sclerotized medially (Fig. 2.21G, H).

ETYMOLOGY: This genus is named after the Madagascan word "Tanindrazana", which stands for "Fatherland" in the nation's motto and represents national unity. The gender is masculine.

DISTRIBUTION: Species are known from all provinces and occur in habitats between 10–1,130 m elevation. Macrohabitats are described as gallery forests, tropical dry forests, mixed tropical forests, low- and high-altitude rainforests, sclerophyl forests, dwarf littoral forests, secondary forests, and dry deciduous forests.

DISCUSSION: Female specimens are unknown for this genus. Approximately half of the specimens belonging to *T. harinhali* have the DFLA subdivided into two pseudosegments instead of three and the antenna is therefore 6-segmented. Specimens from the same locality may have 6- or 7-segmented antenna and this polymorphism can be observed even within one individual.

Identification key to the males of species of Tanindrazanus

1. Clypeal apex not elevated relative to labral base (Fig. 2.13C–F, I–K)..2
- Clypeal apex slightly to distinctly elevated relative to labral base (Fig. 2.13G, H).......................3
2. Head elongate, nearly cylindrical; postocular broad in dorsal view (Fig. 2.13B); labial segment II longer than III; forefemora slender .... *brunneus*, new species
- Head subtriangular (Fig. 2.13G, H); postocular narrow in dorsal view (Fig. 2.13A); labial segment II and III subequal in length; forefemora incrassate..................... *joffrevillus*, new species
3. Anterior pronotal lobe laterally carinate 4
- Anterior pronotal lobe not laterally carinate...6
4. Body length ≥20 mm; head ventrally flat; labial segment II shorter than III; red and black or orange and black 5

- Body length <20 mm; head ventrally with shallow anteromedial depression; labial segment II longer than III; dull orange .... *bemaraha*, new species

5. Red and black; forefemora slightly incrassate; sternal intersegmental sutures carinulate between II and III and laterally between III–V..................................... *hannajagodae*, new species

- Orange and black; forefemora slender; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI... *irwini*, new species

6. Eye reaching dorsal head surface...7

- Eye not reaching dorsal head surface 11

7. Eye reaching ventral head surface 8

- Eye not reaching ventral head surface...*tenebricus*, new species

8. Pronotal transverse suture complete, not divided by paramedian ridges.....................................9

- Pronotal transverse suture incomplete, divided by paramedian ridges (Fig. 2.15B)........................ ....*amboasaricus*, new species

9. Eye about half head length; posterior pronotal lobe smooth; dorsal laterotergite II very slightly expanded laterally; sternal intersegmental sutures carinulate between II–V..................................... .... *vohiparara*, new species

- Eye about one-third head length; posterior pronotal lobe smooth or striated; dorsal laterotergite II not distinctly expanded laterally; sternal intersegmental suture carinulation patterns not as previously mentioned... 10

10. Pale to dark brown coloration; synthlipsis about width of eye; postocular narrow in dorsal view; posterior pronotal lobe striated; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VII .... *marginatus*, new species

- Red and pale to dark brown coloration; synthlipsis less than width of eye; postocular broad in dorsal view; posterior pronotal lobe smooth; sternal intersegmental sutures carinulate between II–V and laterally between V–VI ....*anjozorobeus*, new species

11. Labial segment II and III not subequal in length 12

- Labial segment II and III subequal in length 14

12. Labial segment II shorter than III 13

- Labial segment II longer than III ....*andohahela*, new species

13. Body length <20 mm; red and black; postclypeus not depressed (Fig. 2.13A); pronotal transverse suture complete, not divided by paramedian ridges ....*marojejy*, new species

- Body length ≥20 mm; dark orange-brown or dark orange-red; postclypeus medially depressed (Fig. 2.13B); pronotal transverse suture incomplete, divided by paramedian ridges (Fig. 2.15B)..... .... *mahafaly*, new species

14. Pronotal transverse suture complete, not divided by paramedian ridges 15

- Pronotal transverse suture incomplete, divided by paramedian ridges (Fig. 2.15B) 18

15. Red and black, pale red and brown, or uniformly dark coloration; anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); forefemora slender 16

- Dull orange with hind femur distally and hind tibia distally black; anterior pronotal lobe without distinct anterolateral projections; forefemora moderately incrassate .... *notatus*, new species

16. Synthlipsis width less that two times width of eye; pale red and brown or uniformly dark brown to blackish coloration 17

- Synthlipsis width two times width of eye; red and black ....*kathrynae*, new species

17. Synthlipsis width about 1.25 times width of eye; uniformly dark brown to blackish coloration .... *simulans*, new species

- Synthlipsis about width of eye; pale red and brown............................ *antananarivo*, new species

18\. Black and pale or tricolored; forefemora slightly to moderately incrassate 19

- Bright orange and black; forefemora slender .... *varicolor*, new species

19\. Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); sternal intersegmental sutures carinulate between II–IV; black and pale ....*nigripes*, new species

- Anterior pronotal lobe without distinct anterolateral projections; sternal intersegmental sutures carinulate between II–VI and laterally between VI and VII; tricolored, dark brown, dull orange, and pale ....*harinhali,* new species

Tanindrazanus amboasaricus, new species

Figs. 2.2, 2.6, 2.9; Map 2.9

DIAGNOSIS: Males are recognized among other species in *Tanindrazanus* by a combination of the following characters: the distinct coloration, synthlipsis about the width of the eye, eye reaching the dorsal and ventral head margins, and the pronotal transverse furrow not continuous. This species is similar to *T. harinhali*, from which it differs by the larger body size; dark brown to blackish head, pronotum, and scutellum; the width of the synthlipsis about the width of an eye; and intersegmental sutures carinulate between sternites II–V.

DESCRIPTION: Medium body size (length: 16.05 mm, holotype; 14.30–16.05 mm). COLORATION: Dark brown with labrum, basal half of scapus, costal margin, and tarsi light brown. Antennifers apically, basal part of hemelytra, trochanters, basal half of femora, and tibiae medially yellowish. Tarsomere III on forelegs with dark brown band in apical part. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; postocular narrow in dorsal view (Fig. 2.13A); synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); eyes about one-third of head length, reaching dorsal and ventral head surfaces; ocelli large, separated by less than half of diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); pedicel about one-fifth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe without anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); legs slender; tarsomeres I and II combined subequal to III on fore- and mid legs, longer on hind legs; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–V; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion tonguelike, apically expanded and rounded.

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality Amboasary, Madagascar.

DISTRIBUTION: Ambovombe in the Amboasary District of the Toliara province (Map 2.9).

DISCUSSION: The coloration on the dorsal surface of the pronotum is sometimes dark brown.

HOLOTYPE: Male: **Madagascar: Toliara:** Amboasary District, Ambovombe, 25.17201°S 46.08971°E, 131 m, 19 Jun 1957, P. Griveaud (MNHN).

PARATYPES: **Madagascar: Toliara:** Amboasary District, Ambovombe, 25.17201°S 46.08971°E, 131 m, 19 Jun 1957, P. Griveaud, 3♂ (MNHN).

Tanindrazanus andohahela, new species

Figs. 2.2, 2.6, 2.9; Map 2.7

DIAGNOSIS: Males recognized among other species in this genus by the longer labial segment II relative to III and slightly incrassate forefemur. This species is similar to *T. bemaraha*, but the shorter labial segment III and lack of anterolateral protuberances on the anterior pronotal lobe distinguish *T. andohahela* from *T. bemaraha*. This species is also similar to *T. notatus*, but differs from it by the slightly incrassate forefemur and lack of black markings on the hind legs.

DESCRIPTION: Medium body size (length: 11.10 mm, holotype; 10.34–11.10 mm). COLORATION: Orange with antennal segments III–IV and basal half of V dark brown, hemelytron basally (except corium) brown, and antennal segment V apically and VI white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-third longer than scape; labial segment III shorter than II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; forefemur slightly incrassate; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21G).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Parc National d' Andohahela, Madagascar.

DISTRIBUTION: Antananarivo, Mahajanga, and Toliara provinces (Map 2.7).

HOLOTYPE: Male: **Madagascar: Toliara:** Parc National d'Andohahela, Ihazofotsy Parcelle III, 24.83083°S 46.53616°E, 80 m, 16 Dec 2002–26 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala (00044865) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 17 Oct 2003–24 Oct 2003, M. Irwin, R. Harin'Hala, 1♂ (00006126) (BMNH), 1♂ (00045559) (USNM); 28 Dec 2003–10 Jan 2004, M. Irwin, R. Harin'Hala, 1♂ (00006093) (UCR); 10 Jan 2004–20 Jan 2004, M. Irwin, R. Harin'Hala, 1♂ (00007177) (CAS), 1♂ (00045466) (SU). **Mahajanga:** 160 km N of Maevatanana on RN 04, Ampijoroa National Park, 16.31933°S 46.81333°E, 43 m, 07 Feb 2005–19 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00045044) (CAS). **Unknown:** 2♂ (00044823, 00044877) (CAS).

Tanindrazanus anjozorobeus, new species

Figs. 2.2, 2.6; Map 2.9

DIAGNOSIS: Males are recognized among other *Tanindrazanus* species by the tricolor body (red, orange, and brown coloration), elevated clypeal apex relative to the labrum, synthlipsis smaller than the width of the eye, and broad postocular in dorsal view. This species is very similar to *T. kathrynae*, but it can be easily distinguished by the larger body size, small width of the synthlipsis, larger eyes that surpass the dorsal and ventral margins of the head in lateral view, very large ocelli separated by less than one-third of the diameter of an ocellus, and lack of anterolateral projections on the pronotum.

DESCRIPTION: Large body size (length: 17.32 mm, holotype; 16.20–17.32 mm). COLORATION: Red with pale orange-brown mandibular and maxillary plates, clypeus, dorsal postocular near ocellar tubercle, labium, anterior pronotal lobe except lateral margins, tibiae except apically, and corium except distally. Remainder of head, lateral margins of anterior pronotal lobe, anterior part of propleura, meso- and metapleura, scutellum, corium distally, forewing membrane, femora and apical part of tibiae, ventrolateral spot on abdominal sternites II–V, and pygophore dark brown to black. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis smaller than the width of eye; interocular sulcus posterior to hind margin of eye; postocular broad in dorsal view (Fig. 2.13A); ocelli very large, separated by less than one-third diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, distinctly surpassing dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe without anterolateral projections; posterior pronotal lobe smooth; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–V and laterally between V and VI; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE longer than basal plate; area of endosomal struts–DPS fusion ovate.

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality Anjozorobe, Madagascar.

DISTRIBUTION: Anjozorobe in the Antananarivo province (Map 2.9).

DISCUSSION: Coloration varies with the pronotal longitudinal furrow either light brown or entirely black and the abdominal sternites dark brown.

HOLOTYPE: Male: **Madagascar: Antananarivo:** Anjozorobe District, Anjozorobe, 18.2619°S 47.6849°E, 1091 m, Dec 1938 (MNHN).

PARATYPES: **Madagascar: Antananarivo:** Anjozorobe District, Anjozorobe, 18.2619°S 47.6849°E, 1091 m, Dec 1938, 3♂ (MNHN).

Tanindrazanus antananarivo, new species

Figs. 2.2, 2.6, 2.9; Map 2.6

DIAGNOSIS: Males recognized among other *Tanindrazanus* species by a combination of the following characters: the dark brown color with pale red abdomen, synthlipsis about the width of the eye, eye not reaching the dorsal and ventral head margins, and continuous pronotal transverse furrow. This species is similar to *T. marginatus* and *T. tenebricus*, but is easily distinguished by the dark brown and pale red color pattern and intersegmental sutures carinulate between sternites II–V and laterally between V and VI.

DESCRIPTION: Medium body size (length: 12.52 mm, holotype; 12.41–14.00 mm). COLORATION: Dark brown with light brown clypeus, antennifer except apically, postocular and neck dorsomedially, head posteroventrally, anteocular laterally and ventrally, labium, basal half of antennal segment V, anterior margin of pronotum, prosternum, corium basally, coxae, trochanters, femora basally, tibiae apically, and tarsi. Meso- and metasterna medially and abdomen, except pygophore, pale red. Distal half of antennal segment V and segments VI and VII white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; postocular narrow in dorsal view (Fig. 2.13A); synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); eyes about one-third of head length, not reaching dorsal and ventral head surfaces; ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III on fore- and mid legs, longer on hind legs; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–V and laterally between V and VI; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality province Antananarivo, Madagascar.

DISTRIBUTION: Northern region of Antananarivo province (Map 2.6).

DISCUSSION: The dorsal surface of the antennifers and postclypeus are light brown in some specimens.

HOLOTYPE: Male: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 16 Jan 2005–27 Jan 2005, M. Irwin, R. Harin'Hala (00006330) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 24 Oct 2003–31 Oct 2003, M. Irwin, R. Harin'Hala, 1♂ (00005367) (CAS); 07 Nov 2003–15 Nov 2003, M. Irwin, R. Harin'Hala, 1♂ (00006334) (CAS); 22 Nov 2003–29 Nov 2003, M. Irwin, R. Harin'Hala, 1♂ (00006333) (CAS); 01 Nov 2004–14 Nov 2004, M. Irwin, R. Harin'Hala, 1♂ (00006336) (CAS); 07 Dec 2004–22 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00006335) (CAS); 22 Dec 2004–06 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00006083) (BMNH); 16 Jan 2005–27 Jan 2005, M. Irwin, R. Harin'Hala, 2♂ (00006331, 00006332) (USNM); 23 Mar 2005–03 Apr 2005, M. Irwin, R. Harin'Hala, 2♂ (00006958, 00006959) (UCR); 03 Apr 2005–17 Apr 2005, M. Irwin, R. Harin'Hala, 1♂ (00006127) (SU).

Tanindrazanus bemaraha, new species

Figs. 2.2, 2.6, 2.9; Map 2.7

DIAGNOSIS: Males are recognized among other species in *Tanindrazanus* by the longer labial segment II relative to III, anterior pronotal lobe with very small anterolateral protuberances, and anterior pronotal lobe slightly carinate laterally. This species is similar to *T. andohahela* and *T. notatus*, but differs from both species by the presence of the anterolateral protuberances and laterally carinate anterior pronotal lobe. *Tanindrazanus bemaraha* is further distinguished from *T. notatus* by the lack of black markings on the hind femur and tibia and longer labial segment II.

DESCRIPTION: Medium body size (length: 13.93 mm, holotype; 13.07–13.93 mm). COLORATION: Orange-brown with dark brown scape except basally, pedicel, and antennal segments III and IV, as well as V basally. Antennal segment V apically and segments VI and VII pale. Wing membrane and distal wing veins brown. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-third longer than scape; labial segment III shorter than II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B), slightly carinate laterally; posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III on mid and hind tarsi, foretarsi missing; wings spread out in specimens. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII;

pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21G).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Tsingy de Bemaraha National Park, Madagascar.

DISTRIBUTION: Tsingy de Bemaraha National Park in the Mahajanga province (Map 2.7).

HOLOTYPE: Male: **Madagascar: Mahajanga:** Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 19.70944°S 44.71806°E, 150 m, 16 Nov 2001–20 Nov 2001, Fisher et al. (00006473) (CAS).

PARATYPE: **Madagascar: Mahajanga:** Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 19.70944°S 44.71806°E, 150 m, 16 Nov 2001–20 Nov 2001, Fisher et al., 1♂ (00005362) (CAS).

Tanindrazanus brunneus, new species

Figs. 2.2, 2.6, 2.9; Map 2.8

DIAGNOSIS: Males recognized among other species in this genus by the very elongate subtriangular (almost cylindrical) head in lateral view, postclypeal depression extending to interocular sulcus, broad postocular in dorsal view, synthlipsis about 2.5 width of an eye, eyes about one-fifth of the head length, and small ocelli on a shallower ocellar tubercle. This species is similar to *T. joffrevillus*, but is distinguished by the preceding characters, labial segment II longer than III, striated posterior pronotal lobe, and slender legs.

DESCRIPTION: Medium body size (length: 10.31 mm, holotype). COLORATION: Orange with pale thoracic pleura and sterna and brown pronotum and wing membrane. Scape, pedicel, antennal segments III and IV, as well as segment V basally and segment VII apically, dark brown. Antennal segment V apically, segment VI, and base of segment VII white. VESTITURE:

As in generic description. STRUCTURE: HEAD: Elongate; ventrally flat; clypeal apex not elevated relative to labrum Fig. 2.13C–F, I–K); postclypeus with very shallow, narrow medial longitudinal depression to interocular sulcus; synthlipsis about 2.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli relatively small, separated by less than diameter of ocellus, located on shallow medial tubercle (Fig. 2.13G); eyes about one-fifth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III shorter than II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); legs slender; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process very flattened in lateral view (Fig. 2.20F); BPE as long as basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the color of the body.

DISTRIBUTION: The only known specimen was collected from Marojejy Nature Reserve in the Antsiranana province (Map 2.8).

HOLOTYPE: Male: **Madagascar**: **Antsiranana**: R.N.I. de Marojejy, 10.0 km NW Manantenina, 14.43333°S 49.76167°E, 750 m, 15 Oct 1996–22 Oct 1996, E. Quinter and T. Nguyen (00078368) (AMNH).

Tanindrazanus hannajagodae, new species

Figs. 2.2, 2.6, 2.9; Map 2.6

DIAGNOSIS: Males are recognized among other *Tanindrazanus* species by the large body size, red and black coloration, flat ventral head surface, labial segment II shorter than III, laterally carinate anterior pronotal lobe, slightly incrassate forefemur, and intersegmental sutures carinulate between sternites II and III and laterally between III–V. This species is similar to *T. marojejy*, *T. mahafaly*, and *T. irwini*, but can be separated from the features mentioned, in particular the coloration and sternal intersegmental carinulation pattern.

DESCRIPTION: Large body size (length: 23.39 mm, holotype; 22.47–23.69 mm). COLORATION: Red with black antenna (except pedicel basally, apical half of segment V, and segment VI), posterior pronotal margin, scutellar processes apically, hemelytron except base of corium, trochanters, femora basally, and posterolateral stripes on abdominal sternites III–VI. Hind tibia dark red and distal half of antennal segment V and segment VI white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally flat; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III longer than II. THORAX: Anterior pronotal lobe without distinct anterolateral projections, laterally carinate; posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur slightly incrassate; tarsomeres I and II combined shorter than III on fore- and mid legs, subequal on hind legs; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded or notched medially; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II and III and laterally between III–V; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion circular.

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after the second author's daughter, Hanna Jagoda Chłond.

DISTRIBUTION: Northern region of the Antsiranana province (Map 2.6).

DISCUSSION: The coloration is variable with the hind femur dark red, the ventral intersegmental sutures black, and the hemelytron light brown in some specimens.

HOLOTYPE: Male: **Madagascar: Antsiranana:** 7 km N of Joffreville, 12.45°S 49.23333°E, 426 m, 11 Feb 2007–18 Feb 2007, M. Irwin, R. Harin'Hala (00006261) (CAS).

PARATYPES: **Madagascar: Antsiranana:** 7 km N of Joffreville, 12.45°S 49.23333°E, 426 m, 20 Jan 2007–27 Jan 2007, M. Irwin, R. Harin'Hala, 1♂ (00006263) (SU); 11 Feb 2007–18 Feb 2007, M. Irwin, R. Harin'Hala, 1♂ (00006262) (UCR). Réserve Spéciale d'Ambre, 3.5 km 235° SW Sakaramy, 12.46888°S 49.24222°E, 325 m, 26 Jan 2001–31 Jan 2001, Fisher et al., 1♂ (00006117) (CAS).

Tanindrazanus harinhali, new species

Figs. 2.2, 2.6, 2.9; Map 2.6

DIAGNOSIS: Males are recognized among other species in this genus by a combination of the following characters: the distinct tricolor pattern (dark brown, orange, and pale yellow), synthlipsis about 1.5 times the width of the eye, eye not reaching the dorsal and ventral head margins, ocelli separated by diameter of ocellus, and the pronotal transverse furrow not continuous. This species is similar to *T. amboasaricus*, but differs by the smaller body size;

orangish head, pronotum, and scutellum; greater synthlipsis width; and intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII.

DESCRIPTION: Medium body size (length: 10.99 mm, holotype; 10.39–11.89 mm). COLORATION: Dark brown with pale yellow mandibular and maxillary plates, postclypeus, antennifer dorsally, scape basally, scutellum medially, corium basally, coxae, trochanters, fore- and mid femora except dorsally, hind femur except apically, foretibia, mid tibia except apically, hind tibia medially, tarsi, laterotergites except posterior half of VII, ventrolateral stripes on abdominal sternites III and IV, lateral margins of sternites II–VI, and anterolateral area of VII, labial segment II basally, labial segment IV, prothorax, and dorsal half of mesopleuron orange. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur slightly incrassate; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE shorter than basal plate; area of endosomal struts–DPS fusion elongate ovoid.

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after Rasolondalao Harin'Hala Hasinjaka, who helped collect a majority of the specimens examined for this species.

DISTRIBUTION: Fianarantsoa and Toliara provinces (Map 2.6).

DISCUSSION: The yellow coloration on the head, legs, and stripes on the abdominal sternites may be reduced in size or absent, and the clypeus, posteroventral head surface, and dorsomedial neck surface may be yellow. Approximately half of the specimens examined have the DFLA subdivided into two pseudosegments instead of three among and within individuals.

HOLOTYPE: Male: **Madagascar: Toliara:** Beza Mahafaly Reserve, Parcelle I near research station, 23.6865°S 44.591°E, 165 m, 28 Nov 2001–04 Dec 2001, R. Harin'Hala (00006418) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 03 Mar 2007–10 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044892) (CAS). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 16 Oct 2001–08 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00006425) (CAS); 09 Aug 2005–25 Aug 2005, M. Irwin, R. Harin'Hala, 1♂ (00006537) (UCR). Radio tower 22 km SW of Ilakaka, near Fianarantsoa/Toliara border, 22.77917°S 45.025°E, 1100 m, 06 Mar 2002–11 Mar 2002, M. Irwin, R. Harin'Hala, 1♂ (00006340) (CAS). **Toliara:** Andohahela Natl Park, Tsimelahy, Parcelle II, 24.93683°S 46.62666°E, 180 m, 27 Dec 2002–06 Jan 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006391) (CAS); 06 Jan 2003–16 Jan 2003, R. Harin'Hala, 1♂ (00006376) (CAS), 1♂ (00006377) (USNM); 08 Mar 2003–18 Mar 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006337, 00006344) (SU); 28 Mar 2003–08 Apr 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006552) (CAS); 22 Jun 2003–29 Jun 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006375) (AMNH); 17 Aug 2003–24 Aug 2003, M. Irwin, F.

Parker, R. Harin'Hala, 1♂ (00006554) (UCR); 09 Nov 2003–20 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006551) (CAS). Berenty Special Reserve, 8 km NW Amboasary, 25.00666°S 46.30333°E, 85 m, 25 Oct 2002–26 Oct 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006340) (CAS); 26 Oct 2002–02 Nov 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006349) (CAS), 1♂ (00006357) (BMNH); 30 Nov 2002–07 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00005359) (SU), 3♂ (00006353–00006355) (CAS); 26 Jan 2003–05 Feb 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006529) (UCR); 24 Mar 2003–03 Apr 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006532, 00045392) (AMNH); 03 May 2003–14 May 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006374) (CAS); 22 Nov 2003–30 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006534) (BMNH); 07 Dec 2003–14 Dec 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006541, 00006542) (USNM); 02 Jan 2004–13 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006547) (CAS); 23 Jan 2004–04 Feb 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006543, 00006546) (MNHN); 04 Feb 2004–15 Feb 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006528, 00006536) (AMNH); 15 Feb 2004–02 Mar 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006358) (SU); 27 May 2004–06 Jun 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006544, 00006545) (CAS); 06 Jun 2004–20 Jun 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006533, 00006553) (USNM); 22 Aug 2004–01 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006530) (UCR). Berenty Special Reserve, 8 km NW Amboasary, 25.021°S 46.3055°E, 35 m, 21 Dec 2003–01 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006346) (CAS); 02 Jan 2004–13 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006359) (UCR); 24 Mar 2004–04 Apr 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006549, 00006550) (CAS); 04 Apr 2004–15 Apr 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006531) (SU); 23 Jun 2004–04 Jul 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006350, 00006351) (AMNH); 04 Jul 2004–18 Jul 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006356) (CAS). Beza Mahafaly

Reserve, Parcelle II near Bellevue, 23.68983°S 44.5755°E, 180 m, 10 Nov 2001–21 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00006424) (MNHN); 18 Dec 2001–25 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00006426) (SU); 16 Jan 2002–18 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00006385) (CAS); 08 Feb 2002–15 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00006540) (UCR). Beza Mahafaly Reserve, Parcelle I near research station, 23.6865°S 44.591°E, 165 m, 15 Oct 2001–10 Nov 2001, M.E. Irwin, F.D. Parker, R. Harin'Hala, 1♂ (00006387) (CAS); 10 Nov 2001–21 Nov 2001, R. Harin'Hala, 1♂ (00006557) (UCR); 21 Nov 2001–28 Nov 2001, R. Harin'Hala, 2♂ (00006341, 00006392) (CAS); 28 Nov 2001–04 Dec 2001, R. Harin'Hala, 1♂ (00006417) (CAS); 04 Dec 2001–11 Dec 2001, R. Harin'Hala, 2♂ (00006345, 00006415) (SU); 11 Dec 2001–18 Dec 2001, R. Harin'Hala, 2♂ (00006132, 00006379) (AMNH); 18 Dec 2001–25 Dec 2001, R. Harin'Hala, 1♂ (00006388) (CAS); 25 Dec 2001–02 Jan 2002, R. Harin'Hala, 1♂ (00006548) (BMNH); 18 Jan 2002–25 Jan 2002, M.E. Irwin, F.D. Parker, R. Harin'Hala, 1♂ (00045278) (BMNH); 25 Jan 2002–01 Feb 2002, R. Harin'Hala, 2♂ (00006389, 00006390) (USNM); 08 Feb 2002–15 Feb 2002, R. Harin'Hala, 2♂ (00006342, 00006402) (CAS); 14 Mar 2002–22 Mar 2002, R. Harin'Hala, 1♂ (00006420) (CAS); 29 Mar 2002–10 Apr 2002, R. Harin'Hala, 1♂ (00006555) (CAS); 29 Apr 2002–19 May 2002, R. Harin'Hala, 1♂ (00006386) (CAS); 19 May 2002–08 Jun 2002, R. Harin'Hala, 1♂ (00006401) (CAS); 08 Jun 2002–18 Jun 2002, R. Harin'Hala, 2♂ (00006421, 00006423) (BMNH); 18 Jun 2002–28 Jun 2002, R. Harin'Hala, 1♂ (00006393) (CAS); 07 Jul 2002–18 Jul 2002, R. Harin'Hala, 1♂ (00006412) (CAS); 28 Jul 2002–09 Aug 2002, R. Harin'Hala, 1♂ (00006338) (CAS); 09 Aug 2002–16 Aug 2002, R. Harin'Hala, 1♂ (00006427) (CAS); 16 Aug 2002–28 Aug 2002, R. Harin'Hala, 2♂ (00006403, 00006404) (USNM); 09 Sep 2002–20 Sep 2002, R. Harin'Hala, 1♂ (00006414) (CAS); 20 Sep 2002–05 Oct 2002, R. Harin'Hala, 1♂ (00006422) (UCR); 20 Oct 2002–28 Oct 2002, R. Harin'Hala, 1♂ (00006380) (CAS); 28 Oct 2002–10 Nov 2002, M.E. Irwin, F.D. Parker,

R. Harin'Hala, 2♂ (00006409, 00006410) (BMNH); 02 Dec 2002–12 Dec 2002, R. Harin'Hala, 2♂ (00006347, 00006348) (CAS); 12 Dec 2002–17 Dec 2002, R. Harin'Hala, 1♂ (00006378) (CAS); 17 Dec 2002–20 Dec 2002, R. Harin'Hala, 1♂ (00006419) (CAS); 20 Dec 2002–24 Dec 2002, R. Harin'Hala, 1♂ (00006095) (CAS); 24 Dec 2002–02 Jan 2003, R. Harin'Hala, 1♂ (00006413) (AMNH); 09 Jan 2003–23 Jan 2003, R. Harin'Hala, 4♂ (00006405–00006408) (CAS); 23 Jan 2003–04 Feb 2003, R. Harin'Hala, 5♂ (00006395–00006399) (MNHN); 04 Feb 2003–16 Feb 2003, R. Harin'Hala, 1♂ (00006400) (SU); 16 Feb 2003–02 Mar 2003, R. Harin'Hala, 1♂ (00006556) (BMNH); 13 Mar 2003–23 Mar 2003, R. Harin'Hala, 2♂ (00006381, 00006382) (USNM); 23 Mar 2003–02 Apr 2003, R. Harin'Hala, 1♂ (00006339) (CAS); 02 Apr 2003–10 Apr 2003, R. Harin'Hala, 1♂ (00006352) (CAS); 29 Apr 2003–07 May 2003, R. Harin'Hala, 1♂ (00006416) (UCR). Parc National d'Andohahela, Ihazofotsy Parcelle III, 24.83083°S 46.53616°E, 80 m, 06 May 2003–13 May 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006343) (SU); 29 Jun 2003–06 Jul 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044843) (UCR); 03 Aug 2003–13 Aug 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00044809, 00044837) (CAS). **Unknown:** 5♂ (00006383, 00006384, 00006535, 00006538, 00006539) (CAS).

Tanindrazanus irwini, new species

Figs. 2.2, 2.6, 2.9, 2.15F; Map 2.7

DIAGNOSIS: Males are recognized among other species in *Tanindrazanus* by the large body size, black coloration with orange markings, flat ventral head surface, labial segment II shorter than III, laterally carinate anterior pronotal lobe, slender legs, and intersegmental sutures carinulate between sternite II–IV and laterally between IV–VI. This species is similar to *T. varicolor*, but differs by the larger body size, flat ventral head surface, labial segment II shorter than III, laterally carinate anterior pronotal lobe, and intersegmental sutures carinulate between sternite II–VI and laterally between VI and VII.

DESCRIPTION: Large body size (length: 22.76 mm, holotype; 18.95–22.76 mm). COLORATION: Dark brown-black with bright orange head dorsally, scape, labium except segment II basally, scutellum medially, hemelytron except posteromedial spot, femora apically, tibiae, tarsi, laterotergites II–V, anterior half of laterotergite VI, sternites III–V, and anterior half of sternite VI except posterolateral stripes. Distal half of antennal segment V and segments VI and VII white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally flat; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III longer than II. THORAX (Fig. 2.15F): Anterior pronotal lobe without distinct anterolateral projections, laterally carinate; posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); legs slender; tarsomeres I and II combined subequal to III; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternite II–IV and laterally between IV–VI; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after Mike Irwin, who helped collect a majority of the specimens examined for this species.

DISTRIBUTION: Marojejy Nature Reserve in the Antsiranana province and near the Andasibe-Mantadia National Park in the Toamasina province (Map 2.7).

DISCUSSION: Coloration is variable with the orange areas reduced or absent on the dorsal head surface, labium, scutellum, femora, hind tibia, and abdomen in some specimens.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 30 May 2005–11 Jun 2005, M. Irwin, R. Harin'Hala (00045088) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 09 Dec 2004–15 Dec 2004, M. Irwin, R. Harin'Hala, 2♂ (00045220, 00045375) (CAS); 25 Dec 2004–30 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00006224) (SU), 1♂ (00006225) (UCR); 05 Jan 2005–10 Jan 2005, M. Irwin, R. Harin'Hala, 2♂ (00006096, 00006097) (CAS); 10 Jan 2005–15 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00006235) (UCR); 15 Jan 2005–26 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00006135) (AMNH); 04 Feb 2005–11 Feb 2005, M. Irwin, R. Harin'Hala, 3♂ (00006233, 00006234, 00006239) (CAS); 11 Feb 2005–18 Feb 2005, M. Irwin, R. Harin'Hala, 3♂ (00006217, 00006241, 00006242) (AMNH); 18 Feb 2005–25 Feb 2005, M. Irwin, R. Harin'Hala, 3♂ (00045603, 00045612, 00045712) (BMNH); 25 Feb 2005–04 Mar 2005, M. Irwin, R. Harin'Hala, 5♂ (00005366, 00006226–00006229) (CAS); 11 Mar 2005–18 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00006232) (UCR); 04 Apr 2005–16 Apr 2005, M. Irwin, R. Harin'Hala, 2♂ (00006499, 00045339) (SU); 16 Apr 2005–28 Apr 2005, M. Irwin, R. Harin'Hala, 6♂ (00007087, 00045004, 00045048, 00045072, 00045405, 00045475) (CAS); 28 Apr 2005–07 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00006221) (UCR); 07 May 2005–18 May 2005, M. Irwin, R. Harin'Hala, 3♂ (00006134, 00006237, 00006238) (USNM); 18 May 2005–30 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00006216) (BMNH), 1♂ (00006243) (USNM); 30 May 2005–11 Jun

2005, M. Irwin, R. Harin'Hala, 4♂ (00007211, 00044957, 00044982, 00045462) (CAS); 28 Jun 2005–13 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00006218) (SU), 1♂ (00006222) (UCR), 4♂ (00006223, 00006230, 00006231, 00006236) (MNHN), 4♂ (00006240, 00006452–00006454) (CAS). **Toamasina:** Lakato env. Near Andasibe-Mantadia National Park, 19.18651°S 48.43856°E, 635 m, 09 Jan 2007–10 Jan 2007, Z. Mráček, 1♂ (MMBC).

Tanindrazanus joffrevillus, new species

Figs. 2.2, 2.6, 2.9; Map 2.6

DIAGNOSIS: Males recognized among other species in this genus by the dull orange coloration, ventrally flat head surface, clypeal apex not elevated relative to the labrum, smooth posterior pronotal lobe, and slightly incrassate forefemur. This species is similar to *T. andohahela*, but is distinguished by dark brown corium, ventrally flat head surface, clypeal apex not elevated relative to the labrum, larger synthlipsis width, subequal lengths of labial segments II and III, smooth posterior pronotal lobe, divided pronotal transverse suture, and intersegmental sutures carinulate between sternites II–VI.

DESCRIPTION: Medium body size (length: 11.19 mm, holotype). COLORATION: Dull orange with thoracic sterna pale and hemelytron, except corium basally, brown. Antennal segments V and VI white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally flat; clypeal apex not elevated relative to labrum (Fig. 2.13C–F, I–K); postclypeus with relatively shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eyes about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur slightly incrassate; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–VI; pygophore process very flattened in lateral view (Fig. 2.20F); BPE as long as basal plate; area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21G).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Joffreville, Madagascar.

DISTRIBUTION: Only one of the two known specimens has locality data. It is known from a locality north of Joffreville in the Antsiranana province (Map 2.6).

HOLOTYPE: Male: **Madagascar: Antsiranana:** 7 km N of Joffreville, 12.33333°S 49.25°E, 360 m, 20 Mar 2001–07 Apr 2001, M. Irwin, R. Harin'Hala (00007256) (CAS). **Unknown**, 1♂ (00044998) (CAS).

PARATYPE: **Madagascar: Unknown**, 1♂ (00044998) (CAS).

Tanindrazanus kathrynae, new species

Figs. 2.2, 2.6, 2.9, 2.13G, 2.15D, 2.19F, 2.20G; Map 2.7

DIAGNOSIS: Males recognized among other *Tanindrazanus* species by the red and black coloration, elevated clypeal apex relative to the labrum, broad postocular in dorsal view, and synthlipsis about two times the width of the eye. This species is very similar to *T. anjozorobeus*, but is distinguished by the smaller body size, smaller eyes that do not surpass the dorsal and ventral margins of the head in lateral view, larger width of the synthlipsis, and the very small anterolateral projections on the pronotum.

DESCRIPTION: Medium body size (length: 12.67 mm, holotype; 11.62–12.67 mm). COLORATION: Red with pale orange-brown mandibular and maxillary plates, clypeus, anterolateral and dorsal margin of eye, labium, anterior pronotal lobe except lateral margins, and corium except distally. Remainder of head except two paramedian dorsal stripes posterior to ocelli, lateral margins of anterior pronotal lobe, anterior part of propleura, meso- and metapleura, scutellum, corium distally, forewing membrane, femora and apical one-third to one-half of fore- and mid tibiae, hind tibiae except small apical part, ventrolateral spot on abdominal sternites II–VI, and pygophore dark brown to black. VESTITURE: As in generic description. STRUCTURE: HEAD (Fig. 2.13G): Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum; postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; postocular broad in dorsal view (Fig. 2.13B); ocelli large, separated by less than diameter of ocellus, located on slightly elevated median tubercle; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about two-fifths longer than scape; labial segment III subequal to II. THORAX (Fig. 2.15D): Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–V and laterally between V and VI; pygophore process subtriangular in lateral view (Fig. 2.20G); BPE longer than basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is a noun in the genitive case and is named in memoriam of the senior author's partner’s mother, Kathryn Carroll.

DISTRIBUTION: Miandritsara Forest in the Fianarantsoa province (Map 2.7).

DISCUSSION: In some specimens, the head and anterior pronotal lobe have reduced red coloration or are entirely black and the median longitudinal suture on the pronotum and the medial area of abdominal sternite VII are black.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Miandritsara Forest, 40 km S Ambositra, 20.79266°S 47.17566°E, 825 m, 13 Nov 2006–22 Nov 2006, M. Irwin, R. Harin'Hala (00006103) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Andringitra Est, Ambalamarovandana, 22.22595°S 46.93418°E, 1500–1600m, 15 Jan 1971–25 Jan 1971, 1♂ (MNHN). Miandritsara Forest, 40 km S Ambositra, 20.79266°S 47.17566°E, 825 m, 23 Oct 2004–03 Nov 2004, M. Irwin, R. Harin'Hala, 1♂ (00045053) (UCR); 05 Jan 2005–18 Jan 2005, M. Irwin, R. Harin'Hala, 2♂ (00044858, 00045506) (CAS), 1♂ (00045608) (SU); 09 Feb 2005–22 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00045383) (AMNH); 22 Feb 2005–05 Mar 2005, M. Irwin, R. Harin'Hala, 2♂ (00044863, 00045360) (CAS), 1♂ (00045626) (USNM); 13 Apr 2005–27 Apr 2005, M. Irwin, R. Harin'Hala, 2♂ (00007062, 00044984) (CAS), 1♂ (00045549) (MNHN); 05 Jan 2006–12 Jan 2006, M. Irwin, R. Harin'Hala, 2♂ (00044818, 00045566) (BMNH); 16 Feb 2006–27 Feb 2006, M. Irwin, R. Harin'Hala, 1♂ (00044832) (BMNH); 27 Feb 2006–08 Mar 2006, M. Irwin, R. Harin'Hala, 1♂ (00045632) (SU); 14 Apr 2006–02 May 2006, M. Irwin, R. Harin'Hala, 2♂ (00006094, 00006298) (CAS), 1♂ (00006312) (MNHN); 13 Nov 2006–22 Nov 2006, M. Irwin, R. Harin'Hala, 2♂ (00006293, 00006299) (AMNH); 01 Dec 2006–10 Dec 2006, M. Irwin, R. Harin'Hala, 1♂ (00006302) (UCR); 10 Dec 2006–19 Dec 2006, M. Irwin, R. Harin'Hala, 2♂ (00006313, 00006314) (CAS); 19 Dec 2006–28 Dec 2006, M. Irwin, R. Harin'Hala, 4♂ (00007053, 00007202, 00045201, 00045365) (CAS); 15 Jan 2007–24 Jan 2007, M. Irwin, R. Harin'Hala, 2♂ (00045083, 00045482) (CAS); 24 Jan 2007–31 Jan 2007, M. Irwin, R. Harin'Hala, 1♂ (00006294) (BMNH); 31 Jan 2007–11 Feb 2007, M. Irwin, R. Harin'Hala, 2♂

(00006315, 00006316) (SU); 11 Feb 2007–20 Feb 2007, M. Irwin, R. Harin'Hala, 1♂ (00006301) (MNHN), 3♂ (00006309–00006311) (CAS); 20 Feb 2007–27 Feb 2007, M. Irwin, R. Harin'Hala, 1♂ (00006297) (USNM); 08 Mar 2007–17 Mar 2007, M. Irwin, R. Harin'Hala, 4♂ (00006303–00006306) (CAS); 17 Mar 2007–26 Mar 2007, M. Irwin, R. Harin'Hala, 1♂ (00006300) (AMNH); 26 Mar 2007–05 Apr 2007, M. Irwin, R. Harin'Hala, 2♂ (00006307, 00006308) (USNM); 05 Apr 2007–14 Apr 2007, M. Irwin, R. Harin'Hala, 2♂ (00006295, 00006296) (UCR).

Tanindrazanus mahafaly, new species

Figs. 2.3, 2.6, 2.9; Map 2.7

DIAGNOSIS: Males are recognized among other species in this genus by a combination of the following characters: the large body size, distinct dark orange-brown to red-orange coloration, labial segment II shorter than III, slightly incrassate forefemur, and only the intersegmental suture between sternites II and III carinulate. This species is similar to *T. irwini*, from which it differs by the dark orange-red color pattern, anteromedially depressed ventral head surface, and carinulation pattern on the sternal intersegmental sutures.

DESCRIPTION: Large body size (length: 19.57 mm, holotype; 18.03–19.92 mm). COLORATION: Dark orange with apical half of pedicel and basiflagellomere, anterior pronotal lobe, metapleuron, and abdomen, except laterotergites, dark reddish brown. Hemelytron bright orange and antennal segments VI and VII pale orange to white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III longer than II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur slightly incrassate; tarsomeres I and II combined subequal to III on fore- and mid legs, longer on hind legs; wings spread in specimens. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II and III; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate; area of endosomal struts–DPS fusion circular.

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Beza Mahafaly Reserve, Madagascar.

DISTRIBUTION: Beza Mahafaly Reserve in the Toliara province (Map 2.7).

DISCUSSION: In some specimens, the head, scutellum, fore- and mid legs, and abdomen are bright red-orange, while the remaining structures are dull orange.

HOLOTYPE: Male: **Madagascar: Toliara:** Beza Mahafaly Reserve, Parcelle I near research station, 23.6865°S 44.591°E, 165 m, 15 Oct 2001–10 Nov 2001, M. Irwin, F. Parker, R. Harin'Hala (00045290) (CAS).

PARATYPES: **Madagascar: Toliara:** Beza Mahafaly Reserve, Parcelle II near Bellevue, 23.68983°S 44.5755°E, 180 m, 21 Nov 2001–28 Nov 2001, R. Harin'Hala, 1♂ (00006244) (CAS). Beza Mahafaly Reserve, Parcelle I near research station, 23.6865°S 44.591°E, 165 m, 04 Dec 2001–11 Dec 2001, R. Harin'Hala, 1♂ (00006245) (CAS); 08 Feb 2002–15 Feb 2002, R. Harin'Hala, 1♂ (00006133) (CAS); 22 Feb 2002–01 Mar 2002, R. Harin'Hala, 1♂ (00006220) (SU); 18 Jun 2002–28 Jun 2002, R. Harin'Hala, 1♂ (00006219) (UCR).

Tanindrazanus marginatus, new species

Figs. 2.3, 2.6, 2.9; Map 2.8

DIAGNOSIS: Males are recognized among other species in this genus by the brownish coloration, synthlipsis about the width of an eye, and large eyes reaching the dorsal and ventral head surfaces. This species is similar to *T. tenebricus* and *T. nigripes*, but differs from both species by the lighter coloration and lateral carinulation on the intersegmental suture between sternites VI and VII. *Tanindrazanus marginatus* is further distinguished from *T. nigripes* by the smaller synthlipsis width.

DESCRIPTION: Medium body size (length: 16.43 mm, holotype; 13.62–17.43 mm). COLORATION: Dark brown with light brown clypeus, postclypeus medially, dorsal margin of ocellar tubercle, labium, basal wing veins, trochanters, femora except apically, tibiae basally, tarsi, and lateral margin of sternites. Distal half of antennal segment V and segments VI and VII white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III on forelegs, slightly longer on mid and hind legs; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternite

II–IV and laterally between IV–VII; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE longer than basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the pale laterotergites.

DISTRIBUTION: Antsiranana, Fianarantsoa, Toamasina, and Toliara provinces (Map 2.8).

DISCUSSION: In some specimens, the dorsal neck surface, thorax, corium, coxae, and laterotergites are light brown and the postclypeus medially dark brown.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1110 m, 08 Apr 2002–15 Apr 2002, M. Irwin, R. Harin'Hala (00006821) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 04 Feb 2005–11 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00006892) (CAS); 18 Mar 2005–25 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00006888) (CAS); 28 Apr 2005–07 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00006908) (USNM); 13 Jul 2005–28 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00006087) (AMNH); 14 Oct 2005–22 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00006850) (SU). Montaigne Francais, 12.325°S 49.33333°E, 150 m, 30 Jan 2001–15 Feb 2001, M. Irwin, R. Harin'Hala, 2♂ (00006833, 00006847) (CAS), 1♂ (00006921) (AMNH); 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006920) (UCR). Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 12 Feb 2001–04 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006932) (CAS). Parc National Montagne d'Ambre, 12.52027°S 49.17916°E, 1125 m, 30 May 2001–06 Jun 2001, M. Irwin, R. Harin'Hala, 1♂ (00006834) (UCR). **Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 13 Jan 2007–20 Jan 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006931) (MNHN); 04 Feb 2007–10 Feb 2007, M. Irwin,

F. Parker, R. Harin'Hala, 4♂ (00006805, 00006806, 00006855, 00006860) (CAS); 10 Feb 2007–17 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006803, 00006804, 00006861) (AMNH); 03 Mar 2007–10 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006941) (UCR); 17 Mar 2007–24 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006936) (SU); 24 Mar 2007–31 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006810) (CAS); 07 Apr 2007–14 Apr 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006937) (CAS); 14 Apr 2007–21 Apr 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006942) (CAS); 06 May 2007–14 May 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006801) (BMNH); 14 May 2007–21 May 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006943) (MNHN); 02 Jun 2007–10 Jun 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006930) (CAS); 07 Jul 2007–14 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006934) (CAS); 14 Jul 2007–19 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006926) (SU); 19 Jul 2007–23 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006927) (SU); 23 Jul 2007–28 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006928) (AMNH); 03 Aug 2007–11 Aug 2007, M. Irwin, F. Parker, R. Harin'Hala, 4♂ (00006811, 00006857, 00006858, 00006938) (USNM); 27 Aug 2007–06 Sep 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006929) (CAS); 06 Sep 2007–13 Sep 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006856, 00006944) (MNHN); 27 Sep 2007–04 Oct 2007, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006807–00006809) (CAS); 25 Oct 2007–08 Nov 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006922) (CAS); 08 Nov 2007–22 Nov 2007, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006812, 00006859, 00006945) (BMNH); 28 Nov 2007–13 Dec 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006935) (USNM); 03 Jan 2008–09 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006907) (SU); 09 Jan 2008–17 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006836) (UCR); 01 Apr 2008–09 Apr 2008, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006887, 00006890) (CAS). Manombo Special Reserve camp site, 32 km SSE of Farafangana, 23.02183°S 47.72°E, 36 m, 10 Oct 2004–21 Oct 2004, M. Irwin, R. Harin'Hala, 1♂ (00045347) (CAS); 23 Nov 2004–05 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00045266) (UCR); 15 Dec 2004–26 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00045207) (AMNH); 26 Dec 2004–05 Jan 2005, M. Irwin, R. Harin'Hala, 3♂ (00045006, 00045195, 00045522) (CAS); 16 Jan 2005–20 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00045467) (SU); 15 Feb 2005–27 Feb 2005, M. Irwin, R. Harin'Hala, 2♂ (00044964, 00045376) (CAS); 24 Apr 2005–10 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00044810) (BMNH); 10 May 2005–22 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00045152) (BMNH); 06 Jun 2005–24 Jun 2005, M. Irwin, R. Harin'Hala, 2♂ (00007190, 00045382) (USNM); 24 Jun 2005–10 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00044842) (MNHN); 10 Jul 2005–27 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00045119) (CAS); 09 Oct 2005–16 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00044946) (UCR). Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 15 Nov 2001–22 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00045415) (CAS); 28 Jan 2002–04 Feb 2002, M. Irwin, R. Harin'Hala, 2♂ (00006879, 00006880) (CAS); 12 Feb 2002–19 Feb 2002, M. Irwin, R. Harin'Hala, 2♂ (00006835, 00006940) (SU); 14 Apr 2002–23 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00045707) (CAS); 03 Jun 2002–13 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (00006904) (MNHN); 13 Jun 2002–23 Jun 2002, M. Irwin, R. Harin'Hala, 1♂ (00006905) (CAS); 16 Feb 2003–26 Feb 2003, M. Irwin, R. Harin'Hala, 2♂ (00006883, 00006884) (USNM); 21 Mar 2003–12 Apr 2003, M. Irwin, R. Harin'Hala, 1♂ (00006891) (BMNH); 04 May 2003–16 May 2003, M. Irwin, R. Harin'Hala, 2♂ (00006885, 00006886) (AMNH); 15 May 2003–28 May 2003, M. Irwin, R. Harin'Hala, 1♂ (00006960) (CAS); 28 May 2003–06 Jun 2003, M. Irwin, R. Harin'Hala, 1♂ (00045034) (UCR). Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1110 m, 19 Feb 2002–26 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00006902) (CAS); 04 Mar 2002–12 Mar 2002, M. Irwin, R. Harin'Hala, 1♂ (00006837) (SU);

26 Mar 2002–31 Mar 2002, M. Irwin, R. Harin'Hala, 3♂ (00006844–00006846) (CAS), 1♂ (00006924) (USNM); 31 Mar 2002–08 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00006903) (USNM); 08 Apr 2002–15 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00006799) (AMNH), 17♂ (00006815–00006820, 00006822–00006830) (CAS), 3♂ (00006843, 00006925, 00006933) (UCR). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 06 Dec 2001–15 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00006917) (CAS); 21 Dec 2001–24 Dec 2001, M. Irwin, R. Harin'Hala, 1♂ (00044908) (UCR); 14 Jan 2002–21 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00045718) (CAS); 28 Jan 2002–04 Feb 2002, M. Irwin, R. Harin'Hala, 1♂ (00099047) (CAS); 09 Apr 2002–16 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00006896) (USNM); 30 Apr 2002–07 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00006839) (AMNH); 07 May 2002–14 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00006802) (CAS); 18 Feb 2003–27 Feb 2003, M. Irwin, R. Harin'Hala, 1♂ (00007112) (MNHN); 09 Mar 2003–20 Mar 2003, M. Irwin, R. Harin'Hala, 1♂ (00006895) (BMNH); 07 May 2003–17 May 2003, M. Irwin, R. Harin'Hala, 2♂ (00006874, 00006875) (SU); 06 Aug 2003–16 Aug 2003, M. Irwin, R. Harin'Hala, 3♂ (00006911–00006913) (CAS), 1♂ (00006919) (BMNH); 28 Sep 2003–08 Oct 2003, M. Irwin, R. Harin'Hala, 1♂ (00006898) (CAS); 18 Oct 2003–26 Oct 2003, M. Irwin, R. Harin'Hala, 1♂ (00006899) (CAS); 17 Dec 2003–30 Dec 2003, M. Irwin, R. Harin'Hala, 2♂ (00006831, 00006832) (CAS); 30 Dec 2003–11 Jan 2004, M. Irwin, R. Harin'Hala, 1♂ (00006914) (CAS); 11 Jan 2004–21 Jan 2004, M. Irwin, R. Harin'Hala, 2♂ (00006881, 00006882) (MNHN); 31 Jan 2004–12 Feb 2004, M. Irwin, R. Harin'Hala, 1♂ (00006894) (CAS); 21 Mar 2004–02 Apr 2004, M. Irwin, R. Harin'Hala, 2♂ (00006796, 00006797) (AMNH); 02 Apr 2004–15 Apr 2004, M. Irwin, R. Harin'Hala, 1♂ (00006840) (USNM); 24 Jun 2004–08 Jul 2004, M. Irwin, R. Harin'Hala, 2♂ (00006838, 00006897) (BMNH); 07 Oct 2004–20 Oct 2004, M. Irwin, R. Harin'Hala, 1♂ (00006918) (UCR); 14 Jan 2005–02 Feb 2005, M. Irwin, R. Harin'Hala, 1♂

(00006868) (SU); 27 Feb 2005–13 Mar 2005, M. Irwin, R. Harin'Hala, 3♂ (00006841, 00006842, 00006916) (CAS); 28 Mar 2005–10 Apr 2005, M. Irwin, R. Harin'Hala, 1♂ (00006900) (BMNH); 25 Sep 2005–07 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00006869) (CAS); 06 Nov 2005–13 Nov 2005, M. Irwin, R. Harin'Hala, 1♂ (00006946) (CAS); 13 Nov 2005–24 Nov 2005, M. Irwin, R. Harin'Hala, 1♂ (00006865) (MNHN); 21 Dec 2005–30 Dec 2005, M. Irwin, R. Harin'Hala, 1♂ (00006866) (BMNH); 20 Jan 2006–29 Jan 2006, M. Irwin, R. Harin'Hala, 2♂ (00006872, 00006873) (SU); 29 Jan 2006–07 Feb 2006, M. Irwin, R. Harin'Hala, 1♂ (00006915) (CAS); 15 Feb 2006–26 Feb 2006, M. Irwin, R. Harin'Hala, 9♂ (00006947–00006950, 00006953–00006957) (CAS); 05 Mar 2006–18 Mar 2006, M. Irwin, R. Harin'Hala, 2♂ (00006854, 00006867) (UCR); 18 Mar 2006–30 Mar 2006, M. Irwin, R. Harin'Hala, 3♂ (00006862–00006864) (MNHN); 13 Apr 2006–24 Apr 2006, M. Irwin, R. Harin'Hala, 1♂ (00006870) (AMNH); 02 May 2006–13 May 2006, M. Irwin, R. Harin'Hala, 2♂ (00006871, 00006901) (MNHN); 20 May 2006–29 May 2006, M. Irwin, R. Harin'Hala, 1♂ (00006893) (CAS); 09 Aug 2006–23 Aug 2006, M. Irwin, R. Harin'Hala, 1♂ (00006800) (USNM); 23 Aug 2006–07 Sep 2006, M. Irwin, R. Harin'Hala, 1♂ (00006853) (CAS); 07 Sep 2006–20 Sep 2006, M. Irwin, R. Harin'Hala, 3♂ (00006851, 00006852, 00006951) (BMNH); 20 Sep 2006–05 Oct 2006, M. Irwin, R. Harin'Hala, 1♂ (00006952) (SU); 01 Nov 2006–11 Nov 2006, M. Irwin, R. Harin'Hala, 1♂ (00044923) (UCR). Parc National d'Isalo, 9.1 km 354° N Ranohira, 22.48166°S 45.46166°E, 725 m, 27 Jan 2003–31 Jan 2003, Fisher et al., 1♂ (00005363) (AMNH), 3♂ (00006876–00006878) (CAS). Ranomafana JIRAMA water works, 21.2485°S 47.45216°E, 690 m, 16 Oct 2001–08 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00005361) (CAS). **Toamasina:** Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 01 Sep 2001–05 Sep 2001, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006889) (CAS). Fampanambo, 15.37550°S 49.62175°E, 108 m, 1962, J. Vadon, 1♂ (MRAC). Mobot Site, Analalava 7 km SW of Foulpointe, 17.69333°S 49.46027°E, 18 m, 21 Dec 2007–28 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00044874) (SU); 18 Jan 2008–25 Jan 2008, M. Irwin, R. Harin'Hala, 2♂ (00006848, 00006909) (CAS), 1♂ (00044801) (USNM); 25 Jan 2008–01 Feb 2008, M. Irwin, R. Harin'Hala, 1♂ (00006923) (CAS), 1♂ (00006939) (AMNH); 21 Mar 2008–28 Mar 2008, M. Irwin, R. Harin'Hala, 1♂ (00006798) (UCR). Mobot Site, Analalava 7 km SW of Foulpointe, 17.70889°S 49.45806°E, 24 m, 15 Sep 2007–21 Sep 2007, M. Irwin, R. Harin'Hala, 1♂ (00006906) (CAS). **Toliara:** Kirindy forest, 60 km NE of Morondava, 20.0665°S 44.65767°E, 45 m, 18 Oct 2003–30 Oct 2003, M. Irwin, R. Harin'Hala, 1♂ (00045067) (CAS). **Unknown:** 3♂ (00006813, 00006814, 00006849) (CAS).

Tanindrazanus marojejy, new species

Figs. 2.3, 2.6, 2.9, 2.20H; Map 2.6

DIAGNOSIS: Males recognized among other *Tanindrazanus* species by the black body with red abdomen and pale orange hemelytra, ventrally flat head surface, broad postocular in dorsal view, labial segment II shorter than segment III, and continuous pronotal transverse furrow. This species is similar to *T. anjozorobeus* and *T. kathrynae*, but is distinguished by the black head, thorax, and legs; pale orange hemelytra; flat ventral head surface; synthlipsis about 1.5 times width of eye; labial segment II shorter than III; and intersegmental sutures carinulate between II and III and laterally between III–VI.

DESCRIPTION: Medium body size (length: 17.53 mm, holotype; 17.05–19.72 mm). COLORATION: Black with antennal segment VI and basal half of segment VII, hemelytron, tarsi, and pretarsi orange and distal half of antennal segment VII pale orange. Abdomen red with anterior margin of sternite II, sternite VII (except small anterolateral spot), laterotergite VII (except anterior margin), and pygophore black. VESTITURE: As in generic description.

STRUCTURE: HEAD: Ventrally flat; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); synthlipsis about 1.5 times width of eye; interocular sulcus posterior to hind margin of eye; ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); postclypeus with shallow, broad depression to middle of interocular area (Fig. 2.13B); postocular moderately broad in dorsal view; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III longer than II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III; hemelytron almost reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between II and III and laterally between III–VI; pygophore process subtriangular in lateral view (Fig. 2.20H); BPE shorter than basal plate; area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21G).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Marojejy Nature Reserve, Madagascar.

DISTRIBUTION: Marojejy Nature Reserve in the Antsiranana province (Map 2.6).

HOLOTYPE: Male: **Madagascar: Antsiranana:** R.N.I. de Marojejy, 11.0 km NW Manantenina, 14.43667°S 49.74167°E, 1225 m, 25 Oct 1996–03 Nov 1996, Eric L. Quinter (00078359) (AMNH).

PARATYPES: **Madagascar: Antsiranana:** Sambava District, R.N. XII Marojejy, Ambatosoratra, 14.38735°S 49.75717°E, 1700m, Nov 1960, P. Soga, 3♂ (MNHN).

Tanindrazanus nigripes, new species

Figs. 2.3, 2.6, 2.9, 2.22E; Map 2.8

DIAGNOSIS: Males recognized among other *Tanindrazanus* species by the dark brown to black coloration with pale yellow markings, synthlipsis about 1.5 times the width of an eye, and eyes not reaching the dorsal and ventral head margins. This species is similar to *T. tenebricus*, but the larger width of the synthlipsis, eyes not reaching the dorsal and ventral head margins, and intersegmental sutures carinulate between sternites II–IV distinguishes *T. marginatus* from *T. tenebricus*.

DESCRIPTION: Medium body size (length: 12.63 mm, holotype; 11.78–12.63 mm). COLORATION: Dark brown to black with mandibular plates dorsally, postocular dorsally except ocellar tubercle, and fore- and mid femora ventrally and laterally pale yellow. Labium light brown except segment II basally and distal two-thirds of antennal segment V and segments VI and VII white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with shallow, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.5 times width of eye; interocular sulcus at (Fig. 2.13B) or posterior to hind margin of eye; postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, not reaching dorsal and ventral head surfaces; pedicel about two-fifths longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur moderately incrassate; tarsomeres I and II combined subequal to III on fore- and mid legs, longer on hind legs; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–IV; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE as long as basal plate (Fig. 2.22E); area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the blackish coloration of the body.

DISTRIBUTION: Antsiranana and Toamasina provinces (Map 2.8).

DISCUSSION: Coloration is variable with the clypeus, postclypeus, coxae, intersternal sutures, median longitudinal depression on sternites, and medial sternites pale yellow in some specimens.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Sakalava Beach, dwarf littoral forest, 12.26277°S 49.3975°E, 10 m, 31 May 2001–07 Jun 2001, M. Irwin, R. Harin'Hala (00006712) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Forêt Ambato, 26.6 km 33° NE Ambanja, 13.46444°S 48.55166°E, 150 m, 08 Dec 2004, B.L. Fisher, 1♂ (00044939) (CAS). Montagne Français, 12.325°S 49.33333°E, 150 m, 15 Feb 2001–06 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006705) (SU), 1♂ (00006717) (USNM); 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00045437) (UCR). Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 26 Jan 2001–29 Jan 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 3♂ (00006715, 00007165, 00007195) (CAS), 1♂ (00007231) (AMNH); 11 Feb 2001–12 Feb 2001, M. Irwin, R. Harin'Hala, 2♂ (00006727, 00045465) (CAS); 04 Mar 2001–19 Mar 2001, M. Irwin, R. Harin'Hala, 4♂ (00006704, 00006710, 00006726, 00045231) (CAS), 1♂ (000045328) (BMNH), 1♂ (000045436) (MNHN), 1♂ (00045500) (SU). Parc National Montagne d'Ambre, 12.51666°S 49.18333°E, 975 m, 25 Jan 2001–11 Feb 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 1♂ (00005368) (UCR); 25 Jan 2001–29 Jan 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 2♂

(00007047, 00007134) (CAS); 11 Feb 2001–04 Mar 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 1♂ (00006145) (BMNH), 1♂ (00006718) (MNHN). Parc National Montagne d'Ambre, 12.52027°S 49.17916°E, 1125 m, 19 Mar 2001–15 Apr 2001, M. Irwin, R. Harin'Hala, 2♂ (00006714, 00006716) (CAS), 1♂ (00006721) (BMNH), 1♂ (00006722) (AMNH); 21 Apr 2001–26 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006703) (UCR); 14 May 2001–30 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00006711) (USNM); 30 May 2001–06 Jun 2001, M. Irwin, R. Harin'Hala, 1♂ (00006706) (CAS), 1♂ (00006713) (MNHN). Sakalava Beach, dwarf littoral forest, 12.26277°S 49.3975°E, 10 m, 07 Apr 2001–22 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006708) (SU); 13 May 2001–16 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00006708) (USNM); 07 Jun 2001–25 Jun 2001, M. Irwin, R. Harin'Hala, 1♂ (00006709) (AMNH); 13 Aug 2001–20 Aug 2001, M. Irwin, R. Harin'Hala, 1♂ (00045396) (CAS); 20 Aug 2001–28 Aug 2001, M. Irwin, R. Harin'Hala, 1♂ (00007143) (UCR). **Toamasina:** Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 08 Oct 2001–16 Oct 2001, M. Irwin, R. Harin'Hala, 1♂ (00006725) (CAS). **Unknown:** 2♂ (00006707, 00045240) (CAS).

Tanindrazanus notatus, new species

Figs. 2.3, 2.6, 2.10, 2.21G; Map 2.6

DIAGNOSIS: Males are recognized among other species in this genus by the distinct dull orange-brown coloration with black markings on the hind legs. *Tanindrazanus notatus* is similar to *T. andohahela* and *T. bemaraha*, but the black apical half of the hind femur and tibia and the subequal lengths of labial segments II and III differentiate *T. notatus* from these species.

DESCRIPTION: Medium body size (length: 10.17 mm, holotype; 10.17–12.24). COLORATION: Orange with apical half of scape, pedicel, antennal segments III–VI, apical half of hind femur, and hind tibia, except basally, dark brown. Apex of corium, membrane, and distal wing veins brown. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe without distinct anterolateral projections; posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; forefemur moderately incrassate; tarsomeres I and II combined subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE shorter than basal plate; area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21G).

ETYMOLOGY: The species epithet is a past participle in the nominative case and is named for the black markings on the hind legs.

DISTRIBUTION: Beroboka village from the Toliara province (Map 2.6).

DISCUSSION: The two specimens examined differ in size (10.17 and 12.24 mm) but are morphologically similar and were collected from the same locality.

HOLOTYPE: Male: **Madagascar: Toliara:** Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 05 Feb 2009–13 Feb 2009, M. Irwin, R. Harin'Hala (00045368) (CAS).

PARATYPE: **Madagascar: Toliara:** Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 19 Dec 2008–27 Dec 2008, M. Irwin, R. Harin'Hala, 1♂ (00044868) (CAS).

Tanindrazanus simulans, new species

Figs. 2.3, 2.6, 2.10

DIAGNOSIS: Males are recognized among other *Tanindrazanus* species by the nearly uniform dark brown to blackish coloration, synthlipsis about 1.25 times wider than the width of an eye, eyes reaching ventral and almost reaching the dorsal head margins, and a continuous pronotal transverse furrow. This species is similar to *T. tenebricus* and *T. nigripes*, but is distinguished by the width of synthlipsis, eyes reaching the ventral head margin but not the dorsal margin, and the pedicel about one-fifth longer than scape.

DESCRIPTION: Medium body size (length: 15.40 mm, holotype; 15.10–15.40 mm). COLORATION: Blackish except postocular part of the head around ocellar tubercle and tarsi pale brown. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about 1.25 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, reaching ventral but not dorsal head surface; pedicel about one-fifth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III on forelegs, longer on mid and hind legs; hemelytra surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternite II–IV and laterally between IV–VI; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE longer than basal plate; area of endosomal struts–DPS fusion ovate.

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named after the similarity to *T. tenebricus*.

DISTRIBUTION: The two known specimens were labeled as originating from "Ivondro." There are at least four localities in the Fianarantsoa, Toamasina, and Toliara provinces that include the name "Ivondro"; we were unable to determine the exact locality.

HOLOTYPE: Male: **Madagascar**: **Unknown:** Reg. S.E. Ivondro, 1939, A. Seyrig (MNHN).

PARATYPE: **Madagascar**: **Unknown:** Reg. S.E. Ivondro, Feb 1940, A. Seyrig, 1♂ (MNHN).

Tanindrazanus tenebricus, new species

Figs. 2.3, 2.6, 2.10, 2.18B; Map 2.8

DIAGNOSIS: Males are recognized among other *Tanindrazanus* species by the blackish coloration with pale markings on the head and pronotum, synthlipsis about the width of an eye, and large eyes reaching only dorsal head. This species is similar to *T. nigripes* and *T. simulans*, from which it differs by the smaller synthlipsis width and eyes reaching the dorsal but not the ventral head surface. *Tanindrazanus tenebricus* is further differentiated from *T. nigripes* by the intersegmental sutures carinulate between sternite II–IV and laterally between IV–VI.

DESCRIPTION: Medium body size (length: 16.37 mm, holotype; 15.40–17.02 mm). COLORATION: Blackish with mandibular plates dorsally, postocular dorsally except ocellar tubercle, posterolateral margin of pronotum, and tarsi pale yellow. Labium light brown, except segment II basally, and antennal segment VI light brown and segment VII white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum (Fig. 2.13G, H); postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13H); postocular narrow in dorsal view

(Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about one-third of head length, reaching dorsal but not ventral head surface; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); legs slender; tarsomeres I and II combined subequal to III on forelegs, longer on mid and hind legs; wings spread out in specimens. ABDOMEN (Fig. 2.18B): Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternite II–IV and laterally between IV–VI; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE longer than basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the dark coloration of the body.

DISTRIBUTION: Specimens are known from the southeastern region of the Fianarantsoa province (Map 2.8). Two specimens were labeled as originating from “Ivondro”. There are at least four localities in the Fianarantsoa, Toamasina, and Toliara provinces that include the name “Ivondro”; we were unable to determine the exact locality.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Manombo Special Reserve camp site, 32 km SSE of Farafangana, 23.02183°S 47.72°E, 36 m, 16 Jan 2005–20 Jan 2005, M. Irwin, R. Harin’Hala (00045483) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 10 Feb 2007–17 Feb 2007, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006723) (CAS); 03 Mar 2007–10 Mar 2007, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006720) (SU); 17 Mar 2007–24 Mar 2007, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006724) (UCR). Manombo Special Reserve camp site, 32 km SSE of

Farafangana, 23.02183°S 47.72°E, 36 m, 10 Oct 2004–21 Oct 2004, M. Irwin, R. Harin'Hala, 2♂ (00007141, 00044862) (CAS); 23 Nov 2004–05 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00044995) (AMNH); 05 Jan 2005–16 Jan 2005, M. Irwin, R. Harin'Hala, 2♂ (00007046, 00045656) (CAS); 16 Jan 2005–20 Jan 2005, M. Irwin, R. Harin'Hala, 2♂ (00045488, 00045723) (BMNH); 13 Mar 2005–26 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00045301) (UCR); 10 Apr 2005–24 Apr 2005, M. Irwin, R. Harin'Hala, 2♂ (00044873, 00045022) (CAS), 1♂ (00045267) (AMNH); 22 May 2005–06 Jun 2005, M. Irwin, R. Harin'Hala, 7♂ (00007118, 00045270, 00045399, 00045403, 00045496, 00045606, 00045721) (CAS); 10 Aug 2005–25 Aug 2005, M. Irwin, R. Harin'Hala, 2♂ (00044828, 00045684) (MNHN); 11 Sep 2005–25 Sep 2005, M. Irwin, R. Harin'Hala, 1♂ (00045104) (CAS), 1♂ (00045196) (USNM); 25 Sep 2005–02 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00007101) (SU), 1♂ (00045477) (UCR). **Unknown:** Reg. S.E. Ivondro, Dec 1938, A. Seyrig, 1♂ (MNHN); 1939, A. Seyrig, 1♂ (MNHN).

Tanindrazanus varicolor, new species

Figs. 2.3, 2.6, 2.7, 2.10, 2.13H, 2.16A, 2.17C, 2.20I, 2.21H; Map 2.7

DIAGNOSIS: Males are recognized among other species in this genus by the distinct black and orange coloration, labial segments II and III subequal in length, and the anterior pronotal lobe with very small anterolateral protuberances. This species is similar to *T. irwini*, but differs by the smaller body size, anteromedial depression on the ventral head surface, and intersegmental sutures carinulate between sternite II–VI and laterally between VI and VII, as well as the diagnostic features mentioned.

DESCRIPTION: Medium body size (length: 15.97 mm, holotype; 15.89–16.12 mm). COLORATION: Dark brown-black with bright orange head, scape, labium, pronotum, scutellum medially, stridulatory groove, meso- and metasternal longitudinal depressions, hemelytron except posteromedial spot, femora except medially on mid leg, tibiae, tarsi, anterior half of laterotergites, sternite III medially, and sternites II–VII anterolaterally. Distal half of antennal segment VII white. VESTITURE: As in generic description. STRUCTURE: HEAD (Fig. 2.13H): Ventrally with shallow anteromedial depression; clypeal apex dorsally elevated relative to labrum; postclypeus with relatively deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); legs slender; tarsomeres I and II combined subequal to III on fore- and mid legs, longer on hind legs; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; dorsal laterotergite II not expanded; intersegmental sutures carinulate between sternite II–VI and laterally between VI and VII; pygophore process subtriangular in lateral view (Fig. 2.20I); BPE as long as basal plate; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the variable color forms of this species.

DISTRIBUTION: Toamasina and the northern region of the Antsiranana provinces (Map 2.7).

DISCUSSION: Some specimens are predominately orange in coloration while others have reduced to absent orange markings on the head, thorax, scutellum, femora, tibiae, and abdomen.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 26 Jan 2001–29 Jan 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala (00006271) (CAS).

PARATYPES: **Madagascar: Antsiranana:** 7 km N of Joffreville, 12.33333°S 49.25°E, 360 m, 20 Mar 2001–07 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006287) (CAS); 27 Apr 2001–13 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00006288) (UCR); 13 May 2001–16 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00006484) (USNM). Montagne Français, 12.325°S 49.33333°E, 150 m, 30 Jan 2001–15 Feb 2001, M. Irwin, R. Harin'Hala, 1♂ (00006279) (SU); 15 Feb 2001–06 Mar 2001, M. Irwin, R. Harin'Hala, 2♂ (00006274, 00006281) (CAS); 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006259) (UCR). Parc National Montagne d'Ambre, 12.52027°S 49.17916°E, 1125 m, 11 Feb 2001–04 Mar 2001, M. Irwin, R. Harin'Hala, 2♂ (00006254, 00006264) (CAS); 19 Mar 2001–15 Apr 2001, M. Irwin, R. Harin'Hala, 3♂ (00006247, 00006256, 00006257) (CAS), 1♂ (00006282) (MNHN); 05 Apr 2001–21 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006136) (BMNH), 1♂ (00006267) (AMNH); 21 Apr 2001–26 Apr 2001, M. Irwin, R. Harin'Hala, 2♂ (00006482, 00006483) (UCR). Parc National Montagne d'Ambre, 12.61666°S 49.15°E, 1116 m, Dec 1968, J. Vadon and A. Peyrieras, 1♂ (MNHN). Parc National Montagne d'Ambre, 12.51666°S 49.18333°E, 975 m, 25 Jan 2001–11 Feb 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 2♂ (00006255, 00006486) (CAS); 04 Mar 2001–19 Mar 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 1♂ (00006266) (UCR). Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 23 Jan 2001, M.E. Irwin, 2♂ (00006116, 00006258) (USNM); 26 Jan 2001–29 Jan 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 2♂ (00006253, 00006272) (CAS), 1♂ (00007065) (SU); 11 Feb 2001–12 Feb 2001, M. Irwin, R. Harin'Hala, 2♂ (00006277, 00006278) (UCR); 04 Mar 2001–19 Mar 2001, M. Irwin, R. Harin'Hala, 3♂ (00006252, 00006275, 00006276) (CAS), 1♂ (00006292) (AMNH); 19 Mar

2001–05 Apr 2001, M. Irwin, R. Harin'Hala, 3♂ (00006289, 00006291, 00006702) (CAS). Sakalava Beach, dwarf littoral forest, 12.26277°S 49.3975°E, 10 m, 15 Feb 2001–06 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006283) (CAS); 06 Mar 2001–20 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006260) (CAS); 20 Mar 2001–07 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006273) (BMNH); 07 Apr 2001–22 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006265) (MNHN); 13 May 2001–16 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00006498) (AMNH); 31 May 2001–07 Jun 2001, M. Irwin, R. Harin'Hala, 1♂ (00006251) (SU); 13 Aug 2001–20 Aug 2001, M. Irwin, R. Harin'Hala, 1♂ (00045641) (USNM); 20 Aug 2001–28 Aug 2001, M. Irwin, R. Harin'Hala, 1♂ (00006485) (UCR). **Toamasina:** 7 km SE of Andasibe National Park headquarters, 18.96266°S 48.45266°E, 1050 m, 23 Mar 2001–07 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006269) (CAS); 09 Apr 2001–23 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00006115) (UCR). Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 31 Jul 2001–15 Aug 2001, M. Irwin, R. Harin'Hala, 1♂ (00006250) (UCR); 08 Oct 2001–16 Oct 2001, M. Irwin, R. Harin'Hala, 1♂ (00006246) (BMNH), 1♂ (00006248) (MNHN), 5♂ (00006249, 00006280, 00006284–00006286) (CAS), 1♂ (00006290) (SU); 07 Nov 2001–16 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00005360) (CAS), 1♂ (00006268) (AMNH). **Unknown:** 1♂ (00006270) (CAS).

Tanindrazanus vohiparara, new species

Figs. 2.3, 2.7, 2.10; Map 2.8

DIAGNOSIS: Males are recognized among other species *Tanindrazanus* by the blackish coloration with pale yellow markings, large eyes reaching dorsal and ventral head margins, smooth posterior pronotal lobe, a very slightly expanded dorsal laterotergite II, and the intersegmental sutures carinulate between sternites II–V. This species is similar to *T. nigripes*, particularly a variant of this species, but is distinguished by the eye about half of head length, smooth posterior pronotal lobe, and expanded dorsal laterotergite II.

DESCRIPTION: Medium body size (length: 11.20 mm, holotype). COLORATION: Black with pale yellow scape basally, antennal segment VII, labial segment III and VI, thoracic sterna except medial longitudinal depression on meso- and metasterna, coxae, trochanters, forefemur ventrally and basally, mid and hind femora except medially, foretibia ventrally, anterior margins of laterotergites, and abdominal sternites except large lateral spots on II–VI and apex of VII. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; clypeal apex slightly elevated relative to labrum (Fig. 2.13G, H); postclypeus with deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, separated by less than diameter of ocellus, located on distinct median tubercle (Fig. 2.13H); eye about half of head length, reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape; labial segment III subequal to II. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow continuous; legs slender; tarsomeres I and II combined subequal to III; wings spread out in specimen. ABDOMEN: Apex rounded; dorsal laterotergite II very slightly expanded; intersegmental sutures carinulate between sternites II–V; pygophore process subtriangular in lateral view (Fig. 2.20H, I); BPE shorter than basal plate; endosomal struts ventrally obscured by semiextended endosoma; area of endosomal struts–DPS fusion ovate (Fig. 2.21H).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality that is part of Ranomafana National Park, Madagascar.

DISTRIBUTION: Ranomafana National Park in the Fianarantsoa province (Map 2.8).

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1100 m, 04 Mar 2002–12 Mar 2002, M. Irwin, R. Harin'Hala (00006139) (CAS).

PARATYPE: **Madagascar: Fianarantsoa:** Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 23 Oct 2005–30 Oct 2005, M. Irwin, R. Harin'Hala, 1♂ (00045227) (CAS).

Toliarus, new genus

Figs. 2.3, 2.7, 2.10, 2.13I, 2.19G, 2.20J, 2.21I, 2.22F; Map 2.9

TYPE SPECIES: *Toliarus trichrous*, new species

DIAGNOSIS: Males recognized by a combination of the following characters: the small body size, ocelli on a shallow median tubercle, large antennal shield that does not conceal antennal insertion in lateral view, 6-segmented antenna, and punctate posterior pronotal lobe. This genus is very similar to *Tanindrazanus*, from which it differs by the smaller body size, 6-segmented antenna, and punctate posterior pronotal lobe.

DESCRIPTION: **MALE:** Macropterous, small body size. COLORATION: Red and black or orange and black. VESTITURE: Dense, semierect to erect, long pale to dark brown setae on head, thorax, legs, corium, and abdomen; setae on tibiae stouter and denser near apex. STRUCTURE: HEAD (Fig. 2.13I): Subtriangular in lateral view, longer than wide in dorsal view, shorter than pronotum; anteocular region longer than postocular; clypeal apex not elevated relative to labrum; maxillary plate not reaching dorsal surface of clypeus (except nearly reaching in a some specimens of *T. trichrous*); postclypeus depressed (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli present, located on shallow median tubercle; distinct constriction between postocular and neck; gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin; antennal shield not concealing antennal insertion in lateral view; antenna inserted dorsally on head; scape surpassing clypeal apex, pedicel slightly curved; flagellum subdivided into BFLA and DFLA; BFLA divided into two pseudosegments; DFLA divided into two pseudosegments; antenna thus appearing 6-segmented; labium slender; labial segment III subequal to II, ventrally straight. THORAX: Pronotum wider than long, anterior margin distinctly concave, collar distinct (Fig. 2.15B); anterior pronotal lobe shorter than posterior lobe (Fig. 2.15B), more than half as wide as posterior lobe, relatively smooth; posterior pronotal lobe weakly punctate; pronotal longitudinal furrow reaching anterior but not posterior margin, foveate posteriorly (Fig. 2.15B); pronotal transverse furrow distinct (Fig. 2.15B); lateral depressions on pronotum distinct (Fig. 2.15B), transversely striated; scutellum with two broadly separated apical processes, disc medially depressed; meso- and metasterna shallowly separated by transverse suture (Fig. 2.15F); mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; MGE with deeply depressed meshlike cuticle that extends dorsally in lateral view (Fig. 2.16A); fossula spongiosa on fore- and mid tibiae; corium restricted to areas adjacent to basal wing veins, with pterostigmalike appearance on anterodistal margin (Fig. 2.17A, C); distal part of R present but not forming cell with M (Fig. 2.17B, C); proximal parts of M and Cu veins separate (Fig. 2.17A, C); distal part of M extending beyond apical junction of M+Cu (Fig. 2.17A, C); base of M+Cu cell shorter than or as wide as Cu+1A cell (Fig. 2.17B, C). ABDOMEN: Dorsal laterotergite II not expanded; sternites shallowly depressed medially (Fig. 2.18C), intersegmental sutures carinulate; spiracles ovoid; pygophore (Figs. 2.19G, 2.20J) process subtriangular in lateral view, directed dorsoposteriad, not surpassing posterior margin of pygophore; DPS apex rounded (Fig. 2.21I); endosomal struts reaching posterior margin of DPS, with anterior and posterior ventral processes (Fig. 2.22G); endosoma medially sclerotized (Fig. 2.21I).

ETYMOLOGY: This genus is named after the locality province of the type species, Toliara, Madagascar. The gender is masculine.

DISTRIBUTION: Species are known from the southern region of the Toliara province and from the Antsiranana province and in habitats between 35–180 m elevation. Macrohabitats are described as gallery forests, spiny forests, dry deciduous forests, and transitional forests.

DISCUSSION: Female specimens are unknown for species currently in this genus. The size of the maxillary plates is polymorphic in *T. trichrous*; in approximately 40% of the specimens, the maxillary plates nearly reach the dorsal clypeal surface when viewed laterally (Fig. 2.13H).

Identification key to the males of species of Toliarus

1. Orange with blackish markings, ocelli separated by a distance about the diameter of an ocellus, medium body size (>10 mm) .... *karinae*, new species

- Tricolored (red and black with dark brown fore wing membrane), ocelli separated by more than diameter of an ocellus; small body size (<10 mm) .... *trichrous*, new species

Toliarus karinae, new species

Figs. 2.3, 2.7; Map 2.9

DIAGNOSIS: Males are similar to *T. trichrous*, but is easily distinguished by the larger body size, distinct orange body with blackish markings on the hemelytra and tibiae, medium sized ocelli, and weak punctuation on the posterior pronotal lobe.

DESCRIPTION: Medium body size (length: 12.10 mm, holotype). COLORATION: Orange with antenna except scape ventrally, clavus, forewing membrane, and apices of tibiae blackish. Antennifer apically white. VESTITURE: As in generic description. STRUCTURE: HEAD: Ventrally with shallow anteromedial depression; postclypeus with relatively deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli medium sized, separated by a distance about the diameter of an ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape. THORAX: Anterior pronotal lobe without distinct anterolateral projections; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur incrassate; tarsomeres I and II subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subquadrate in caudal view, with truncate apex; BPE as long as basal plate (Fig. 2.22F); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21I).

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after the second author's wife, Karina Wieczorek.

DISTRIBUTION: The only known specimen was collected from the Ankarana Reserve in the Antsiranana province (Map 2.9).

HOLOTYPE: Male: **Madagascar: Antsiranana:** Ankarana Reserve, 12.91688°S 49.14355°E, 155m, no date provided, J. Vadon and A. Peyrieras (MNHN).

Toliarus trichrous, new species

Figs. 2.3, 2.7, 2.10, 2.13I, 2.19G, 2.20J, 2.21I, 2.22F; Map 2.9

DIAGNOSIS: Males are recognized from *T. karinae* by the smaller body size, red and black coloration, and more punctate posterior pronotal lobe. Males are most similar to *Tanindrazanus anjozorobeus* and *Tanindrazanus kathrynae*, but the smaller body size, red anteocular region and abdominal sternites (except black pygophore), black postocular region, 6-segmented antenna, and punctate posterior pronotal lobe distinguishes *T. trichrous* from these species.

DESCRIPTION: Small body size (length: 7.22 mm, holotype; 7.22–8.97 mm). COLORATION: Red with black head ventrolaterally below eye, postocular except ventrolateral spot, neck except dorsomedially, anterior pronotal and propleural lobes, prosternum, medial pronotal longitudinal furrow on posterior pronotal lobe, meso- and metapleura, scutellum, apical half of hind femur, hind tibia medially, abdominal sternite VII apically, and pygophore. Hemelytron dark brown, except red corium. VESTITURE: As in generic description. STRUCTURE: HEAD (Fig. 2.13I): Ventrally with shallow anteromedial depression; postclypeus with relatively deep, narrow medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli small, separated by more than diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; pedicel about one-fourth longer than scape. THORAX: Anterior pronotal lobe without distinct anterolateral projections; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); forefemur incrassate; tarsomeres I and II subequal to III; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subtriangular in lateral view (Fig. 2.20J), apex rounded; BPE as long as basal plate (Fig. 2.22F); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21I).

ETYMOLOGY: The species epithet is an adjective and is named for the body coloration.

DISTRIBUTION: Specimens were collected from the southern region of Toliara (Map 2.9).

DISCUSSION: Coloration varies with the posterior pronotal lobe and posterior propleural lobe either uniformly black, black with red lateral margins, or uniformly red. The hind femur may be more extensively black, and the black medial spot on abdominal sternite VII varies in size.

HOLOTYPE: Male: **Madagascar: Toliara:** Beza Mahafaly Reserve, Parcelle II near Bellevue, 23.68983°S 44.5755°E, 180 m, 21 Nov 2001–28 Nov 2001, R. Harin’Hala (00006163) (CAS).

PARATYPES: **Madagascar: Toliara:** Andohahela Natýl Park, Tsimelahy, Parcelle II, 24.93683°S 46.62666°E, 180 m, 09 Dec 2002–16 Dec 2002, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006494) (CAS); 16 Dec 2002–17 Dec 2002, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006185, 00006186) (CAS); 15 Feb 2003–26 Feb 2003, M. Irwin, F. Parker, R. Harin’Hala, 5♂ (00006513–00006517) (CAS); 18 Mar 2003–28 Mar 2003, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006184, 00006519) (USNM); 28 Mar 2003–08 Apr 2003, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006155, 00006497) (BMNH); 19 Apr 2003–26 Apr 2003, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006168, 00006169) (MNHN); 29 Jun 2003–10 Jul 2003, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006183, 00006518) (AMNH); 17 Aug 2003–24 Aug 2003, M. Irwin, F. Parker, R. Harin’Hala, 5♂ (00006176–00006180) (CAS); 11 Oct 2003–19 Oct 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006162) (SU); 15 Jan 2004–28 Jan 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006493) (UCR). Berenty Special Reserve, 8 km NW Amboasary, 25.00666°S 46.30333°E, 85 m, 25 Oct 2002–26 Oct 2002, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006153, 00006156) (CAS); 09 Nov 2002–16 Nov 2002, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006167) (UCR); 30 Nov 2002–07 Dec 2002, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006171) (CAS); 14 Dec 2002–16 Dec 2002, M. Irwin, F. Parker, R. Harin’Hala, 3♂ (00006181, 00006182, 00006501) (AMNH); 26 Jan 2003–05 Feb 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006507) (SU); 24 Apr 2003–03 May 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006506) (CAS); 25 May 2003–04 Jun 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006202) (USNM); 22 Nov 2003–30 Nov 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006490) (BMNH); 30 Nov 2003–07 Dec 2003, M. Irwin, F. Parker, R.

Harin’Hala, 1♂ (00006520) (BMNH); 07 Dec 2003–14 Dec 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006492) (UCR); 21 Dec 2003–02 Jan 2004, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006504, 00006522) (CAS); 13 Jan 2004–23 Jan 2004, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006505, 00006510) (MNHN); 04 Feb 2004–15 Feb 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006500) (CAS); 02 Mar 2004–11 Mar 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006509) (CAS); 05 Apr 2004–15 Apr 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006503) (AMNH); 06 Jun 2004–20 Jun 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006489) (CAS); 11 Jul 2004–25 Jul 2004, M. Irwin, F. Parker, R. Harin’Hala, 3♂ (00006511, 00006512, 00006521) (CAS); 07 Aug 2004–22 Aug 2004, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006487, 00006488) (USNM); 22 Aug 2004–01 Sep 2004, M. Irwin, F. Parker, R. Harin’Hala, 2♂ (00006495, 00006496) (SU); 01 Sep 2004–08 Sep 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006508) (UCR). Berenty Special Reserve, 8 km NW Amboasary, 25.021°S 46.3055°E, 35 m, 10 Jun 2003–19 Jun 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006502) (CAS); 08 Nov 2003–15 Nov 2003, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00005364) (CAS); 21 Dec 2003–01 Jan 2004, M. Irwin, F. Parker, R. Harin’Hala, 3♂ (00006175, 00006189, 00006190) (MNHN); 24 Mar 2004–04 Apr 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006491) (SU); 23 Jun 2004–04 Jul 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006157) (BMNH), 1♂ (00006158) (CAS); 04 Jul 2004–18 Jul 2004, M. Irwin, F. Parker, R. Harin’Hala, 1♂ (00006170) (UCR). Beza Mahafaly Reserve, Parcelle II near Bellevue, 23.68983°S 44.5755°E, 180 m, 10 Nov 2001–21 Nov 2001, M. Irwin, R. Harin’Hala, 1♂ (00006208) (CAS); 04 Dec 2001–11 Dec 2001, M. Irwin, R. Harin’Hala, 1♂ (00006204) (UCR). Beza Mahafaly Reserve, Parcelle I near research station, 23.6865°S 44.591°E, 165 m, 21 Nov 2001–28 Nov 2001, R. Harin’Hala, 3♂ (00006154, 00006161, 00006188) (CAS); 04 Dec 2001–11 Dec 2001, R. Harin’Hala, 1♂ (00006213) (CAS); 18 Dec 2001–25 Dec 2001, R. Harin’Hala, 2♂ (00006193, 00006203) (SU); 22 Feb 2002–01 Mar 2002, R. Harin'Hala, 1♂ (00045647) (CAS); 29 Apr 2002–19 May 2002, R. Harin'Hala, 1♂ (00006205) (BMNH); 28 Jul 2002–09 Aug 2002, R. Harin'Hala, 1♂ (00006160) (CAS); 09 Sep 2002–20 Sep 2002, R. Harin'Hala, 1♂ (00006209) (CAS); 28 Oct 2002–10 Nov 2002, M.E. Irwin, F.D. Parker, R. Harin'Hala, 1♂ (00006191) (CAS); 10 Nov 2002–22 Nov 2002, R. Harin'Hala, 2♂ (00006199, 00006215) (USNM); 02 Dec 2002–12 Dec 2002, R. Harin'Hala, 3♂ (00006150, 00006151, 00006212) (AMNH); 12 Dec 2002–17 Dec 2002, R. Harin'Hala, 1♂ (00006187) (CAS); 17 Dec 2002–20 Dec 2002, R. Harin'Hala, 1♂ (00006214) (CAS); 20 Dec 2002–24 Dec 2002, R. Harin'Hala, 1♂ (00006164) (UCR); 24 Dec 2002–02 Jan 2003, R. Harin'Hala, 2♂ (00006210, 00006211) (CAS); 09 Jan 2003–23 Jan 2003, R. Harin'Hala, 1♂ (00006192) (CAS); 04 Feb 2003–16 Feb 2003, R. Harin'Hala, 1♂ (00006194) (BMNH); 02 Mar 2003–13 Mar 2003, R. Harin'Hala, 2♂ (00006159, 00006165) (CAS); 13 Mar 2003–23 Mar 2003, R. Harin'Hala, 2♂ (00006197, 00006198) (BMNH); 23 Mar 2003–02 Apr 2003, R. Harin'Hala, 2♂ (00006086, 00006152) (CAS); 02 Apr 2003–10 Apr 2003, R. Harin'Hala, 3♂ (00006166) (SU), 3♂ (00006172–00006174) (CAS); 10 Apr 2003–21 Apr 2003, R. Harin'Hala, 2♂ (00006206, 00006207) (CAS); 21 Apr 2003–29 Apr 2003, R. Harin'Hala, 1♂ (00006196) (UCR). Cap Ste Marie Special Reserve, 74 km S of Tsihombe, 25.58766°S 45.163°E, 37 m, 18 May 2003–26 May 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006200) (CAS), 1♂ (00006201) (UCR). Parc National d'Andohahela, Ihazofotsy Parcelle III, 24.83083°S 46.53616°E, 80 m, 15 Jan 2003–26 Jan 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00007162) (BMNH), 3♂ (00045213, 00045297, 00045312) (MNHN); 24 Aug 2003–03 Sep 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045633) (CAS); 12 Nov 2003–23 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045242) (UCR); 17 Dec 2003–19 Dec 2003, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00007208, 00044928, 00045630) (USNM); 14 Jan 2004–28 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00007185) (AMNH), 6♂

(00044953, 00045131, 00045203, 00045298, 00045597, 00045634) (CAS), 2♂ (00045700, 00045726) (SU). **Unknown:** 1♂ (00006195) (CAS).

Toxopus Bergroth, 1905

Figs. 2.3, 2.4, 2.7, 2.10, 2.11, 2.12, 2.13B, 2.13J, 2.13K, 2.14, 2.15B, 2.19H, 2.19I, 2.20K, 2.20L, 2.21J–L, 2.22G, 2.22H, 2.23E; Maps 2.10–2.13

Toxopus Bergroth, 1905: 374.

TYPE SPECIES: *Toxopus politus* Bergroth, 1905

REVISED DIAGNOSIS: Male recognized by the shiny dark brown to blackish coloration with pale yellow markings, meso- and metasterna not completely separated by distinct transverse suture, dorsal laterotergite II expanded laterally, and laterotergites transversely bicolored. Females recognized by the apterous condition, shiny dark brown to blackish coloration sometimes with pale yellow markings, head about as wide as anterior margin of pronotum, 7-segmented antenna with short vestiture, scape as long as distance between anterior margin of eye and apex of head, eye about half head height, anterior pronotal lobe much longer than posterior lobe, fore- and mid trochanters with small papillae, and abdominal tergites I–III declinate toward posterior with remaining tergites oriented horizontally. This genus is most similar to *Rochonia* Distant, 1913, from which it differs by the relatively smooth head and pronotum, hemelytron reaching or surpassing abdominal apex, and dorsal laterotergite II expanded.

REDESCRIPTION: **MALE:** Macropterous, medium body size. COLORATION: Shiny dark brown to black with pale yellow markings. VESTITURE: Sparse to dense, semierect to erect, long pale to dark brown setae on head, thorax, legs, corium, and abdomen; setae on tibiae stouter and denser near apex. STRUCTURE: HEAD (Fig. 2.13B, J, K): Ovoid or subquadrate; shorter than pronotum; clypeal apex not elevated relative to labrum; maxillary plate not reaching dorsal surface of clypeus; postclypeus depressed; distinct constriction between postocular and neck; gula moderately swollen ventrolaterally, not distinctly produced beyond ventral head margin; ocelli present; antennal shield not concealing antennal insertion in lateral view; scape surpassing clypeal apex; flagellum subdivided into BFLA and DFLA; BFLA divided into two pseudosegments; DFLA divided into three pseudosegments; antenna thus appearing 7-segmented; labial segment III subequal to II. THORAX (Fig. 2.15B): Pronotum wider than long, anterior margin distinctly concave, collar distinct; anterior pronotal lobe shorter than posterior lobe, more than half as wide as posterior lobe, relatively smooth; pronotal longitudinal furrow reaching anterior but not posterior margin of pronotum, foveate posteriorly; pronotal transverse furrow distinct; lateral depressions on posterior pronotal lobe distinct; scutellum with two moderately separated apical processes, disc medially depressed; meso- and metasterna not completely separated by distinct transverse suture (Fig. 2.15E); mesosternum with medial and paramedial longitudinal depressions; metasternum medially longitudinally depressed; MGE with deeply depressed meshlike cuticle that extends dorsally in lateral view (Fig. 2.16A); forefemur slightly to strongly incrassate; fossula spongiosa on fore- and mid tibiae; tarsomeres I and II combined subequal to III; corium restricted to areas adjacent to basal wing veins, with pterostigmalike appearance on anterodistal margin (Fig. 2.17A, C); distal part of R present but not forming cell with M (Fig. 2.17B, C); proximal parts of M and Cu separate (Fig. 2.17A, C); distal part of M extending beyond apical junction of M+Cu (Fig. 2.17A, C); base of M+Cu cell shorter than or as wide as Cu+1A cell (Fig. 2.17B, C). ABDOMEN: Dorsal laterotergite II expanded; sternites shallowly depressed medially (Fig. 2.18C), intersegmental sutures carinulate; spiracles ovoid; pygophore process subtriangular in lateral view (Fig. 2.20K, L), directed dorsoposteriad, apex rounded; DPS apex rounded (Fig. 2.21J–L). **FEMALE:** Differs from males in the following characteristics: apterous; reduced yellow markings; head larger, about as wide as anterior pronotal margin, shorter or longer than pronotum; postclypeus not depressed (Fig. 2.13A); antennal shield not expanded; antennal vestiture much shorter; scape as long as distance between anterior eye margin and apex of head; ocelli absent; eyes small, about half head height; labial segments II shorter than or subequal to segment III; collar barely distinct; anterior pronotal lobe longer than and as wide as posterior lobe (Fig. 2.15A), without distinct anterolateral projections; pronotal longitudinal furrow reduced to deep medial depression near posterior margin of anterior pronotal lobe (Fig. 2.15A); lateral depressions on posterior pronotal lobe obsolete; scutellum weakly developed; meso- and metasterna platelike with shallow, wide medial longitudinal depression; MGE reduced, shallow, not extending dorsally in lateral view (Fig. 2.16B, C); fore- and mid trochanters with patches of small papillae (Fig. 2.16D, E); hind femur slightly curved in dorsal view; fossula spongiosa larger; dorsal laterotergite II not expanded; abdominal tergites I–III declinate toward posterior, intersegmental sutures carinulate, remaining tergites oriented horizontally, intersegments not carinulate; sternites flat; external genitalia short, platelike (Fig. 2.23E).

DISTRIBUTION: Species are known from all provinces and in habitats between 7–1,360 m elevation. Macrohabitats include tropical dry forests, dwarf littoral forests, low-altitude dense humid forests, low-altitude littoral rainforests, high-altitude rainforests, spiny forests, gallery forests, sclerophyl forests, montane rainforest, dry deciduous forests, and transitional forests.

DISCUSSION: Bergroth (1905) described this genus from a single female specimen. He emphasized the overall head structure and strongly curved hind tibia as diagnostic for this genus. However, head shape and structure is variable among species in some ectrichodiine genera (e.g., *Microstemmatoides* Putshkov, 1985, *Daraxa* Stål, 1859, *Gibbosella*) and the leg armature can vary among and within species. As examples, the presence and location of patches of papillae on the femora and trochanters may differ among species of *Rhiginia* Stål, 1859, males and females of the same species in *Racelda* Signoret, 1863, and apterous and. macropterous forms within species of *Glymmatophora*. Similarly, femoral and tibial spines may vary in presence, size, or number in species of *Glymmatophora*. Finally, the curvature of the hind tibia can vary between species in a genus (straight or slightly curved in *Pothea* Amyot and Serville. 1843, *Katanga* Schouteden, 1903, *Centraspis* Schaum, 1862) and within species (straight or slightly curved in females of *Ectrichodia crux* [Thunberg] 1783). Curvature and robustness of the hind tibia in females of *Toxopus politus* Bergroth, 1905, appears to be fairly extreme, and we found this character variable in two female specimens that we assign to *Toxopus*: one specimen has a more robust and strongly curved hind tibia than the other. We are unable to definitively assign either specimen to *T. politus* based on the original description; the holotype of *T. politus* is missing and could not be examined for confirmation (see discussion for *T. politus*). Comparison of these two specimens with a female with cylindrical head and slender, slightly curved hind tibia revealed many morphological similarities: apterous, shiny blackish coloration, head about as wide as anterior margin of pronotum, 7-segmented antenna with short vestiture, scape as long as distance between anterior eye margin and apex of head, eyes small, and abdominal tergites I–III declinate toward posterior, among several other features. Given the abundance of morphological similarities between these females and known variability in head shape and leg structure in other Ectrichodiinae genera, the genus is here redescribed to accommodate females with various head shapes and slender, less curved, and unarmed hind tibia. Based on morphology, geographic proximity, and molecules, we also associated the female with the cylindrical head and slender hind legs with males of a new species, *T. griswoldi*, enabling us to describe *Toxopus* males for the first time. Attempts to associate the other two females with conspecific males based on morphology, geography, and molecules failed. These two females remain undescribed for the time being since, based on head shape, presence of a ventral medial depression on the head, and geographic proximity, they could represent females of any of the following species: *T.*

ampitavananima, *T. basalis*, *T. brucei*, *T. namoroka*, *T. parkeri*, *T. signoretii*, *T. simulans*, *T. steineri*, *T. tibialis*, and *T. vazimba*.

The monotypic genus *Rochonia* was described by Distant from one macropterous male specimen from the Seychelles in 1913. The holotype of *R. galeatus* Distant, 1913, which is fairly damaged and has the ventral surface not visible, was examined at the BMNH. It is clear that *Rochonia* shares many morphological features with *Toxopus*, while few characters distinguish the two genera (see differential diagnosis for *Toxopus*). Based on these morphological similarities, *Toxopus* may in fact belong to *Rochonia*. We refrain from synonymizing *Toxopus* with *Rochonia* until additional specimens of *Rochonia* become available that will allow examination of ventral characters, antennal segmentation, and intraspecific variation. Future phylogenetic analyses including *Rochonia* and *Toxopus* may also provide support for synonymy.

Identification key to the males of species of Toxopus

1. Head cylindrical (Fig. 2.13J) 2

- Head subquadrate (Fig. 2.13A) or ovoid (Fig. 2.13F) 9

2. Head ventrally flat..3

- Head with medial depression either restricted to anteocular region or extending to postocular 4

3. Pedicel not distinctly curved; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI..*insignis*, new species

- Pedicel slightly curved; sternal intersegmental sutures carinulate between II and III and laterally between III–VI ....*fisheri*, new species

4. Head with ventral anteromedial depression; postocular broad in dorsal view (Fig. 2.13B); sublateral antennal insertion; pronotal transverse suture incomplete, divided by paramedian ridges (Fig. 2.15B)..5

- Head with ventral medial depression extending to postocular; postocular narrow in dorsal view (Fig. 2.13A); dorsal antennal insertion; pronotal transverse suture complete, not divided by paramedian ridges .... *melobrunneus*, new species

5. Posterior pronotal lobe smooth; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI... *toliara*, new species

- Posterior pronotal lobe striated; sternal intersegmental suture carinulation pattern not as previously mentioned..6

6. Synthlipsis width 1.5 times width of eye; sternal intersegmental sutures carinulate between II and III and laterally between III and IV..*antsiranana*, new species

- Synthlipsis width two times width of eye; sternal intersegmental suture carinulation pattern not as previously mentioned 7

7. Postclypeal depression extending to interocular sulcus; sternal intersegmental sutures carinulate between II and III and laterally between III–V .... *ambohitantely*, new species

- Postclypeal depression extending to middle of interocular area (Fig. 2.13B); sternal intersegmental suture carinulation pattern not as previously mentioned...8

8. Postclypeal depression relatively broad; ventral margin of labial segment III convex (Fig. 2.13J, D, E, F); sternal intersegmental sutures carinulate between II and III and laterally between III–VII ....*italaviana*, new species

- Postclypeal depression narrow; ventral margin of labial segment III straight (Fig. 2.13G–I, K); sternal intersegmental sutures carinulate between II–IV and laterally between IV–VII .... *griswoldi*, new species

9. Anteocular region as long as postocular (Fig. 2.13J).. 10

- Anteocular region longer than postocular (Fig. 2.13K).. 11

10. Postclypeal depression extending to interocular sulcus; ventral margin of labial segment III straight (Fig. 2.13G–I, K); posterior pronotal lobe striated ....*pallidus*, new species

- Postclypeal depression extending to middle of interocular area; ventral margin of labial segment III convex (Fig. 2.13C–F, J); posterior pronotal lobe smooth ....*farafangana*, new species

11. Head about as long as wide in dorsal view 12

- Head longer than wide in dorsal view 16

12. Synthlipsis about width of eye; eye reaching dorsal head surface in lateral view; sternal intersegmental sutures carinulate between II and III and laterally between III–V ....*toamasina*, new species

- Synthlipsis at least 1.5 times width of eye; eye not reaching dorsal head surface in lateral view; carinulation patterns on the sternal intersegmental sutures not as previously mentioned 13

13. Synthlipsis about 1.5 times width of eye 14

- Synthlipsis about two times width of eye 15

14. Head ventrally with anteromedial depression; eye not distinctly reaching ventral head surface in lateral view; sternal intersegmental sutures carinulate between II–VI ....*tibialis*, new species

- Head with medial depression extending along entire ventral head surface; eye reaching or nearly reaching ventral head surface in lateral view; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI ....*basalis*, new species

15. Posterior pronotal lobe weakly transversely striated; sternal intersegmental sutures carinulate between II–VI ....*parkeri*, new species

- Posterior pronotal lobe smooth; sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI...*brucei*, new species

16. Only sternal intersegmental suture between II and III carinulate 17

- Multiple sternal intersegmental sutures carinulate 18

17. Synthlipsis about two times width of eye; postocular broad in dorsal view (Fig. 2.13B); posterior pronotal lobe smooth .... *miandritsara*, new species

- Synthlipsis about 1.5 times width of eye; postocular narrow in dorsal view (Fig. 2.13A); posterior pronotal lobe weakly transversely striated ....*simulans*, new species

18. Synthlipsis at least 1.5 times width of eye; eye not distinctly reaching dorsal head surface... 19

- Synthlipsis about width of eye; eye reaching or nearly reaching dorsal head surface .... *signoretii* (Reuter), new combination

19. Synthlipsis about two times width of eye; anterior pronotal lobe with distinct, small anterolateral protuberances (Fig. 2.15B); posterior pronotal lobe smooth 20

- Synthlipsis about 1.5 times width of eye; anterior pronotal lobe without distinct anterolateral protuberances; posterior pronotal lobe weakly transversely striated .... *ampitavananima*, new species

20. Ventral surface of labial segment III straight (Fig. 2.13G–I, K); sternal intersegmental sutures carinulate between II–VI and laterally between VI and VII.. 21

- Ventral surface of labial segment III convex (Fig. 2.13C–F, J); sternal intersegmental sutures carinulate between II–IV and laterally between IV–VI...................................*steineri*, new species

21. Interocular sulcus near hind margin of eye (Fig. 2.13B); head, including postclypeal depression, anterior pronotal lobe, and legs reddish brown.........................*namoroka*, new species

- Interocular sulcus anterior to hind margin of eye; head dark brown with postclypeal depression and labium pale; anterior pronotal lobe generally dark brown; legs dark brown and pale................. .... *vazimba*, new species

Identification key to the females of species of Toxopus

1. Hind tibia distinctly curved, armed with small papillae (Fig. 2.16D, E); shiny dark brown to black; basal part of scape and antennal segments V–VII entirely, except basal half of V, pale; dorsal surface of femora basally, foretibia ventrally except basally and apically, rings on mid and hind tibiae, and tarsi pale to brown (based on original description)....................... *politus* Bergroth

- Hind tibia not distinctly curved, unarmed; shiny blackish with extensive pale to brown markings ....*griswoldi*, new species

Toxopus ambohitantely, new species

Figs. 2.3, 2.7, 2.10, 2.13J; Map 2.11

DIAGNOSIS: Males are recognized among other *Toxopus* species by the moderately dense vestiture, coloration, elongate cylindrical head in lateral view, relatively deep postclypeal depression that reaches the interocular sulcus, sublateral antennal insertion, labial segment III ventrally convex, and intersegmental sutures carinulate between sternites II and III and laterally between III–V. This species is similar to *T. italaviana*, *T. griswoldi*, *T. insignis*, *T. fisheri*, *T. antsiranana*, and *T. toliara*, but is distinguished from them by the intersegmental sutures carinulate between sternites II and III and laterally between III–V, subtriangular pygophore process, and endosoma medially sclerotized.

DESCRIPTION: **MALE:** Body length: 9.93 mm (holotype), 9.83–10.18 mm. COLORATION: Blackish with pale yellow corium basally, trochanters, femora except dorsoapical half, fore- and mid tibiae medially, hind tibia subbasally and medially, anterior half of laterotergites, abdominal sternites medially (except anterior, posterior, and lateral margins), sternites II–VI anterolaterally, and lateral margin of sternite VII. Antennal segments VI and VII, hemelytron, and tarsi brown. VESTITURE: Moderately dense; other features as in generic description. STRUCTURE: HEAD

(Fig. 2.13J): Cylindrical in lateral view; longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region longer than postocular; postclypeus with deep, narrow medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus posterior to hind margin of eye; postocular broad in dorsal view (Fig. 2.13B); ocelli small, located on shallow median tubercle, separated by a distance less than or equal to diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-fourth longer than scape, slightly curved; labium slender; labial segment III ventrally convex. THORAX: Anterior pronotal lobe with relatively small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded, sinuate, or medially notched; intersegmental sutures carinulate between sternites II and III and laterally between III–V; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion ovate; endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Ambohitantely, Madagascar.

DISTRIBUTION: Antananarivo, Antsiranana, Mahajanga, and Toamasina provinces (Map 2.11).

DISCUSSION: In some specimens, the base of the scape, antennal segments VI and VII, scutellar processes, femora, tibiae, and corium are more pale yellow than dark brown. The labium may be light brown.

HOLOTYPE: Male: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 15 Oct 2004–01 Nov 2004, M. Irwin, F. Parker, R. Harin'Hala (00006782) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 31 Oct 2003–07 Nov 2003, M. Irwin, R. Harin'Hala, 3♂ (00006788–00006790) (CAS); 05 Mar 2004–19 Mar 2004, M. Irwin, R. Harin'Hala, 1♂ (00006791) (CAS); 19 Mar 2004–28 Mar 2004, M. Irwin, R. Harin'Hala, 1♂ (00006778) (SU); 15 Oct 2004–01 Nov 2004, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006779–00006781) (USNM), 2♂ (00006783, 00006784) (CAS), 3♂ (00006785–00006787) (MNHN); 01 Nov 2004–14 Nov 2004, M. Irwin, R. Harin'Hala, 1♂ (00006792) (UCR); 17 Apr 2005–26 Apr 2005, M. Irwin, R. Harin'Hala, 2♂ (00044905, 00045071) (AMNH), 2♂ (00045364, 00045369) (BMNH). **Antsiranana:** Parc National Montagne d'Ambre, 12.51666°S 49.18333°E, 975 m, 04 Mar 2001–19 Mar 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 1♂ (00006120) (CAS). Sakalava Beach, dwarf littoral forest, 12.26277°S 49.3975°E, 10 m, 15 Feb 2001–06 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006794) (USNM); 22 Apr 2001–27 Apr 2001, M. Irwin, R. Harin'Hala, 1♂ (00045583) (SU). **Mahajanga:** Reserve Speciale de Bemarivo, 23.8 km 223° SW Besalampy, 16.925°S 44.36833°E, 30 m, 19 Nov 2002–23 Nov 2002, Fisher et al., 1♂ (00006793) (CAS). **Toamasina:** 7 km SE of Andasibe National Park headquarters, 18.96266°S 48.45266°E, 1050 m, 07 Jan 2001–22 Jan 2001, M. Irwin, R. Harin'Hala, 1♂ (00007142) (CAS). Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 01 Sep 2001–05 Sep 2001, M. Irwin, R. Harin'Hala, 1♂ (00006795) (MNHN); 19 Sep 2001–26 Sep 2001, M. Irwin, R. Harin'Hala, 1♂ (00045254) (UCR).

Toxopus ampitavananima, new species

Figs. 2.3, 2.7, 2.10, 2.22G; Map 2.12

DIAGNOSIS: Males are recognized among other *Toxopus* species by the subquadrate head shape in lateral view that is longer than wide in dorsal view, anterior pronotal lobe without anterolateral protuberances, and intersegmental sutures carinulate between sternites II and III and laterally between III–VI. This species is similar to *T. vazimba*, but the smaller synthlipsis width, interocular sulcus located near the hind margin of the eye, eye one-half of the head length in lateral view, anterior pronotal lobe lacking distinct anterolateral protuberances, striated posterior pronotal lobe, intersegmental sutures carinulate between sternites II and III and laterally between III–VI, and BPE as long as the basal plate distinguish *T. ampitavananima* from *T. vazimba*.

DESCRIPTION: **MALE:** Body length: 10.67 mm (holotype), 10.50–11.91 mm. COLORATION: Blackish with pale yellow mandibular and maxillary plates dorsally, postclypeal medial longitudinal depression, anterolateral area anterior of interocular sulcus, scape basally, pedicel basally, antennal segment III basally, antennal segment IV apically, antennal segments VI and VII, anterior pronotal lobe anterolaterally, posterior margin of posterior pronotal lobe, stridulatory process, meso- and metasterna, scutellar processes apically, corium basally, coxae, trochanters, forefemur basally and ventrally, mid femur basally and subapically, hind femur except medially, foretibia except basally, mid tibia except subbasally, hind tibia apically, tarsi, anterior half of laterotergites, abdominal sternites II–V except medially and laterally, ventrolateral anterior margin of sternite VI, and lateral margin of abdomen except apex of sternite VII. Labium and remainder of pronotum brown. VESTITURE: Moderately dense; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); longer than wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about half of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe without anterolateral projections; posterior pronotal lobe weakly to strongly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly to strongly transversely striated; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III and laterally between III–VI; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21K); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Ampitavananima Forest, Madagascar.

DISTRIBUTION: Antsiranana, Fianarantsoa, Toamasina, and Toliara provinces (Map 2.12).

DISCUSSION: The coloration in this species is variable: the pale yellow coloration on the head and scutellum may be reduced, the anterior pronotal lobe may have more pale yellow coloration throughout, the posterior pronotal lobe may be dark brown, and the entire ventromedial abdominal surface may be pale yellow or nearly so.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 14 Apr 2007–21 Apr 2007, M. Irwin, F. Parker, R. Harin'Hala (00006768) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 04 Mar 2001–19 Mar 2001, M. Irwin, R. Harin'Hala, 1♂ (00006719) (CAS). **Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 13 Jan 2007–20 Jan 2007, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006771–00006773) (CAS); 04 Feb 2007–10 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006762–00006764) (CAS); 10 Feb 2007–17 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006766) (UCR); 17 Feb 2007–24 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006740) (CAS); 10 Mar 2007–17 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 4♂ (00006743–00006746) (BMNH), 2♂ (00006755, 00006756) (UCR); 17 Mar 2007–24 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006741) (SU); 24 Mar 2007–31 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006769) (CAS); 07 Apr 2007–14 Apr 2007, M. Irwin, F. Parker, R. Harin'Hala, 4♂ (00006737–00006739, 00006753) (MNHN), 1♂ (00006754) (CAS); 21 Apr 2007–29 Apr 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006761) (CAS); 06 May 2007–14 May 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006770) (USNM); 14 May 2007–21 May 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006775) (USNM); 21 May 2007–25 May 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006752) (USNM); 25 May 2007–02 Jun 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006767) (USNM); 02 Jun 2007–10 Jun 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006760) (CAS); 01 Jul 2007–07 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006765) (CAS); 14 Jul 2007–19 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006742) (CAS); 19 Jul 2007–23 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006747, 00006748) (SU); 23 Jul 2007–28 Jul 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂

(00006121, 00006735) (CAS); 13 Sep 2007–20 Sep 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006776) (CAS); 27 Sep 2007–04 Oct 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006774) (CAS); 04 Oct 2007–11 Oct 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006751) (CAS); 11 Oct 2007–18 Oct 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006758, 00044833) (AMNH); 25 Oct 2007–08 Nov 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006736) (AMNH); 03 Jan 2008–09 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006731) (AMNH); 09 Jan 2008–17 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006750) (CAS); 17 Jan 2008–24 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006749) (CAS); 02 Mar 2008–08 Mar 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006759) (SU); 16 Mar 2008–22 Mar 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006732) (UCR). Manombo Special Reserve camp site, 32 km SSE of Farafangana, 23.02183°S 47.72°E, 36 m, 26 Dec 2004–05 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00045458) (CAS); 10 May 2005–22 May 2005, M. Irwin, R. Harin'Hala, 2♂ (00045398, 00045685) (CAS); 22 May 2005–06 Jun 2005, M. Irwin, R. Harin'Hala, 1♂ (00045378) (SU); 10 Jul 2005–27 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00007067) (UCR). **Toamasina:** Mobot Site, Analalava 7 km SW of Foulpointe, 17.69333°S 49.46027°E, 18 m, 29 Feb 2008–07 Mar 2008, M. Irwin, R. Harin'Hala, 1♂ (00044815) (CAS). **Toliara:** Forêt Ivohibe 55.0 km N Tolagnaro, 24.56888°S 47.20388°E, 200 m, 02 Dec 2006–04 Dec 2006, B.L. Fisher et al., 1♂ (00006733) (CAS). **Unknown:** 1♂ (00006757) (CAS).

Toxopus antsiranana, new species

Figs. 2.3, 2.7, 2.10; Map 2.10

DIAGNOSIS: Males are recognized among other species in this genus by a combination of the following characters: the coloration, elongate cylindrical head in lateral view, synthlipsis 1.5

times width of an eye, antenna inserted sublaterally on the head, labial segment III ventrally straight, and intersegmental sutures carinulate between sternites II and III and laterally between III and IV. Males are similar to males of *T. italaviana*, *T. griswoldi*, *T. insignis*, *T. fisheri*, and *T. toliara*, but are distinguished by the smaller synthlipsis width and intersegmental sutures carinulate between sternites II and III and laterally between III and IV.

DESCRIPTION: **MALE:** Body length: 12.21 mm (holotype), 11.10–12.21 mm. COLORATION: Blackish with pale yellow mandibular plates dorsally, postclypeus between antennifers, antennifer, labial segment IV except basally, scape basally, pedicel basally, base of antennal segment III, antennal segment VII, metasternum laterally, corium basally, mid and hind coxae posteriorly, trochanters, forefemur basally and subapically, mid and hind femora except medially, foretibia medially and subbasally, mid tibia subbasally and subapically, hind tibia basally and subapically, tarsi, anterior half of laterotergites, and abdominal sternites medially and anterolaterally. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Cylindrical in lateral view (Fig. 2.13J); longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli small, located on shallow median tubercle (Fig. 2.13J), separated by a distance less than or equal to diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-fourth longer than scape, slightly curved; labium slender; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe weakly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded or sinuate; intersegmental sutures carinulate between sternites II and III and laterally between III and IV; pygophore process curved in lateral view (Fig. 2.20K), elongate in caudal view (Fig. 2.19H), surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21K); endosoma with sclerotized, hairlike, denticles on posterior margin (Fig. 2.21J, K).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the Antsiranana province in Madagascar, where the type specimen was collected.

DISTRIBUTION: Toamasina and southern region of Antsiranana provinces (Map 2.10).

DISCUSSION: Coloration varies with the dorsal area between antennifers sometimes brown.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.67944°S 50.18361°E, 240 m, 26 Nov 2004, B.L. Fisher (00044804) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.67944°S 50.18361°E, 240 m, 26 Nov 2004, B.L. Fisher, 1♂ (00045129) (CAS). Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 25 Dec 2004–30 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00044835) (CAS); 05 Jan 2005–10 Jan 2005, M. Irwin, R. Harin'Hala, 3♂ (00006128, 00006970, 00007099) (UCR); 25 Feb 2005–04 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00045652) (CAS); 18 Mar 2005–25 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00006098) (CAS); 25 Mar 2005–04 Apr 2005, M. Irwin, R. Harin'Hala, 1♂ (00006100) (SU); 18 May 2005–30 May 2005, M. Irwin, R. Harin'Hala, 1♂ (00007189) (SU). **Toamasina:** Fampanambo, 15.37550°S 49.62175°E, 108 m, Feb 1959, J. Vadon, 2♂, (MRAC); Feb 1961, J. Vadon, 2♂, (MRAC). Ivoloina Zoological Park, 12 km NW of

Toamasina, 18.05933°S 49.35790°E, 29 m, 16 Nov 2000 – 20 Nov 2000, Dolin and Andreeva, 1♂ (TLMF). Nosy Mangabe, 15.49324°S 49.76776°E, 266 m, 27 Dec 2003, R. Dolin, 1♂ (TLMF). Périnet (Andasibe), 18.82666°S 48.44778°E, 1119 m, 19 Dec 2001 – 31 Dec 2001, V. Dolin, 1♂ (TLMF). **Unknown:** 1♂ (00007191) (CAS).

Toxopus basalis, new species

Figs. 2.3, 2.7, 2.10, 2.22H; Map 2.11

DIAGNOSIS: Males recognized among other species in *Toxopus* by the coloration, sparse vestiture, head as long as wide, synthlipsis 1.5 times width of an eye, interocular sulcus anterior to the hind margin of the eye, eye reaching the ventral head margin, striated posterior pronotal lobe, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI. Males are similar to males of *T. steineri*, *T. namoroka*, and *T. vazimba*, but differs from these species by the characters mentioned. This species is most similar to *T. brucei,* but is distinguished by the smaller width of the synthlipsis relative to the eye, interocular sulcus anterior to the hind margin of the eye, larger eye in lateral view, eye not reaching ventral head margin, and striated posterior pronotal lobe.

DESCRIPTION: **MALE:** Body length: 13.01 mm (holotype), 11.49–13.01 mm. COLORATION: Blackish with pale yellow postclypeal medial longitudinal depression, labial segment IV, scape basally, meso- and metasterna, corium basally, mid and hind coxae, trochanters, forefemur ventrally and basally, mid and hind femora basally, tibiae medially, tarsi, anterior half of laterotergites, abdominal sternites II–VI medially (except at margins of II and III and posteromedial spots on III–VI), and anterolateral spots on sternites. VESTITURE: Very sparse; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); as long as wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about 1.5 times width of eye; interocular sulcus anterior to hind margin of eye; postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about half of head length, not reaching dorsal head surface, reaching ventral head surface; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe weakly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly transversely striated; hemelytron surpassing tergite VII and not reaching, reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the pale basal part of the femora.

DISTRIBUTION: Mahajanga and northern region of Toliara provinces (Map 2.11).

DISCUSSION: The coloration of the medial longitudinal depression on the postclypeus is narrowly or broadly pale yellow in some specimens. The variability of antennal color patterns could not be fully assessed because parts of the antennae are missing in most specimens. In one specimen, the basal antennal segments are light brown with segments V–VII pale yellow. This may be a variant as all other specimens have a dark brown to black scape and pedicel. It is likely that segments V–VII are always pale yellow.

HOLOTYPE: Male: **Madagascar: Toliara:** Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 03 Dec 2008–11 Dec 2008, M. Irwin, R. Harin'Hala (00045571) (CAS).

PARATYPES: **Madagascar: Mahajanga:** 160 km N of Maevatanana on RN 04, Ampijoroa National Park, 16.31933°S 46.81333°E, 43 m, 07 Feb 2005–19 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00045511) (CAS). **Toliara:** Beroboka village, 45 km NE Morondava, 19.9775°S 44.66533°E, 128 m, 16 Oct 2008–24 Oct 2008, M. Irwin, R. Harin'Hala, 1♂ (00045574) (CAS); 09 Nov 2008–17 Nov 2008, M. Irwin, R. Harin'Hala, 1♂ (00044958) (CAS); 17 Nov 2008–25 Nov 2008, M. Irwin, R. Harin'Hala, 2♂ (00007161, 00045159) (USNM); 19 Dec 2008–27 Dec 2008, M. Irwin, R. Harin'Hala, 1♂ (00044937) (UCR). Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 30 Oct 2007–06 Nov 2007, M. Irwin, R. Harin'Hala, 2♂ (00006972, 00006975) (BMNH), 1♂ (00006977) (CAS); 22 Nov 2007–30 Nov 2007, M. Irwin, R. Harin'Hala, 2♂ (00007073, 00044898) (CAS), 2♂ (00045223, 00045525) (SU); 17 Nov 2008–25 Nov 2008, M. Irwin, R. Harin'Hala, 1♂ (00045070) (CAS); 25 Nov 2008–03 Dec 2008, M. Irwin, R. Harin'Hala, 1♂ (00045705) (UCR). **Unknown:** 1♂ (00045556) (CAS).

Toxopus brucei, new species

Figs. 2.3, 2.7, 2.10; Map 2.12

DIAGNOSIS: Males recognized among other species in this genus by the coloration, sparse vestiture, head as long as wide, smooth posterior pronotal lobe, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI. This species is similar to *T. steineri*, *T. namoroka*, and *T. vazimba*, but differs from these species by the features mentioned.

This species is most similar to *T. basalis*, from which it differs by the larger synthlipsis width, interocular sulcus near the hind margin of the eye, smaller eye width in lateral view, eye not reaching ventral head margin, and smooth posterior pronotal lobe.

DESCRIPTION: **MALE:** Body length: 12.61 mm (holotype), 11.00–12.70 mm. COLORATION: Blackish with pale yellow scape basally, antennal segments VI and VII, corium basally, trochanters, forefemur ventrally, mid and hind femora basally, tibiae medially, tarsi, anterior half of laterotergites, abdominal sternites III–VI medially except at margins, and anterolateral spots on sternites. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); as long as wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe smooth; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded or sinuate; intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L);

endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: This species epithet is a noun in the genitive case and is named after the senior author's uncle, Thomas Allen Bruce.

DISTRIBUTION: Mahajanga and south-central region of Toamasina provinces (Map 2.12).

DISCUSSION: The coloration is slightly variable with antennal segment V pale yellow, the corium, except basally, brown, the meso- and metasterna and sternite II with a medial yellow spot, and the medial spots on the sternites are not be bordered by dark brown margins.

HOLOTYPE: Male: **Madagascar: Mahajanga:** Besalampy District, Analangidro dry forest, 7 km NE of Besalampy, 16.6915°S 44.5235°E, 09 Oct 2007–16 Oct 2007, M. Irwin, R. Harin'Hala (00007133) (CAS).

PARATYPES: **Madagascar: Mahajanga:** Besalampy District, Analangidro dry forest, 7 km NE of Besalampy, 16.6915°S 44.5235°E, 61 m, 02 Oct 2007–09 Oct 2007, M. Irwin, R. Harin'Hala, 1♂ (00007039) (CAS); 09 Oct 2007–16 Oct 2007, M. Irwin, R. Harin'Hala, 1♂ (00007217) (SU); 14 Dec 2007–21 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00045338) (UCR). Besalampy District, Marofototra dry forest, 17 km W of Besalampy, 16.72166°S 44.42366°E, 52 m, 26 Nov 2007–03 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00044822) (CAS), 1♂ (00044972) (BMNH); 10 Dec 2007–17 Dec 2007, M. Irwin, R. Harin'Hala, 2♂ (00007043, 00007156) (AMNH), 2♂ (00007160, 00007170) (USNM), 2♂ (00007182, 00007223) (CAS), 1♂ (00045011) (BMNH); 17 Dec 2007–24 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00045155) (SU). Besalampy District, Marofototra palm forest, 17 km W of Besalampy, 16.71666°S 44.41666°E, 11 m, 10 Dec 2007–17 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00045286) (CAS). Maintirano District Asondrodava dry forest, 15 km N of Maintirano, 17.96533°S 44.0355°E, 61 m, 03 Dec 2007–10 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00006140) (CAS); 10 Dec 2007–17 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00007012) (UCR). Maintirano District, 50 km E of Maintirano, 18.004°S 44.452°E, 274 m, 25 Oct 2007–01 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00007193) (CAS). Namoroka village, Befatika Andranovory, 7 km NW Vilanandro village, 16.47333°S 45.39133°E, 122 m, 09 Nov 2007–16 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00007131) (CAS). Reserve Speciale de Bemarivo, 23.8 km 223° SW Besalampy, 16.925°S 44.36833°E, 30 m, 19 Nov 2002–23 Nov 2002, Fisher et al., 1♂ (00006149) (CAS). **Toamasina:** Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 05 Sep 2001–19 Sep 2001, M. Irwin, R. Harin'Hala, 1♂ (00044971) (CAS).

Toxopus farafangana, new species

Figs. 2.3, 2.7, 2.10; Map 2.11

DIAGNOSIS: Males are recognized among other *Toxopus* species by the coloration, ovoid head shape in lateral view, anteocular region as long as postocular, broad postocular, labial segment III ventrally convex, smooth posterior pronotal lobe, and BPE shorter than the basal plate. Males are similar to *T. pallidus*, but the dark brown to blackish posterior propleural lobe and thoracic sterna, predominately dark brown to blackish ventral abdominal surface, interocular sulcus near the hind margin of the eye, labial segment III ventrally convex, smooth posterior pronotal lobe, and BPE shorter than the basal plate distinguish *T. farafangana* from *T. pallidus*.

DESCRIPTION: **MALE:** Body length: 10.19 mm (holotype), 9.05–10.66 mm. COLORATION: Blackish with pale yellow anterior margin of antennifer, antennal segment V (except basally) and VI and VII, corium basally, mid and hind trochanters, forefemur ventrally, mid and hind femora basally and subapically, foretibia subbasally and apically, mid and hind tibiae apically and medially, tarsi, anterior half of laterotergites, small posterior paramedian stripes on abdominal sternites II–VII, lateral margin of sternites II and III, and anterolateral margin of sternites IV–VII. Labium except basal two-thirds of segment II, posterior pronotal lobe, and remainder of corium brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region as long as postocular (Fig. 2.13J); postclypeus with deep, broad medial longitudinal depression to middle of interocular area; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular moderately broad in dorsal view (Fig. 2.13B); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium slender; labial segment III shorter than II, ventrally convex (Fig. 2.13J). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly transversely striated; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore, apex rounded; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion ovate; endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after a locality near which known specimens were collected.

DISTRIBUTION: Southeastern region of the Fianarantsoa province (Map 2.11).

DISCUSSION: In some specimens, the coloration is slightly variable with the posterior pronotal lobe dark brown and the abdominal ventrolateral pale yellow spots sometimes larger on some sternites or absent.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 17 Feb 2007–24 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala (00007034) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 13 Jan 2007–20 Jan 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00044948, 00044974) (CAS); 20 Jan 2007–26 Jan 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006147, 00007265) (CAS); 26 Jan 2007–04 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00044798, 00045114) (CAS), 2♂ (00045438, 00045524) (BMNH); 26 Jan 2007–04 Feb 2007, M. Irwin, R. Harin'Hala, 1♂ (00045049) (UCR); 04 Feb 2007–10 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00007080, 00007207) (CAS); 17 Feb 2007–24 Feb 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00007230) (SU); 24 Feb 2007–03 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045346) (CAS); 03 Mar 2007–10 Mar 2007, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00007173, 00007175, 00007252) (USNM); 06 Sep 2007–13 Sep 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00007052) (CAS); 08 Nov 2007–22 Nov 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045221) (SU); 20 Dec 2007–27 Dec 2007, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00045003, 00045332) (AMNH); 03 Jan 2008–09 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044965) (CAS); 09 Jan 2008–17 Jan 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044938) (UCR); 16 Mar 2008–22 Mar 2008, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006729, 00044968) (CAS). Manombo Special Reserve camp site, 32 km SSE of Farafangana, 23.02183°S 47.72°E, 36 m, 12 Nov 2004–23 Nov 2004, M. Irwin, R. Harin'Hala, 1♂ (00045531) (CAS); 15 Dec 2004–26 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00044890) (SU); 16 Jan 2005–20 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00045258) (UCR).

Toxopus fisheri, new species

Figs. 2.3, 2.7, 2.10, 2.19H, 2.20K, 2.21J; Map 2.12

DIAGNOSIS: Males are recognized among other species in this genus by the sparse vestiture, coloration, elongate cylindrical head in lateral view, ventrally flat head surface, sublateral antennal insertion, labial segment III ventrally straight, and intersegmental sutures carinulate between sternites II and III and laterally between III–VI. This species is similar to *T. italaviana*, *T. griswoldi*, *T. antsiranana*, and *T. toliara*, but differs from these species by the ventrally flat head surface. *Toxopus fisheri* are also similar to *T. insignis*, from which it differs by the dark brown to blackish postclypeal depression, pale yellow maxillary plates and antennifers, and intersegmental sutures carinulate between sternites II and III and laterally between III–VI.

DESCRIPTION: **MALE:** Body length: 10.19 mm (holotype), 9.84–11.09 mm. COLORATION: Blackish with pale yellow maxillary plates dorsally, antennifer, scape basally, pedicel basally, base of antennal segment III, antennal segment VII, corium basally, coxae, trochanters, forefemur basally and subapically, mid and hind femora except medially, foretibia medially except lateral spots, mid and hind tibiae subbasally and medially, tarsi, laterotergites II and VII, anterior half of laterotergites III–VI, and abdominal sternites laterally and medially except intersternal sutures. Antennal segments V, VI, and apex of VII and labium brown. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Cylindrical in lateral view (Fig. 2.13J); longer than wide in dorsal view; ventrally flat; anteocular region longer than postocular (Fig. 2.13K); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli small, located on shallow median tubercle (Fig. 2.13J), separated by a distance less than or equal to diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about two-fifths longer than scape, slightly curved; labium slender; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe weakly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III and laterally between III–VI; pygophore process curved in lateral view (Fig. 2.20K), elongate in caudal view (Fig. 2.19H), surpassing dorsal margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion ovate (Fig. 2.21J); endosoma with sclerotized, hairlike, denticles on posterior margin (Fig. 2.21J).

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after Brian Fisher, who collected the majority of specimens examined for this species.

DISTRIBUTION: Antsiranana province (Map 2.12).

DISCUSSION: The coloration varies with the small medial longitudinal stripe on the postclypeus, meso- and metasterna, and mid tibia medially pale yellow in some specimens.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Forêt de Binara, 7.5 km 230° SW Daraina, 13.255°S 49.61666°E, 375 m, 01 Dec 2003, B.L. Fisher (00045439) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Forêt Bekaraoka, 6.8 km 60° ENE Daraina, 13.00277°S 49.01166°E, 150 m, 07 Dec 2003, B.L. Fisher, 1♂ (00045028) (UCR), 1♂ (00045100) (SU), 2♂ (00045143, 00045592) (CAS). Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 12.97°S 49.7°E, 175 m, 10 Dec 2003, B.L. Fisher, 1♂ (00045087) (CAS), 2♂ (00045141, 00045148) (SU), 1♂ (00045636) (UCR). Forêt de Binara, 7.5 km 230° SW Daraina, 13.255°S 49.61666°E, 375 m, 01 Dec 2003, B.L. Fisher, 1♂ (00045469) (CAS). Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 15 Dec 2004–20 Dec 2004, M. Irwin, R. Harin'Hala, 1♂ (00006969) (CAS); 05 Jan 2005–10 Jan 2005, M. Irwin, R. Harin'Hala, 1♂ (00006968) (UCR). Rés. Analamerana, 28.4 km 99° Anivorano-Nord, 12.74666°S 49.49472°E, 60 m, 05 Dec 2004, B.L. Fisher, 1♂ (00045431) (CAS).

Toxopus griswoldi, new species

Figs. 2.3, 2.4, 2.7, 2.10, 2.23E; Map 2.10

DIAGNOSIS: Males recognized among other *Toxopus* species by the small body size, sparse vestiture, coloration, elongate cylindrical head in lateral view, sublateral antennal insertion, labial segment III ventrally straight, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VII. In addition to the generic diagnostic characters, the slender, slightly curved hind tibia distinguishes females of this species from other known *Toxopus* females. Males are similar to *T. italaviana*, *T. insignis*, *T. fisheri*, *T. antsiranana*, and *T. toliara*, but differs from these species by the small body size. The sparse vestiture further distinguishes this species from *T. italaviana*, *T. antsiranana*, and *T. toliara*, while the intersegmental sutures carinulate between sternites II–IV and laterally between IV–VII differentiate *T. griswoldi* from *T. insignis* and *T. fisheri*.

DESCRIPTION: **MALE:** Body length: 9.28 mm (holotype), 8.74–9.76 mm. COLORATION: Blackish with pale yellow clypeus; antennifer; scape except apically, antennal segment VII except apically, collar, posterolateral pronotal margins, meso- and metasterna medially, scutellar processes, corium basally, coxae, trochanters, forefemur basally and subapically, mid and hind femora except medially, tibiae medially, tarsi, laterotergite II, anterior area of laterotergites III–

VII, and abdominal sternites medially and laterally. Antennal segment VI and apex of VII and labium brown. VESTITURE: Very sparse; other features as in generic description. STRUCTURE: HEAD: Cylindrical in lateral view (Fig. 2.13J); longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area (Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli small, located on shallow median tubercle (Fig. 2.13J), separated by diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-fourth longer than scape, slightly curved; labium slender; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–IV and laterally between IV–VII; pygophore process curved in lateral view (Fig. 2.20K), elongate in caudal view (Fig. 2.19H), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21K); endosoma with sclerotized, hairlike, denticles on posterior margin (Fig. 2.21J, K). **FEMALE:** Body length: 11.75 mm; in addition to characters mentioned in the generic description: STRUCTURE: HEAD: Synthlipsis about 3.5 times width of eye. THORAX: Hind tibia slender, slightly curved. ABDOMEN: Intersegmental sutures carinulate laterally between sternites II–VI; external genitalia as in plate 23E; bursa copulatrix membranous, damaged; vermiform gland and lateral spermatheca missing.

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after Charles Griswold, who collected the only known female specimen known for this species.

DISTRIBUTION: Mahajanga, Toliara, and the northern area of the Antananarivo provinces (Map 2.10).

DISCUSSION: Some specimens have pale yellow mandibular plates. The female specimen was associated with males based on morphology, geographic proximity, and molecular data (COI pairwise genetic distance 0.76%).

HOLOTYPE: Male: **Madagascar: Toliara:** Cap Ste Marie Special Reserve, 74 km S of Tsihombe, 25.58766°S 45.163°E, 37 m, 23 Nov 2003–30 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala (00045173) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 28 Dec 2003–10 Jan 2004, M. Irwin, R. Harin'Hala, 1♂ (00045139) (CAS); 14 Nov 2004–29 Nov 2004, M. Irwin, R. Harin'Hala, 1♂ (00045132) (UCR). **Mahajanga:** Ambovomamy Belambo, 20 km NW of Port Berger, 15.45116°S 47.61333°E, 33 m, 28 Oct 2007–06 Nov 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045234) (CAS); 23 Nov 2007–08 Dec 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044962) (SU); 08 Dec 2007–11 Dec 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045233) (AMNH); 26 Oct 2008–01 Nov 2008, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00044994, 00045075) (CAS), 2♂ (00045386, 00045645) (USNM); 16 Nov 2008–23 Nov 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045056) (CAS); 23 Nov 2008–30 Nov 2008, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045692) (UCR). Analamanitra Forest, 14 km NE of Misinjo, 16.13333°S 45.7°E, 20 m, 23 Oct 2007–30 Oct 2007, M. Irwin, R. Harin'Hala, 1♂ (00045008) (CAS); 30 Oct 2007–16 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00007148) (AMNH); 16 Nov 2007–20 Nov 2007, M. Irwin, R. Harin'Hala, 3♂ (00007096, 00007176, 00045025) (MNHN); 20 Nov 2007–04 Dec 2007, M.

Irwin, R. Harin'Hala, 2♂ (00044799, 00044896) (USNM). Anjiaabo, 3 km N Baly village, 16.059°S 45.27416°E, 7 m, 07 Nov 2007–24 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00007214) (CAS). Besalampy District, Analangidro dry forest, 7 km NE of Besalampy, 16.6915°S 44.5235°E, 61 m, 24 Sep 2007–02 Oct 2007, M. Irwin, R. Harin'Hala, 1♂ (00044806) (CAS); 18 Nov 2007–25 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00044886) (SU). Besalampy District, Marofototra dry forest, 17 km W of Besalampy, 16.72166°S 44.42366°E, 52 m, 19 Nov 2007–26 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00044880) (CAS); 26 Nov 2007–03 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00044885) (SU). Namoroka 53 km from Soalala 3 km N Vilanandro Village, 16.47333°S 45.39133°E, 122 m, 16 Nov 2007–23 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00007171) (BMNH), 1♂ (00007212) (CAS). Namoroka village, Befatika Andranovory, 7 km NW Vilanandro village, 16.47333°S 45.39133°E, 122 m, 02 Nov 2007–09 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00045002) (CAS). Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 16.40666°S 45.31°E, 100 m, 12 Nov 2002–16 Nov 2002, Fisher et al., 1♂ (00045095) (CAS), 1♂ (00045133) (SU); 12 Nov 2002–16 Nov 2002, Fisher et al., 1♀ (00045042) (CAS). Parc National de Namoroka, 17.8 km 329° WNW Vilanandro, 16.37666°S 45.32666°E, 100 m, 08 Nov 2002–12 Nov 2002, Fisher et al., 1♂ (00006435) (CAS). **Toliara:** Beroboka village, 45 km NE Morondava, 19.9775°S 44.66533°E, 128 m, 30 Sep 2008–08 Oct 2008, M. Irwin, R. Harin'Hala, 1♂ (00044841) (CAS); 08 Oct 2008–16 Oct 2008, M. Irwin, R. Harin'Hala, 1♂ (00045649) (AMNH); 09 Nov 2008–17 Nov 2008, M. Irwin, R. Harin'Hala, 2♂ (00044915, 00045565) (CAS); 11 Dec 2008–19 Dec 2008, M. Irwin, R. Harin'Hala, 1♂ (00045695) (UCR). Beroboka village, 45 km NE Morondava, 19.9775°S 44.82483°E, 131 m, 14 Oct 2007–18 Oct 2007, M. Irwin, R. Harin'Hala, 1♂ (00045110) (CAS); 18 Oct 2007–26 Oct 2007, M. Irwin, R. Harin'Hala, 2♂ (00044859, 00045096) (BMNH); 17 Nov 2008–25 Nov 2008, M. Irwin, R. Harin'Hala, 1♂ (00044814) (AMNH), 1♂ (00045041) (CAS); 05 Feb 2009–13 Feb

2009, M. Irwin, R. Harin'Hala, 1♂ (00045208) (CAS). Cap Ste Marie Special Reserve, 74 km S of Tsihombe, 25.58766°S 45.163°E, 37 m, 23 Nov 2003–30 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045379) (CAS). Parc National d'Andohahela, Ihazofotsy Parcelle III, 24.83083°S 46.53616°E, 80 m, 16 Dec 2002–26 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045333) (CAS); 21 Apr 2003–28 Apr 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00045635) (UCR).

Toxopus insignis, new species

Figs. 2.4, 2.7, 2.10, 2.14; Map 2.13

DIAGNOSIS: Males are recognized among other species in *Toxopus* by the sparse vestiture, coloration, elongate cylindrical head in lateral view, sublateral antennal insertion, straight pedicel, and labial segment III ventrally straight. This species is similar to *T. italaviana*, *T. griswoldi*, *T. fisheri*, *T. antsiranana*, and *T. toliara*, from which it differs by the straight pedicel. The ventrally flat head surface further differentiates *T. insignis* males from the mentioned species, except for *T. fisheri*, which can be discerned from by the pale yellow postclypeal depression, dark brown maxillary plates and antennifers, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI.

DESCRIPTION: **MALE:** Body length: 10.43 mm (holotype), 9.73–11.41 mm. COLORATION: Blackish with pale yellow postclypeal medial longitudinal depression, interocular sulcus, scape basally, posterior margin of mesosternum, corium basally, mid and hind coxae anteriorly, trochanters, forefemur ventrally and subapically, mid and hind femora basally and subapically, fore- and mid tibiae medially, small subbasal and subapical band on hind tibia, anterior half of laterotergites, and sternites laterally and medially except intersternal suture. Antennal segments VI and VII, labium, and rest of hind tibia brown. VESTITURE: Very sparse;

other features as in generic description. STRUCTURE: HEAD: Cylindrical in lateral view (Fig. 2.13J); longer than wide in dorsal view; ventrally flat; anteocular region longer than postocular (Fig. 2.13K); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli small, located on shallow median tubercle (Fig. 2.13J), separated by less than diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about one-third longer than scape, not distinctly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; pygophore process curved in lateral view (Fig. 2.20K), elongate in caudal view (Fig. 2.19H), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior ventral processes (Fig. 2.22G), posteriorly obscured by endosoma; area of endosomal struts–DPS fusion short, subquadrate; endosoma with sclerotized, hairlike, denticles on posterior margin (Fig. 2.21J, K).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the pale interocular sulcus.

DISTRIBUTION: Mahajanga and northern Antananarivo provinces (Map 2.13).

DISCUSSION: The pale yellow subapical band on the femora is sometimes absent.

HOLOTYPE: Male: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 14 Nov 2004–29 Nov 2004, M. Irwin, R. Harin'Hala (00045091) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 31 Oct 2003–07 Nov 2003, M. Irwin, R. Harin'Hala, 1♂ (00045115) (CAS); 07 Nov 2003–15 Nov 2003, M. Irwin, R. Harin'Hala, 1♂ (00045662) (UCR); 15 Oct 2004–01 Nov 2004, M. Irwin, R. Harin'Hala, 2♂ (00007098, 00045080) (CAS), 2♂ (00045147, 00045265) (SU), 3♂ (00045426, 00045594, 00045670) (AMNH); 01 Nov 2004–14 Nov 2004, M. Irwin, R. Harin'Hala, 1♂ (00045051) (UCR), 5♂ (00045057, 00045125, 00045130, 00045140, 00045671) (CAS), 1♂ (00045702) (SU); 14 Nov 2004–29 Nov 2004, M. Irwin, R. Harin'Hala, 3♂ (00044920, 00045009, 00045065) (AMNH), 6♂ (00044920, 00045009, 00045065, 00045073, 00045081, 00045082) (BMNH), 14♂ (00045090, 00045098, 00045108, 00045113, 00045116, 00045121, 00045122, 00045135, 00045138, 00045149, 00045160, 00045162, 00045168, 00045169, 00045664, 00045665, 00045668) (CAS), 2♂ (00045679, 00045690) (SU), 2♂ (00045696, 00045697) (UCR); 29 Nov 2004–07 Dec 2004, M. Irwin, R. Harin'Hala, 2♂ (00044856, 00045030) (UCR), 3♂ (00045031, 00045040, 00045043) (USNM), 13♂ (00045046, 00045055, 00045058, 00045060, 00045066, 00045084, 00045103, 00045126, 00045146, 00045150, 00045151, 00045158, 00045164) (CAS), 6♂ (00045165, 00045659, 00045661, 00045666, 00045673, 00045703) (MNHN), 2♂ (00045724, 00045725) (SU); 22 Dec 2004–06 Jan 2005, M. Irwin, R. Harin'Hala, 3♂ (00007068, 00045145, 00045587) (USNM). **Mahajanga:** Analamanitra Forest, 14 km NE of Misinjo, 16.13333°S 45.7°E, 20 m, 16 Nov 2007–20 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00007229) (CAS). Parc National Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Vazimba, 19.14194°S 44.82805°E, 50 m, 06 Nov 2001–10 Nov 2001, Fisher et al., 1♂ (00045054) (CAS). Réserve forestière Beanka, 50.7 km E

Maintirano, 17.88027°S 44.46888°E, 140 m, 28 Oct 2009–31 Oct 2009, B.L. Fisher et al., 1♂ (00006910) (CAS); 1♂ (00007081) (UCR).

Toxopus italaviana, new species

Figs. 2.4, 2.7, 2.10, 2.13B, 2.15B; Map 2.12

DIAGNOSIS: Males are recognized among other *Toxopus* species by the moderately dense vestiture, elongate cylindrical head shape in lateral view, broad postclypeal longitudinal depression, relatively large ocelli, antenna inserted sublaterally on the head, and labial segment III ventrally convex. This species is similar to *T. griswoldi*, *T. insignis*, *T. fisheri*, *T. antsiranana*, and *T. toliara*, but is distinguished by the diagnostic characters mentioned. The slightly larger ocelli further distinguish *T. italaviana* from the other species, except *T. toliara*. The intersegmental sutures carinulate between sternites II and III and laterally between III–VII also distinguish males of *T. italaviana* from these species, with the exception of *T. griswoldi*.

DESCRIPTION: **MALE:** Body length: 10.58 mm (holotype), 10.25–10.63 mm. COLORATION: Blackish with pale yellow mandibular and maxillary plates dorsally, postclypeus except laterally above eye, antennifer, scape basally, antennal segment VII basally, labial segment II ventroapically, labial segment III ventrobasally, anterolateral projections of pronotum, mesosternum anteromedially and posterolaterally, metasternum medially, corium basally, coxae, trochanters, forefemur basally and ventrally, mid femur basally and subapically, hind femur basally and apically, foretibia except basally, mid tibia except apically, hind tibia except medially and apically, laterotergite II, anterior half of dorsal laterotergites III–VII, ventral laterotergites III–VII, and abdominal sternites medially and laterally. Antennal segment VI and apex of VII, remainder of labium, and corium brown. VESTITURE: Moderately dense; other features as in generic description. STRUCTURE: HEAD (Fig. 2.13B): Cylindrical in lateral view

(Fig. 213J); longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region longer than postocular (Fig. 2.13K); synthlipsis about two times width of eye; interocular sulcus near hind margin of eye; postclypeus with shallow, broad medial longitudinal depression to middle of interocular area; postocular moderately broad in dorsal view; ocelli large, located on shallow median tubercle (Fig. 2.13J), separated by a distance less than or equal to diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about two-fifths longer than scape, slightly curved; labium stout; labial segment III ventrally convex (Fig. 2.13J). THORAX (Fig. 2.15B): Anterior pronotal lobe with small anterolateral projections; posterior pronotal lobe weakly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges; lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III and laterally between III–VII; pygophore process curved in lateral view (Fig. 2.20K), elongate in caudal view (Fig. 2.19H), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior ventral processes (Fig. 2.22G), posteriorly obscured by endosoma; area of endosomal struts–DPS fusion short, subquadrate; endosoma with sclerotized, hairlike, denticles on posterior margin (Fig. 2.21J, K).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Italaviana, Madagascar.

DISTRIBUTION: Italaviana, near the Antananarivo-Fianarantsoa border (Map 2.12).

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Italaviana, 35 km SSE of Antsirabe, 20.17333°S 47.086°E, 1360 m, 27 Feb 2005–13 Mar 2005, M. Irwin, R. Harin'Hala (00006433) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Italaviana, 35 km SSE of Antsirabe, 20.17333°S 47.086°E, 1360 m, 09 Dec 2002–19 Dec 2002, M. Irwin, R. Harin'Hala, 1♂ (00006965) (CAS); 10 Mar 2003–20 Mar 2003, M. Irwin, R. Harin'Hala, 1♂ (00006431) (CAS), 1♂ (00006966) (UCR); 15 Jul 2003–26 Jul 2003, M. Irwin, R. Harin'Hala, 4♂ (00006438, 00006439, 00006441, 00006445) (CAS), 2♂ (00006449, 00006450) (USNM); 16 Oct 2003–26 Oct 2003, M. Irwin, R. Harin'Hala, 2♂ (00006961, 00006963) (SU); 22 Jan 2004–04 Feb 2004, M. Irwin, R. Harin'Hala, 1♂ (00006962) (CAS); 24 Mar 2004–08 Apr 2004, M. Irwin, R. Harin'Hala, 1♂ (00006428) (CAS), 2♂ (00006429, 00006430) (BMNH); 27 Feb 2005–13 Mar 2005, M. Irwin, R. Harin'Hala, 1♂ (00006432) (UCR).

Toxopus melobrunneus, new species

Figs. 2.4, 2.7, 2.10; Map 2.11

DIAGNOSIS: Males are recognized among other species in *Toxopus* by a combination of the following characters: the large body size, coloration, cylindrical head shape in lateral view, smooth posterior pronotal lobe and lateral depressions, continuous pronotal transverse furrow, and intersegmental sutures carinulate between sternites II and III. Males are similar to males of *T. italaviana*, *T. griswoldi*, *T. insignis*, *T. fisheri*, *T. ambohitantely*, *T. antsiranana*, and *T. toliara*, but the continuous pronotal transverse suture and intersegmental sutures carinulate between sternites II and III distinguish *T. melobrunneus* from these species. The subtriangular pygophore process and medial endosomal sclerotization pattern further differentiate *T. melobrunneus* from these species, except from *T. ambohitantely*.

DESCRIPTION: **MALE:** Body length: 14.95 mm (holotype), 13.96–14.95 mm. COLORATION: Blackish with pale yellow area anterior to interocular sulcus, lateral and posterolateral margins of ocellar tubercle, anterolaterally from interocular sulcus, antennal segments V (except basally) and VI and VII, margins and longitudinal depression of metasternum, corium basally, femora basally, foretibia ventrally, anterior area of laterotergites III–VII, abdominal sternites II medially, anterolateral spots on sternites II–VII, and ventrolateral spots on sternites III–VII. VESTITURE: Dense; other features as in generic description. STRUCTURE: Head: Cylindrical in lateral view (Fig. 2.13J); longer than wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about 1.5 times width of eye; interocular sulcus posterior to hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on distinct median tubercle (Fig. 2.13H), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium slender; labial segment III ventrally straight (Fig. 2.13K). Thorax: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow continuous; lateral depressions of posterior pronotal lobe smooth; hemelytron surpassing abdominal apex. Abdomen: Apex rounded; intersegmental sutures carinulate between sternites II and III; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L); endosoma medially sclerotized (Fig. 2.21L).

Etymology: The species epithet is an adjective in the nominative case and is named for the mostly dark brown legs.

Distribution: Northern Fianarantsoa and southeastern Toliara provinces (Map 2.11).

DISCUSSION: Some specimens have more pale yellow on the ventral femoral and tibial surfaces and laterotergites, and can be reduced on the abdomen.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 30 Dec 2005–08 Jan 2006, M. Irwin, R. Harin'Hala (00007059) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Belle Vue at Talatakely, 21.2665°S 47.42016°E, 1020 m, 04 May 2003–16 May 2003, M. Irwin, R. Harin'Hala, 1♂ (00007037) (CAS), 1♂ (00007129) (UCR). Parc National Ranomafana, radio tower at forest edge, 21.251°S 47.40716°E, 1130 m, 07 May 2002–14 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00044926) (CAS), 1♂ (00044926) (USNM); 25 Jul 2002–03 Aug 2002, M. Irwin, R. Harin'Hala, 1♂ (00045238) (SU); 06 Jul 2003–17 Jul 2003, M. Irwin, R. Harin'Hala, 1♂ (00045291) (CAS); 12 Feb 2004–23 Feb 2004, M. Irwin, R. Harin'Hala, 1♂ (00007009) (CAS); 24 Jun 2004–08 Jul 2004, M. Irwin, R. Harin'Hala, 1♂ (00045275) (USNM); 12 Jul 2005–25 Jul 2005, M. Irwin, R. Harin'Hala, 1♂ (00044927) (USNM); 06 Nov 2005–13 Nov 2005, M. Irwin, R. Harin'Hala, 1♂ (00007127) (CAS); 07 Sep 2006–20 Sep 2006, M. Irwin, R. Harin'Hala, 2♂ (00007028, 00007196) (SU); 11 Nov 2006–18 Nov 2006, M. Irwin, R. Harin'Hala, 2♂ (00044935, 00044941) (UCR). **Toliara:** Forêt Ivohibe 55.0 km N Tolagnaro, 24.56888°S 47.20388°E, 200 m, 02 Dec 2006–04 Dec 2006, B.L. Fisher et al., 1♂ (00006728) (CAS). **Unknown:** 3♂ (00044925, 00044932, 00045243) (CAS).

Toxopus miandritsara, new species

Figs. 2.4, 2.7, 2.11; Map 2.10

DIAGNOSIS: Males are recognized among other species in this genus by a combination of the following characters: the coloration, ovoid head shape in lateral view, anteocular region longer than postocular, broad postocular, antenna inserted slightly sublaterally on the head, and smooth posterior pronotal lobe and lateral depressions. This species is similar to *T. simulans* and *T. toamasina*, but differs from these species by the light brown proximal part of the veins on the hemelytra, dark brown ventral abdominal surface, larger synthlipsis width, broad postocular, slight sublateral antennal insertion on the head, and smooth posterior pronotal lobe and lateral depressions. *Toxopus miandritsara* is further differentiated from *T. toamasina* by the intersegmental sutures carinulate between sternites II and III.

DESCRIPTION: **MALE:** Body length: 10.06 mm (holotype), 9.51–10.06 mm. COLORATION: Blackish with pale yellow corium basally, proximal wing veins, mid and hind coxae basally, mid and hind trochanters, femora basally and ventrally, foretibia subbasally and apically, mid and hind tibiae medially and apically, anterior one-third of laterotergites, and lateral margin of abdominal sternites II–VI. Mandibular and maxillary plates, labium, remainder of corium, and tarsi brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; ventrally with shallow medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli large, located on shallow median tubercle (Fig. 2.13J), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted slightly sublaterally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally convex (Fig. 2.13J). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions on pronotum smooth; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion hexagonal; endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Miandritsara Forest, Madagascar.

DISTRIBUTION: Miandritsara Forest in the Fianarantsoa province (Map 2.10).

DISCUSSION: The transverse suture between the meso- and metasterna and the ventrolateral spots on the anterior abdominal sternites are pale yellow in some specimens.

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Miandritsara Forest, 40 km S Ambositra, 20.79266°S 47.17566°E, 825 m, 26 Mar 2007–05 Apr 2007, M. Irwin, R. Harin'Hala (00044852) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** Miandritsara Forest, 40 km S Ambositra, 20.79266°S 47.17566°E, 825 m, 13 Nov 2006–22 Nov 2006, M. Irwin, R. Harin'Hala, 1♂ (00044848) (CAS); 22 Nov 2006–01 Dec 2006, M. Irwin, R. Harin'Hala, 1♂ (00044826) (CAS); 10 Dec 2006–19 Dec 2006, M. Irwin, R. Harin'Hala, 1♂ (00006148) (UCR); 28 Dec 2006–04 Jan 2007, M. Irwin, R. Harin'Hala, 2♂ (00044834, 00044970) (CAS), 1♂ (00044973) (SU); 31 Jan 2007–11 Feb 2007, M. Irwin, R. Harin'Hala, 1♂ (00006481) (UCR).

Toxopus namoroka, new species

Figs. 2.4, 2.7, 2.11; Map 2.13

DIAGNOSIS: Males are recognized among other *Toxopus* species by a combination of the following characters: the distinctive dark and pale coloration with red-brownish head and thoracic markings, sparse vestiture, narrow postclypeal depression, smooth posterior pronotal lobe, and intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII. Males are similar to males of *T. steineri*, *T. basalis*, *T. vazimba*, and *T. brucei*, but differs from these species by the very distinctive red-brown head and thorax, narrow postclypeal depression, eye about one-fourth of the head length, and intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII.

DESCRIPTION: **MALE:** Body length: 11.44 mm (holotype), 11.44–11.56 mm. COLORATION: Blackish with reddish-brown head, labium, scape, pedicel, antennal segment V, anterior pronotal lobe except pronotal longitudinal furrow, dorsal half of anterior propleural lobe, anterior margin of mesopleuron, scutellum, and legs (except coxae posteriorly and femora basally). Antennal segments VI and VII, corium basally, anterior half of laterotergites, abdominal sternites III–VI medially except at margins, and anterolateral spots on sternites pale yellow. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); longer than wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with shallow, narrow medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about one-fourth of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-third longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe smooth; wings spread out in specimens. ABDOMEN:

Apex rounded or sinuate; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the type locality, Tsingy de Namoroka National Park, Madagascar.

DISTRIBUTION: Tsingy de Namoroka National Park in the Mahajanga province (Map 2.13).

DISCUSSION: The medial pale yellow spots on the abdominal sternites may be divided by a brown medial longitudinal stripe, and the pale yellow spot on sternite VI may be reduced.

HOLOTYPE: Male: **Madagascar: Mahajanga:** Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 16.40666°S 45.31°E, 100 m, 12 Nov 2002–16 Nov 2002, Fisher et al. (00045251) (CAS).

PARATYPE: **Madagascar: Mahajanga:** Parc National de Namoroka, 16.9 km 317° NW Vilanandro, 16.40666°S 45.31°E, 100 m, 12 Nov 2002–16 Nov 2002, Fisher et al., 1♂ (00006477) (CAS).

Toxopus pallidus, new species

Figs. 2.4, 2.7, 2.11; Map 2.12

DIAGNOSIS: Males are recognized among other species in *Toxopus* by the smaller body size, coloration, ovoid head shape in lateral view, anteocular regions as long as postocular, labial segment III ventrally straight, and BPE as long as the basal plate. This species is similar to *T. farafangana*, from which it differs by the the pale yellow posterior propleural lobe and thoracic sterna, predominately pale to pale yellow ventral abdominal surface, interocular sulcus posterior to the hind margin of the eye, labial segment III ventrally straight, striated posterior pronotal lobe, and BPE as long as the basal plate. This species is also similar to *T. simulans*, but is distinguished by the slightly smaller body size, ventral head depression restricted to the anteocular region, anteocular as long as postocular, broader postocular, labial segment III ventrally straight, and intersegmental sutures carinulate between sternites II and III.

DESCRIPTION: **MALE:** Body length: 9.10 mm (holotype), 8.85–9.10 mm. COLORATION: Blackish with pale yellow scape basally, antennal segment V (except basally) and VI and VII; posterior propleural lobe, ventral half of mesopleuron, metapleuron, thoracic sterna, corium basally, coxae, trochanters, fore- and mid femora ventrally and basally, hind femur basally, foretibia ventrally, mid and hind tibiae except subbasally and apically, anterior margin of dorsal laterotergites, ventral laterotergites, abdominal sternites except lateral medial spots, and margins of pygophore. Labium and posterior pronotal lobe brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region as long as postocular (Fig. 2.13J); postclypeus with deep, narrow medial longitudinal depression to interocular sulcus; synthlipsis about 1.5 times width of eye; interocular sulcus posterior to hind margin of eye (Fig. 2.13B); postocular broad in dorsal view (Fig. 2.13B); ocelli large, located on shallow median tubercle (Fig. 2.13J), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), ventrally obscured by endosoma; area of endosomal struts–DPS fusion ovate; endosoma missing.

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the pale body coloration.

DISTRIBUTION: Ranomafana National Park in the Fianarantsoa province (Map 2.12).

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** Parc National de Ranomafana, Vatoharanana River, 4.1 km 231° SW Ranomafana, 21.29°S 47.43333°E, 1100 m, 27 Mar 2003–31 Mar 2003, Fisher et al. (00045432) (CAS).

PARATYPE: **Madagascar: Fianarantsoa:** Parc National Ranomafana, Vohiparara, at broken bridge, 21.22616°S 47.36983°E, 1110 m, 08 Apr 2002–15 Apr 2002, M. Irwin, R. Harin'Hala, 1♂ (00007192) (CAS).

Toxopus parkeri, new species

Figs. 2.4, 2.7, 2.11, 2.13K; Map 2.11

DIAGNOSIS: Males are recognized among other species in *Toxopus* by a combination of the following characters: the coloration, dense vestiture, subquadrate head in lateral view that is as long as wide in dorsal view, and ventrally depressed head surface, synthlipsis two times width of an eye, interocular sulcus anterior to the hind margin of the eye, intersegmental sutures carinulate between sternites II–VI; and BPE as long as basal plate. Males are very similar to *T. basalis*, *T. tibialis*, and *T. brucei*, but differ by the smaller body size, larger synthlipsis width, and interocular sulcus located anterior to the hind margin of the eye. The smaller eye size relative to the head length, the eyes not reaching the dorsal and ventral margins, larger synthlipsis width, and intersegmental sutures carinulate between sternites II–VI separate *T. parkeri* from *T. basalis*. The striated lateral depressions on the posterior pronotal lobe and intersegmental sutures carinulate between sternites II–VI differentiate *T. parkeri* from *T. brucei*.

DESCRIPTION: **MALE:** Body length: 12.22 mm (holotype), 11.52–13.34 mm. COLORATION: Blackish with pale yellow clypeus, postclypeal medial longitudinal depression, bases of scape and pedicel, antennal segment V (except basally) and VI and VII, meso- and metasterna, corium basally, forecoxa posteriorly, mid and hind coxae except laterally, trochanters, forefemur except dorsally, mid and hind femora basally, foretibia except basally, mid and hind tibiae medially, tarsi, anterior half of laterotergites, and abdominal sternites (except pygophore) medially and laterally. Scape and pedicel medially, antennal segment IV and base of V, and postclypeal medial longitudinal depression brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD (Fig. 2.13K): Subquadrate in lateral view; as long as wide in dorsal view; ventrally with shallow medial depression; anteocular region longer than postocular; postclypeus with shallow, broad medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus anterior to hind margin of eye; postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle, separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight. THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded or sinuate; intersegmental sutures carinulate between sternites II–VI; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after Frank Parker, who is one of the main CAS collectors for the taxonomic inventory of Madagascar.

DISTRIBUTION: Antananarivo, Mahajanga, and Toliara provinces (Map 2.11).

DISCUSSION: The antennae and postclypeus vary with respect to the extent of the dark brown coloration.

HOLOTYPE: Male: **Madagascar: Toliara:** Parc National d'Andohahela, Ihazofotsy Parcelle III, 24.83083°S 46.53616°E, 80 m, 16 Dec 2002–26 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala (00044875) (CAS).

PARATYPES: **Madagascar: Antananarivo:** 46 km NE of Ankazobe: Ambohitantely, 18.198°S 47.2815°E, 700 m, 20 Jan 2004–01 Feb 2004, M. Irwin, R. Harin'Hala, 1♂ (00006973) (UCR), 1♂ (00006974) (CAS). **Mahajanga:** Maintirano District Asondrodava dry forest, 15 km N of Maintirano, 17.96533°S 44.0355°E, 61 m, 03 Dec 2007–10 Dec 2007, M. Irwin, R. Harin'Hala, 1♂ (00007075) (CAS). **Toliara:** Parc National d'Andohahela, Ihazofotsy Parcelle III, 24.83083°S 46.53616°E, 80 m, 16 Dec 2002–26 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00044884) (CAS); 24 Feb 2003–06 Mar 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00007091, 00044897) (SU), 2♂ (00045204, 00045249) (CAS), 1♂ (00045381) (UCR); 21 Apr 2003–28 Apr 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00045052, 00045377) (USNM). **Unknown:** 1♂ (00006976) (CAS).

Toxopus politus Bergroth, 1905

Map 2.13

Toxopus politus Bergroth, 1905: 375

DISTRIBUTION: According to the original description, the type specimen was collected from Nosy Be Island off the northwest coast of Madagascar (Map 2.13).

DISCUSSION: We do not redescribe this species, since the only known specimen could not be located, and none of the specimens examined by us correspond to this species. Many of Bergroth's type specimens are deposited in the Zoological Museum, University of Helsinki, but Jansson & Coscarón (1989: appendix I) reported the female holotype of *T. politus* to be missing (or away on loan) from that collection. The specimen is still absent (Larry Huldén, personal commun.). Correspondence with other major European collections did not offer any further leads, and we speculate that the type specimen may be lost. The three female specimens of *Toxopus* examined during our study do not appear to be conspecific with *T. politus* based on differences in color patterns, ventral abdominal structure (segment VI medially longer than V in *T. politus*; subequal in female specimens), and locality information. A potential neotype designation will therefore have to await availability of additional *Toxopus* specimens.

Toxopus signoretii (Reuter), 1887, new combination

Fig. 2.12; Map 2.13

Cleptria signoretii Reuter, 1887: 107

REVISED DIAGNOSIS: Males are recognized among other *Toxopus* species by a combination of the following characters: the coloration, large body size, subquadrate head shape in lateral view that is as long as it is wide in dorsal view, eye reaching dorsal head surface, and synthlipsis about the width of an eye. This species is very similar to *T. tibialis*, *T. basalis*, and *T. parkeri*, but differs by the slightly larger body size, smaller synthlipsis width, and intersegmental sutures carinulate between sternites entirely between II–III and laterally between III–VI. *Toxopus signoretii* can be further differentiated from *T. parkeri* by the sparse vestiture, interocular sulcus near the hind margin of the eye, and eye about half width of the head lengths and not reaching the dorsal head surface. The interocular sulcus near the hind margin of the eye and the eye not reaching the dorsal but reaching the ventral head surface further distinguish *T. signoretii* from *T. basalis*. This species differs from *T. tibialis* by the sparse vestiture, ventral medial longitudinal depression on the head extending onto postocular surface, and eye about half width of the head lengths and not reaching the dorsal head surface.

REDESCRIPTION: **MALE:** Body length: 12.20 mm (holotype). COLORATION: Brownish with pale yellow postclypeal medial longitudinal depression, base of scape, corium basally, trochanters, forefemur basally and ventrally, mid and hind femora except dorsomedially, foretibia except basally, mid and hind tibiae medially, mid tarsi (fore- and hind missing), anterior half of dorsal laterotergites, and abdominal sternites (except pygophore) paramedially and laterally. VESTITURE: Sparse; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); about as long as wide in dorsal view; ventrally with longitudinal depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); ocelli large, located on distinct median tubercle (Fig. 2.13H), separated by less than diameter of ocellus; postocular narrow in dorsal view (Fig. 2.13A); eye about half of head length, reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about as long as scape, curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); posterior pronotal lobe smooth; lateral depressions of posterior pronotal lobe smooth; hemelytron nearly reaching abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites entirely between II–III and laterally between III–VI.

DISTRIBUTION: The holotype and one juvenile were collected from Nosy Be Island off the northwest coast of Madagascar (Map 2.13). One specimen was collected from Vohemar, which is on the northeast coast of Madagascar.

DISCUSSION: The redescription is based on habitus images and Reuter's (1887) original description of the holotype. The original description indicates that one immature specimen was collected (coll. Stumpff) in "Loucoubé," which is currently known as the Natural Reserve of Lokobe on Nosy Be Island. Reuter described this species in the genus *Cleptria* Stål, 1859, but did not provide arguments for assigning it to that genus. This species is transferred to *Toxopus* based on the 7-segmented antenna, head being longer than or as long as the width, subequal lengths of labial segments II and III, and apterous females, which are features differentiating *Toxopus* from *Cleptria*.

HOLOTYPE: Male: **Madagascar: Antsiranana:** Nosy Be, 13.31502°S 48.25926°E, 155 m (NMW).

PARATYPE: **Madagascar: Antsiranana:** Nosy Be, 13.31502°S 48.25926°E, 155 m, 1 juv. (MNHN).

OTHER MATERIAL EXAMINED: **Madagascar: Antsiranana:** Vohémar, 13.37028°S 50.00337°E, 6 m, 1♂ (MNHN). **Unknown:** 1♂ (NMW).

Toxopus simulans, new species

Figs. 2.4, 2.7, 2.11; Map 2.13

DIAGNOSIS: Males recognized among other *Toxopus* species by the coloration, ovoid head shape in lateral view that is longer than wide in dorsal view, anteocular region longer than postocular, narrow postocular, and labial segment III ventrally convex. This species is most similar to *T. pallidus*, but the slightly larger body size, ventral medial depression extending along the entire head surface, longer anteocular region relative to the postocular, interocular sulcus located near the hind margin of the eye, narrower postocular in dorsal view, and ventrally convex labial segment III distinguishes this species from *T. pallidus*.

DESCRIPTION: **MALE:** Body length: 11.53 mm (holotype), 10.89–11.62 mm. COLORATION: Blackish with pale yellow antennal segments V (except basally) and VI and VII, meso- and metasterna, coxae, trochanters, forefemur ventrally, mid and hind femora except large subapical band, mid and hind tibiae medially, tarsi, anterior one-third of dorsal laterotergites, ventral laterotergites, and abdominal sternites (except pygophore) medially and laterally. Mandibular and maxillary plates, postclypeal medial longitudinal depression, labium, posterior pronotal lobe, corium, and lateral longitudinal band across sternites varying shades of brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); longer than wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, narrow medial longitudinal depression to interocular sulcus; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on distinct median tubercle (Fig. 2.13H), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally convex (Fig. 2.13J). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe weakly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion short, subquadrate; endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a participle in the nominative case and is named for the similar body coloration with *Toxopus pallidus*.

DISTRIBUTION: Toamasina and northern Antsiranana provinces (Map 2.13).

HOLOTYPE: Male: **Madagascar: Antsiranana:** Parc National Montagne d'Ambre, 12.51444°S 49.18138°E, 960 m, 04 Mar 2001–19 Mar 2001, M. Irwin, R. Harin'Hala (00045508) (CAS).

PARATYPES: **Madagascar: Antsiranana:** Parc National Montagne d'Ambre, 12.52027°S 49.17916°E, 1125 m, 14 May 2001–30 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00007226) (CAS). Sakalava Beach, dwarf littoral forest, 12.26277°S 49.3975°E, 10 m, 20 Aug 2001–28 Aug 2001, M. Irwin, R. Harin'Hala, 1♂ (00045363) (CAS). 7 km N of Joffreville, 12.33333°S 49.25°E, 360 m, 13 May 2001–16 May 2001, M. Irwin, R. Harin'Hala, 1♂ (00045123) (SU). **Toamasina:** Botanic Garden near entrance to Andasibe National Park, 18.92633°S 48.40783°E, 1025 m, 01 Nov 2001–07 Nov 2001, M. Irwin, R. Harin'Hala, 1♂ (00007048) (UCR). **Unknown:** 1♂ (00045124) (CAS).

Toxopus steineri, new species

Figs. 2.4, 2.7, 2.11; Map 2.12

DIAGNOSIS: Males recognized among other species in *Toxopus* by the coloration, dense vestiture, narrow postclypeal depression, ventrally straight labial segment III, smooth posterior pronotal lobe, and intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI. This species is similar to *T. namoroka*, *T. basalis*, *T. vazimba*, and *T. brucei*, but the dark brown to blackish ventral abdominal surface, narrow postclypeal depression, and ventrally straight labial segment III distinguishes *T. steineri* from these other species.

DESCRIPTION: **MALE:** Body length: 11.14 mm (holotype), 11.00–11.59 mm. COLORATION: Blackish with pale yellow bases of scape and pedicel, antennal segment V distally and segments VI and VII, posterolateral margins of pronotum, lateral areas of transverse sulcus between meso- and metasterna, coxae, trochanters, base forefemur, forefemur subapically and ventrally, mid and hind femora basally and apically, foretibia medially, mid tibia except subbasally and apically, hind tibia basally, foretarsi, mid and hind tarsi basally, corium basally, anterior one-third to half of laterotergites, and abdominal sternites laterally except posterior two-thirds of segments VI and VII. Maxillary plates dorsally, postclypeal longitudinal depression, paramedially along interocular sulcus, basal half of antennal segment V, labium, mid and hind tarsi apically, and anterior margin of corium (except basally) dark yellow to brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); longer than wide in dorsal view; ventrally with deep longitudinal depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, narrow medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about two-fifths longer than scape, slightly curved; labium stout; labial segment III ventrally convex (Fig. 2.13J). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), ventrally obscured by semiextended endosoma; area of endosomal struts–DPS fusion subquadrate; endosoma sclerotized medially (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in the genitive case and is named after Ranomafana, Madagascar, which is near the type locality.

DISTRIBUTION: Known from a single locality west of Ranomafana in the Fianarantsoa province (Map 2.12).

HOLOTYPE: Male: **Madagascar: Fianarantsoa:** 7 km W Ranomafana, 21.25923°S 47.38664°E, 900 m, 23 Feb 1990–28 Feb 1990, W.E. Steiner (00026334) (USNM).

PARATYPES: **Madagascar: Fianarantsoa:** 7 km W Ranomafana, 21.25923°S 47.38664°E, 900 m, 23 Feb 1990–28 Feb 1990, W.E. Steiner, 3♂ (00026332, 00026333, 00026335) (USNM).

Toxopus tibialis, new species

Figs. 2.4, 2.7, 2.11; Map 2.11

DIAGNOSIS: Males are recognized among other species in *Toxopus* by a combination of the following characters: the relatively larger body size, moderately dense vestiture, head as long as it is wide in dorsal view, ventral depression on the head restricted to the anteocular region, eye about one-third of head length, eye not reaching dorsal or ventral head margins, and intersegmental sutures carinulate between sternites II–VI. Males are most similar to *T. basalis* and *T. parkeri*, from which it differs by the larger body size, ventral anteromedial depression on the head, and interocular sulcus located near the hind margin of the eye. The denser vestiture, smaller eye size that does not reach the dorsal and ventral head margins, and intersegmental sutures carinulate between sternites II–VI further differentiates *T. tibialis* from *T. basalis*. A smaller synthlipsis width further distinguished *T. tibialis* from *T. parkeri*.

DESCRIPTION: **MALE:** Body length: 14.52 mm (holotype), 13.89–15.40 mm. COLORATION: Blackish with pale yellow clypeus, dorsal margins of mandibular and maxillary plates, postclypeal medial longitudinal depression, antennifer, scape basally, antennal segments V–VII, mesosternum except medial longitudinal depression, metasternum medially, corium basally, mid and hind coxae, trochanters, base of forefemur, for femur ventrally and subbasally, mid and hind femora except small apical and large medial bands, tibiae medially, tarsi, anterior half of laterotergites, and abdominal sternites (except pygophore) medially, and lateral margin of sternites. Labium brown. VESTITURE: Moderately dense; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); as long as wide in dorsal view; ventrally with deep anteromedial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about 1.5 times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on distinct median tubercle (Fig. 2.13H), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe weakly transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–VI; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is an adjective in the nominative case and is named for the pale coloration of the tibia.

DISTRIBUTION: Antsiranana and Mahajanga provinces in Madagascar (Map 2.11).

DISCUSSION: The clypeus, mandibular and maxillary plates, and postclypeus are slightly darker in some specimens.

HOLOTYPE: Male: Male: **Madagascar: Antsiranana:** Forêt Ambanitaza, 26.1 km 347° Antalaha, 14.67944°S 50.18361°E, 240 m, 26 Nov 2004, B.L. Fisher (00045457) (CAS).

PARATYPES: **Madagascar: Antsiranana:** 7 km N of Joffreville, 12.33333°S 49.25°E, 360 m, 22 Jan 2001–26 Jan 2001, M.E. Irwin, E.L. Schlinger, R. Harin'Hala, 1♂ (00044821) (CAS). Forêt d'Ampondrabe, 26.3 km 10° NNE Daraina, 12.97°S 49.7°E, 175 m, 10 Dec 2003, B.L. Fisher, 1♂ (00045701) (CAS). Marojejy National Park, 5 km W Manantenina village, Camp Mantella, 14.43816°S 49.774°E, 490 m, 11 Feb 2005–18 Feb 2005, M. Irwin, R. Harin'Hala, 1♂ (00045492) (SU). **Mahajanga:** Réserve forestière Beanka, 50.2 km E Maintirano, 18.02638°S 44.05055°E, 250 m, 19 Oct 2009–26 Oct 2009, B.L. Fisher et al., 1♂ (00044854) (UCR). **Unknown:** 1♂ (00045637) (CAS).

Toxopus toamasina, new species

Figs. 2.4, 2.7, 2.11; Map 2.10

DIAGNOSIS: Males are recognized among other species in this genus by the coloration, ovoid head shape in lateral view that is as long as it is wide in dorsal view, synthlipsis about as wide as an eye, narrow postocular, eye about half the length of the head in lateral view and reaching the dorsal and ventral head margins, and intersegmental sutures carinulate between sternites II and III and laterally between III–V. This species is similar to *T. simulans*, but differs by the generally darker coloration, apex of corium light brown, head as long as it is wide, smaller synthlipsis width, eye one-half of the head length in lateral view, eye height relative to dorsal and ventral head margins, labial segment III ventrally straight, and intersegmental sutures carinulate between sternites II and III and laterally between III–V.

DESCRIPTION: **MALE:** Body length: 12.04 mm (holotype), 11.22–12.41 mm. COLORATION: Blackish with pale yellow margins of ocellar tubercle except posteromedial area, antennal segments V (except basally) and VI and VII, mid and hind coxae, trochanters, forefemur except dorsally, mid and hind femora except subapically, mid and hind tibiae except subbasally and apically, tarsi, anterior half of dorsal laterotergites, ventral laterotergites, paramedial spots on abdominal sternites II–VI, and lateral margin of abdomen. Labium, posterolateral pronotal lobe, and corium apically brown. VESTITURE: Moderately dense; other features as in generic description. STRUCTURE: HEAD: Ovoid in lateral view (Fig. 2.13F); as long as wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on distinct median tubercle (Fig. 2.13H), separated by less than diameter of ocellus; eye about half of head length, reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe transversely striated; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe transversely striated; hemelytron surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II and III and laterally between III–V; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore; BPE as long as basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21J, K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21K); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the Toamasina province in Madagascar, where all known specimens were collected.

DISTRIBUTION: Eastern region the Toamasina province (Map 2.10).

DISCUSSION: In some specimens, the scutellar processes and abdominal sternite II are pale yellow, the pale yellow ventrolateral abdominal spots vary in size.

HOLOTYPE: Male: **Madagascar: Toamasina:** Parcelle E3, Tampolo, 17.28333°S 49.43333°E, 10 m, 14 Apr 2004, Malagasy Ant Team (00006478) (CAS).

PARATYPES: **Madagascar: Toamasina:** Mobot Site, Analalava 7 km SW of Foulpointe, 17.69333°S 49.46027°E, 18 m, 03 Jan 2008–11 Jan 2008, M. Irwin, R. Harin'Hala, 2♂ (00007095, 00044942) (CAS); 11 Jan 2008–18 Jan 2008, M. Irwin, R. Harin'Hala, 1♂ (00006394) (CAS); 22 Feb 2008–29 Feb 2008, M. Irwin, R. Harin'Hala, 1♂ (00045546) (SU); 04 Apr 2008–11 Apr 2008, M. Irwin, R. Harin'Hala, 1♂ (00007056) (SU); 18 Apr 2008–25 Apr 2008, M. Irwin, R. Harin'Hala, 1♂ (00007078) (UCR); 25 Apr 2008–02 May 2008, M. Irwin, R.

Harin'Hala, 1♂ (00045537) (UCR). Parcelle E3, Tampolo, 17.28333°S 49.43333°E, 10 m, 14 Apr 2004, Malagasy Ant Team, 1♂ (00007218) (CAS).

Toxopus toliara, new species

Figs. 2.4, 2.7, 2.11, 2.21K; Map 2.10

DIAGNOSIS: Males are recognized among other *Toxopus* species by the coloration, moderately dense vestiture, elongate cylindrical head in lateral view, relatively large ocelli, antenna inserted sublaterally on the head, ventrally straight labial segment III, and smooth posterior pronotal lobe. This species is similar to *T. italaviana*, *T. griswoldi*, *T. insignis*, *T. fisheri*, and *T. antsiranana*, but is distinguished by the diagnostic features mentioned.

DESCRIPTION: **MALE:** Body length: 11.02 mm (holotype), 10.39–12.54 mm. COLORATION: Blackish with pale yellow maxillary plates dorsally; antennifers postclypeal medial longitudinal depression, paramedian longitudinal stripes on postclypeus anterior of interocular sulcus that extend laterally along interocular sulcus, labium, scape basally, antennal segment VII, collar, pronotum anterolaterally, anterolateral margin of posterior pronotal lobe, meso- and metasterna medially except transverse sulcus, corium basally, coxae, trochanters, fore- and mid femora basally and subapically, hind femur except medially, foretibia basally and medially except lateral spots, base of mid tibia, mid tibia subbasally and medially, hind tibia basally and subapically, tarsi, anterior half of laterotergites, and abdominal sternites laterally and medially, except intersternal sutures. Antennal segments V and VI and remainder of corium brown. VESTITURE: Moderately dense; other features as in generic description. STRUCTURE: HEAD: Cylindrical in lateral view (Fig. 2.13J); longer than wide in dorsal view; ventrally with shallow anteromedial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with shallow, narrow medial longitudinal depression to middle of interocular area

(Fig. 2.13B); synthlipsis about two times width of eye; interocular sulcus near hind margin of eye (Fig. 2.13B); postocular moderately broad in dorsal view; ocelli large, located on shallow median tubercle (Fig. 2.13J), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted sublaterally on head; pedicel about two-fifths longer than scape, slightly curved; labium slender; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly to strongly transversely striated; hemelytron reaching or surpassing abdominal apex. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–IV and laterally between IV–VI; pygophore process curved in lateral view (Fig. 2.20K), elongate in caudal view (Fig. 2.19H), surpassing posterior margin of pygophore; BPE shorter than basal plate; endosomal struts reaching posterior margin of DPS (Fig. 2.21K), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate subquadrate (Fig. 2.21K); endosoma with sclerotized, hairlike, denticles on posterior margin (Fig. 2.21K).

ETYMOLOGY: The species epithet is a noun in apposition and is named after the Toliara province in Madagascar, where a majority of the specimens examined were collected.

DISTRIBUTION: Fianarantsoa, Mahajanga, and Toliara provinces (Map 2.10).

DISCUSSION: The coloration is highly variable with the pale yellow markings more extensive or reduced on the head, pronotum, scutellar processes, and legs.

HOLOTYPE: Male: **Madagascar: Toliara:** Berenty Special Reserve, 8 km NW Amboasary, 25.021°S 46.3055°E, 35 m, 28 Feb 2004–24 Mar 2004, M. Irwin, F. Parker, R. Harin'Hala (00006598) (CAS).

PARATYPES: **Madagascar: Fianarantsoa:** 50 km S of Farafangana, Mahabo Mananivo, Ampitavananima Forest, 23.12983°S 47.717°E, 34 m, 06 Sep 2007–13 Sep 2007, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006614) (CAS). **Mahajanga:** Besalampy District, Marofototra dry forest, 17 km W of Besalampy, 16.72166°S 44.42366°E, 52 m, 19 Nov 2007–26 Nov 2007, M. Irwin, R. Harin'Hala, 1♂ (00044907) (CAS). **Toliara:** Andohahela Natl Park, Tsimelahy, Parcelle II, 24.93683°S 46.62666°E, 180 m, 27 Dec 2002–06 Jan 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006639, 00006643) (CAS); 05 Feb 2003–15 Feb 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006674) (CAS); 15 Feb 2003–26 Feb 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006628) (BMNH); 18 Mar 2003–28 Mar 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006626) (CAS); 29 Jun 2003–10 Jul 2003, M. Irwin, F. Parker, R. Harin'Hala, 6♂ (00006618, 00006627, 00006629, 00006630, 00006632, 00006634) (USNM); 17 Aug 2003–24 Aug 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006676) (CAS); 01 Oct 2003–11 Oct 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006647, 00006669) (SU); 30 Oct 2003–09 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006660, 00006666) (CAS); 30 Nov 2003–11 Dec 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006673, 00006675) (UCR); 21 Dec 2003–23 Dec 2003, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006579–00006581) (AMNH); 15 Jan 2004–28 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006609–00006611) (CAS); 28 Jan 2004–12 Feb 2004, M. Irwin, F. Parker, R. Harin'Hala, 6♂ (00006625, 00006633, 00006636, 00006638, 00006640, 00006644) (BMNH); 06 Mar 2004–18 Mar 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006617) (UCR). Berenty Special Reserve, 8 km NW Amboasary, 25.00666°S 46.30333°E, 85 m, 25 Oct 2002–26 Oct 2002, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006649, 00006663) (AMNH); 02 Nov 2002–09 Nov 2002, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006667, 00006681) (CAS); 30 Nov 2002–07 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006622) (UCR); 07 Dec 2002–14 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂

(00006665) (SU); 14 Dec 2002–16 Dec 2002, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006615) (CAS); 27 Dec 2002–07 Jan 2003, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006436, 00006442, 00006446) (USNM), 11♂ (00006448, 00006451, 00006601–00006608, 00006664) (CAS); 26 Jan 2003–05 Feb 2003, M. Irwin, F. Parker, R. Harin'Hala, 7♂ (00006695–00006701) (CAS); 24 Mar 2003–03 Apr 2003, M. Irwin, F. Parker, R. Harin'Hala, 6♂ (00006566–00006570, 00045618) (CAS); 14 Apr 2003–24 Apr 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00005357, 00006624) (AMNH); 24 Apr 2003–03 May 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006599, 00006600) (MNHN); 14 May 2003–25 May 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006595, 00006596) (CAS); 25 May 2003–04 Jun 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006679) (UCR); 04 Jun 2003–10 Jun 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006646, 00006678) (CAS); 08 Nov 2003–15 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006677) (CAS); 22 Nov 2003–30 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006525–00006527) (MNHN); 14 Dec 2003–21 Dec 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006577, 00006578) (CAS); 21 Dec 2003–02 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006592, 00006593) (CAS); 02 Jan 2004–13 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006558) (SU); 13 Jan 2004–23 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006561, 00006562) (CAS); 04 Feb 2004–15 Feb 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006571, 00006572) (CAS); 15 Feb 2004–02 Mar 2004, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006619, 00006621, 00006680) (BMNH); 02 Mar 2004–11 Mar 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006559, 00006560) (CAS); 05 Apr 2004–15 Apr 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006563, 00006564) (MNHN); 30 Apr 2004–01 May 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006443) (SU); 14 May 2004–27 May 2004, M. Irwin, F. Parker, R. Harin'Hala, 4♂ (00006582–00006585) (CAS); 20 Jun 2004–30 Jun 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006657) (CAS); 30 Jun 2004–11 Jul 2004, M. Irwin, F.

Parker, R. Harin'Hala, 2♂ (00006691, 00006692) (CAS); 25 Jul 2004–07 Aug 2004, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006574–00006576) (MNHN); 22 Aug 2004–01 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006565) (SU); 01 Sep 2004–08 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006591) (UCR). Berenty Special Reserve, 8 km NW Amboasary, 25.021°S 46.3055°E, 35 m, 10 Jun 2003–19 Jun 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006524) (CAS); 22 Nov 2003–30 Nov 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006694) (UCR); 07 Dec 2003–14 Dec 2003, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006689, 00006690) (AMNH); 21 Dec 2003–01 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006682, 00006683) (CAS); 02 Jan 2004–13 Jan 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006686) (SU); 15 Feb 2004–28 Feb 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006620) (CAS); 28 Feb 2004–24 Mar 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006597) (CAS); 24 Mar 2004–04 Apr 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006573, 00006685) (USNM); 04 Apr 2004–15 Apr 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006594) (CAS); 29 Apr 2004–11 Jun 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006612, 00006613) (BMNH); 23 Jun 2004–04 Jul 2004, M. Irwin, F. Parker, R. Harin'Hala, 3♂ (00006468, 00006650, 00006684) (AMNH); 04 Jul 2004–18 Jul 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006623) (MNHN); 31 Jul 2004–15 Aug 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006693) (CAS); 29 Aug 2004–08 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006589) (SU); 08 Sep 2004–21 Sep 2004, M. Irwin, F. Parker, R. Harin'Hala, 2♂ (00006687, 00006688) (CAS); 21 Sep 2004–07 Oct 2004, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006590) (UCR). Beza Mahafaly Reserve, Parcelle II near Bellevue, 23.68983°S 44.5755°E, 180 m, 16 Jan 2002–18 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00006637) (CAS); 18 Jan 2002–25 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00044812) (UCR). Beza Mahafaly Reserve, Parcelle I near research station, 23.6865°S 44.591°E, 165 m, 15 Oct 2001–10 Nov 2001, M.E.

Irwin, F.D. Parker, R. Harin'Hala, 1♂ (00045584) (CAS); 10 Nov 2001–21 Nov 2001, R. Harin'Hala, 1♂ (00006586) (UCR); 21 Nov 2001–28 Nov 2001, R. Harin'Hala, 2♂ (00006099, 00006118) (SU); 28 Nov 2001–04 Dec 2001, R. Harin'Hala, 1♂ (00006653) (CAS); 04 Dec 2001–11 Dec 2001, R. Harin'Hala, 2♂ (00006645, 00006670) (BMNH); 18 Dec 2001–25 Dec 2001, R. Harin'Hala, 2♂ (00006119, 00006437) (CAS), 2♂ (00006635, 00006642) (MNHN); 16 Jan 2002–18 Jan 2002, R. Harin'Hala, 2♂ (00006654, 00006659) (USNM); 01 Feb 2002–08 Feb 2002, R. Harin'Hala, 1♂ (00006668) (USNM); 10 Apr 2002–29 Apr 2002, R. Harin'Hala, 2♂ (00006658, 00006662) (CAS); 08 Jun 2002–18 Jun 2002, R. Harin'Hala, 2♂ (00006440, 00006444) (AMNH); 28 Jun 2002–07 Jul 2002, R. Harin'Hala, 1♂ (00006434) (UCR); 07 Jul 2002–18 Jul 2002, R. Harin'Hala, 1♂ (00006652) (CAS); 09 Sep 2002–20 Sep 2002, R. Harin'Hala, 2♂ (00006648, 00006651) (SU); 20 Sep 2002–05 Oct 2002, R. Harin'Hala, 1♂ (00006656) (CAS); 09 Jan 2003–23 Jan 2003, R. Harin'Hala, 1♂ (00006641) (CAS); 21 Apr 2003–29 Apr 2003, R. Harin'Hala, 1♂ (00006616) (UCR). Cap Ste Marie Special Reserve, 74 km S of Tsihombe, 25.58766°S 45.163°E, 37 m, 02 Jun 2003–10 Jun 2003, M. Irwin, F. Parker, R. Harin'Hala, 1♂ (00006447) (CAS). Mikea Forest, NW of Manombo, 22.90366°S 43.4755°E, 30 m, 06 Jan 2002–16 Jan 2002, M. Irwin, R. Harin'Hala, 1♂ (00006661) (CAS); 28 Mar 2002–08 Apr 2002, M. Irwin, R. Harin'Hala, 2♂ (00006587, 00006588) (SU); 29 Apr 2002–09 May 2002, M. Irwin, R. Harin'Hala, 1♂ (00006672) (UCR); 06 Mar 2003–17 Mar 2003, M. Irwin, R. Harin'Hala, 1♂ (00006671) (UCR); 27 Jul 2003–03 Aug 2003, M. Irwin, R. Harin'Hala, 2♂ (00006631, 00006655) (CAS).

Toxopus vazimba, new species

Figs. 2.4, 2.7, 2.11, 2.19I, 2.20L, 2.21L; Map 2.10

DIAGNOSIS: Males recognized among other species in *Toxopus* by the coloration, dense vestiture, interocular sulcus anterior to the hind margin of the eye, smooth posterior pronotal lobe, and intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII. This species is similar to *T. steineri*, *T. namoroka*, *T. basalis*, and *T. brucei*, but is distinguished from these species by the features mentioned.

DESCRIPTION: **MALE:** Body length: 11.27 mm (holotype), 11.27–12.71 mm. COLORATION: Blackish with pale yellow clypeus, postclypeal medial longitudinal depression, antennifer, scape basally, pedicel basally, antennal segment VII, anterolateral and anteromedial margins of pronotum, meso- and metasterna, corium basally, coxae, trochanters, forefemur ventrally and basally, mid and hind femora basally, fore- and mid tibiae except lateral stripes, hind tibia except apically, tarsi, anterior areas of laterotergites, abdominal sternites medially, lateral margin of sternite II, anterolateral and posterolateral margins of sternites III–VI, and anterolateral margin of sternite VII. Labium and antennal segment VI brown. VESTITURE: Dense; other features as in generic description. STRUCTURE: HEAD: Subquadrate in lateral view (Fig. 2.13K); longer than wide in dorsal view; ventrally with deep medial depression; anteocular region longer than postocular (Fig. 2.13K); postclypeus with deep, broad medial longitudinal depression to interocular sulcus; synthlipsis about two times width of eye; interocular sulcus anterior to hind margin of eye; postocular narrow in dorsal view (Fig. 2.13A); ocelli large, located on shallow median tubercle (Fig. 2.13K), separated by less than diameter of ocellus; eye about one-third of head length, not reaching dorsal and ventral head surfaces; antenna inserted dorsally on head; pedicel about one-fourth longer than scape, slightly curved; labium stout; labial segment III ventrally straight (Fig. 2.13K). THORAX: Anterior pronotal lobe with very small anterolateral projections (Fig. 2.15B); posterior pronotal lobe smooth; pronotal transverse furrow divided by paramedian longitudinal ridges (Fig. 2.15B); lateral depressions of posterior pronotal lobe weakly transversely striated; wings spread out in specimens. ABDOMEN: Apex rounded; intersegmental sutures carinulate between sternites II–VI and laterally between VI and VII; pygophore process subtriangular in caudal view (Fig. 2.19I), not surpassing posterior margin of pygophore, apex rounded; BPE shorter than basal plate; endosomal struts not reaching posterior margin of DPS (Fig. 2.21L), with anterior and posterior ventral processes (Fig. 2.22G); area of endosomal struts–DPS fusion elongate ovoid (Fig. 2.21L); endosoma medially sclerotized (Fig. 2.21L).

ETYMOLOGY: The species epithet is a noun in apposition and is named after Tombeau Vazimba, Madagascar.

DISTRIBUTION: Known from Tsingy de Bemaraha National Park in the Mahajanga province in Madagascar (Map 2.10).

HOLOTYPE: Male: **Madagascar: Mahajanga:** Parc National Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Vazimba, 19.14194°S 44.82805°E, 50 m, 06 Nov 2001–10 Nov 2001, Fisheret al. (00006964) (CAS).

PARATYPES: **Madagascar: Mahajanga:** Parc National Tsingy de Bemaraha, 3.4 km 93°E Bekopaka, Tombeau Vazimba, 19.14194°S 44.82805°E, 50 m, 06 Nov 2001–10 Nov 2001, Fisher et al., 1♂ (00006472) (CAS), 1♂ (00006730) (SU), 1♂ (00006967) (UCR). Parc National Tsingy de Bemaraha, 10.6 km ESE 123° Antsalova, 19.70944°S 44.71806°E, 150 m, 16 Nov 2001–20 Nov 2001, Fisheret al., 1♂ (00007109) (CAS).

Conclusion

The Madagascan invertebrate fauna has not been thoroughly documented, but the situation is improving thanks to large taxonomic surveys such as the one that has enabled this taxonomic project. Prior to our monograph, only 10 described species of millipede assassin bugs were known from the island. Here, we described 63 new species and three new genera of Ectrichodiinae that are endemic to Madagascar. This drastic increase in described diversity presents an opportunity to investigate the timing and origin of Madagascan Ectrichodiinae using phylogenetic, divergence dating, and biogeographic analyses; a companion paper investigating these questions is in press (Forthman & Weirauch, in press). Phylogenetic studies of Madagascan plants, vertebrates, and some invertebrates support close relationships to either Afrotropical or Oriental lineages (see Vences, 2004; Yoder & Nowak, 2006; Warren et al., 2010). Assuming their monophyly, Afrotropical-Madagascan relationships are evident in the genera *Glymmatophora* and *Maraenaspis*; both genera have the bulk of species restricted to mainland Africa. Other Madagascan genera, e.g., *Gibbosella* and *Marojejycoris*, share morphological similarities with Afrotropical taxa, e.g., *Synavecoris*, such as the drab coloration, ovoid head shape, and circular spiracles. However, male specimens of *Gibbosella* also share some morphological features (e.g., distal part of M and Cu fused or nearly so; dorsal laterotergites with posterior tubercles) with Oriental taxa, such as *Caecina* Stål, 1863, and *Bannania* Hsiao, 1973. Only formal phylogenetic analyses including comprehensive taxon sampling in the Afrotropical and Oriental regions, as well as morphological and molecular characters, will shed light on the phylogenetic relationships and origins of Madagascan Ectrichodiinae.

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Figure 2.1. Dorsal habitus of *Gibbosella* species, *Glymmatophora carolae*, and *Glymmatophora crassipes*.

Gibbosella
andasibe ♂

Gibbosella
betampona ♂

Gibbosella
brunalvus ♂

Gibbosella
brunalvus ♀

Gibbosella
conisimilis ♂

Gibbosella
elongata ♂

Gibbosella
fulva ♂

Gibbosella
mantella ♂

Gibbosella
megafrons ♂

Gibbosella
nitida ♂

Gibbosella
notoconica ♂

Gibbosella
pallidacorium ♂

Gibbosella
pallidalata ♂

Gibbosella
planiscutum ♂

Gibbosella
planiscutum ♀

Gibbosella
quadocris ♂

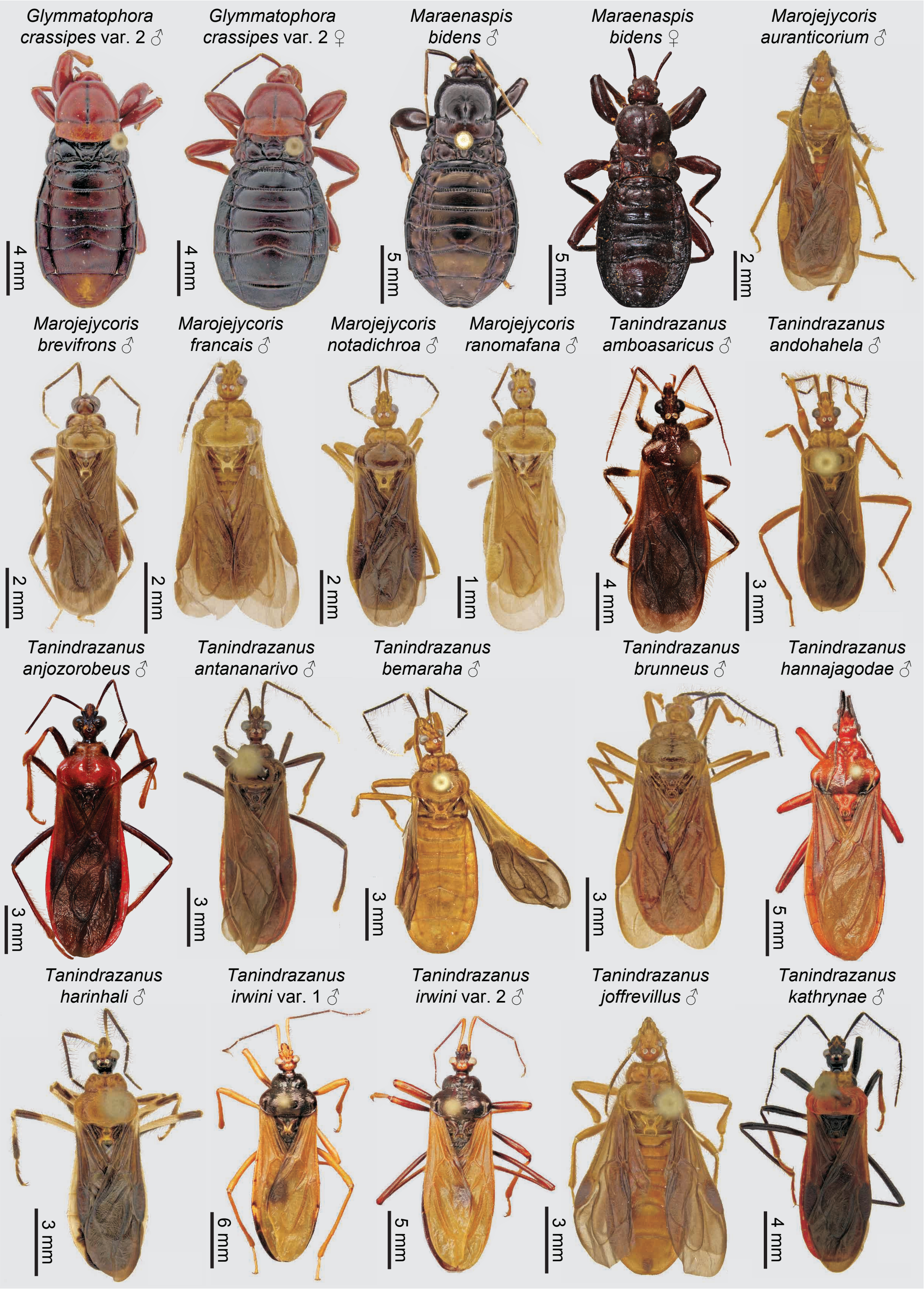
Gibbosella
vangocris ♂

Glymmatophora
carolae ♂

Glymmatophora
crassipes var. 1 ♂

Glymmatophora
crassipes var. 1 ♀

Figure 2.2. Dorsal habitus of *Glymmatophora crassipes*, *Maraenaspis bidens*, *Marojejycoris* species, and *Tanindrazanus* species (*T. amboasaricus* – *T. kathrynae*).



Glymmatophora crassipes var. 2 ♂

Glymmatophora crassipes var. 2 ♀

Maraenaspis bidens ♂

Maraenaspis bidens ♀

Marojejycoris auranticorium ♂

Marojejycoris brevifrons ♂

Marojejycoris francais ♂

Marojejycoris notadichroa ♂

Marojejycoris ranomafana ♂

Tanindrazanus amboasaricus ♂

Tanindrazanus andohahela ♂

Tanindrazanus anjozorobeus ♂

Tanindrazanus antananarivo ♂

Tanindrazanus bemaraha ♂

Tanindrazanus brunneus ♂

Tanindrazanus hannajagodae ♂

Tanindrazanus harinhali ♂

Tanindrazanus irwini var. 1 ♂

Tanindrazanus irwini var. 2 ♂

Tanindrazanus joffrevillus ♂

Tanindrazanus kathrynae ♂

Figure 2.3. Dorsal habitus of *Tanindrazanus* species (*T. mahafaly* – *T. vohiparara*), *Toliarus* species, and *Toxopus* species (*T. ambohitantely* – *T. griswoldi* [male]).

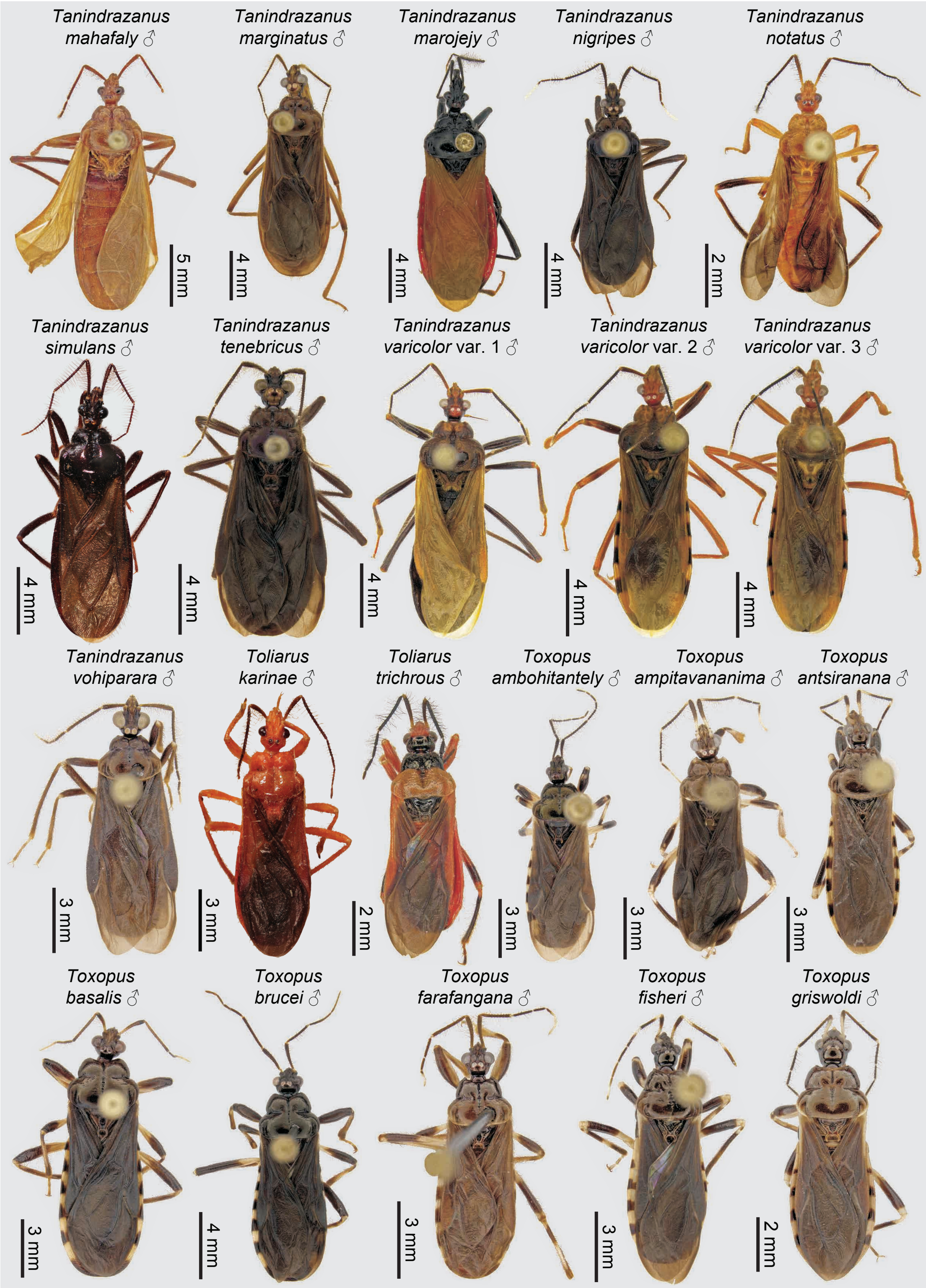

Tanindrazanus mahafaly ♂
5 mm
Tanindrazanus marginatus ♂
4 mm
Tanindrazanus marojejy ♂
4 mm
Tanindrazanus nigripes ♂
4 mm
Tanindrazanus notatus ♂
2 mm
Tanindrazanus simulans ♂
4 mm
Tanindrazanus tenebricus ♂
4 mm
Tanindrazanus varicolor var. 1 ♂
4 mm
Tanindrazanus varicolor var. 2 ♂
4 mm
Tanindrazanus varicolor var. 3 ♂
4 mm
Tanindrazanus vohiparara ♂
3 mm
Toliarus karinae ♂
3 mm
Toliarus trichrous ♂
2 mm
Toxopus ambohitantely ♂
3 mm
Toxopus ampitavananima ♂
3 mm
Toxopus antsiranana ♂
3 mm
Toxopus basalis ♂
3 mm
Toxopus brucei ♂
4 mm
Toxopus farafangana ♂
3 mm
Toxopus fisheri ♂
3 mm
Toxopus griswoldi ♂
2 mm

Figure 2.4. Dorsal habitus of *Toxopus* species (*T*. *griswoldi* [female] – *T*. *vazimba*).

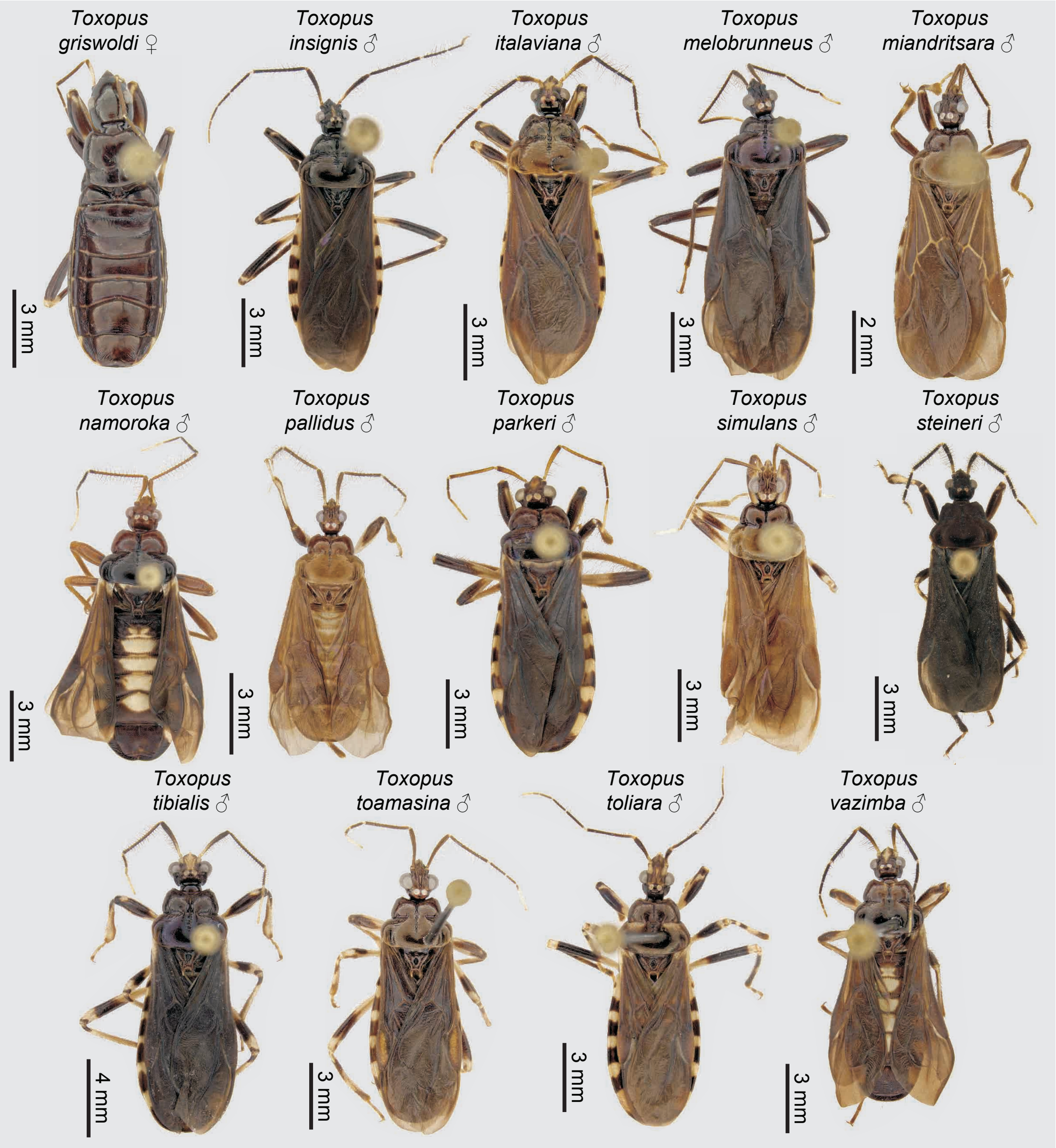

Toxopus griswoldi ♀
Toxopus insignis ♂
Toxopus italaviana ♂
Toxopus melobrunneus ♂
Toxopus miandritsara ♂
3 mm
3 mm
3 mm
3 mm
2 mm
Toxopus namoroka ♂
Toxopus pallidus ♂
Toxopus parkeri ♂
Toxopus simulans ♂
Toxopus steineri ♂
3 mm
3 mm
3 mm
3 mm
3 mm
Toxopus tibialis ♂
Toxopus toamasina ♂
Toxopus toliara ♂
Toxopus vazimba ♂
4 mm
3 mm
3 mm
3 mm

Figure 2.5. Lateral habitus of *Gibbosella* species, *Glymmatophora* species, *Maraenaspis bidens,* and *Marojejycoris* species (*M. auranticorium – M. francais*).

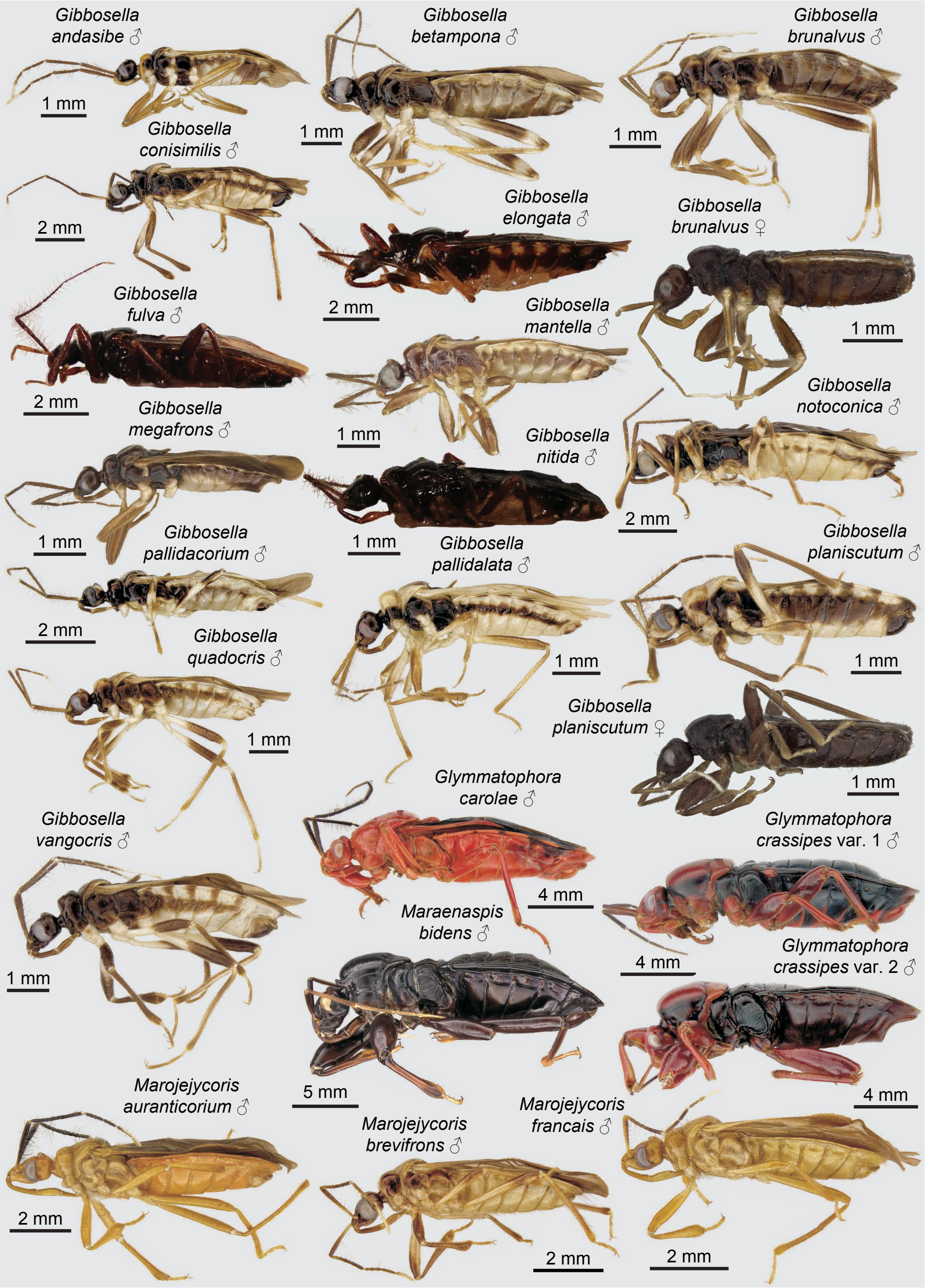
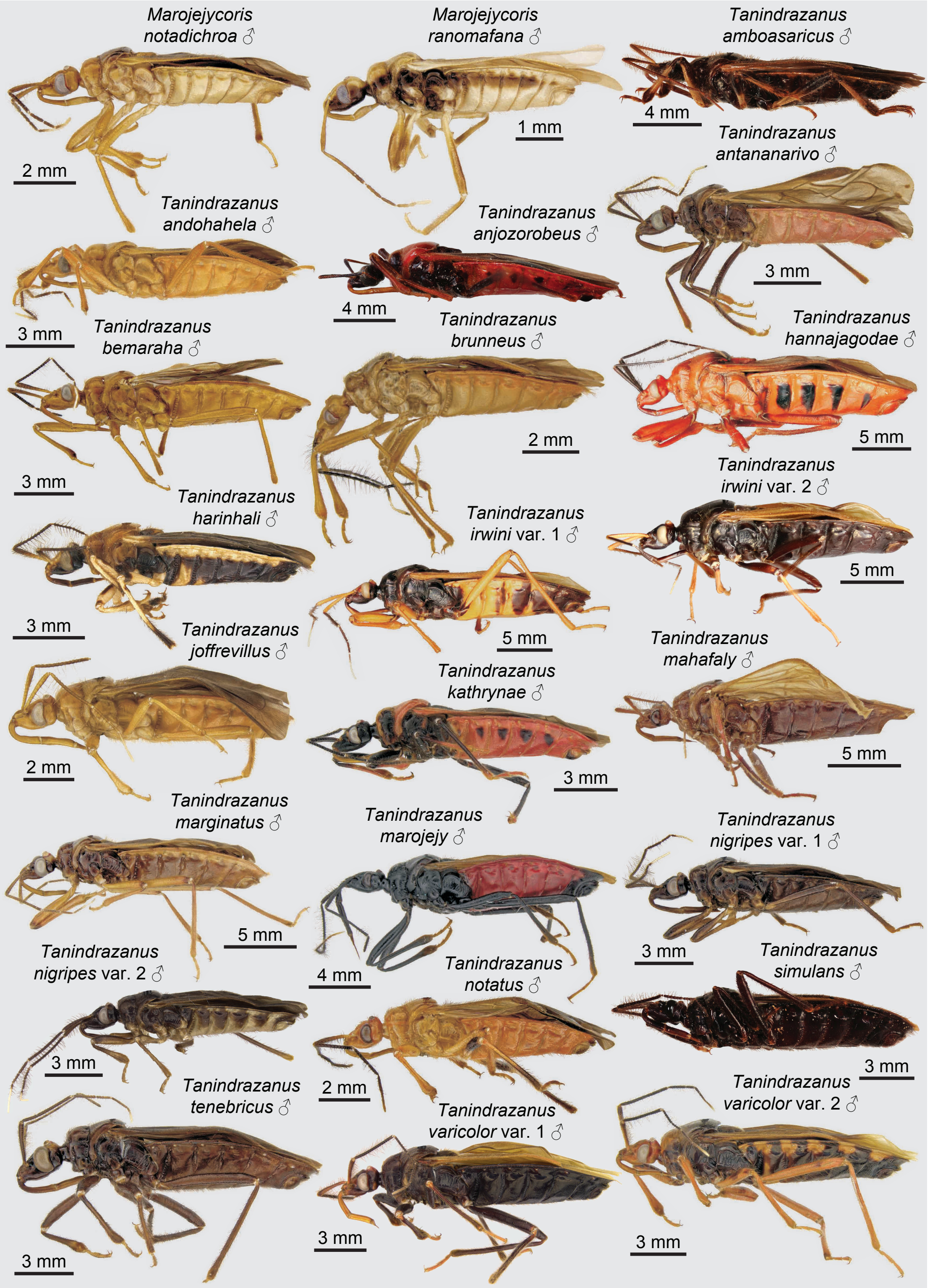

Gibbosella andasibe ♂
1 mm
Gibbosella betampona ♂
1 mm
Gibbosella brunalvus ♂
1 mm
Gibbosella conisimilis ♂
2 mm
Gibbosella elongata ♂
2 mm
Gibbosella brunalvus ♀
1 mm
Gibbosella fulva ♂
2 mm
Gibbosella mantella ♂
1 mm
Gibbosella notoconica ♂
2 mm
Gibbosella megafrons ♂
1 mm
Gibbosella nitida ♂
1 mm
Gibbosella pallidacorium ♂
2 mm
Gibbosella pallidalata ♂
1 mm
Gibbosella planiscutum ♂
1 mm
Gibbosella quadocris ♂
1 mm
Gibbosella planiscutum ♀
1 mm
Glymmatophora carolae ♂
4 mm
Gibbosella vangocris ♂
1 mm
Glymmatophora crassipes var. 1 ♂
4 mm
Maraenaspis bidens ♂
5 mm
Glymmatophora crassipes var. 2 ♂
4 mm
Marojejycoris auranticorium ♂
2 mm
Marojejycoris brevifrons ♂
2 mm
Marojejycoris francais ♂
2 mm

Figure 2.6. Lateral habitus of *Marojejycoris notadichroa*, *Marojejycoris francais*, and *Tanindrazanus* species (*T. amboasaricus* – *T. varicolor*).



Marojejycoris notadichroa ♂
2 mm
Marojejycoris ranomafana ♂
1 mm
Tanindrazanus amboasaricus ♂
4 mm
Tanindrazanus antananarivo ♂
3 mm
Tanindrazanus andohahela ♂
3 mm
Tanindrazanus anjozorobeus ♂
4 mm
Tanindrazanus bemaraha ♂
3 mm
Tanindrazanus brunneus ♂
2 mm
Tanindrazanus hannajagodae ♂
5 mm
Tanindrazanus harinhali ♂
3 mm
Tanindrazanus irwini var. 1 ♂
5 mm
Tanindrazanus irwini var. 2 ♂
5 mm
Tanindrazanus joffrevillus ♂
2 mm
Tanindrazanus kathrynae ♂
3 mm
Tanindrazanus mahafaly ♂
5 mm
Tanindrazanus marginatus ♂
5 mm
Tanindrazanus marojejy ♂
4 mm
Tanindrazanus nigripes var. 1 ♂
3 mm
Tanindrazanus nigripes var. 2 ♂
3 mm
Tanindrazanus notatus ♂
2 mm
Tanindrazanus simulans ♂
3 mm
Tanindrazanus tenebricus ♂
3 mm
Tanindrazanus varicolor var. 1 ♂
3 mm
Tanindrazanus varicolor var. 2 ♂
3 mm

Figure 2.7. Lateral habitus of *Tanindrazanus varicolor*, *Tanindrazanus vohiparara*, *Toliarus* species, and *Toxopus* species.

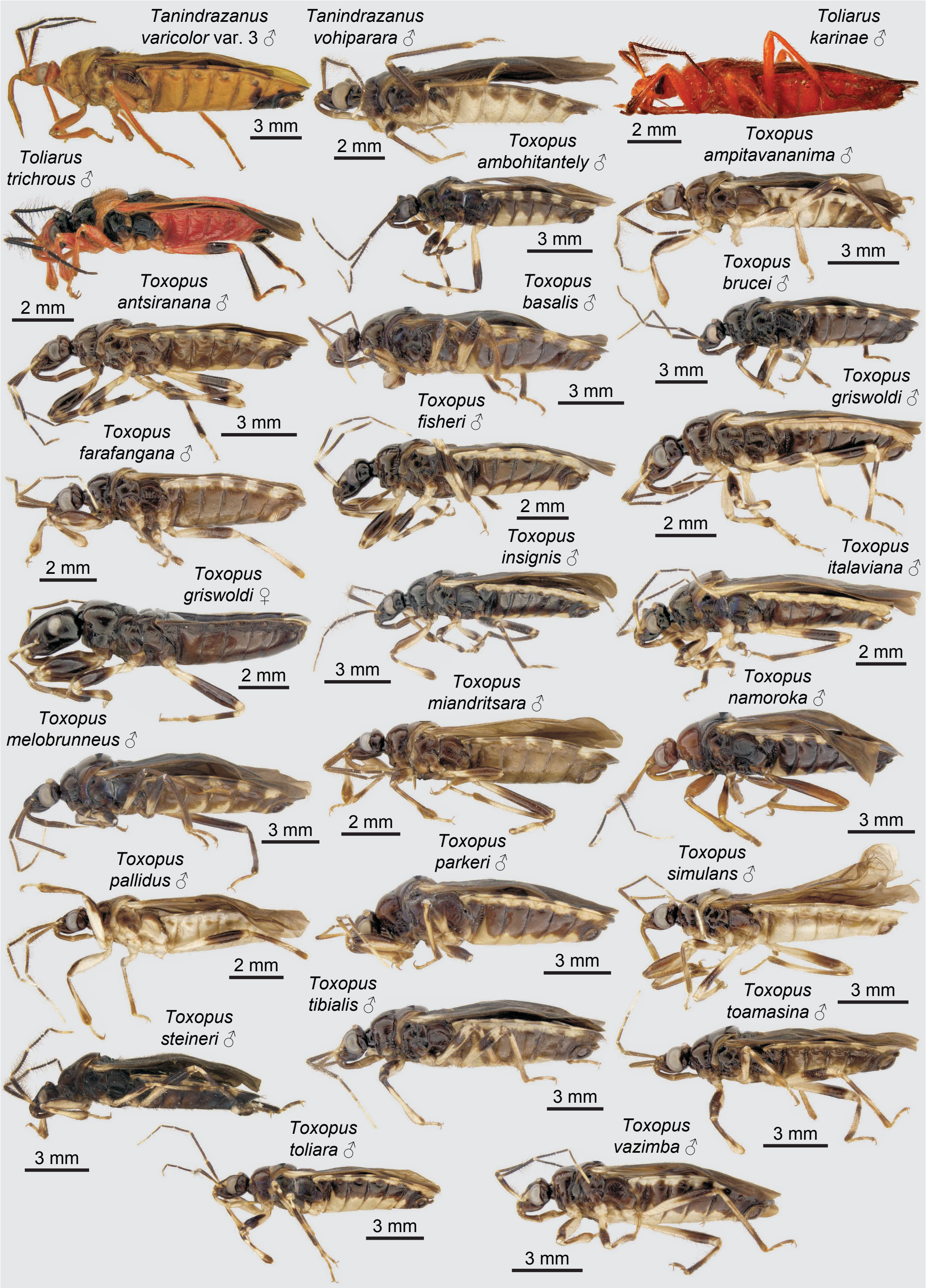

Tanindrazanus varicolor var. 3 ♂
3 mm
Tanindrazanus vohiparara ♂
2 mm
Toliarus karinae ♂
2 mm
Toliarus trichrous ♂
2 mm
Toxopus ambohitantely ♂
3 mm
Toxopus ampitavananima ♂
3 mm
Toxopus antsiranana ♂
3 mm
Toxopus basalis ♂
3 mm
Toxopus brucei ♂
3 mm
Toxopus griswoldi ♂
Toxopus farafangana ♂
2 mm
Toxopus fisheri ♂
2 mm
Toxopus insignis ♂
2 mm
Toxopus italaviana ♂
Toxopus griswoldi ♀
2 mm
3 mm
Toxopus miandritsara ♂
2 mm
Toxopus namoroka ♂
Toxopus melobrunneus ♂
3 mm
2 mm
Toxopus parkeri ♂
3 mm
Toxopus pallidus ♂
2 mm
Toxopus simulans ♂
3 mm
Toxopus steineri ♂
3 mm
Toxopus tibialis ♂
3 mm
Toxopus toamasina ♂
3 mm
Toxopus toliara ♂
3 mm
Toxopus vazimba ♂
3 mm

Figure 2.8. Ventral habitus of *Gibbosella* species, *Glymmatophora* species, and *Maraenaspis bidens*.

Gibbosella andasibe ♂

Gibbosella betampona ♂

Gibbosella brunalvus ♂

Gibbosella brunalvus ♀

Gibbosella conisimilis ♂

Gibbosella mantella ♂

Gibbosella megafrons ♂

Gibbosella notoconica ♂

Gibbosella pallidacorium ♂

Gibbosella pallidalata ♂

Gibbosella planiscutum ♂

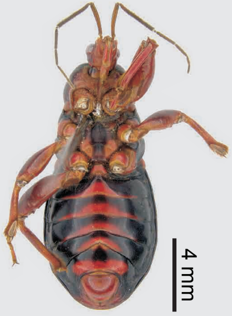
Gibbosella planiscutum ♀

Gibbosella quadocris ♂

Gibbosella vangocris ♂

Glymmatophora carolae ♂

Glymmatophora crassipes var. 1 ♂



Glymmatophora crassipes var. 1 ♀

Glymmatophora crassipes var. 2 ♂

Maraenaspis bidens ♂

Maraenaspis bidens ♀

Figure 2.9. Ventral habitus of *Marojejycoris* species and *Tanindrazanus* species (*T. amboasaricus* – *T. nigripes*).

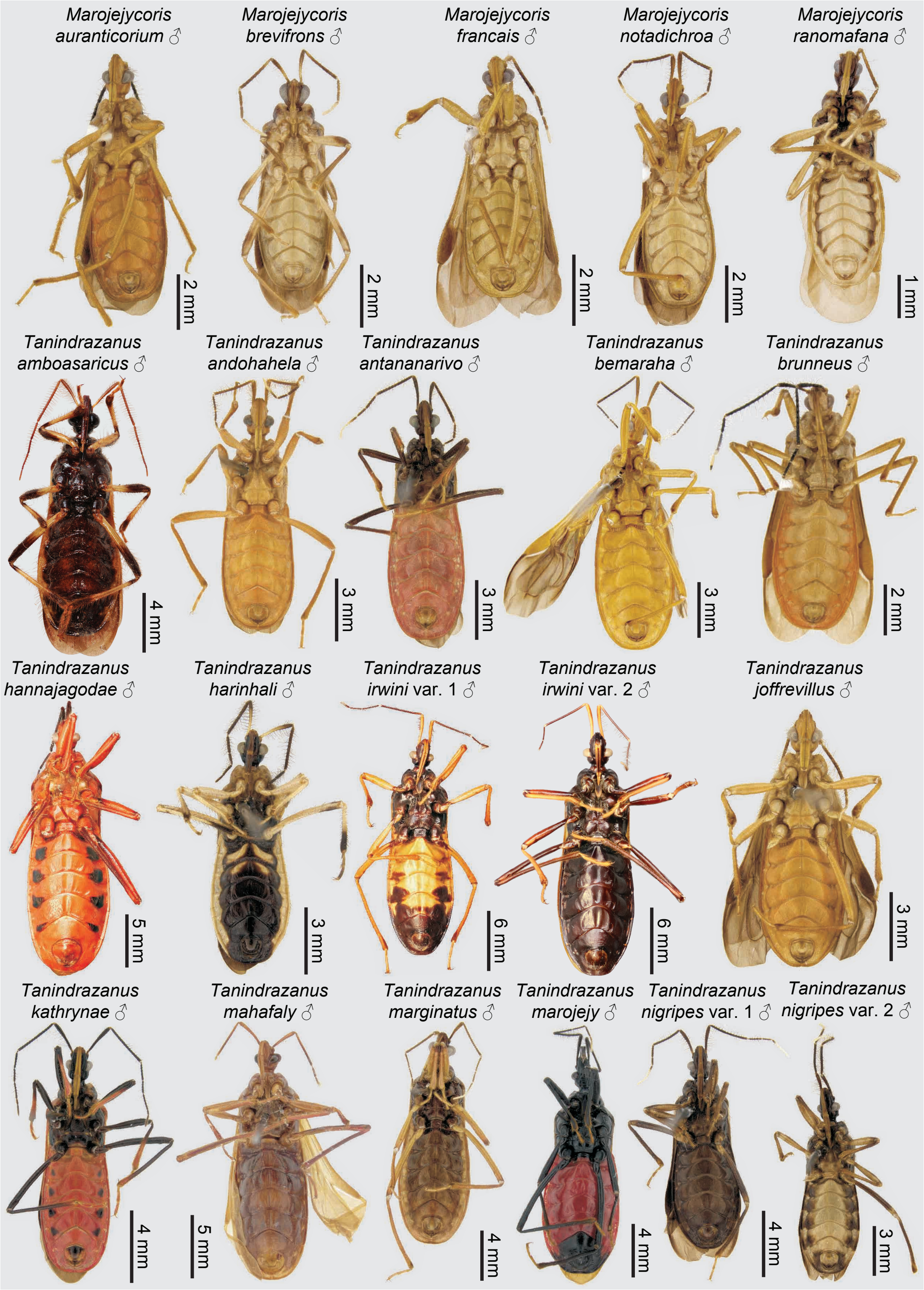

Marojejycoris auranticorium ♂
2 mm
Marojejycoris brevifrons ♂
2 mm
Marojejycoris francais ♂
2 mm
Marojejycoris notadichroa ♂
2 mm
Marojejycoris ranomafana ♂
1 mm
Tanindrazanus amboasaricus ♂
4 mm
Tanindrazanus andohahela ♂
3 mm
Tanindrazanus antananarivo ♂
3 mm
Tanindrazanus bemaraha ♂
3 mm
Tanindrazanus brunneus ♂
2 mm
Tanindrazanus hannajagodae ♂
5 mm
Tanindrazanus harinhali ♂
3 mm
Tanindrazanus irwini var. 1 ♂
6 mm
Tanindrazanus irwini var. 2 ♂
6 mm
Tanindrazanus joffrevillus ♂
3 mm
Tanindrazanus kathrynae ♂
4 mm
Tanindrazanus mahafaly ♂
5 mm
Tanindrazanus marginatus ♂
4 mm
Tanindrazanus marojejy ♂
4 mm
Tanindrazanus nigripes var. 1 ♂
4 mm
Tanindrazanus nigripes var. 2 ♂
3 mm

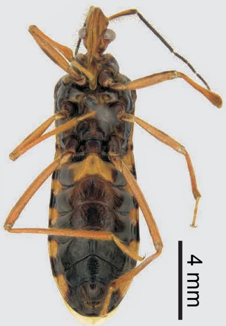
Figure 2.10. Ventral habitus of *Tanindrazanus* species (*T*. *notatus* – *T*. *vohiparara*), *Toliarus trichrous*, and *Toxopus* species (*T*. *ambohitantely* – *T*. *melobrunneus*).


Tanindrazanus notatus ♂


Tanindrazanus simulans ♂


Tanindrazanus tenebricus ♂


Tanindrazanus varicolor var. 1 ♂


Tanindrazanus varicolor var. 2 ♂


Tanindrazanus varicolor var. 3 ♂


Tanindrazanus vohiparara ♂


Toliarus trichrous ♂


Toxopus ambohitantely ♂


Toxopus ampitavananima ♂


Toxopus antsiranana ♂


Toxopus basalis ♂


Toxopus brucei ♂


Toxopus farafangana ♂


Toxopus fisheri ♂


Toxopus griswoldi ♂


Toxopus griswoldi ♀


Toxopus insignis ♂


Toxopus italaviana ♂


Toxopus melobrunneus ♂

Figure 2.11. Ventral habitus of *Toxopus* species (*T*. *miandritsara* – *T*. *vazimba*).

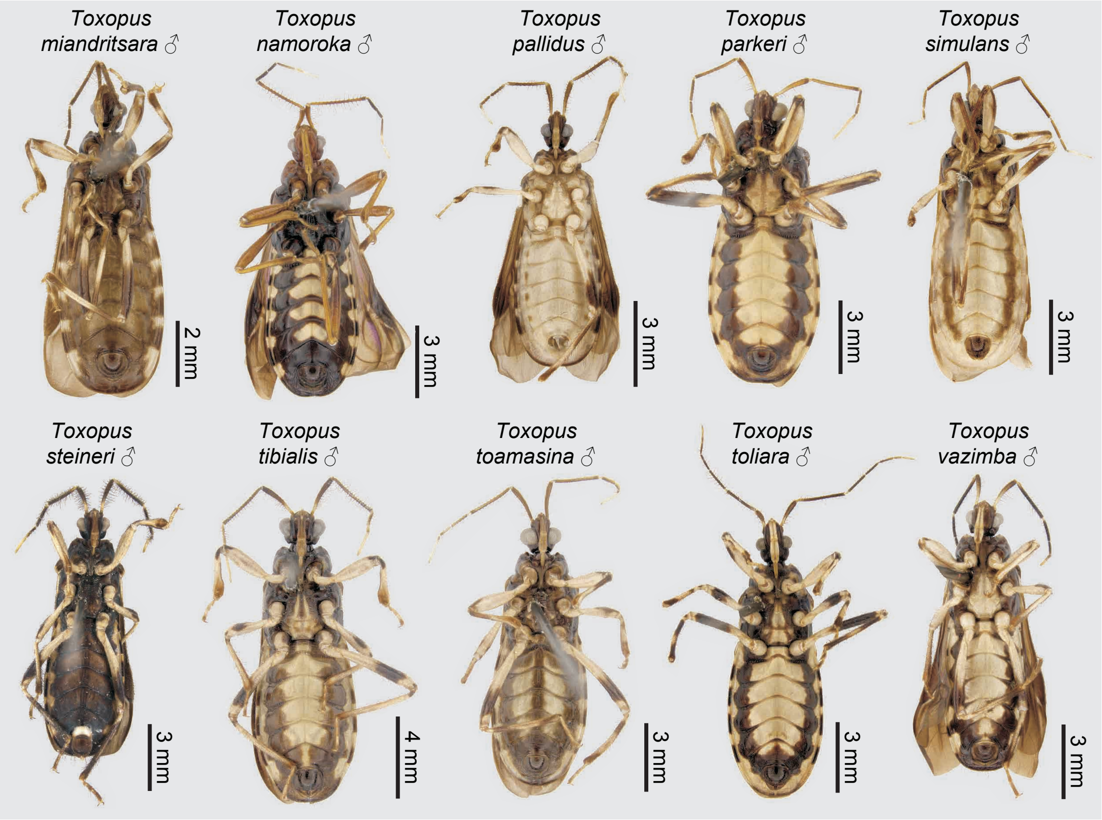
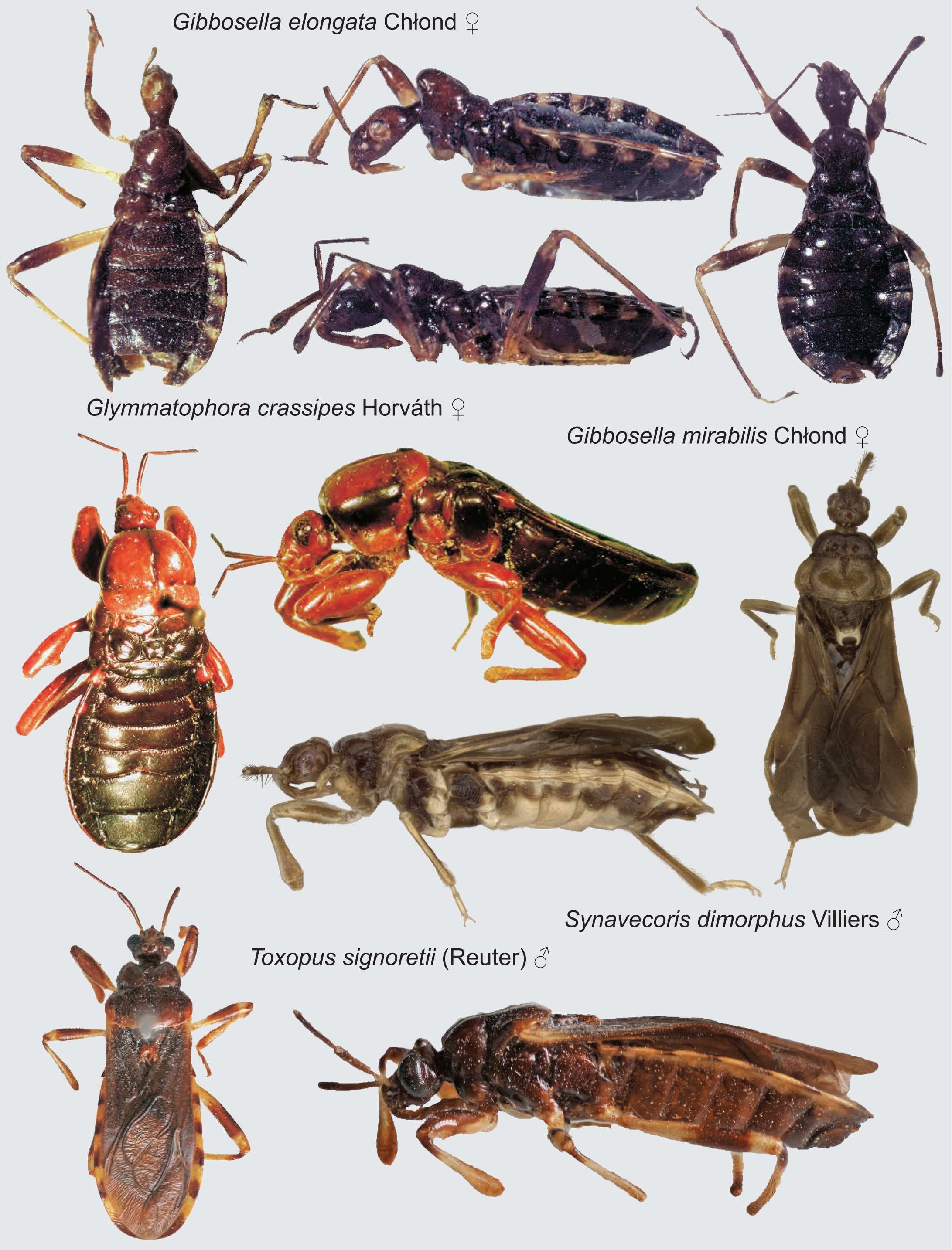

Toxopus miandritsara ♂
2 mm
Toxopus namoroka ♂
3 mm
Toxopus pallidus ♂
3 mm
Toxopus parkeri ♂
3 mm
Toxopus simulans ♂
3 mm
Toxopus steineri ♂
3 mm
Toxopus tibialis ♂
4 mm
Toxopus toamasina ♂
3 mm
Toxopus toliara ♂
3 mm
Toxopus vazimba ♂
3 mm

Figure 2.12. Dorsal and lateral habitus of holotypes of *Gibbosella elongata*, *Gi. mirabilis*, *Glymmatophora crassipes*, *Synavecoris dimorphus*, and *Toxopus signoretii*.



Gibbosella elongata Chłond ♀

Glymmatophora crassipes Horváth ♀

Gibbosella mirabilis Chłond ♀

Synavecoris dimorphus Villiers ♂

Toxopus signoretii (Reuter) ♂

Figure 2.13. Dorsal (A., B.) and lateral (C.–K.) head structures. A. *Glymmatophora crassipes*, B. *Toxopus italaviana*, C. *Gibbosella mantella*, D. *Glymmatophora crassipes*, E. *Maraenaspis bidens*, F. *Marojejycoris brevifrons*, G. *Tanindrazanus kathrynae*, H. *Tanindrazanus varicolor*, I. *Toliarus trichrous*, J. *Toxopus ambohitantely*, K. *Toxopus parkeri*.

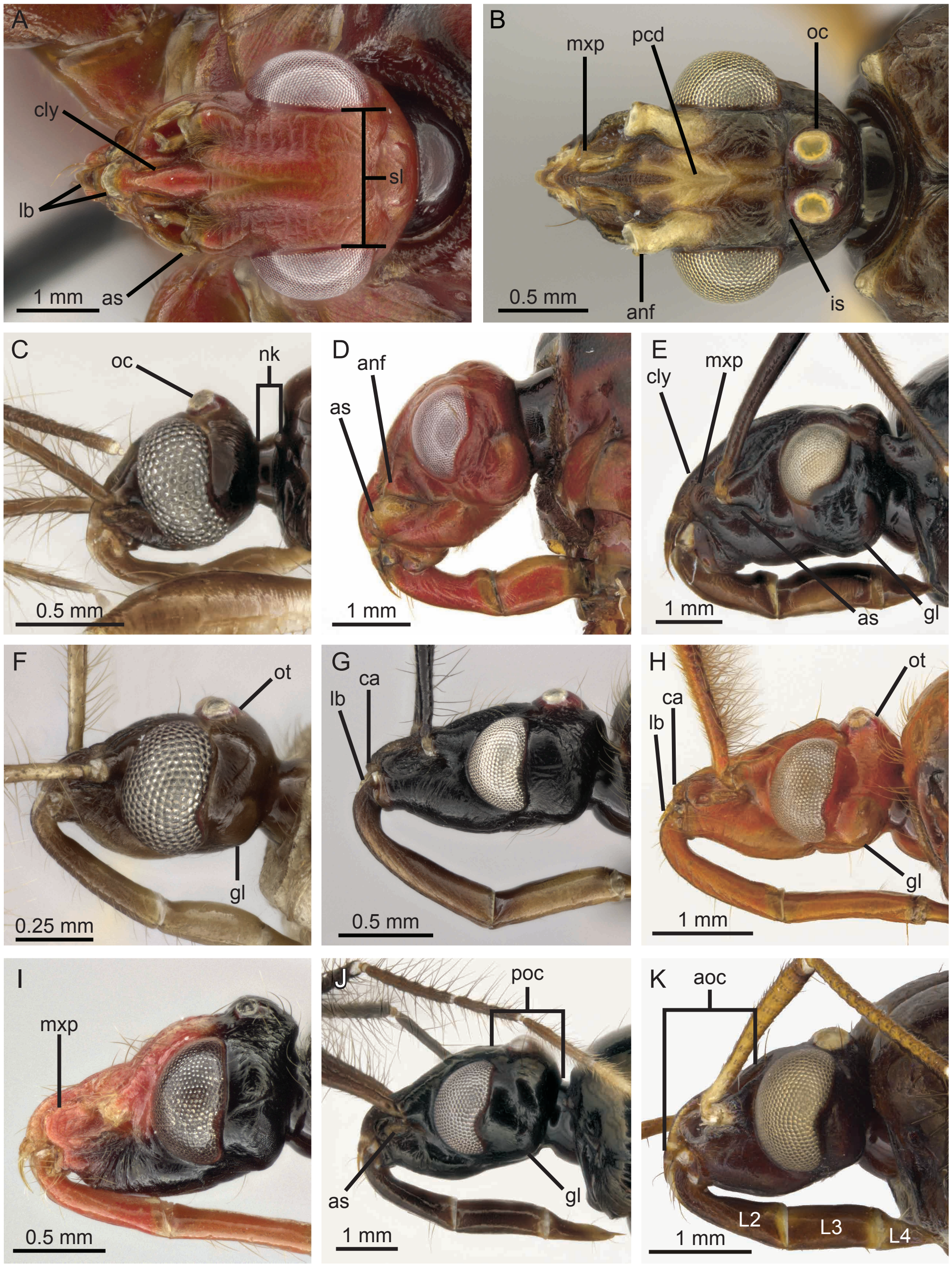

A
cly
sl
lb
1 mm
as
B
mxp
pcd
oc
0.5 mm
anf
is
C
oc
nk
0.5 mm
D
anf
as
1 mm
E
cly
mxp
1 mm
as
gl
F
ot
gl
0.25 mm
G
ca
lb
0.5 mm
H
ot
ca
lb
gl
1 mm
I
mxp
0.5 mm
J
poc
as
gl
1 mm
K
aoc
L2
L3
L4
1 mm

Figure 2.14. Lateral antennal morphology of *Toxopus insignis*. A. Antenna, B. basiflagellomere, C. distiflagellomere.

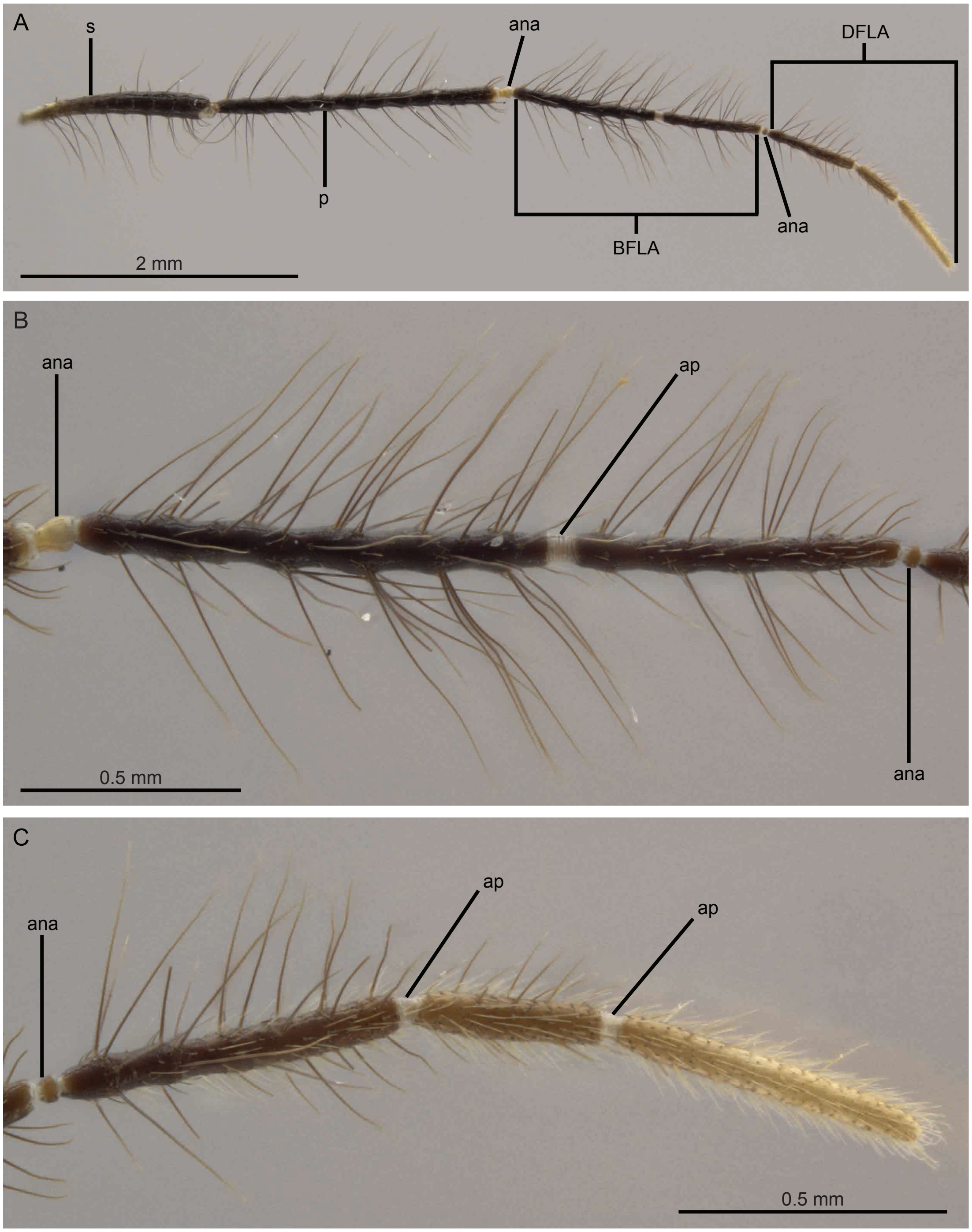

A
s
ana
DFLA
p
BFLA
ana
2 mm
B
ana
ap
ana
0.5 mm
C
ana
ap
ap
0.5 mm

Figure 2.15. Dorsal (A., B.), lateral (C., D.), and ventral (E., F.) thoracic structures. A. *Maraenaspis bidens*, B. *Toxopus italaviana*, C. *Gibbosella conisimilis*, D. *Tanindrazanus kathrynae*, E. *Glymmatophora crassipes*, F. *Tanindrazanus irwini*.

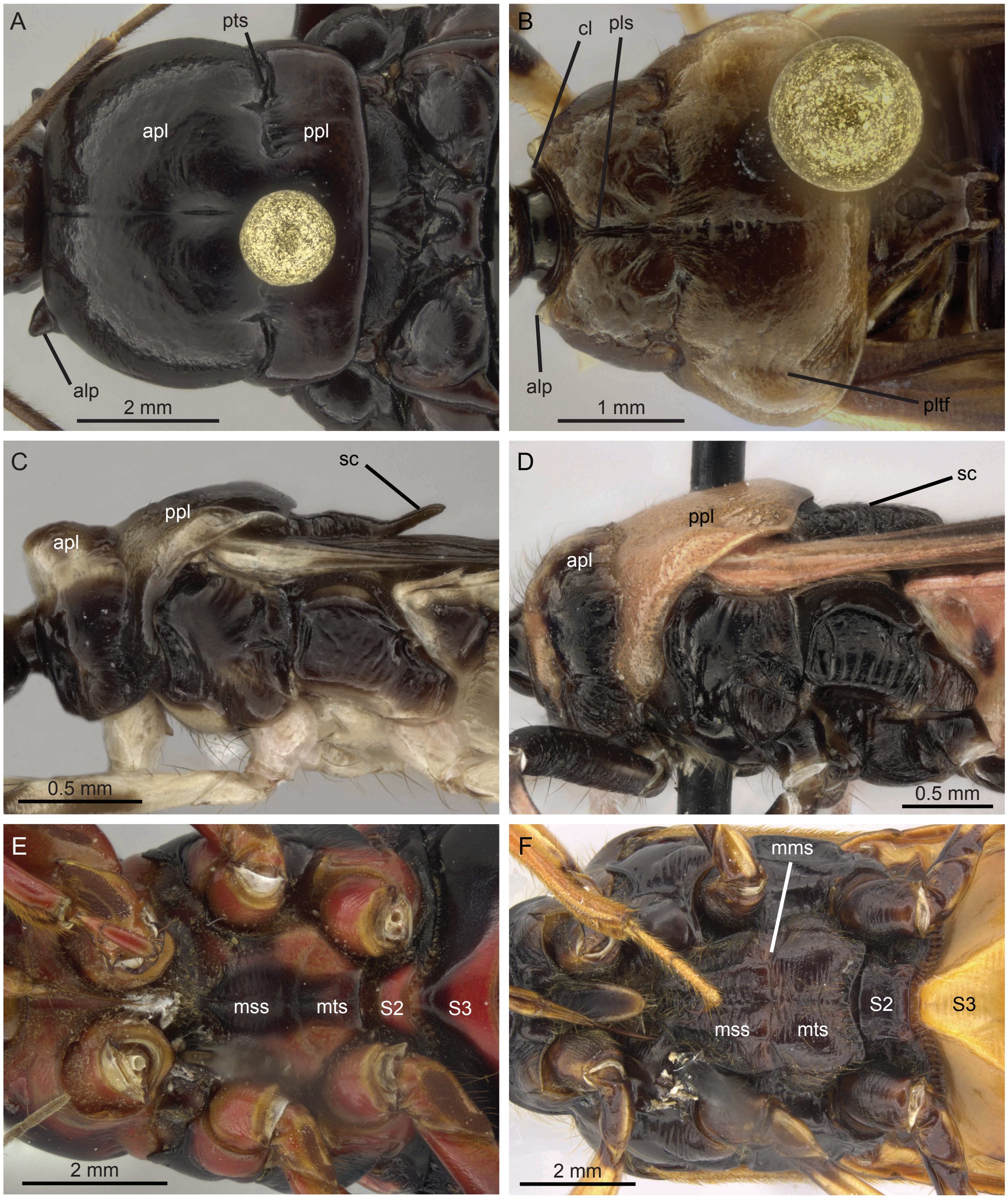

A
pts
apl
ppl
alp
2 mm
B
cl
pls
alp
pltf
1 mm
C
sc
ppl
apl
0.5 mm
D
sc
ppl
apl
0.5 mm
E
mss
mts
S2
S3
2 mm
F
mms
mss
mts
S2
S3
2 mm

Figure 2.16. Metathoracic gland evaporatorium (A.–C.) and femoral armature (D., E.). A. *Tanindrazanus varicolor* (lateral), B. *Glymmatophora crassipes* (lateral), C. *Glymmatophora carolae* (ventral), D. *Gibbosella* sp., E. *Glymmatophora crassipes*.

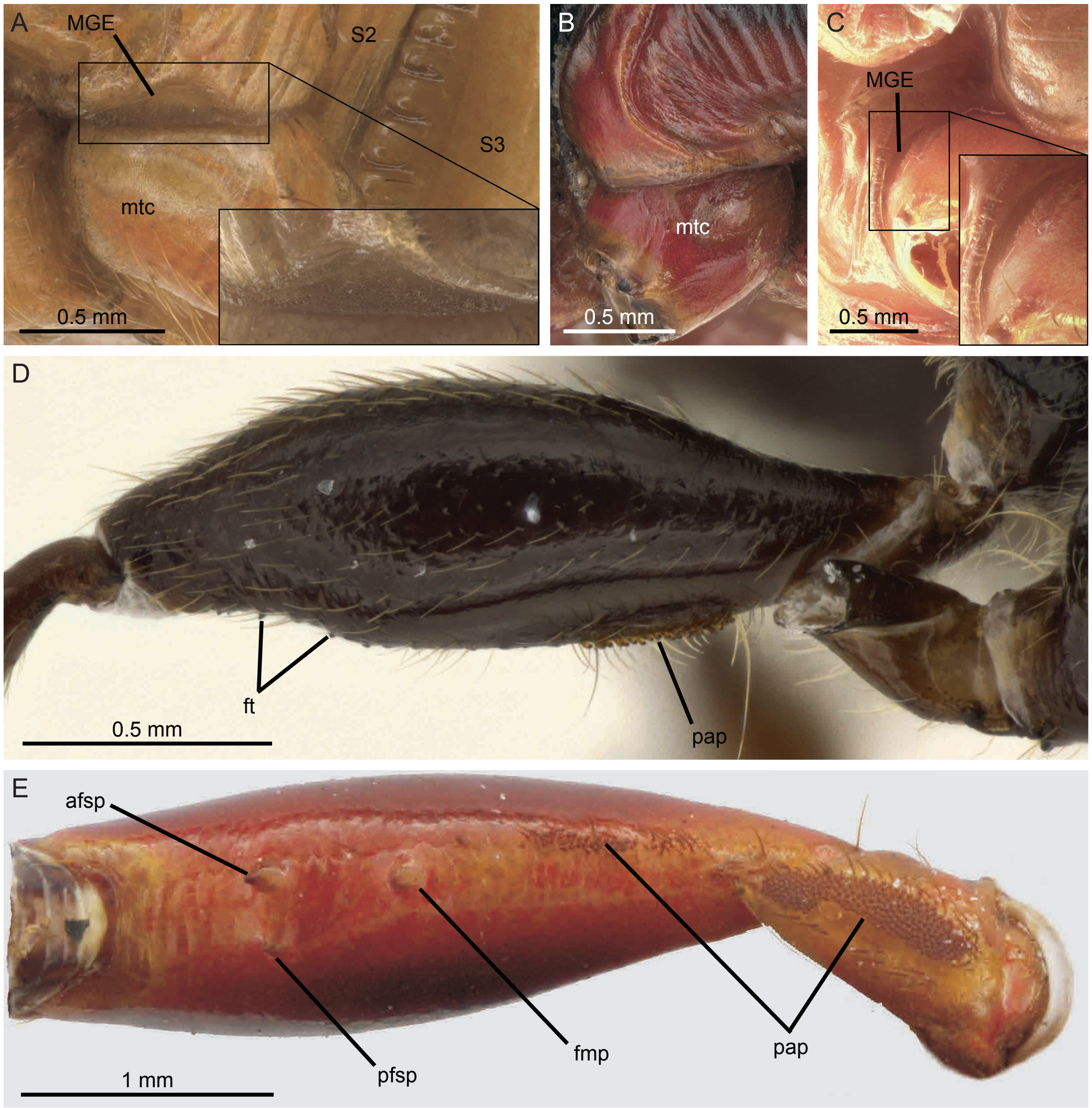

A
MGE
S2
S3
mtc
0.5 mm
B
mtc
0.5 mm
C
MGE
0.5 mm
D
ft
0.5 mm
pap
E
afsp
pfsp
fmp
pap
1 mm

Figure 2.17. Wing morphology. A. *Gibbosella planiscutum*, B. *Glymmatophora carolae*, C. *Tanindrazanus varicolor*.


A
exM
1A
Cu
M
M+Cu
Cu
M
co
R
cp
1 mm
B
R
M
co
M+Cu
Cu
1A
R
3 mm
C
R
M
Cu
M
exM
Cu
co
R
cp
3 mm

Figure 2.18. Lateral (A., B.) and ventral (C.) abdominal morphology. A. *Gibbosella conisimilis*, B. *Tanindrazanus tenebricus*, C. *Distirogaster* sp.

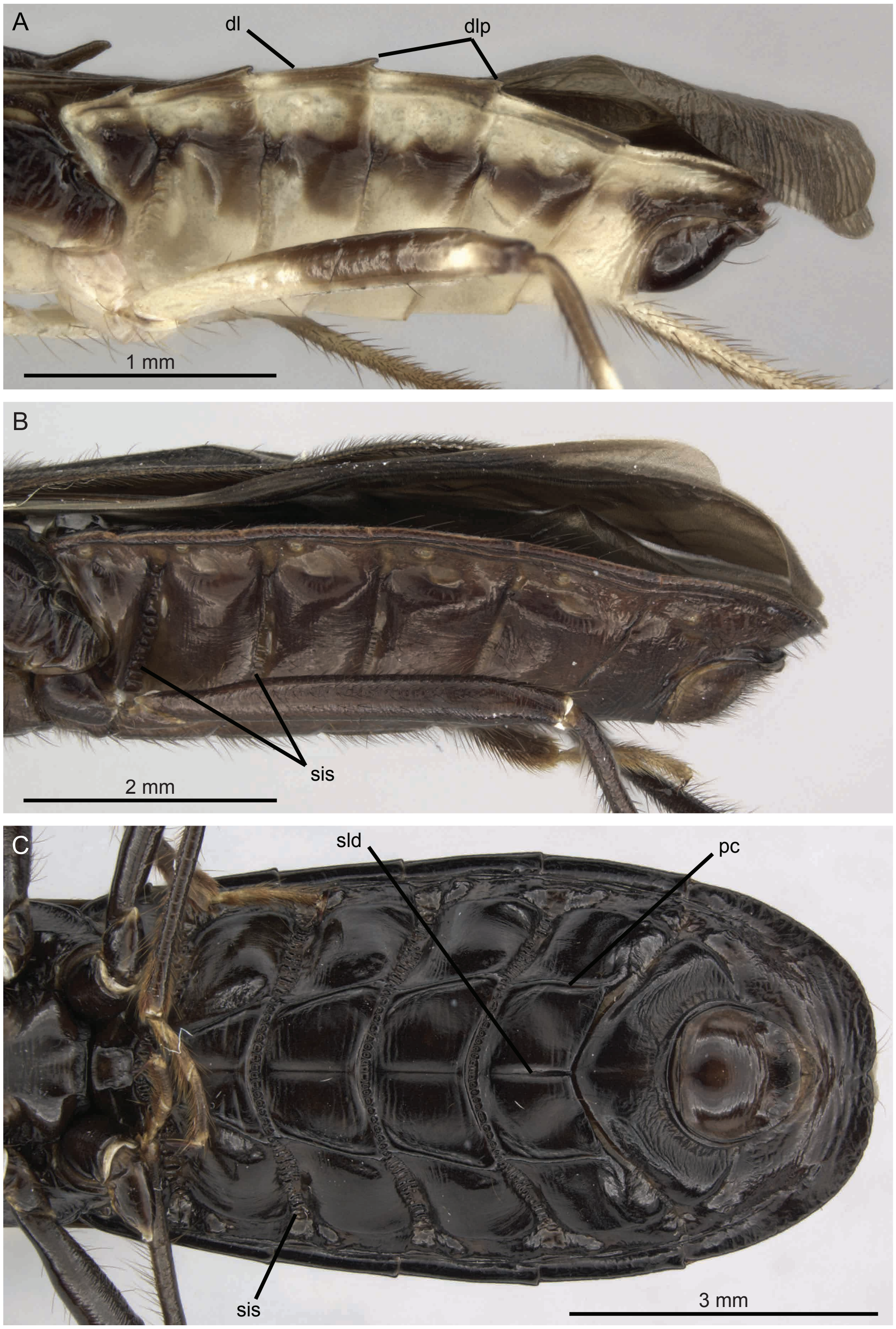

A
dl
dlp
1 mm
B
sis
2 mm
C
sld
pc
sis
3 mm

Figure 2.19. Pygophore morphology in caudal view. A. *Gibbosella quadocris*, B. *Gibbosella vangocris*, C. *Glymmatophora crassipes*, D. *Maraenaspis bidens*, E. *Marojejycoris auranticorium*, F. *Tanindrazanus kathrynae*, G. *Toliarus trichrous*, H. *Toxopus fisheri*, I. *Toxopus vazimba*.

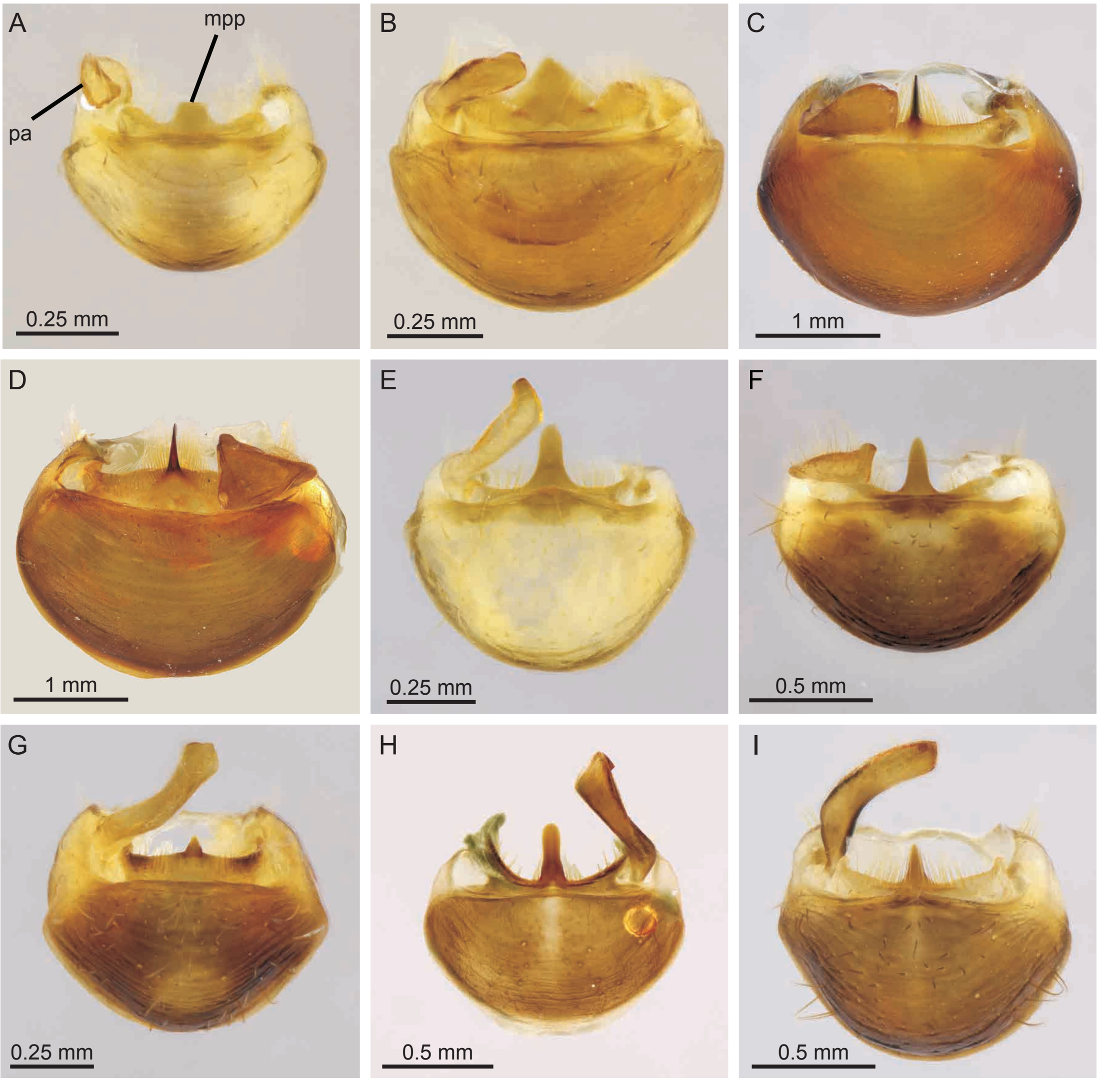

A
mpp
pa
0.25 mm
B
0.25 mm
C
1 mm
D
1 mm
E
0.25 mm
F
0.5 mm
G
0.25 mm
H
0.5 mm
I
0.5 mm

Figure 2.20. Pygophore morphology in lateral view. A. *Gibbosella notoconica*, B. *Gibbosella quadocris*, C. *Gibbosella vangocris*, D. *Glymmatophora carolae*, E. *Maraenaspis bidens*, F. *Marojejycoris auranticorium*, G. *Tanindrazanus kathrynae*, H. *Tanindrazanus marojejy*, I. *Tanindrazanus varicolor*, J. *Toliarus trichrous*, K. *Toxopus fisheri*, L. *Toxopus vazimba*.

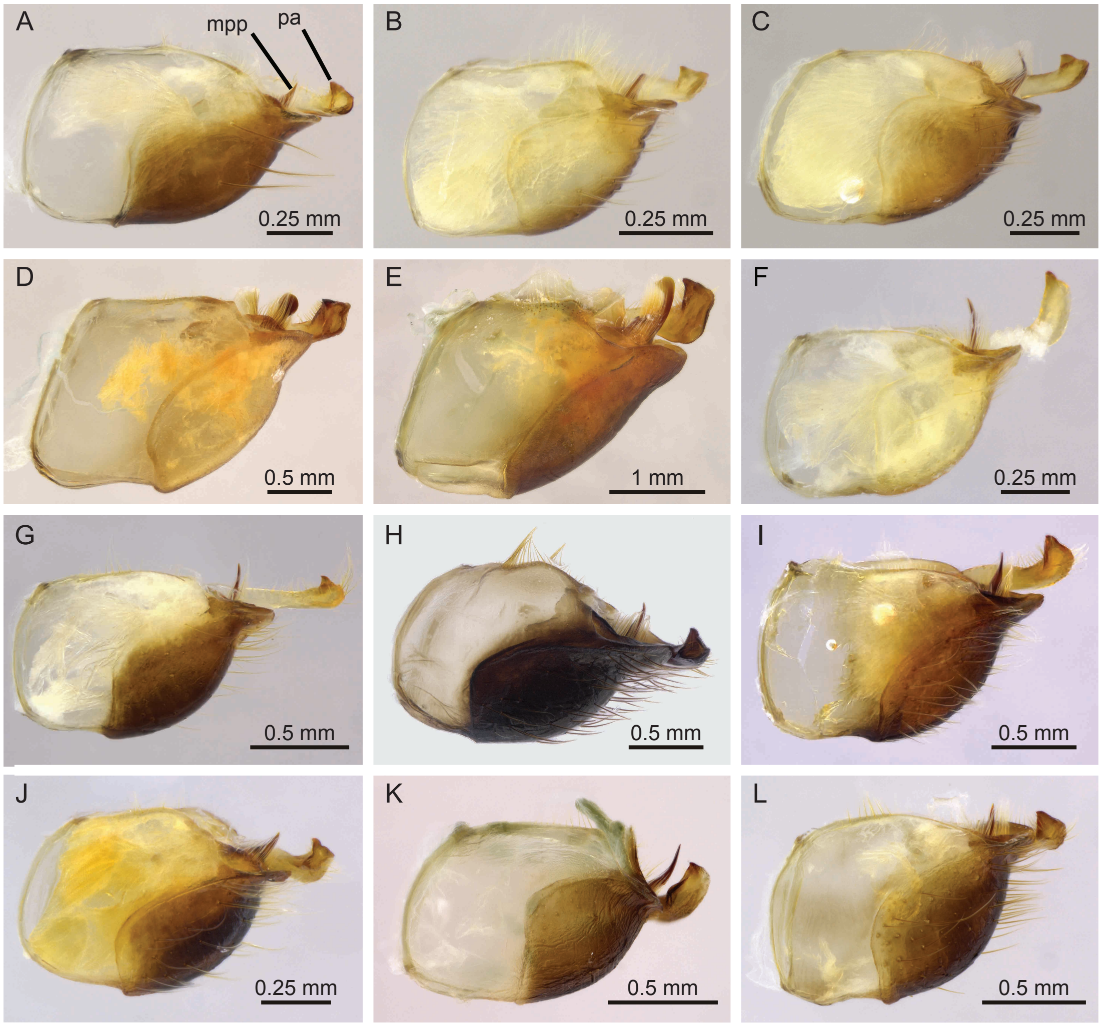

A
mpp
pa
0.25 mm
B
0.25 mm
C
0.25 mm
D
0.5 mm
E
1 mm
F
0.25 mm
G
0.5 mm
H
0.5 mm
I
0.5 mm
J
0.25 mm
K
0.5 mm
L
0.5 mm

Figure 2.21. Phallus morphology in dorsal view. A. *Gibbosella notoconica*, B. *Gibbosella vangocris*, C. *Glymmatophora carolae*, D. *Glymmatophora crassipes*, E. *Maraenaspis bidens*, F. *Marojejycoris brevifrons*, G. *Tanindrazanus notatus*, H. *Tanindrazanus varicolor*, I. *Toliarus trichrous*, J. *Toxopus fisheri*, K. *Toxopus toliara*, L. *Toxopus vazimba*.

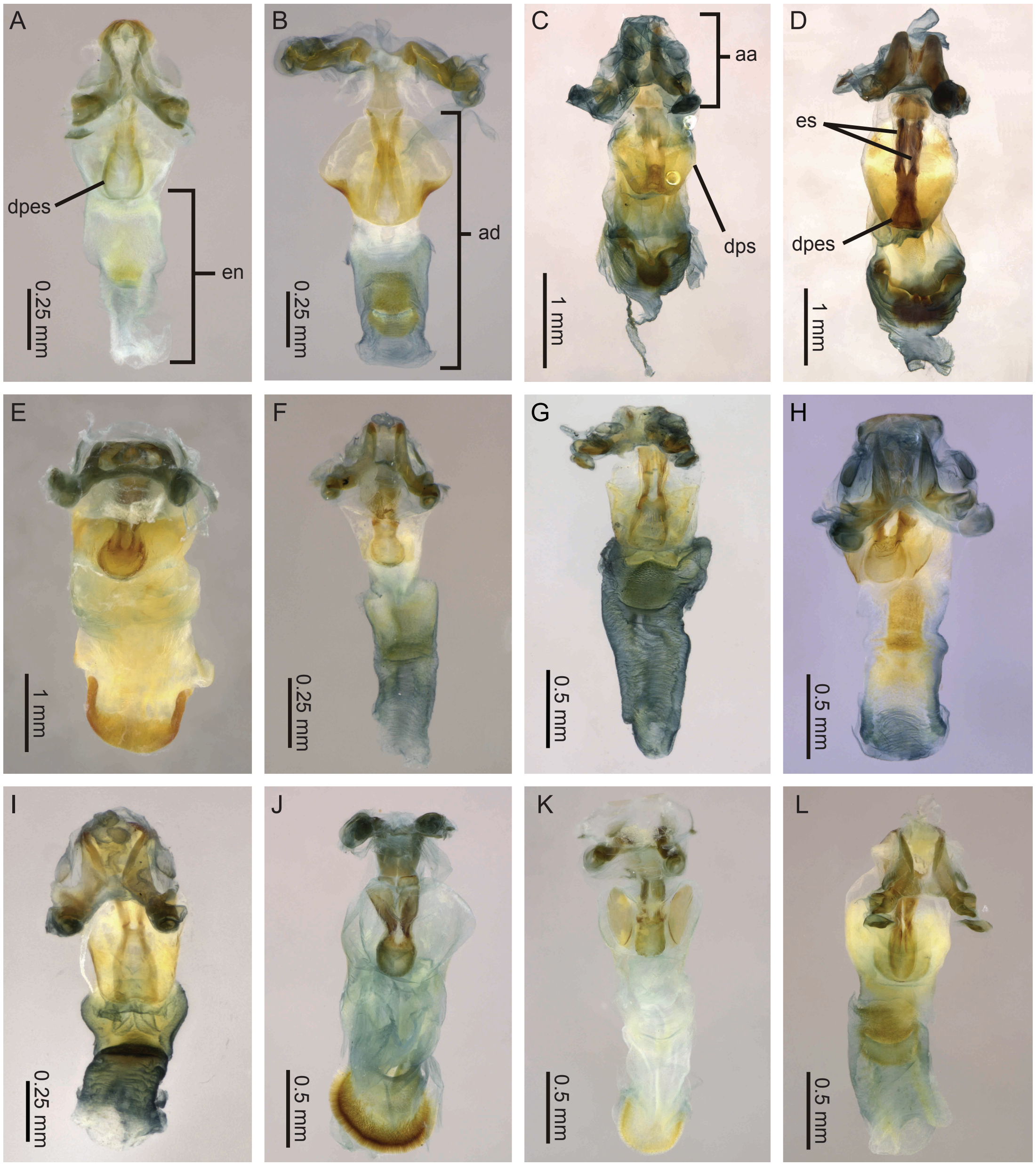

A
dpes
en
0.25 mm
B
ad
0.25 mm
C
aa
dps
1 mm
D
es
dpes
1 mm
E
1 mm
F
0.25 mm
G
0.5 mm
H
0.5 mm
I
0.25 mm
J
0.5 mm
K
0.5 mm
L
0.5 mm

Figure 2.22. Phallus morphology in lateral view. A. *Gibbosella vangocris*, B. *Glymmatophora crassipes*, C. *Maraenaspis bidens*, D. *Marojejycoris francais*, E. *Tanindrazanus nigripes*, F. *Toliarus trichrous*, G. *Toxopus ampitavananima*, H. *Toxopus basalis*.

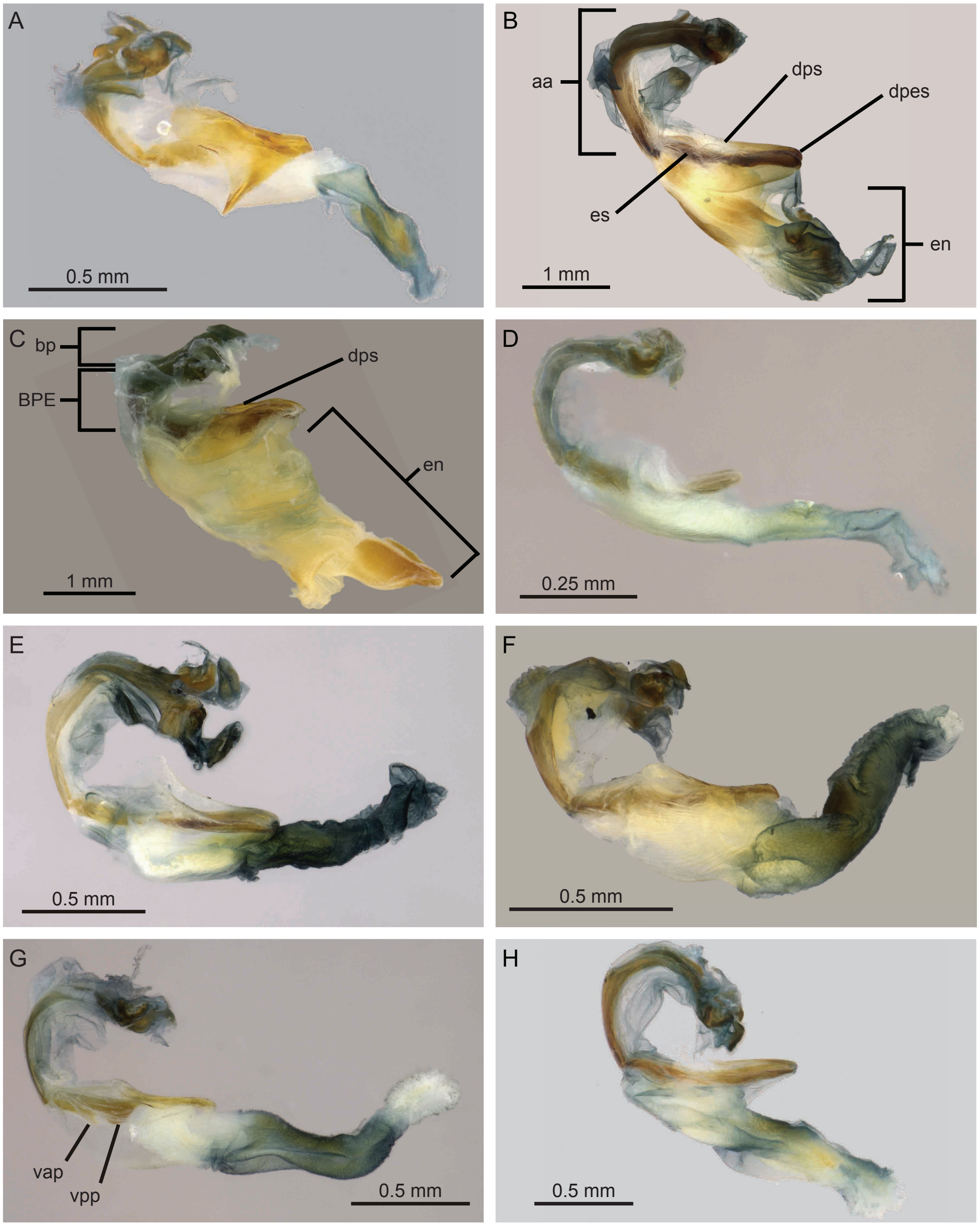

A
0.5 mm
B
aa
dps
dpes
es
en
1 mm
C
bp
BPE
dps
en
1 mm
D
0.25 mm
E
0.5 mm
F
0.5 mm
G
vap
vpp
0.5 mm
H
0.5 mm

Figure 2.23. Female external (A.–E., caudal view) and internal (F., dorsal view) genitalic morphology. A. *Gibbosella brunalvus*, B. *Gibbosella planiscutum*, C. *Glymmatophora crassipes* var. 1, D. *Glymmatophora crassipes* var. 2, E. *Toxopus griswoldi*, F. *Glymmatophora crassipes* var. 2.

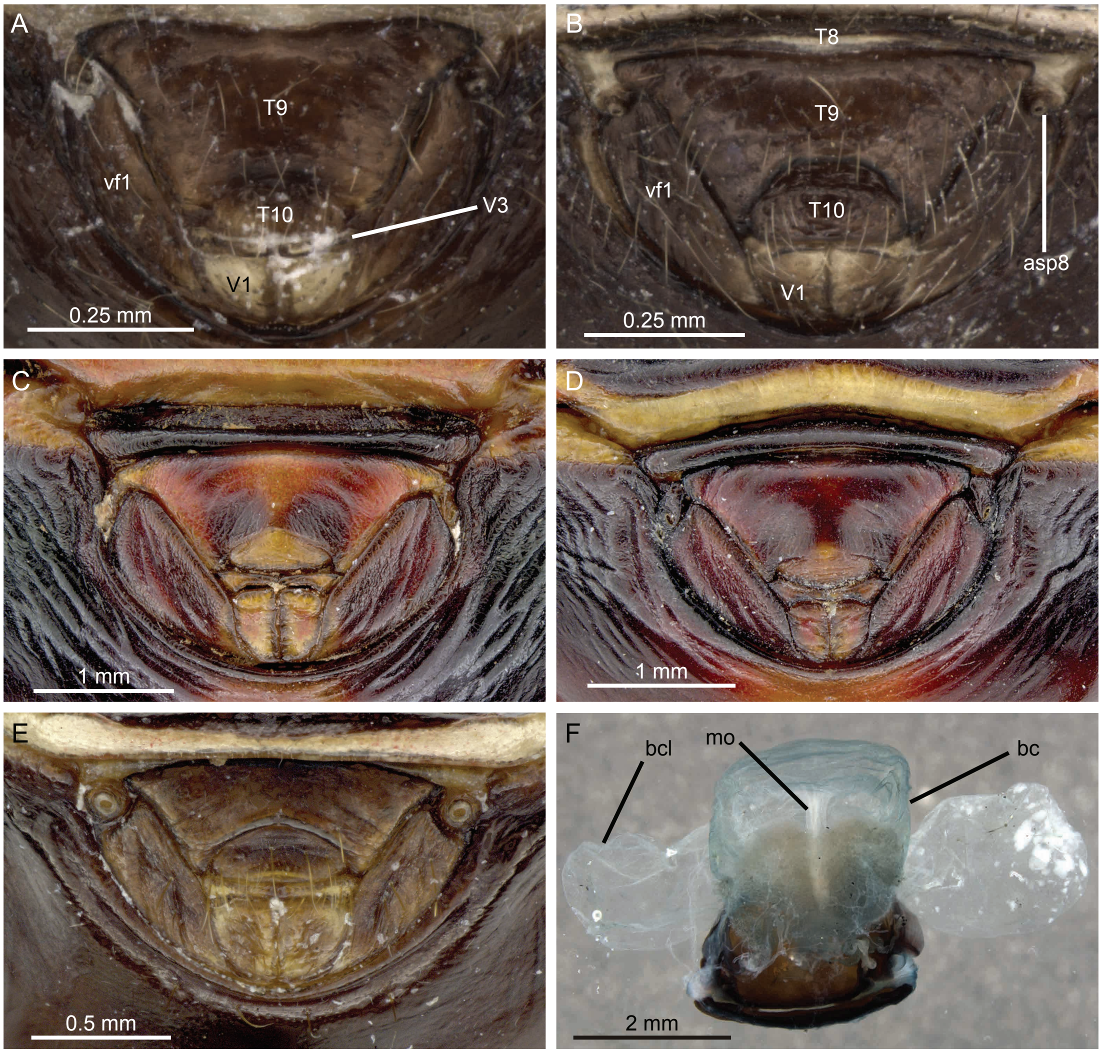

A
T9
vf1
T10
V3
V1
0.25 mm
B
T8
T9
vf1
T10
asp8
V1
0.25 mm
C
1 mm
D
1 mm
E
0.5 mm
F
bcl
mo
bc
2 mm

Figure 2.24. Dorsal habitus of the eight females that cannot by associated with male-based species using molecular, morphological, and geographic data. Five females are assigned to *Gibbosella* based on morphological similarities, while three females cannot be assigned to any genera.


Gibbosella sp.
UCR_ENT 00045079


Gibbosella sp.
UCR_ENT 00045157


Gibbosella sp.
UCR_ENT 00045452


Gibbosella sp.
UCR_ENT 00045569

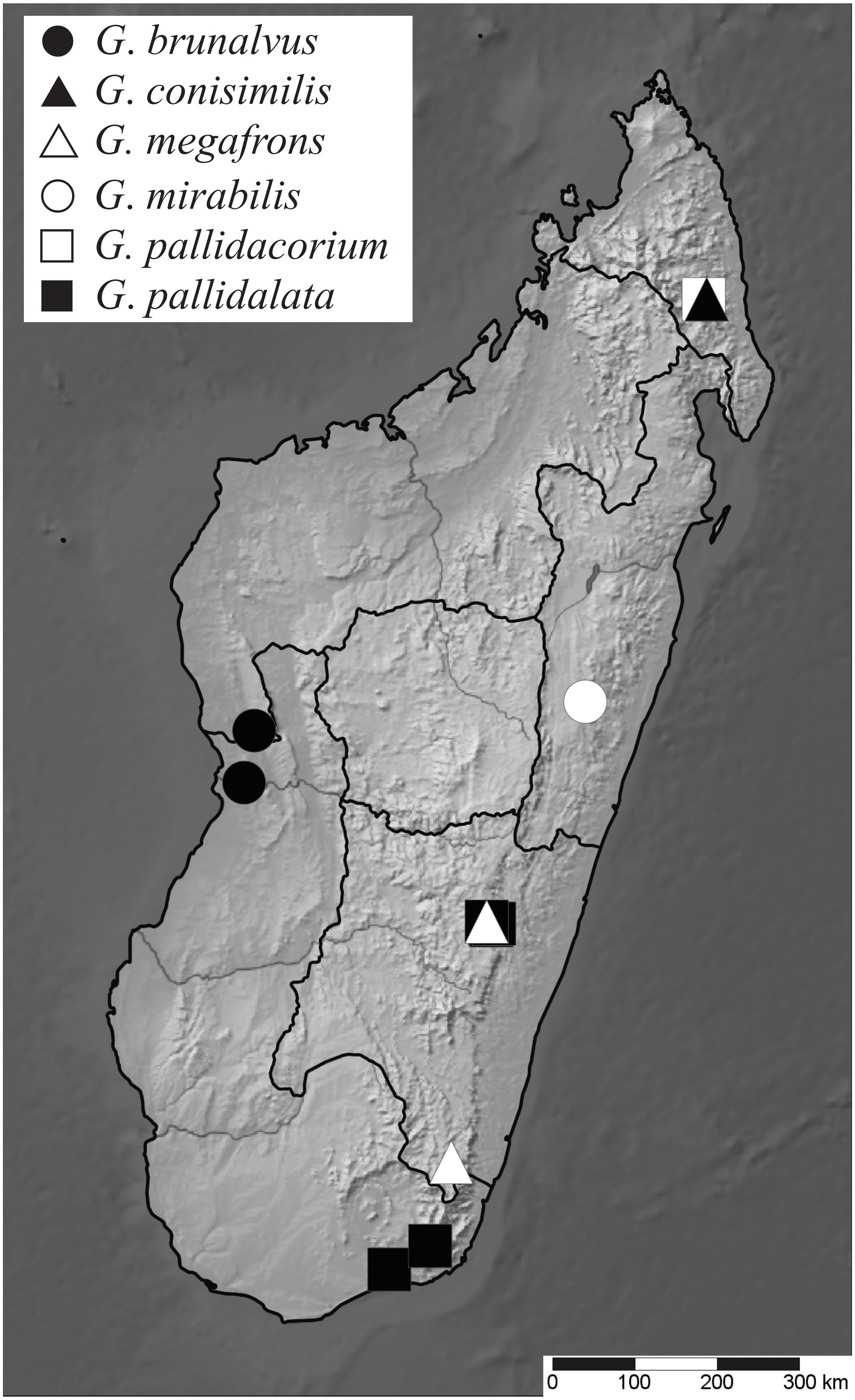

Gibbosella sp.
UCR_ENT 00045646


Undetermined sp.
UCR_ENT 00044794

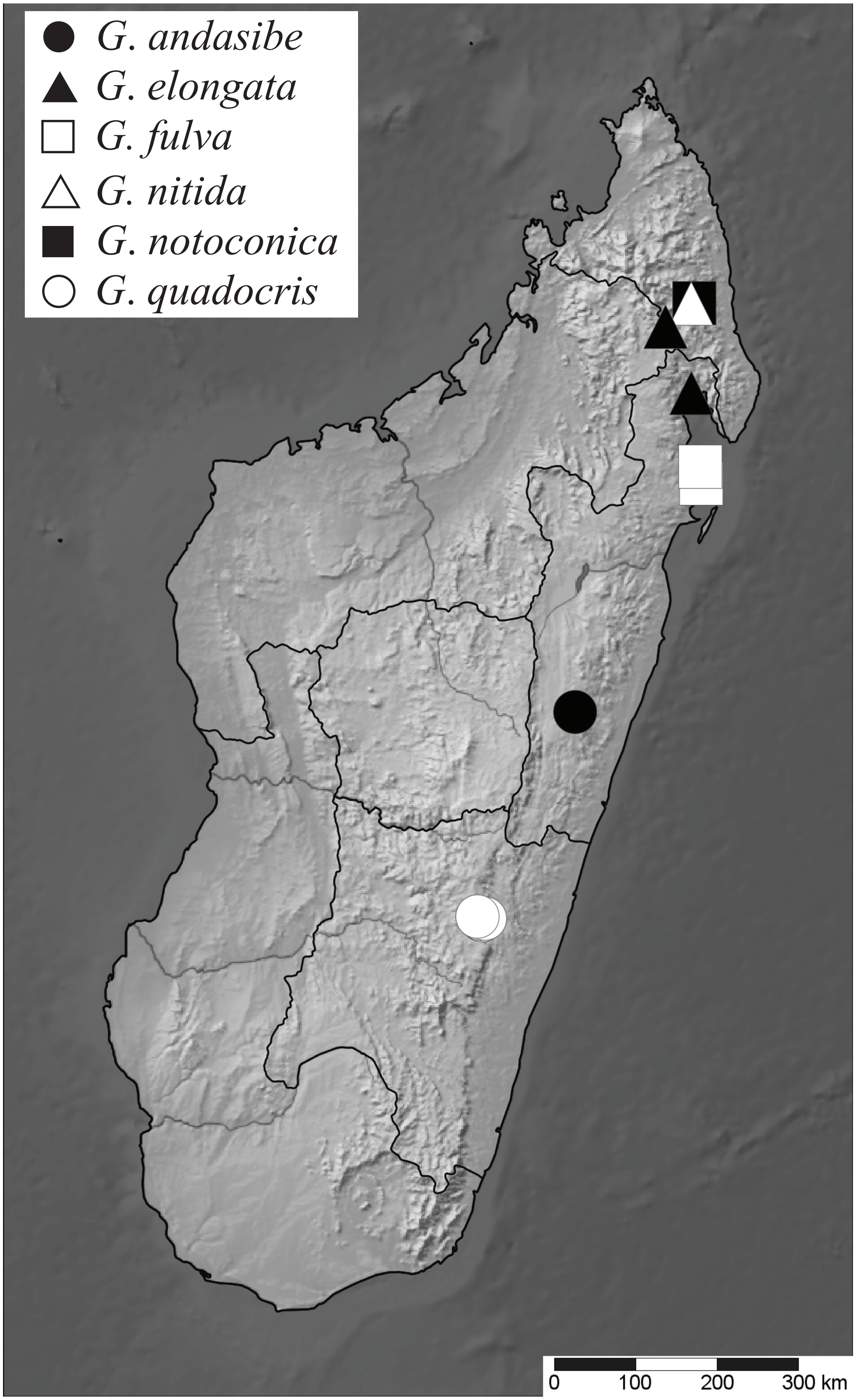

Undetermined sp.
UCR_ENT 00045353


Undetermined sp.
UCR_ENT 00045654

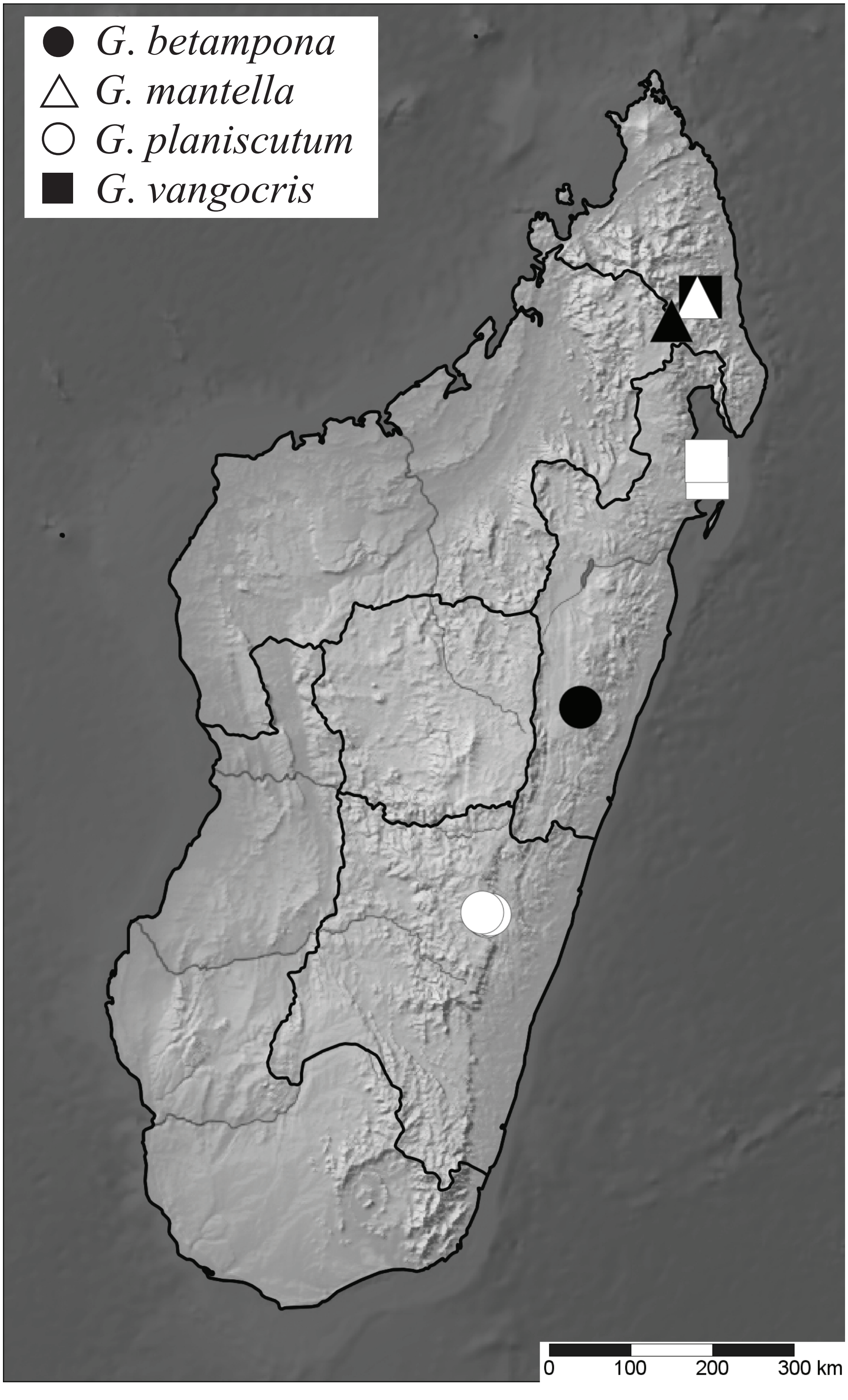
Map 2.1. Localities of *Gibbosella brunalvus*, *G*. *conisimilis*, *G. megafrons*, *G*. *mirabilis*, *G. pallidacorium*, and *G*. *pallidalata*.


● G. brunalvus
▲ G. conisimilis
△ G. megafrons
○ G. mirabilis
☐ G. pallidacorium
■ G. pallidalata
0
100
200
300 km

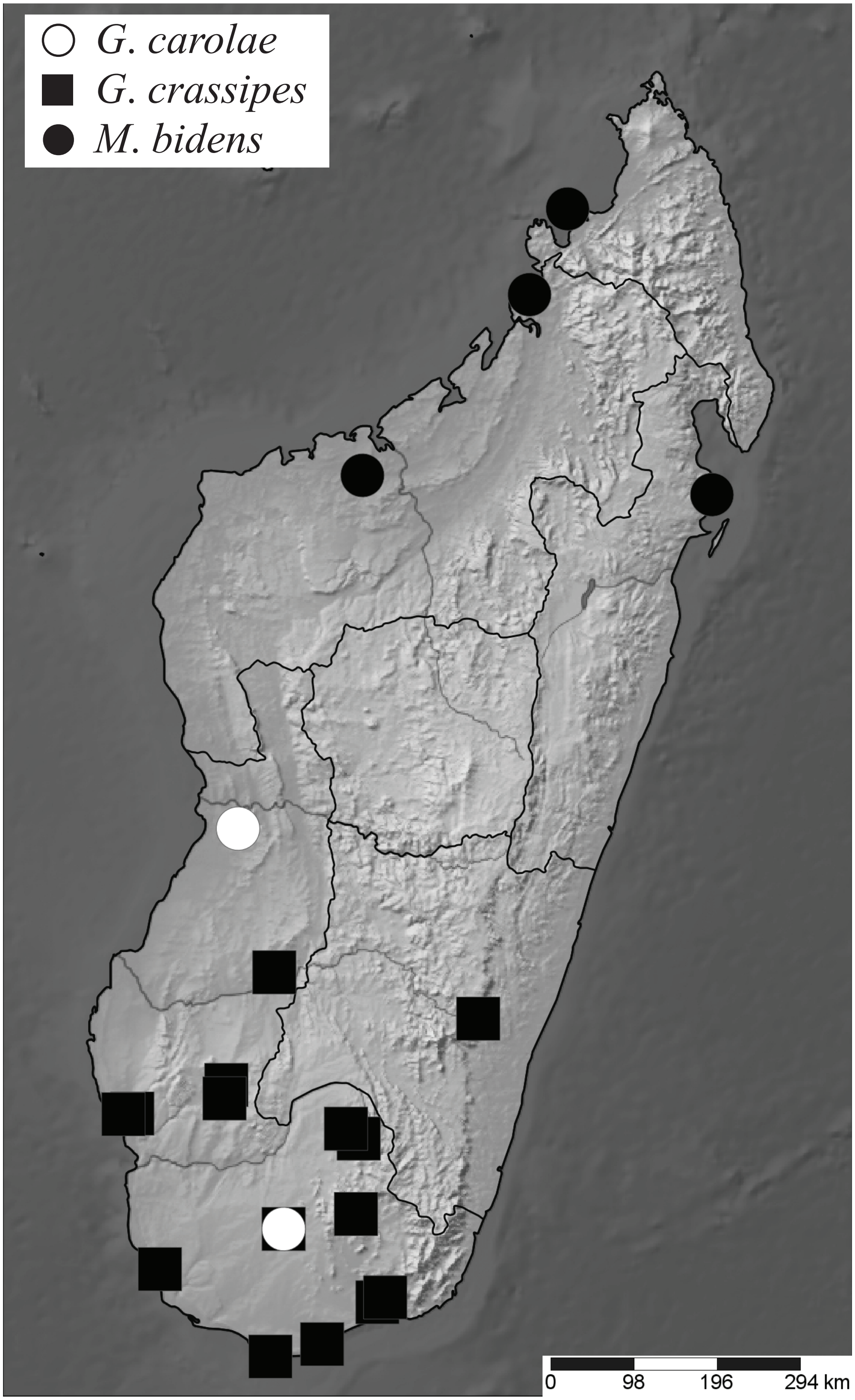
Map 2.2. Localities of *Gibbosella andasibe*, *G*. *elongata*, *G. fulva*, *G*. *nitida*, *G*. *notoconica* and *G*. *quadocris*.


● G. andasibe
▲ G. elongata
□ G. fulva
△ G. nitida
■ G. notoconica
○ G. quadocris
0
100
200
300 km

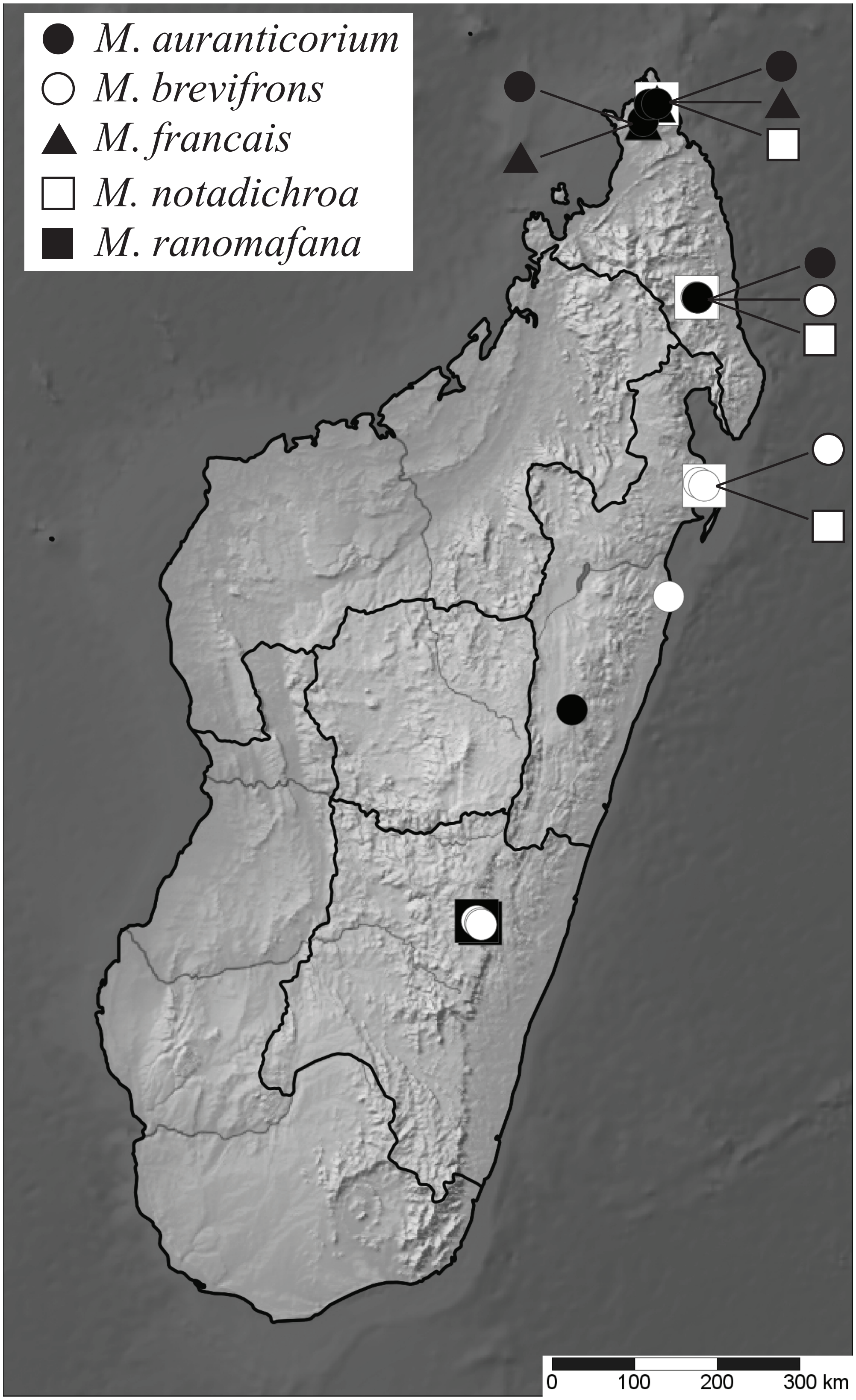
Map 2.3. Localities of *Gibbosella betampona*, *G*. *mantella*, *G. planiscutum*, and *G*. *vangocris*.


● G. betampona
△ G. mantella
○ G. planiscutum
■ G. vangocris
0
100
200
300 km

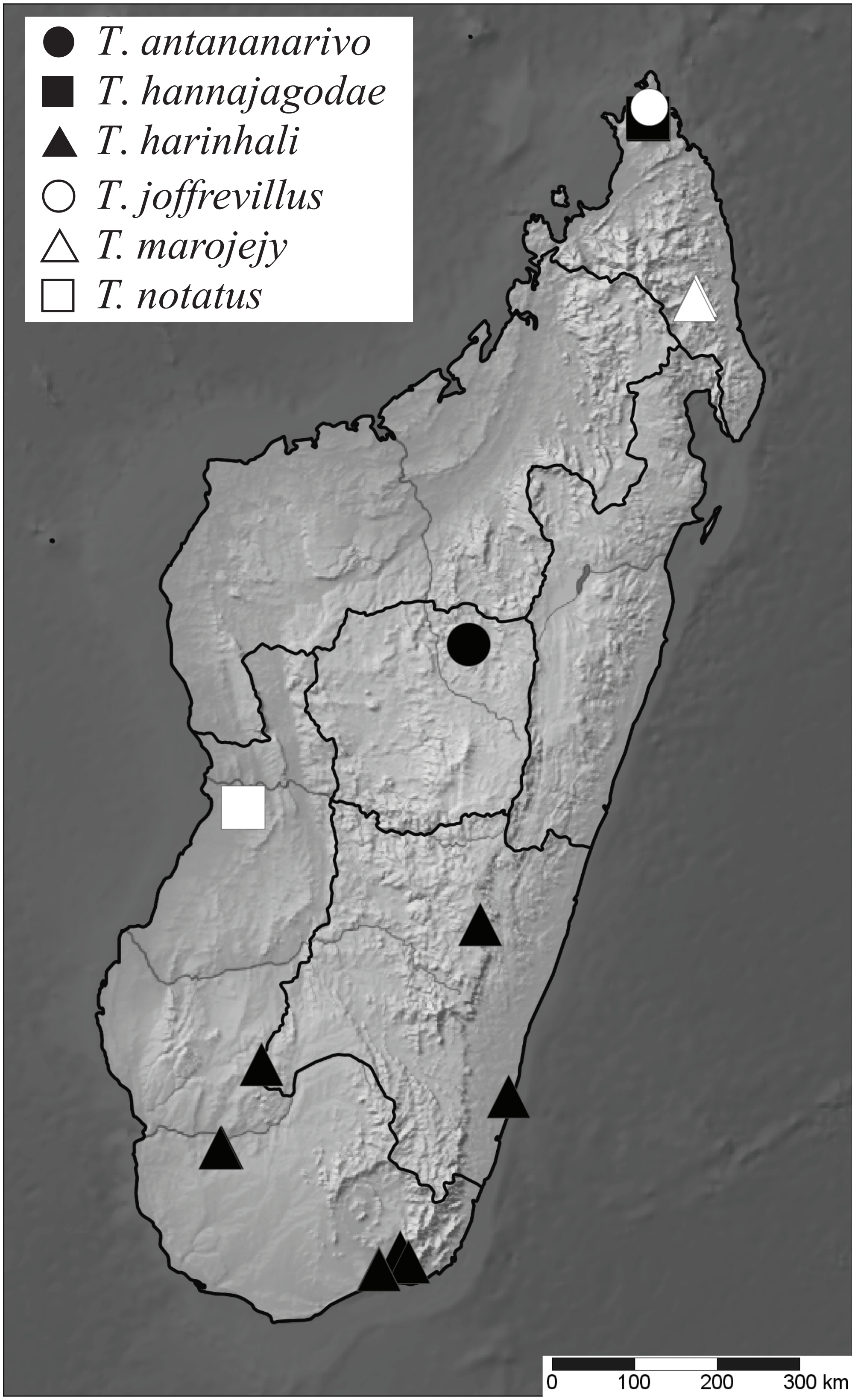
Map 2.4. Localities of *Glymmatophora* species and *Maraenaspis bidens*.


○ G. carolae
■ G. crassipes
● M. bidens
0
98
196
294 km

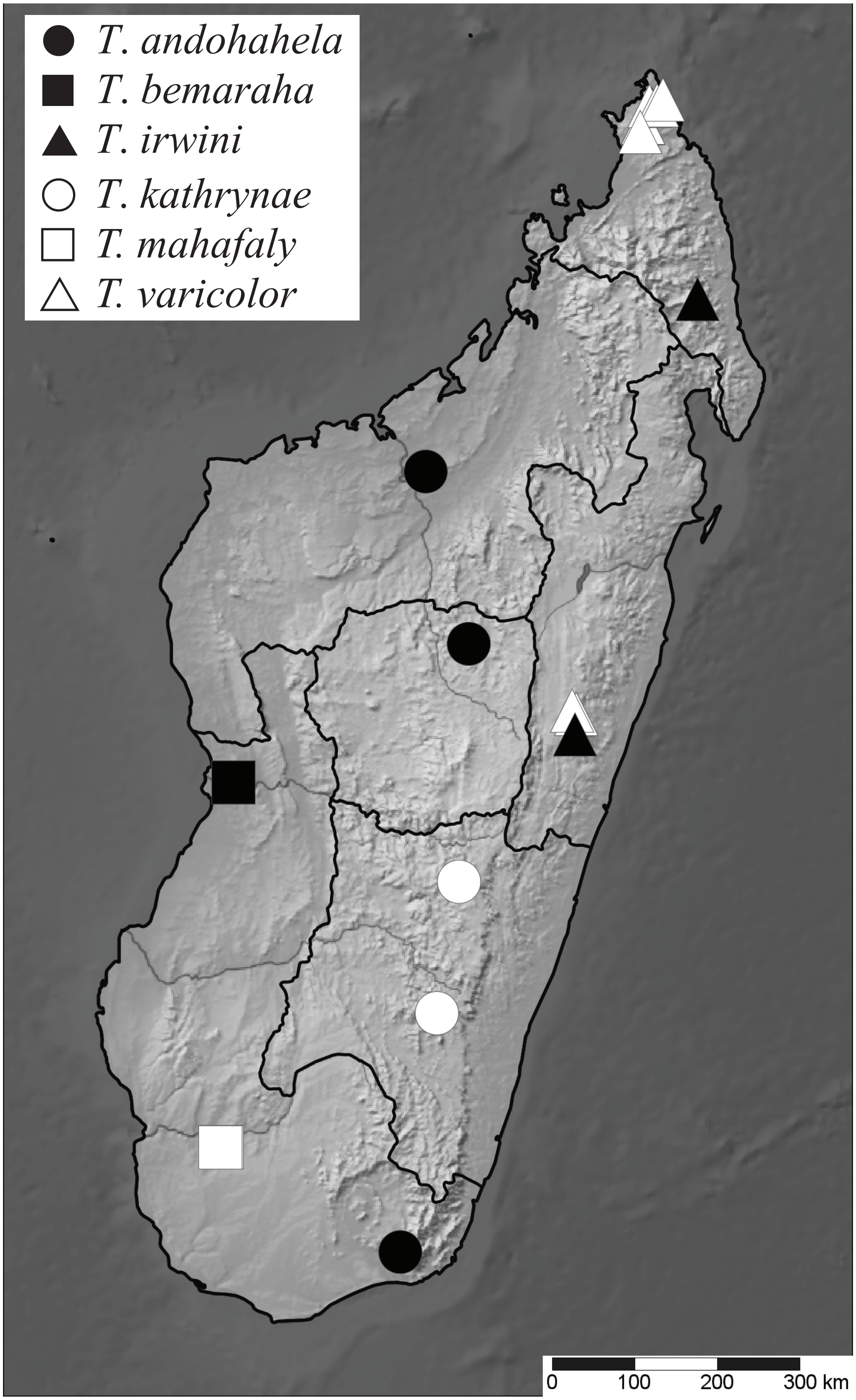
Map 2.5. Localities of *Marojejycoris* species.


● M. auranticorium
○ M. brevifrons
▲ M. francais
☐ M. notadichroa
■ M. ranomafana
0
100
200
300 km

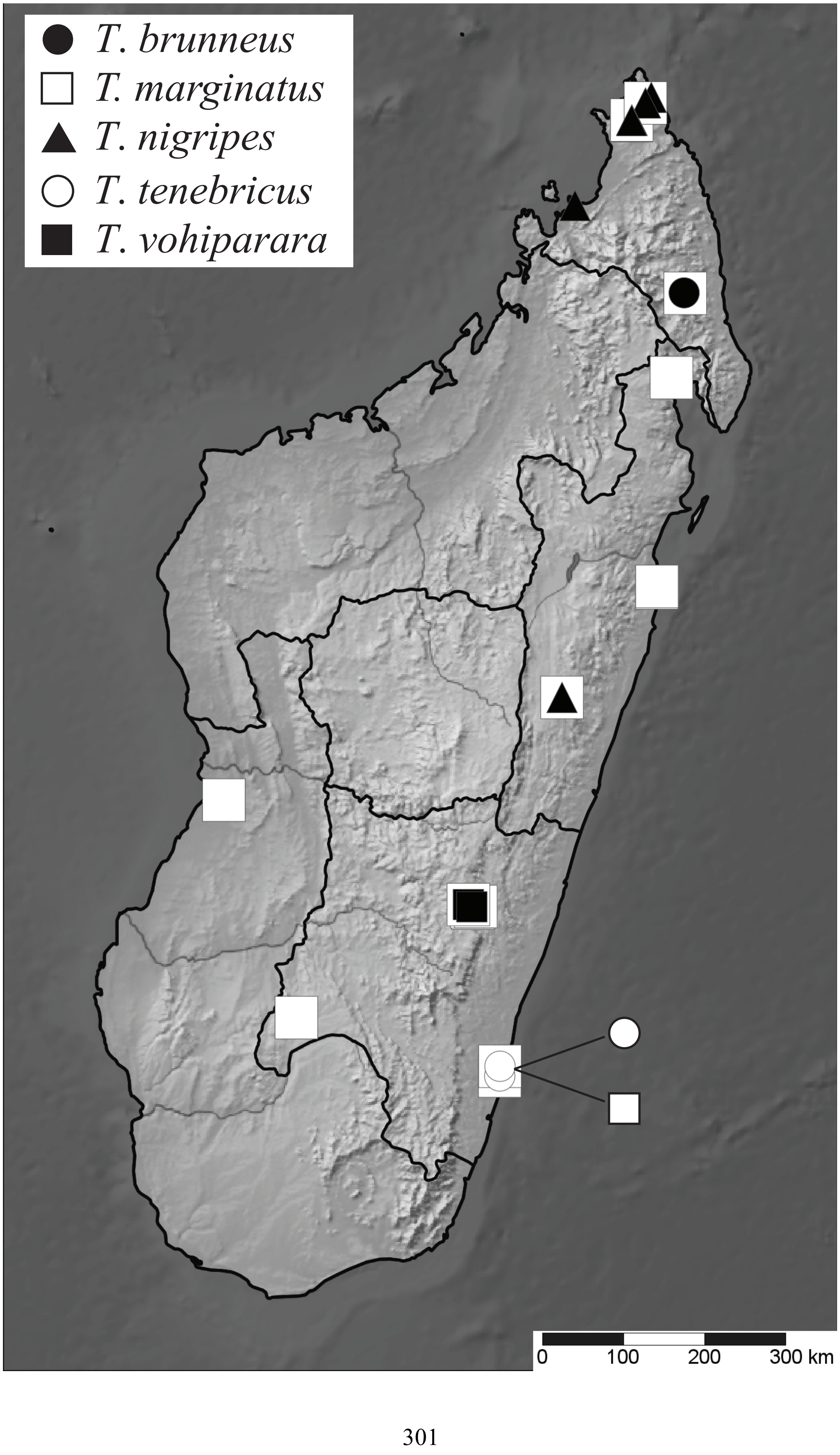
Map 2.6. Localities of *Tanindrazanus antananarivo*, *T. hannajagodae*, *T. harinhali*, *T. joffrevillus*, *T. marojejy*, and *T. notatus*.

● T. antananarivo
■ T. hannajagodae
▲ T. harinhali
○ T. joffrevillus
△ T. marojejy
□ T. notatus
0
100
200
300 km

Map 2.7. Localities of *Tanindrazanus andohahela*, *T. bemaraha*, *T. irwini*, *T. kathrynae*, *T. mahafaly*, and *T. varicolor*.


● T. andohahela
■ T. bemaraha
▲ T. irwini
○ T. kathrynae
□ T. mahafaly
△ T. varicolor
0
100
200
300 km

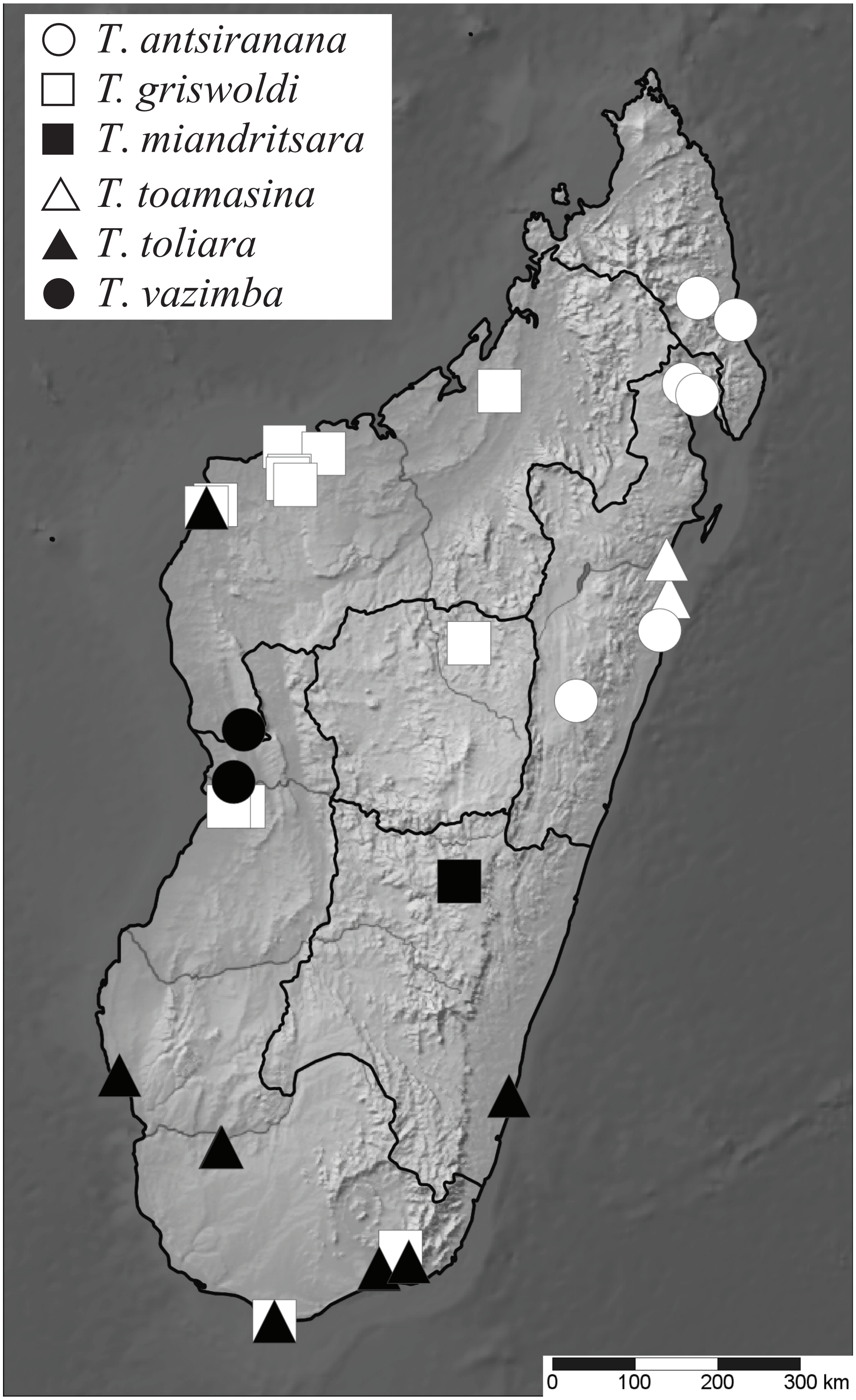
Map 2.8. Localities of *Tanindrazanus brunneus*, *T. marginatus*, *T. nigripes*, *T. tenebricus*, and *T. vohiparara*.


● T. brunneus
☐ T. marginatus
▲ T. nigripes
○ T. tenebricus
■ T. vohiparara
0
100
200
300 km

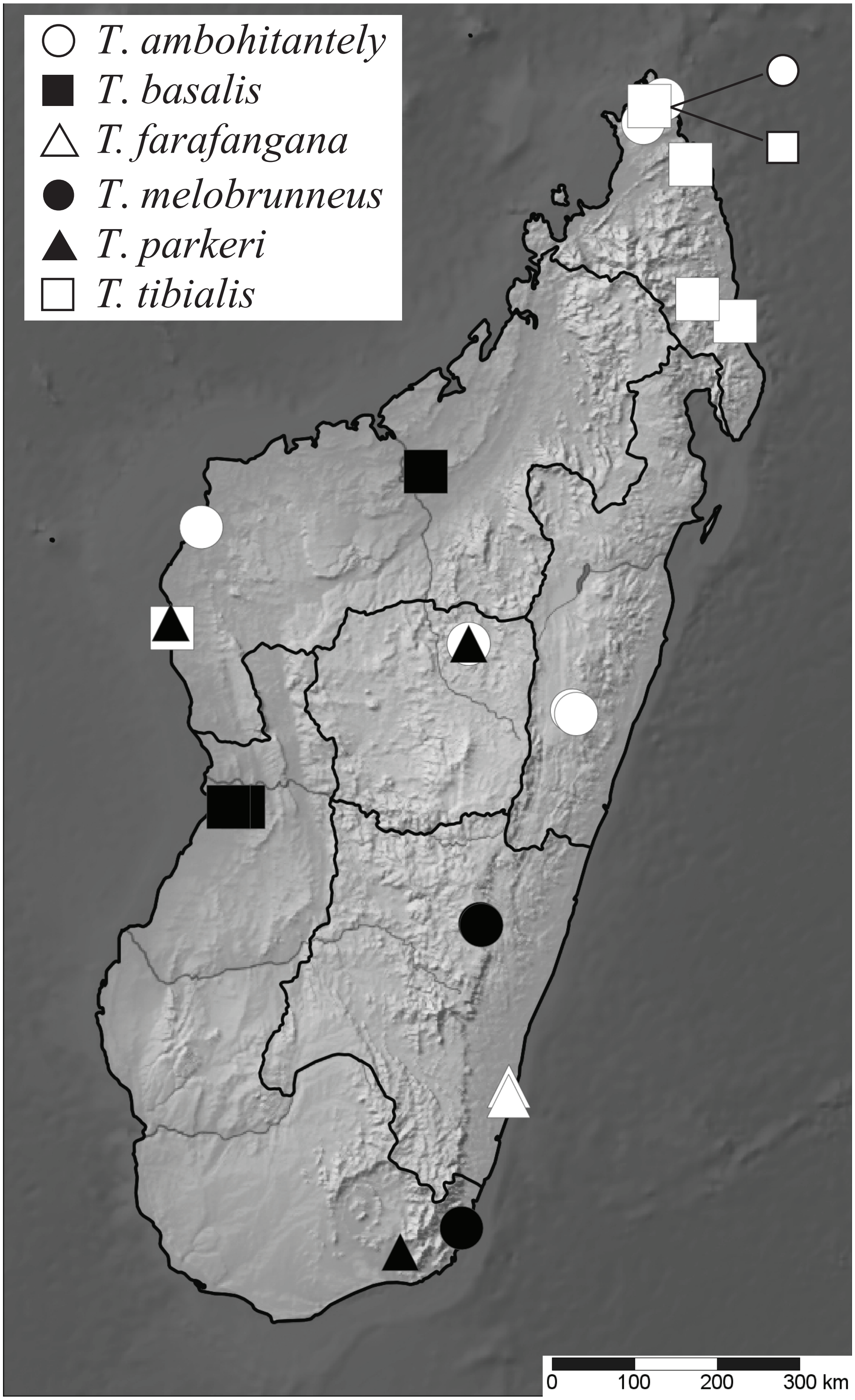
Map 2.9. Localities of *Tanindrazanus amboasaricus*, *Ta*. *anjozorobeus*, and *Toliarus* (*To*.) species.


● *Ta. amboasaricus*
■ *Ta. anjozorobeus*
▲ *To. karinae*
○ *To. trichrous*
0
100
200
300 km

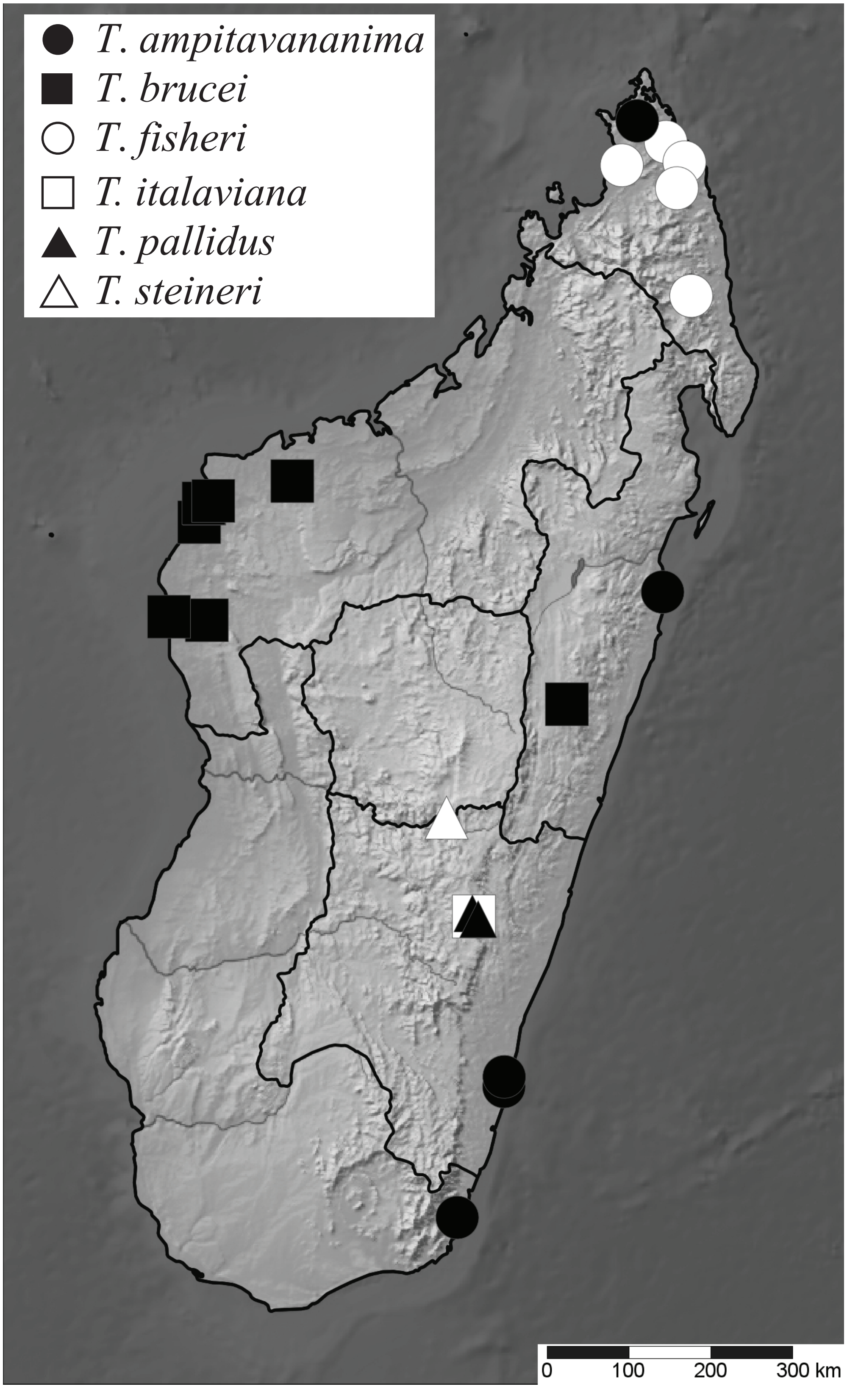
Map 2.10. Localities of *Toxopus antsiranana*, *T. griswoldi*, *T. miandritsara*, *T. toamasina*, *T. toliara*, and *T. vazimba*.


○ T. antsiranana
□ T. griswoldi
■ T. miandritsara
△ T. toamasina
▲ T. toliara
● T. vazimba
0
100
200
300 km

Map 2.11. Localities of *Toxopus ambohitantely*, *T. basalis*, *T. farafangana*, *T. melobrunneus*, *T. parkeri*, and *T. tibialis*.

○ T. ambohitantely
■ T. basalis
△ T. farafangana
● T. melobrunneus
▲ T. parkeri
□ T. tibialis
0
100
200
300 km

Map 2.12. Localities of *Toxopus ampitavananima*, *T. brucei*, *T. fisheri*, *T. italaviana*, *T. pallidus*, and *T. steineri*.


● T. ampitavananima
■ T. brucei
○ T. fisheri
☐ T. italaviana
▲ T. pallidus
△ T. steineri
0
100
200
300 km

Map 2.13. Localities of *Toxopus insignis*, *T. namoroka*, *T. politus*, *T. signoretii*, and *T. simulans*.

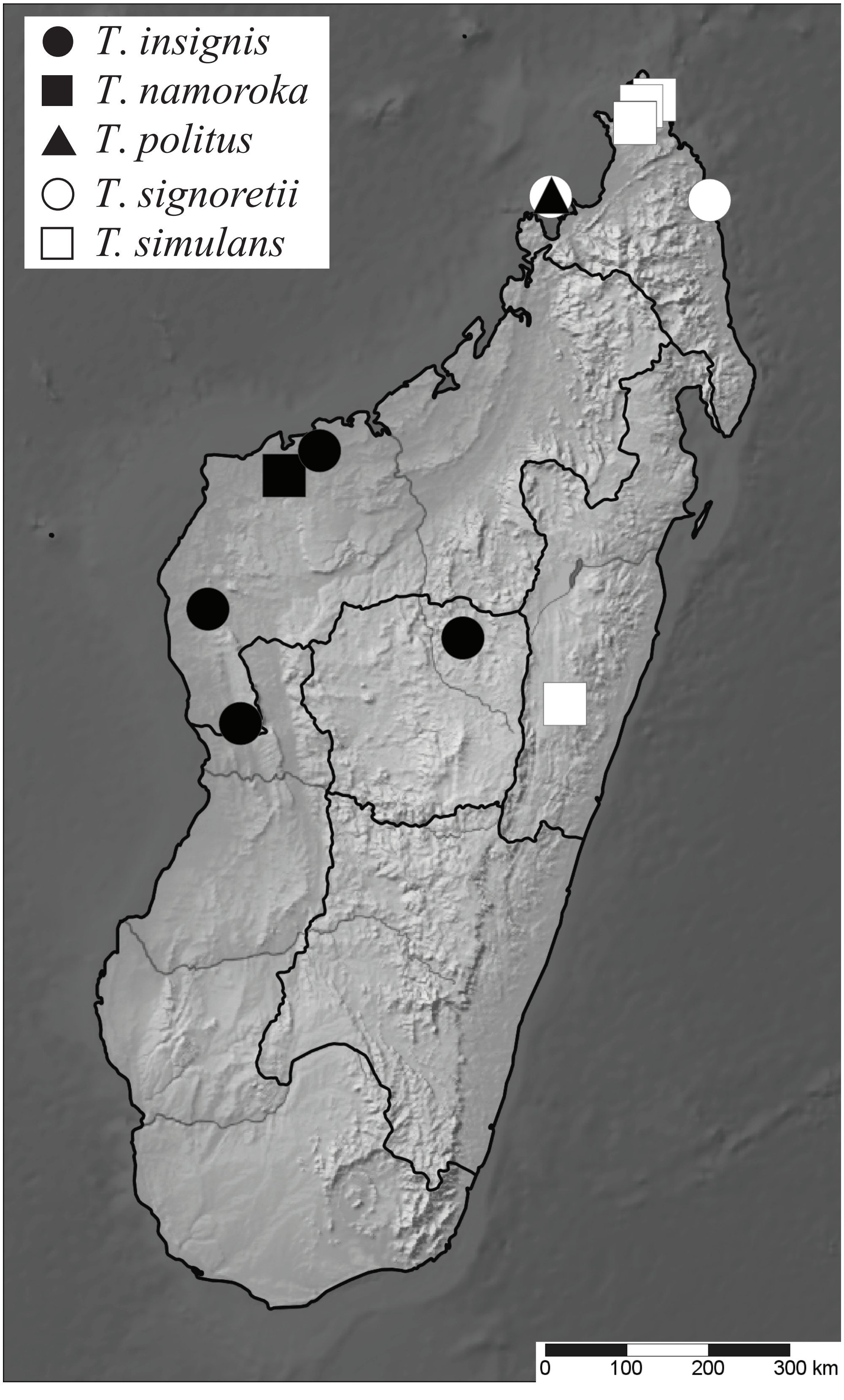

● T. insignis
■ T. namoroka
▲ T. politus
○ T. signoretii
□ T. simulans
0
100
200
300 km

Table 2.1. Measurements (in mm). Abbreviations: Cly-Abd, clypeus to abdomen; AOc, anteocular; POc, postocular; APr, anterior pronotal lobe; PPr, posterior pronotal lobe; Scu, scutellum; Sca, scape; Ped, pedicel; Syn, synthlipsis; SD, standard deviation.

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Gibbosella andasibe n. sp.																
Male (*N* = 1)	Measurements	4.31	3.64	0.60	0.11	0.23	0.30	0.52	0.36	0.77	0.76	0.55	0.31	0.65	1.08	1.25
Gibbosella betampona n. sp.																
Male (*N* = 1)	Measurements	7.02	6.40	0.91	0.24	0.23	0.54	0.82	0.75	1.16	1.35	0.88	0.34	1.19	1.77	2.28
Gibbosella brunalvus n. sp.																
Male (*N* = 5)	Mean	5.05	4.93	0.85	0.21	0.27	0.44	0.67	0.55	0.95	1.04	0.69	0.36	0.93	1.36	1.60
	SD	0.10	0.15	0.03	0.02	0.02	0.02	0.04	0.05	0.03	0.02	0.03	0.01	0.04	0.07	0.06
	Range	0.24	0.34	0.06	0.04	0.05	0.04	0.09	0.13	0.06	0.05	0.07	0.02	0.09	0.15	0.13
	Min.	4.92	4.79	0.81	0.20	0.25	0.42	0.62	0.49	0.91	1.03	0.66	0.34	0.88	1.30	1.54
	Max.	5.16	5.13	0.88	0.24	0.30	0.46	0.71	0.62	0.98	1.08	0.73	0.36	0.97	1.45	1.67
Female (*N* = 1)	Measurements	4.54	4.54	0.92	0.25	0.30	0.69	0.22	0.31	0.64	0.69	0.64	0.39	0.97	0.90	1.79
Gibbosella conisimilis n. sp.																
Male (*N* = 3)	Mean	8.82	8.07	1.32	0.32	0.36	0.61	1.14	0.99	1.22	1.62	1.10	0.51	1.34	2.19	2.76
	SD	0.25	0.32	0.05	0.00	0.01	0.03	0.06	0.13	0.03	0.02	0.02	0.03	0.05	0.09	0.16
	Range	0.49	0.58	0.10	0.01	0.02	0.06	0.12	0.25	0.06	0.04	0.04	0.07	0.10	0.17	0.30
	Min.	8.61	7.86	1.27	0.32	0.36	0.57	1.10	0.88	1.20	1.60	1.08	0.48	1.29	2.12	2.65
	Max.	9.10	8.44	1.37	0.33	0.37	0.64	1.21	1.12	1.26	1.64	1.12	0.54	1.40	2.30	2.95
Gibbosella elongata Chłond, 2010																
Male (*N* = 1)	Measurements	10.50	9.90	1.70	0.62	0.47	0.80	1.28	0.91	1.89	2.21	1.40	0.48	1.49	2.44	3.45
Gibbosella fulva n. sp.																
Male (*N* = 2)	Mean	7.58	7.39	1.14	0.37	0.42	0.71	1.02	0.80	1.03	1.56	0.90	0.39	1.41	2.21	2.44
	SD	0.03	0.02	0.02	0.01	0.00	0.01	0.01	0.00	0.03	0.01	0.01	0.00	0.01	0.01	0.02
	Range	0.04	0.03	0.03	0.01	0.00	0.01	0.02	0.00	0.04	0.02	0.01	0.00	0.01	0.02	0.03
	Min.	7.56	7.37	1.12	0.36	0.42	0.70	1.01	0.80	1.01	1.55	0.90	0.39	1.41	2.20	2.42
	Max.	7.60	7.40	1.15	0.37	0.42	0.71	1.03	0.80	1.05	1.57	0.91	0.39	1.42	2.22	2.45
Gibbosella mantella n. sp.																
Male (*N* = 1)	Measurements	5.79	5.42	0.88	0.19	0.21	0.53	0.70	0.61	1.14	1.21	0.85	0.27	1.07	1.52	1.96

Table 2.1. (Continued).

Species			Length										Width				
			Total	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Gibbosella megafrons n. sp.																	
	Male ($N = 2$)	Mean	4.94	4.42	0.75	0.19	0.27	0.37	0.93	0.53	1.02	1.01	0.60	0.35	0.78	1.31	1.58
		SD	1.00	0.90	0.14	0.08	0.04	0.04	0.52	0.10	0.07	0.12	0.07	0.00	0.11	0.28	0.38
		Range	1.41	1.27	0.20	0.12	0.06	0.06	0.73	0.13	0.10	0.18	0.10	0.00	0.15	0.39	0.54
		Min.	4.24	3.78	0.65	0.13	0.24	0.34	0.57	0.47	0.97	0.92	0.55	0.35	0.70	1.12	1.31
		Max.	5.65	5.05	0.85	0.25	0.30	0.40	1.30	0.60	1.07	1.10	0.65	0.35	0.85	1.51	1.85
Gibbosella nitida n. sp.																	
	Male ($N = 1$)	Measurements	5.30	4.75	0.90	0.33	0.35	0.45	0.62	0.52	0.85	0.89	0.65	0.35	0.90	1.45	1.61
Gibbosella notoconica n. sp.																	
	Male ($N = 2$)	Mean	9.62	9.01	1.37	0.34	0.33	0.64	1.27	1.06	1.53	1.90	1.29	0.48	1.35	2.27	3.31
		SD	0.67	0.67	0.09	0.02	0.04	0.01	0.09	0.17	0.06	0.19	0.13	0.04	0.08	0.15	0.27
		Range	0.95	0.95	0.13	0.02	0.05	0.02	0.13	0.25	0.09	0.26	0.18	0.06	0.11	0.21	0.39
		Min.	9.15	8.53	1.31	0.33	0.31	0.63	1.21	0.94	1.49	1.76	1.20	0.45	1.30	2.17	3.11
		Max.	10.09	9.48	1.43	0.35	0.36	0.65	1.33	1.18	1.57	2.03	1.39	0.52	1.40	2.38	3.50
Gibbosella pallidacorium n. sp.																	
	Male ($N = 1$)	Measurements	6.76	5.78	0.84	0.20	0.23	0.35	0.81	0.65	1.04	1.34	0.86	0.30	0.97	1.67	1.89
Gibbosella pallidalata n. sp.																	
	Male ($N = 5$)	Mean	5.68	5.18	0.90	0.24	0.29	0.41	0.70	0.58	1.07	1.10	0.66	0.36	0.96	1.52	1.83
		SD	0.22	0.18	0.07	0.03	0.04	0.01	0.05	0.06	0.03	0.03	0.02	0.01	0.03	0.04	0.07
		Range	0.57	0.46	0.18	0.08	0.10	0.03	0.15	0.15	0.09	0.08	0.04	0.03	0.07	0.09	0.15
		Min.	5.36	4.88	0.82	0.20	0.23	0.39	0.63	0.50	1.02	1.06	0.63	0.34	0.91	1.47	1.75
		Max.	5.93	5.34	1.00	0.27	0.33	0.42	0.78	0.65	1.11	1.14	0.67	0.37	0.98	1.56	1.89
Gibbosella planiscutum n. sp.																	
	Male ($N = 5$)	Mean	5.50	5.32	0.88	0.24	0.27	0.52	0.68	0.50	0.95	1.08	0.72	0.38	1.02	1.47	1.83
		SD	0.27	0.38	0.08	0.03	0.03	0.02	0.05	0.05	0.07	0.07	0.03	0.03	0.06	0.10	0.17
		Range	0.68	0.99	0.20	0.06	0.08	0.05	0.13	0.11	0.16	0.16	0.08	0.07	0.15	0.20	0.42
		Min.	5.28	4.91	0.77	0.21	0.24	0.50	0.60	0.48	0.85	0.98	0.68	0.35	0.97	1.38	1.67
		Max.	5.96	5.90	0.97	0.27	0.32	0.55	0.73	0.58	1.01	1.14	0.76	0.42	1.12	1.58	2.09

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Gibbosella planiscutum n. sp.																
Female (*N* = 5)	Mean	4.92	4.92	0.86	0.26	0.27	0.71	0.25	0.33	0.71	0.75	0.68	0.42	1.07	0.96	1.86
	SD	0.20	0.20	0.01	0.04	0.02	0.01	0.03	0.04	0.04	0.07	0.03	0.01	0.03	0.04	0.06
	Range	0.28	0.28	0.02	0.05	0.03	0.02	0.05	0.05	0.06	0.10	0.04	0.01	0.04	0.06	0.08
	Min.	4.78	4.78	0.85	0.23	0.25	0.70	0.23	0.30	0.68	0.70	0.66	0.41	1.05	0.93	1.82
	Max.	5.06	5.06	0.87	0.29	0.29	0.73	0.28	0.36	0.74	0.80	0.70	0.42	1.09	0.99	1.90
Gibbosella quadocris n. sp.																
Female (*N* = 5)	Mean	6.46	5.57	0.95	0.25	0.30	0.49	0.78	0.65	1.06	1.22	0.72	0.37	1.02	1.61	1.93
	SD	0.22	0.20	0.06	0.04	0.02	0.01	0.04	0.05	0.06	0.08	0.02	0.02	0.04	0.08	0.04
	Range	0.56	0.46	0.15	0.11	0.04	0.03	0.09	0.11	0.15	0.21	0.05	0.04	0.10	0.21	0.11
	Min.	6.23	5.33	0.88	0.21	0.28	0.47	0.76	0.59	1.00	1.12	0.70	0.35	0.97	1.53	1.87
	Max.	6.79	5.78	1.03	0.33	0.32	0.50	0.85	0.70	1.15	1.33	0.76	0.39	1.07	1.74	1.99
Gibbosella vangocris n. sp.																
Male (*N* = 5)	Mean	8.20	7.25	1.22	0.38	0.36	0.60	0.99	0.87	1.40	1.59	0.90	0.42	1.26	2.04	2.60
	SD	0.43	0.30	0.06	0.04	0.02	0.02	0.09	0.04	0.05	0.11	0.04	0.03	0.05	0.08	0.13
	Range	1.15	0.81	0.14	0.08	0.05	0.06	0.23	0.11	0.12	0.29	0.11	0.07	0.13	0.20	0.36
	Min.	7.55	6.80	1.14	0.34	0.34	0.57	0.85	0.83	1.34	1.48	0.84	0.39	1.17	1.91	2.38
	Max.	8.70	7.61	1.28	0.42	0.39	0.63	1.09	0.95	1.45	1.77	0.95	0.46	1.31	2.11	2.74
Glymmatophora carolae n. sp.																
Male (*N* = 4)	Mean	15.77	15.77	2.22	0.80	0.63	1.75	2.58	1.30	2.40	2.94	2.34	1.22	3.74	5.32	5.66
	SD	0.84	0.84	0.45	0.24	0.08	0.18	0.14	0.17	0.23	0.31	0.05	0.05	0.09	0.14	0.63
	Range	2.01	2.01	0.88	0.46	0.18	0.34	0.35	0.36	0.48	0.68	0.11	0.11	0.19	0.31	1.39
	Min.	14.90	14.90	1.82	0.56	0.53	1.57	2.42	1.17	2.26	2.69	2.30	1.19	3.67	5.20	5.10
	Max.	16.91	16.91	2.70	1.02	0.71	1.91	2.77	1.53	2.74	3.37	2.41	1.30	3.86	5.51	6.49
Glymmatophora crassipes Horváth, 1914																
Male (*N* = 5)	Mean	17.94	17.94	3.19	1.43	0.52	3.23	1.41	1.23	2.25	2.56	2.36	1.27	4.85	4.83	7.85
	SD	1.54	1.54	0.32	0.16	0.07	0.34	0.14	0.13	0.29	0.35	0.19	0.09	0.39	0.42	0.99
	Range	4.08	4.08	0.70	0.31	0.19	0.85	0.34	0.30	0.70	0.77	0.45	0.23	0.90	0.99	2.40
	Min.	15.52	15.52	2.80	1.29	0.45	2.70	1.28	1.12	1.90	2.13	2.10	1.10	4.20	4.11	6.30
	Max.	19.60	19.60	3.50	1.60	0.64	3.55	1.62	1.42	2.60	2.90	2.55	1.33	5.10	5.10	8.70

Table 2.1. (Continued).

Species		Length										Width				
		Total	Clyp -Abd	Head	AOc	POc	APr	PPr	Scu	Sca	Ped	Head	Syn	APr	PPr	Abd
Glymmatophora crassipes Horváth, 1914																
Female (*N* = 5)	Mean	20.78	20.78	3.36	1.44	0.85	3.57	1.57	1.51	2.36	2.52	2.53	1.43	5.40	5.27	9.29
	SD	2.24	2.24	0.41	0.28	0.23	0.50	0.13	0.12	0.05	0.16	0.30	0.22	0.68	0.80	1.18
	Range	5.60	5.60	1.12	0.72	0.65	1.26	0.30	0.28	0.10	0.30	0.70	0.50	1.56	1.75	2.80
	Min.	18.30	18.30	2.88	1.18	0.55	2.84	1.40	1.37	2.30	2.40	2.20	1.20	4.64	4.45	7.90
	Max.	23.90	23.90	4.00	1.90	1.20	4.10	1.70	1.65	2.40	2.70	2.90	1.70	6.20	6.20	10.70
Maraenaspis bidens (Reuter), 1887																
Male (*N* = 2)	Mean	21.85	21.85	3.25	1.26	0.64	3.93	1.33	1.63	3.33	3.75	2.66	1.53	5.11	5.03	9.21
	SD	0.32	0.32	0.20	0.21	0.02	0.54	0.01	0.03	0.05	0.19	0.08	0.05	0.32	0.31	0.34
	Range	0.45	0.45	0.28	0.30	0.03	0.77	0.01	0.04	0.07	0.27	0.11	0.08	0.45	0.44	0.48
	Min.	21.63	21.63	3.11	1.41	0.65	3.55	1.34	1.61	3.30	3.61	2.72	1.57	4.88	4.81	8.97
	Max.	22.08	22.08	3.39	1.41	0.65	4.32	1.34	1.65	3.37	3.88	2.72	1.57	5.34	5.25	9.45
Female (*N* = 2)	Mean	22.15	22.15	3.65	1.60	1.15	3.74	1.72	1.37	2.90	—	2.78	1.61	4.88	4.14	8.26
	SD	1.20	1.20	0.21	0.14	0.07	0.09	0.04	0.06	0.00	—	0.14	0.03	0.03	0.05	0.07
	Range	1.70	1.70	0.30	0.20	0.10	0.13	0.06	0.08	0.00	—	0.20	0.04	0.04	0.07	0.10
	Min.	21.30	21.30	3.50	1.50	1.10	3.67	1.69	1.33	2.90	—	2.78	1.61	4.88	4.10	8.21
	Max.	23.00	23.00	3.80	1.70	1.20	3.80	1.75	1.41	2.90	—	2.98	1.65	4.92	4.17	8.31
Marojejycoris auranticorium n. sp.																
Male (*N* = 4)	Mean	9.35	8.96	1.71	0.57	0.57	0.66	1.16	0.77	1.56	1.82	1.20	0.59	1.66	2.46	2.84
	SD	0.34	0.29	0.07	0.02	0.03	0.10	0.06	0.06	0.07	0.09	0.04	0.06	0.04	0.04	0.14
	Range	0.69	0.64	0.16	0.04	0.07	0.22	0.12	0.14	0.18	0.20	0.08	0.14	0.10	0.10	0.30
	Min.	8.96	8.54	1.64	0.55	0.53	0.54	1.13	0.68	1.47	1.69	1.14	0.53	1.60	2.41	2.70
	Max.	9.65	9.18	1.80	0.59	0.59	0.76	1.25	0.82	1.65	1.88	1.22	0.67	1.69	2.51	3.00
Marojejycoris brevifrons n. sp.																
Male (*N* = 5)	Mean	7.19	6.58	1.23	0.30	0.34	0.51	0.87	0.66	1.26	1.33	0.97	0.35	1.28	1.88	2.16
	SD	0.96	0.66	0.08	0.04	0.02	0.05	0.07	0.07	0.09	0.11	0.04	0.02	0.11	0.13	0.17
	Range	2.28	1.50	0.21	0.11	0.05	0.13	0.17	0.18	0.22	0.26	0.10	0.06	0.22	0.29	0.41
	Min.	5.63	5.63	1.08	0.24	0.31	0.44	0.79	0.60	1.13	1.18	0.93	0.31	1.15	1.73	1.99
	Max.	7.91	7.13	1.29	0.35	0.36	0.57	0.95	0.77	1.34	1.44	1.02	0.37	1.36	2.02	2.40

Table 2.1. (Continued).

Species		Length										Width				
		Total	Clyp -Abd	Head	AOc	POc	APr	PPr	Scu	Sca	Ped	Head	Syn	APr	PPr	Abd
Marojejycoris francais n. sp.																
Female (*N* = 2)	Mean	6.99	6.50	1.15	0.39	0.34	0.50	0.90	0.63	0.93	1.27	0.89	0.44	1.34	1.92	2.19
	SD	0.62	0.46	0.04	0.05	0.06	0.01	0.04	0.08	0.09	0.11	0.06	0.00	0.11	0.15	0.16
	Range	0.87	0.65	0.06	0.07	0.09	0.02	0.05	0.12	0.12	0.15	0.09	0.01	0.15	0.22	0.22
	Min.	6.55	6.18	1.12	0.35	0.30	0.49	0.87	0.57	0.87	1.19	0.84	0.44	1.27	1.81	2.08
	Max.	7.42	6.82	1.18	0.42	0.39	0.51	0.93	0.69	1.00	1.34	0.93	0.44	1.42	2.03	2.30
Marojejycoris notadichroa n. sp.																
Male (*N* = 5)	Mean	8.46	7.94	1.44	0.48	0.47	0.65	1.03	0.78	1.29	1.46	1.35	0.56	1.56	2.19	2.54
	SD	0.45	0.54	0.09	0.03	0.05	0.02	0.08	0.03	0.08	0.05	0.65	0.04	0.11	0.18	0.31
	Range	1.01	1.33	0.24	0.08	0.12	0.05	0.22	0.07	0.21	0.13	1.50	0.09	0.25	0.46	0.71
	Min.	8.08	7.40	1.33	0.44	0.41	0.62	0.90	0.74	1.22	1.41	1.00	0.53	1.42	1.95	2.18
	Max.	9.09	8.73	1.57	0.52	0.53	0.67	1.12	0.81	1.43	1.54	2.51	0.62	1.67	2.41	2.88
Marojejycoris ranomafana n. sp.																
Male (*N* = 2)	Mean	6.20	5.46	1.01	0.25	0.38	0.48	0.71	0.55	1.12	1.18	0.70	0.37	1.10	1.56	1.87
	SD	0.18	0.06	0.01	0.02	0.00	0.07	0.01	0.07	0.04	0.05	0.03	0.00	0.00	0.01	0.04
	Range	0.25	0.08	0.02	0.03	0.00	0.10	0.01	0.10	0.06	0.07	0.04	0.00	0.00	0.01	0.06
	Min.	6.08	5.41	1.00	0.24	0.37	0.43	0.70	0.50	1.09	1.15	0.68	0.37	1.10	1.56	1.84
	Max.	6.33	5.50	1.02	0.27	0.38	0.52	0.71	0.61	1.15	1.21	0.72	0.37	1.10	1.57	1.90
Tanindrazanus amboasaricus n. sp.																
Male (*N* = 4)	Mean	15.91	15.06	2.74	1.11	0.69	1.19	1.92	1.17	2.29	2.99	2.03	0.75	2.47	3.83	5.03
	SD	1.25	0.85	0.27	0.09	0.07	0.10	0.14	0.08	0.09	0.20	0.15	0.11	0.04	0.31	0.36
	Range	2.70	1.75	0.60	0.22	0.17	0.20	0.30	0.18	0.20	0.45	0.30	0.25	0.09	0.65	0.80
	Min.	14.60	14.30	2.45	1.02	0.62	1.10	1.80	1.05	2.20	2.75	1.90	0.60	2.42	3.50	4.70
	Max.	17.30	16.05	3.05	1.24	0.79	1.30	2.10	1.23	2.40	3.20	2.20	0.85	2.51	4.15	5.50
Tanindrazanus andohahela n. sp.																
Male (*N* = 4)	Mean	10.83	10.77	1.94	0.73	0.49	0.88	1.35	0.90	1.52	1.99	1.46	0.65	2.01	2.86	3.44
	SD	0.42	0.32	0.12	0.10	0.03	0.06	0.04	0.04	0.08	0.08	0.06	0.04	0.10	0.11	0.15
	Range	1.03	0.77	0.25	0.22	0.05	0.13	0.10	0.10	0.18	0.18	0.14	0.09	0.19	0.25	0.32
	Min.	10.34	10.34	1.78	0.58	0.47	0.79	1.31	0.86	1.41	1.89	1.38	0.60	1.92	2.75	3.22
	Max.	11.36	11.10	2.04	0.80	0.53	0.92	1.41	0.96	1.59	2.07	1.52	0.69	2.11	3.00	3.54

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Tanindrazanus anjozorobeus n. sp.																
Male (*N* = 3)	Mean	17.02	16.91	2.99	0.97	1.07	1.01	2.23	1.55	2.32	3.08	2.37	0.74	2.71	4.32	5.72
	SD	0.45	0.61	0.33	0.13	0.22	0.12	0.20	0.04	0.04	0.02	0.01	0.02	0.08	0.03	0.11
	Range	0.83	1.12	0.59	0.23	0.41	0.22	0.35	0.07	0.08	0.04	0.02	0.04	0.15	0.05	0.22
	Min.	16.50	16.20	2.61	0.83	0.81	0.88	2.00	1.51	2.27	3.06	2.36	0.72	2.65	4.30	5.60
	Max.	17.33	17.32	3.20	1.06	1.22	1.10	2.35	1.58	2.35	3.10	2.38	0.76	2.80	4.35	5.82
Tanindrazanus antananarivo n. sp.																
Male (*N* = 5)	Mean	13.26	12.81	2.20	0.79	0.61	0.87	1.58	1.14	1.90	2.39	1.64	0.65	2.09	3.30	4.27
	SD	0.82	0.67	0.17	0.09	0.08	0.12	0.11	0.08	0.09	0.11	0.08	0.02	0.09	0.19	0.39
	Range	1.99	1.59	0.43	0.23	0.20	0.32	0.26	0.18	0.22	0.29	0.20	0.06	0.21	0.46	1.00
	Min.	12.71	12.41	2.04	0.70	0.48	0.71	1.45	1.07	1.82	2.28	1.58	0.63	2.04	3.17	3.88
	Max.	14.69	14.00	2.47	0.93	0.69	1.03	1.71	1.25	2.04	2.56	1.78	0.69	2.25	3.63	4.88
Tanindrazanus bemaraha n. sp.																
Male (*N* = 2)	Mean	13.50	13.50	2.48	0.96	0.62	1.09	1.63	1.15	2.12	2.77	1.69	0.80	2.27	3.45	4.40
	SD	0.61	0.61	0.17	0.01	0.06	0.05	0.09	0.00	0.00	0.08	0.00	0.05	0.04	0.06	0.07
	Range	0.86	0.86	0.23	0.02	0.09	0.06	0.13	0.01	0.01	0.11	0.01	0.07	0.06	0.08	0.09
	Min.	13.07	13.07	2.36	0.95	0.57	1.05	1.56	1.14	2.11	2.71	1.68	0.77	2.24	3.41	4.35
	Max.	13.93	13.93	2.60	0.97	0.66	1.12	1.69	1.15	2.12	2.83	1.69	0.83	2.30	3.50	4.44
Tanindrazanus brunneus n. sp.																
Male (*N* = 1)	Measurements	10.77	10.31	1.91	0.79	0.54	0.75	1.41	1.11	1.90	2.44	1.26	0.70	1.89	2.86	3.54
Tanindrazanus hannajagodae n. sp.																
Male (*N* = 3)	Mean	23.33	23.18	3.33	1.35	0.74	1.73	3.34	2.12	3.52	4.51	2.76	1.25	3.83	6.41	7.98
	SD	0.75	0.64	0.27	0.12	0.05	0.17	0.12	0.21	0.10	0.09	0.03	0.04	0.12	0.29	0.09
	Range	1.37	1.22	0.51	0.22	0.09	0.31	0.24	0.42	0.18	0.18	0.06	0.08	0.24	0.58	0.17
	Min.	22.47	22.47	3.02	1.26	0.68	1.63	3.24	1.93	3.46	4.44	2.73	1.21	3.69	6.10	7.91
	Max.	23.84	23.69	3.53	1.48	0.77	1.93	3.48	2.35	3.63	4.62	2.79	1.29	3.94	6.68	8.08

Table 2.1. (Continued).

Species		Length										Width				
		Total	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Tanindrazanus harinhali n. sp.																
Male (N = 5)	Mean	11.35	11.01	1.77	0.61	0.53	0.89	1.62	0.83	1.72	2.13	1.44	0.70	2.05	3.08	3.60
	SD	0.58	0.59	0.10	0.04	0.04	0.09	0.09	0.11	0.10	0.12	0.09	0.07	0.15	0.19	0.25
	Range	1.61	1.50	0.29	0.10	0.09	0.24	0.25	0.22	0.28	0.31	0.23	0.17	0.36	0.51	0.60
	Min.	10.57	10.39	1.62	0.55	0.50	0.76	1.50	0.70	1.57	1.96	1.34	0.63	1.92	2.87	3.37
	Max.	12.18	11.89	1.91	0.65	0.59	1.00	1.75	0.92	1.85	2.27	1.57	0.80	2.28	3.38	3.97
Tanindrazanus irwini n. sp.																
Male (N = 5)	Mean	21.28	21.05	3.31	1.40	0.73	1.39	2.91	1.65	3.25	4.19	2.54	1.13	3.54	5.57	6.44
	SD	1.31	1.37	0.26	0.21	0.09	0.10	0.25	0.18	0.09	0.10	0.08	0.06	0.17	0.32	0.49
	Range	3.44	3.82	0.62	0.52	0.23	0.24	0.64	0.39	0.22	0.26	0.21	0.14	0.45	0.86	1.26
	Min.	19.32	18.95	2.91	1.08	0.64	1.32	2.54	1.52	3.11	4.05	2.42	1.05	3.28	5.04	5.83
	Max.	22.76	22.76	3.53	1.60	0.87	1.56	3.18	1.90	3.33	4.31	2.64	1.19	3.73	5.90	7.09
Tanindrazanus joffrevillus n. sp.																
Male (N = 1)	Measurements	11.19	11.19	1.99	0.70	0.59	1.03	1.37	1.00	1.82	2.36	1.58	0.83	2.15	2.95	3.84
Tanindrazanus kathrynae n. sp.																
Male (N = 5)	Mean	12.61	12.27	2.25	0.87	0.65	0.89	1.66	1.02	1.69	2.35	1.48	0.73	2.08	3.26	3.86
	SD	0.41	0.39	0.04	0.05	0.02	0.07	0.15	0.12	0.12	0.21	0.06	0.05	0.11	0.17	0.11
	Range	1.08	1.05	0.10	0.14	0.06	0.16	0.40	0.28	0.30	0.50	0.17	0.12	0.29	0.42	0.31
	Min.	12.20	11.62	2.22	0.80	0.62	0.81	1.41	0.87	1.57	2.22	1.41	0.66	1.95	3.01	3.69
	Max.	13.28	12.67	2.32	0.93	0.67	0.97	1.81	1.15	1.88	2.72	1.58	0.78	2.24	3.43	3.99
Tanindrazanus mahafaly n. sp.																
Male (N = 5)	Mean	18.96	18.96	2.72	0.91	0.76	1.32	2.49	1.82	2.64	3.24	2.37	0.98	3.21	5.12	6.08
	SD	0.77	0.77	0.13	0.08	0.05	0.07	0.17	0.16	0.08	0.13	0.19	0.03	0.09	0.18	0.19
	Range	1.89	1.89	0.35	0.19	0.12	0.17	0.40	0.32	0.20	0.32	0.47	0.08	0.22	0.45	0.42
	Min.	18.03	18.03	2.50	0.77	0.68	1.24	2.29	1.64	2.53	3.05	2.24	0.94	3.09	4.86	5.88
	Max.	19.92	19.92	2.85	0.97	0.81	1.40	2.69	1.96	2.72	3.37	2.71	1.02	3.31	5.31	6.30

Table 2.1. (Continued).

Species		Length										Width				
		Total	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Tanindrazanus marginatus n. sp.																
Male (*N* = 5)	Mean	15.53	15.33	2.66	0.97	0.58	0.97	1.96	1.33	2.25	2.80	2.08	0.76	2.43	3.95	5.51
	SD	1.81	1.67	0.23	0.06	0.08	0.09	0.25	0.10	0.32	0.33	0.20	0.06	0.20	0.43	0.68
	Range	4.01	3.81	0.58	0.16	0.17	0.19	0.53	0.26	0.66	0.69	0.43	0.14	0.46	0.94	1.40
	Min.	13.62	13.62	2.42	0.92	0.50	0.89	1.69	1.21	1.90	2.44	1.85	0.69	2.22	3.45	4.78
	Max.	17.63	17.43	3.00	1.07	0.68	1.07	2.21	1.47	2.56	3.14	2.29	0.84	2.68	4.39	6.18
Tanindrazanus marojejy n. sp.																
Male (*N* = 4)	Mean	18.43	18.22	2.96	1.32	0.73	1.47	2.59	1.25	2.88	3.72	2.05	0.92	3.25	4.97	6.57
	SD	0.98	1.19	0.31	0.15	0.17	0.19	0.19	0.06	0.39	0.30	0.10	0.16	0.16	0.10	0.43
	Range	2.40	2.67	0.75	0.33	0.41	0.44	0.38	0.12	0.95	0.73	0.22	0.39	0.32	0.21	0.95
	Min.	17.20	17.05	2.61	1.12	0.52	1.28	2.42	1.19	2.37	3.32	1.93	0.71	3.10	4.89	6.15
	Max.	19.60	19.72	3.36	1.45	0.93	1.72	2.80	1.31	3.32	4.05	2.15	1.10	3.42	5.10	7.10
Tanindrazanus nigripes n. sp.																
Male (*N* = 5)	Mean	12.72	12.26	2.20	0.93	0.55	0.90	1.56	1.06	1.77	2.42	1.56	0.74	2.20	3.23	4.00
	SD	0.43	0.33	0.07	0.06	0.09	0.09	0.06	0.12	0.09	0.08	0.02	0.01	0.06	0.06	0.16
	Range	0.89	0.85	0.18	0.13	0.20	0.20	0.17	0.33	0.20	0.18	0.05	0.03	0.17	0.14	0.36
	Min.	12.37	11.78	2.09	0.86	0.45	0.83	1.47	0.90	1.64	2.35	1.53	0.72	2.13	3.16	3.84
	Max.	13.26	12.63	2.27	0.99	0.65	1.03	1.64	1.23	1.84	2.54	1.58	0.75	2.30	3.30	4.20
Tanindrazanus notatus n. sp.																
Male (*N* = 2)	Mean	11.48	11.20	1.85	0.66	0.45	0.92	1.52	0.92	1.79	2.19	1.44	0.69	2.04	3.03	3.61
	SD	1.85	1.46	0.18	0.04	0.05	0.14	0.30	0.00	0.17	0.30	0.15	0.06	0.22	0.46	0.64
	Range	2.62	2.06	0.25	0.06	0.07	0.19	0.43	0.00	0.24	0.42	0.21	0.08	0.32	0.65	0.91
	Min.	10.17	10.17	1.73	0.63	0.42	0.82	1.31	0.92	1.68	1.98	1.33	0.65	1.88	2.71	3.15
	Max.	12.79	12.24	1.98	0.68	0.49	1.01	1.74	0.92	1.91	2.40	1.55	0.73	2.20	3.36	4.06
Tanindrazanus simulans n. sp.																
Male (*N* = 2)	Mean	16.10	15.25	2.79	1.36	0.69	1.34	2.11	1.18	2.37	2.68	1.89	0.81	2.43	3.93	4.93
	SD	0.14	0.21	0.01	0.04	0.01	0.04	0.12	0.03	0.04	0.04	0.01	0.00	0.05	0.03	0.09
	Range	0.20	0.30	0.02	0.06	0.02	0.05	0.17	0.04	0.06	0.05	0.02	0.00	0.07	0.04	0.13
	Min.	16.00	15.10	2.78	1.33	0.68	1.31	2.02	1.16	2.34	2.65	1.89	0.81	2.43	3.91	4.86
	Max.	16.20	15.40	2.80	1.39	0.70	1.36	2.19	1.20	2.40	2.70	1.91	0.81	2.50	3.95	4.99

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Tanindrazanus tenebricus n. sp.																
Male (*N* = 5)	Mean	16.15	16.12	2.80	0.97	0.74	1.25	2.01	1.35	2.55	3.23	2.34	0.87	2.74	4.13	5.48
	SD	0.64	0.62	0.22	0.18	0.06	0.07	0.16	0.08	0.11	0.16	0.06	0.03	0.10	0.21	0.28
	Range	1.63	1.63	0.56	0.43	0.15	0.18	0.36	0.21	0.29	0.41	0.14	0.07	0.23	0.59	0.63
	Min.	15.40	15.40	2.61	0.85	0.69	1.15	1.82	1.22	2.39	3.01	2.28	0.83	2.61	3.83	5.13
	Max.	17.02	17.02	3.17	1.28	0.84	1.33	2.18	1.43	2.68	3.43	2.42	0.90	2.85	4.41	5.76
Tanindrazanus varicolor n. sp.																
Male (*N* = 5)	Mean	16.31	16.00	2.53	0.98	0.64	1.06	2.26	1.18	2.31	2.98	2.01	0.94	2.58	4.20	4.95
	SD	0.18	0.08	0.05	0.09	0.07	0.02	0.03	0.04	0.07	0.09	0.04	0.04	0.05	0.09	0.11
	Range	0.41	0.23	0.13	0.19	0.18	0.06	0.06	0.08	0.18	0.23	0.09	0.11	0.12	0.22	0.27
	Min.	16.07	15.89	2.48	0.89	0.57	1.03	2.23	1.14	2.21	2.90	1.97	0.87	2.51	4.06	4.77
	Max.	16.48	16.12	2.61	1.08	0.75	1.09	2.29	1.22	2.39	3.13	2.05	0.98	2.63	4.28	5.04
Tanindrazanus vohiparara n. sp.																
Male (*N* = 1)	Measurements	12.11	11.20	1.96	0.73	0.33	0.68	1.54	0.99	1.68	2.04	1.78	0.59	1.91	3.00	3.65
Toliarus karinae n. sp.																
Male (*N* = 1)	Measurements	12.10	11.70	2.20	1.05	0.60	1.10	1.48	1.05	2.15	1.85	1.50	0.80	2.24	2.98	3.80
Toliarus trichrous n. sp.																
Male (*N* = 5)	Mean	8.98	8.22	1.55	0.60	0.39	0.69	1.19	0.73	1.23	1.57	1.20	0.64	1.62	2.42	2.57
	SD	0.62	0.76	0.06	0.03	0.04	0.10	0.14	0.09	0.10	0.11	0.12	0.06	0.20	0.27	0.32
	Range	1.58	1.76	0.14	0.08	0.07	0.21	0.30	0.23	0.27	0.31	0.29	0.14	0.47	0.66	0.78
	Min.	8.10	7.22	1.47	0.58	0.36	0.57	1.04	0.60	1.12	1.42	1.07	0.58	1.36	2.06	2.20
	Max.	9.68	8.97	1.61	0.65	0.43	0.78	1.34	0.83	1.39	1.73	1.36	0.72	1.83	2.72	2.98
Toxopus ambohitantely n. sp.																
Male (*N* = 5)	Mean	10.51	9.99	1.66	0.61	0.44	0.81	1.27	1.01	1.55	1.82	1.22	0.66	1.93	2.74	3.30
	SD	0.24	0.13	0.06	0.04	0.04	0.06	0.04	0.10	0.05	0.05	0.02	0.01	0.05	0.09	0.05
	Range	0.55	0.35	0.17	0.09	0.10	0.12	0.10	0.22	0.14	0.13	0.05	0.03	0.13	0.24	0.13
	Min.	10.22	9.83	1.55	0.57	0.39	0.76	1.20	0.90	1.50	1.76	1.19	0.64	1.87	2.64	3.23
	Max.	10.78	10.18	1.72	0.65	0.48	0.87	1.30	1.12	1.63	1.89	1.24	0.67	2.00	2.88	3.36

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Toxopus ampitavananima n. sp.																
Male (*N* = 5)	Mean	11.34	11.20	1.80	0.56	0.42	1.00	1.37	1.16	1.78	2.09	1.64	0.79	2.23	3.17	3.63
	SD	0.62	0.66	0.10	0.05	0.04	0.11	0.10	0.03	0.12	0.21	0.14	0.04	0.14	0.24	0.39
	Range	1.32	1.41	0.25	0.10	0.10	0.26	0.22	0.08	0.29	0.56	0.35	0.10	0.31	0.53	0.92
	Min.	10.71	10.50	1.65	0.52	0.38	0.88	1.26	1.11	1.60	1.78	1.52	0.76	2.11	2.86	3.31
	Max.	12.03	11.91	1.91	0.62	0.48	1.13	1.48	1.20	1.89	2.33	1.87	0.85	2.42	3.39	4.22
Toxopus antsiranana n. sp.																
Male (*N* = 3)	Mean	12.18	11.81	2.12	0.76	0.47	1.05	1.57	1.10	1.76	2.19	1.58	0.66	2.26	3.24	3.99
	SD	0.61	0.62	0.09	0.07	0.04	0.07	0.12	0.10	0.21	0.26	0.14	0.05	0.10	0.10	0.38
	Range	1.19	1.11	0.17	0.14	0.07	0.14	0.22	0.17	0.38	0.52	0.25	0.10	0.17	0.19	0.66
	Min.	11.51	11.10	2.04	0.70	0.43	0.98	1.43	0.99	1.52	1.91	1.43	0.61	2.15	3.13	3.55
	Max.	12.70	12.21	2.21	0.84	0.51	1.12	1.65	1.16	1.90	2.43	1.68	0.71	2.32	3.32	4.21
Tanindrazanus basalis n. sp.																
Male (*N* = 5)	Mean	12.39	12.24	1.77	0.56	0.35	1.06	1.61	1.25	1.73	2.13	1.72	0.76	2.54	3.44	4.27
	SD	0.69	0.66	0.12	0.07	0.04	0.04	0.12	0.14	0.07	0.07	0.10	0.03	0.14	0.22	0.19
	Range	1.45	1.52	0.31	0.20	0.11	0.08	0.32	0.30	0.19	0.18	0.23	0.07	0.31	0.51	0.45
	Min.	11.62	11.49	1.57	0.45	0.30	1.02	1.45	1.13	1.65	2.02	1.62	0.73	2.40	3.21	3.97
	Max.	13.07	13.01	1.88	0.64	0.41	1.10	1.77	1.43	1.84	2.20	1.85	0.80	2.70	3.72	4.43
Toxopus brucei n. sp.																
Male (*N* = 5)	Mean	11.93	11.84	1.73	0.52	0.40	1.18	1.55	1.17	1.70	2.06	1.74	0.88	2.58	3.42	4.17
	SD	0.75	0.80	0.11	0.06	0.04	0.06	0.13	0.17	0.09	0.15	0.14	0.04	0.11	0.27	0.31
	Range	1.64	1.70	0.27	0.15	0.09	0.15	0.28	0.36	0.23	0.41	0.31	0.10	0.26	0.58	0.64
	Min.	11.06	11.00	1.59	0.44	0.37	1.10	1.41	0.99	1.57	1.85	1.59	0.84	2.44	3.14	3.87
	Max.	12.70	12.70	1.86	0.59	0.46	1.24	1.69	1.35	1.80	2.26	1.90	0.94	2.70	3.73	4.51
Toxopus farafangana n. sp.																
Male (*N* = 5)	Mean	9.89	9.81	1.64	0.46	0.41	0.95	1.18	0.97	1.36	1.71	1.38	0.58	1.91	2.72	3.52
	SD	0.72	0.66	0.17	0.06	0.04	0.09	0.11	0.14	0.09	0.13	0.08	0.04	0.15	0.21	0.27
	Range	1.73	1.61	0.42	0.18	0.10	0.23	0.30	0.37	0.22	0.34	0.21	0.09	0.36	0.50	0.68
	Min.	9.14	9.05	1.47	0.36	0.37	0.86	1.01	0.81	1.27	1.54	1.30	0.54	1.76	2.47	3.16
	Max.	10.87	10.66	1.89	0.54	0.47	1.09	1.30	1.18	1.48	1.88	1.51	0.63	2.12	2.97	3.84

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Toxopus fisheri n. sp.																
Male (*N* = 5)	Mean	10.95	10.29	1.89	0.66	0.48	0.97	1.34	0.96	1.38	1.95	1.37	0.65	2.08	2.85	3.45
	SD	0.44	0.48	0.09	0.10	0.05	0.07	0.10	0.10	0.16	0.21	0.06	0.05	0.05	0.12	0.13
	Range	1.09	1.26	0.23	0.25	0.12	0.16	0.27	0.27	0.39	0.45	0.15	0.12	0.11	0.25	0.35
	Min.	10.50	9.84	1.76	0.54	0.42	0.89	1.18	0.82	1.27	1.72	1.30	0.61	2.02	2.70	3.26
	Max.	11.59	11.09	1.99	0.79	0.55	1.05	1.45	1.09	1.67	2.17	1.45	0.72	2.13	2.95	3.61
Toxopus griswoldi n. sp.																
Male (*N* = 5)	Mean	9.61	9.39	1.76	0.59	0.47	0.89	1.24	0.84	1.32	1.66	1.39	0.73	2.05	2.68	3.23
	SD	0.41	0.42	0.08	0.08	0.04	0.06	0.07	0.18	0.07	0.08	0.06	0.03	0.08	0.13	0.28
	Range	1.01	1.02	0.21	0.21	0.09	0.15	0.18	0.48	0.17	0.22	0.16	0.09	0.24	0.32	0.69
	Min.	8.98	8.74	1.65	0.51	0.40	0.82	1.15	0.66	1.25	1.52	1.34	0.69	1.92	2.47	2.84
	Max.	9.99	9.76	1.87	0.71	0.49	0.97	1.34	1.14	1.43	1.74	1.49	0.78	2.16	2.79	3.53
Female (*N* = 1)	Measurements	11.75	11.75	2.73	1.02	0.76	1.68	0.68	0.47	1.28	1.70	1.77	1.13	2.66	2.60	3.88
Toxopus insignis n. sp.																
Male (*N* = 5)	Mean	11.58	10.59	1.79	0.58	0.45	0.95	1.44	0.96	1.65	2.16	1.45	0.72	2.13	3.10	3.90
	SD	0.75	0.74	0.13	0.07	0.02	0.08	0.11	0.06	0.11	0.13	0.06	0.04	0.15	0.27	0.37
	Range	1.74	1.67	0.31	0.18	0.04	0.19	0.29	0.13	0.25	0.28	0.14	0.10	0.32	0.58	0.92
	Min.	10.75	9.73	1.68	0.52	0.43	0.86	1.30	0.88	1.49	2.00	1.39	0.66	1.97	2.77	3.44
	Max.	12.49	11.41	1.99	0.70	0.47	1.05	1.60	1.01	1.74	2.27	1.52	0.76	2.29	3.35	4.36
Toxopus italaviana n. sp.																
Male (*N* = 5)	Mean	11.44	10.42	1.81	0.62	0.45	1.01	1.48	0.99	1.51	2.17	1.46	0.78	2.24	3.06	3.85
	SD	0.28	0.17	0.06	0.05	0.03	0.03	0.06	0.08	0.08	0.16	0.04	0.06	0.07	0.10	0.18
	Range	0.76	0.38	0.15	0.14	0.08	0.08	0.13	0.19	0.22	0.39	0.08	0.13	0.18	0.26	0.46
	Min.	11.09	10.25	1.71	0.54	0.42	0.96	1.41	0.91	1.37	2.05	1.43	0.69	2.17	2.95	3.60
	Max.	11.86	10.63	1.86	0.69	0.49	1.04	1.54	1.10	1.59	2.44	1.51	0.82	2.35	3.21	4.06

Table 2.1. (Continued).

Species		Length										Width				
		Total	Clyp -Abd	Head	AOc	POc	APr	PPr	Scu	Sca	Ped	Head	Syn	APr	PPr	Abd
Toxopus melobrunneus n. sp.																
Male (*N* = 5)	Mean	14.66	14.29	2.18	0.72	0.48	0.96	1.84	1.35	2.14	2.77	1.75	0.74	2.49	3.82	4.93
	SD	0.49	0.39	0.13	0.08	0.02	0.09	0.17	0.11	0.06	0.27	0.07	0.03	0.10	0.19	0.20
	Range	1.28	1.00	0.35	0.20	0.06	0.22	0.41	0.23	0.18	0.69	0.15	0.07	0.24	0.50	0.53
	Min.	14.15	13.96	1.99	0.62	0.43	0.85	1.73	1.24	2.06	2.54	1.68	0.70	2.41	3.63	4.62
	Max.	15.43	14.95	2.33	0.82	0.50	1.07	2.13	1.47	2.24	3.23	1.83	0.78	2.65	4.13	5.15
Toxopus miandritsara n. sp.																
Male (*N* = 2)	Mean	10.05	9.79	1.58	0.54	0.39	0.81	1.20	0.83	1.31	1.64	1.20	0.59	1.81	2.71	3.24
	SD	0.44	0.39	0.01	0.01	0.04	0.00	0.04	0.04	0.07	0.10	0.00	0.03	0.08	0.15	0.01
	Range	0.62	0.55	0.02	0.02	0.06	0.01	0.05	0.06	0.11	0.14	0.00	0.04	0.11	0.22	0.01
	Min.	9.73	9.51	1.57	0.53	0.36	0.80	1.17	0.80	1.25	1.57	1.19	0.58	1.76	2.61	3.23
	Max.	10.36	10.06	1.58	0.55	0.42	0.81	1.23	0.86	1.36	1.72	1.20	0.61	1.87	2.82	3.24
Toxopus namoroka n. sp.																
Male (*N* = 2)	Mean	11.50	11.50	1.84	0.64	0.44	1.13	1.52	1.24	1.79	2.37	1.68	0.88	2.47	3.30	3.89
	SD	0.08	0.08	0.14	0.04	0.04	0.06	0.02	0.14	0.04	0.11	0.02	0.02	0.03	0.06	0.17
	Range	0.11	0.11	0.20	0.06	0.06	0.09	0.02	0.19	0.05	0.15	0.03	0.02	0.04	0.09	0.25
	Min.	11.44	11.44	1.75	0.61	0.42	1.09	1.51	1.15	1.76	2.30	1.67	0.86	2.45	3.26	3.77
	Max.	11.56	11.56	1.94	0.66	0.47	1.18	1.53	1.34	1.81	2.45	1.69	0.89	2.49	3.35	4.01
Toxopus pallidus n. sp.																
Male (*N* = 2)	Mean	9.26	8.98	1.40	0.40	0.39	0.74	1.16	0.99	1.37	1.70	1.16	0.56	1.73	2.56	3.02
	SD	0.23	0.17	0.09	0.07	0.01	0.03	0.04	0.06	0.00	0.00	0.00	0.00	0.00	0.06	0.08
	Range	0.32	0.25	0.13	0.10	0.01	0.04	0.06	0.09	0.00	0.00	0.00	0.01	0.00	0.09	0.11
	Min.	9.10	8.85	1.34	0.35	0.39	0.72	1.13	0.95	1.37	1.70	1.16	0.56	1.73	2.52	2.96
	Max.	9.42	9.10	1.47	0.45	0.40	0.76	1.18	1.03	1.37	1.70	1.16	0.56	1.74	2.60	3.07
Toxopus parkeri n. sp.																
Male (*N* = 5)	Mean	12.51	12.22	1.80	0.61	0.37	1.12	1.63	1.43	1.67	2.15	1.85	0.89	2.73	3.62	4.47
	SD	0.79	0.69	0.09	0.07	0.03	0.06	0.12	0.16	0.12	0.13	0.13	0.05	0.19	0.26	0.33
	Range	2.07	1.82	0.23	0.16	0.06	0.14	0.32	0.38	0.30	0.32	0.32	0.14	0.46	0.63	0.83
	Min.	11.77	11.52	1.69	0.55	0.33	1.04	1.47	1.27	1.57	2.04	1.74	0.84	2.57	3.43	4.09
	Max.	13.84	13.34	1.92	0.71	0.39	1.18	1.79	1.66	1.87	2.36	2.05	0.98	3.03	4.06	4.92

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Toxopus signoretii (Reuter) 1887																
Male (*N* = 1)	Measurements	12.10	12.20	2.30	0.90	0.62	1.40	1.70	1.46	1.89	2.50	2.15	0.98	2.83	3.75	4.20
Toxopus simulans n. sp.																
Male (*N* = 4)	Mean	11.96	11.30	1.79	0.55	0.40	0.99	1.43	0.93	1.73	2.06	1.55	0.68	2.17	3.18	3.90
	SD	0.22	0.34	0.08	0.06	0.03	0.04	0.07	0.04	0.01	0.05	0.04	0.03	0.06	0.06	0.20
	Range	0.46	0.74	0.17	0.15	0.07	0.08	0.17	0.08	0.02	0.11	0.08	0.07	0.13	0.16	0.37
	Min.	11.70	10.89	1.69	0.47	0.36	0.95	1.35	0.88	1.72	2.01	1.53	0.66	2.12	3.09	3.70
	Max.	12.16	11.62	1.85	0.62	0.43	1.03	1.51	0.96	1.74	2.11	1.60	0.72	2.24	3.25	4.08
Toxopus steineri n. sp.																
Male (*N* = 3)	Mean	11.48	11.24	1.89	0.59	0.49	0.88	1.53	1.31	1.69	1.94	1.52	0.76	2.22	3.12	3.57
	SD	0.42	0.31	0.10	0.06	0.04	0.07	0.10	0.12	0.08	0.02	0.02	0.03	0.08	0.03	0.26
	Range	0.76	0.59	0.20	0.12	0.09	0.13	0.20	0.22	0.15	0.04	0.04	0.05	0.16	0.05	0.48
	Min.	11.00	11.00	1.80	0.53	0.45	0.81	1.43	1.23	1.64	1.93	1.50	0.74	2.15	3.10	3.38
	Max.	11.76	11.59	2.00	0.65	0.53	0.95	1.63	1.45	1.79	1.96	1.53	0.80	2.31	3.15	3.87
Toxopus tibialis n. sp.																
Male (*N* = 3)	Mean	14.80	14.60	2.28	0.64	0.49	1.48	1.92	1.50	2.22	2.73	2.34	1.10	3.08	4.18	4.99
	SD	0.53	0.76	0.16	0.10	0.02	0.03	0.16	0.14	0.02	0.12	0.08	0.06	0.09	0.24	0.24
	Range	1.01	1.50	0.32	0.17	0.03	0.06	0.30	0.28	0.03	0.24	0.17	0.11	0.17	0.47	0.45
	Min.	14.39	13.89	2.10	0.58	0.47	1.44	1.79	1.36	2.20	2.62	2.25	1.04	2.98	3.98	4.72
	Max.	15.40	15.40	2.43	0.75	0.50	1.50	2.09	1.65	2.24	2.86	2.42	1.16	3.14	4.45	5.17
Toxopus toamasina n. sp.																
Male (*N* = 5)	Mean	12.21	12.02	1.87	0.54	0.41	1.09	1.50	1.16	1.77	2.21	1.83	0.72	2.39	3.30	4.16
	SD	0.35	0.48	0.07	0.04	0.04	0.10	0.10	0.10	0.04	0.06	0.08	0.03	0.11	0.16	0.18
	Range	0.88	1.20	0.20	0.10	0.11	0.24	0.24	0.21	0.11	0.15	0.21	0.08	0.29	0.41	0.47
	Min.	11.69	11.22	1.77	0.49	0.36	1.00	1.32	1.06	1.72	2.15	1.73	0.69	2.20	3.04	3.85
	Max.	12.57	12.41	1.97	0.59	0.46	1.23	1.56	1.27	1.83	2.30	1.94	0.77	2.50	3.44	4.32

Table 2.1. (Continued).

		Length										Width				
Species		**Total**	**Clyp -Abd**	**Head**	**AOc**	**POc**	**APr**	**PPr**	**Scu**	**Sca**	**Ped**	**Head**	**Syn**	**APr**	**PPr**	**Abd**
Toxopus toliara n. sp.																
Male (*N* = 5)	Mean	11.63	11.33	1.99	0.69	0.47	1.02	1.41	1.13	1.43	2.09	1.52	0.74	2.19	3.10	3.85
	SD	0.96	0.93	0.19	0.10	0.04	0.07	0.20	0.13	0.17	0.28	0.12	0.05	0.16	0.35	0.48
	Range	2.28	2.15	0.47	0.27	0.10	0.17	0.49	0.29	0.43	0.67	0.30	0.12	0.39	0.87	1.19
	Min.	10.68	10.39	1.74	0.57	0.41	0.95	1.24	1.02	1.24	1.89	1.40	0.68	1.96	2.74	3.22
	Max.	12.96	12.54	2.21	0.84	0.51	1.12	1.74	1.30	1.67	2.57	1.70	0.80	2.35	3.61	4.41
Toxopus vazimba n. sp.																
Male (*N* = 4)	Mean	11.99	11.99	2.00	0.65	0.45	1.05	1.62	1.16	1.74	2.25	1.71	0.89	2.50	3.38	3.79
	SD	0.59	0.59	0.14	0.06	0.04	0.20	0.11	0.13	0.09	0.10	0.08	0.02	0.13	0.21	0.17
	Range	1.44	1.44	0.30	0.15	0.09	0.46	0.26	0.29	0.20	0.24	0.18	0.04	0.30	0.45	0.37
	Min.	11.27	11.27	1.79	0.56	0.40	0.77	1.46	1.01	1.66	2.10	1.62	0.87	2.31	3.08	3.63
	Max.	12.71	12.71	2.09	0.71	0.49	1.23	1.71	1.30	1.86	2.34	1.80	0.91	2.61	3.52	4.00

Table 2.2. GenBank accession numbers of COI sequences. F – female; M – male; USI – unique specimen identifier; RCW – ethanol specimen collection number.

Species	**Sex**	**USI (UCR_ENT)**	**RCW**	**GenBank accession no.**
Distirogaster tarsalis (Signoret), 1860	M	00006366	2898	KR606396
Distirogaster n. sp.	M	00088090	3018	KR606395
Distirogaster n. sp.	M	00006369	2928	KR606394
Distirogaster n. sp.	M	00007158	2881	KR606393
Distirogaster n. sp.	F	00007088	2880	KR606392
Gibbosella conisimilis n. sp.	M	00045495	2962	KR606400
Gibbosella conisimilis n. sp.	M	00045427	2996	KR606401
Gibbosella notoconica n. sp.	M	00044813	2908	KR606402
Gibbosella notoconica n. sp.	M	00045558	2913	KR606403
Gibbosella pallidalata n. sp.	M	00045653	2939	KR606404
Gibbosella planiscutum n. sp.	M	00045296	2952	KR606405
Gibbosella quadocris n. sp.	M	00044860	2938	KR606406
Gibbosella quadocris n. sp.	M	00045651	2969	KR606407
Gibbosella quadocris n. sp.	M	00007257	2988	KR606408
Gibbosella quadocris n. sp.	M	00007166	2989	KR606409
Gibbosella sp.	F	00045157	2854	KR606410
Gibbosella sp.	F	00045452	2887	KR606411
Gibbosella sp.	F	00045079	2890	KR606412
Gibbosella sp.	F	00045646	2892	KR606413
Gibbosella sp.	F	00045569	3306	KR606414
Glymmatophora crassipes Horváth, 1914	M	00088087	3020	KR606415
Marojejycoris auranticorium n. sp.	M	00045555	2924	KR606416
Marojejycoris brevifrons n. sp.	M	00006480	2923	KR606417
Marojejycoris ranomafana n. sp.	M	00048057	2944	KR606418
Tanindrazanus bemaraha n. sp.	M	00006473	2964	KR606419
Tanindrazanus harinhali n. sp.	M	00006553	2889	KR606420
Tanindrazanus irwini n. sp.	M	00045339	2925	KR606421
Tanindrazanus joffrevillus n. sp.	M	00007256	2918	KR606422
Tanindrazanus marginatus n. sp.	M	00006887	2902	KR606423
Tanindrazanus nigripes n. sp.	M	00006725	2899	KR606424
Tanindrazanus nigripes n. sp.	M	00045465	2961	KR606425
Tanindrazanus nigripes n. sp.	M	00045328	2990	KR606426
Tanindrazanus nigripes n. sp.	M	00045228	2991	KR606427
Tanindrazanus nigripes n. sp.	M	00006705	2993	KR606428
Tanindrazanus notatus n. sp.	M	00044868	3312	KR606429
Tanindrazanus tenebricus n. sp.	M	00006723	2931	KR606430
Tanindrazanus varicolor n. sp.	M	00006250	2921	KR606431
Tanindrazanus varicolor n. sp.	M	00006485	2922	KR606432

Table 2.2. (Continued).

Species	**Sex**	**USI (UCR_ENT)**	**RCW**	**GenBank accession no.**
Tanindrazanus varicolor n. sp.	M	00006482	2949	KR606433
Toxopus ampitavananima n. sp.	M	00006732	3002	KR606434
Toxopus antsiranana n. sp.	M	00007189	2955	KR606435
Toxopus antsiranana n. sp.	M	00007191	2956	KR606436
Toxopus basalis n. sp.	M	00045525	2907	KR606437
Toxopus brucei n. sp.	M	00045338	2901	KR606438
Toxopus brucei n. sp.	M	00045286	2912	KR606439
Toxopus brucei n. sp.	M	00007133	3008	KR606440
Toxopus brucei n. sp.	M	00007043	3009	KR606441
Toxopus brucei n. sp.	M	00044971	3011	KR606442
Toxopus farafangana n. sp.	M	00045332	2884	KR606443
Toxopus farafangana n. sp.	M	00006729	2906	KR606444
Toxopus farafangana n. sp.	M	00044965	3006	KR606445
Toxopus fisheri n. sp.	M	00045431	2910	KR606446
Toxopus griswoldi n. sp.	M	00006435	2916	KR606448
Toxopus griswoldi n. sp.	F	00045042	2894	KR606447
Toxopus italaviana n. sp.	M	00006428	2934	KR606449
Toxopus melobrunneus n. sp.	M	00045243	2994	KR606450
Toxopus miandritsara n. sp.	M	00044852	2919	KR606451
Toxopus miandritsara n. sp.	M	00006148	3007	KR606452
Toxopus namoroka n. sp.	M	00045251	2917	KR606453
Toxopus pallidus n. sp.	M	00045432	2957	KR606454
Toxopus parkeri n. sp.	M	00006973	3010	KR606455
Toxopus simulans n. sp.	M	00045124	2980	KR606456
Toxopus toamasina n. sp.	M	00007056	2951	KR606457
Toxopus toliara n. sp.	M	00006589	2933	KR606458
Toxopus toliara n. sp.	M	00006468	2966	KR606459
Toxopus toliara n. sp.	M	00006688	2997	KR606460
Toxopus toliara n. sp.	M	00006580	3001	KR606461
Toxopus vazimba n. sp.	M	00006472	2953	KR606462
Ectrichodiinae sp.	F	00045353	2891	KR606397
Ectrichodiinae sp.	F	00044794	2893	KR606398
Ectrichodiinae sp.	F	00045654	2895	KR606399

Chapter 3: Phylogenetics and biogeography of the endemic Madagascan millipede assassin bugs (Hemiptera: Reduviidae: Ectrichodiinae)

Abstract

For at least the past 80 my, Madagascar, a major biodiversity hotspot, has been isolated from all other landmasses. This long-term isolation, along with geologic and climatic factors within Madagascar and throughout the Indian Ocean, has undoubtedly influenced the evolution of the island's biota. However, few systematic analyses incorporating modern divergence dating and biogeographic analyses have focused on Madagascan insects. The diverse Madagascan millipede assassin bugs (Heteroptera: Reduviidae: Ectrichodiinae) offer an opportunity to contribute to a limited body of insect-related research that explores Madagascar's historical biogeography. A molecular dataset (COI mtDNA and 18S, 28S D2 and D3-D5 rDNAs) for 56 taxa (39 ingroup) and a combined morphological (145 characters) and molecular dataset for 110 taxa (93 ingroup) are analyzed with maximum likelihood (ML) and parsimony approaches. Based on the molecular ML phylogeny, divergence times were estimated using fossil and secondary calibrations and biogeographic analyses performed using DIVA, DEC, and DEC+j models to determine the role and patterns of vicariance and dispersal in the origin of Madagascan Ectrichodiinae. Results indicate that Ectrichodiinae in Madagascar do not form a monophyletic group, different clades are closely related to Afrotropical and Oriental lineages, and have colonized the island via transoceanic dispersal at least twice from the Oriental region and once from the Afrotropical region in the last ~68 my. Additionally, the DEC+j and DIVA models infer a single out-of-Madagascar dispersal event to the Afrotropical region. Oceanic and geologic factors that may have facilitated dispersal between these three regions are discussed. Results of the combined analyses are used to explore character support for Madagascan taxa and inform taxonomic

diagnoses. Our results are congruent with the small but growing body of biogeographic research supporting Cenozoic transoceanic dispersal for Madagascan invertebrates to and from Oriental and Afrotropical regions.

Introduction

Madagascar, the fourth largest island on Earth, is one of the world's biodiversity hotspots with more than 13,000 plant, 900 vertebrate, and 5,800 invertebrate species known (Goodman & Benstead, 2005; Phillipson et al., 2006). For non-invasive species, ~86% of invertebrates, ~50% of birds, more than 95% of other vertebrates, and more than 90% of vascular plants are endemic to the island (Goodman & Benstead, 2005; Yoder & Nowak, 2006; Phillipson et al., 2006; Buerki et al., 2013). Numerous phylogenetic studies have provided evidence that a large proportion of Madagascar's biota is closely related to African lineages (~37% of plants, ~30% of vertebrates, ~58% of invertebrates [see Yoder & Nowak, 2006]). However, a significant proportion of the biota is closely related to Oriental taxa (see Vences, 2004; Yoder & Nowak, 2006; Warren et al., 2010); about 32% of plants, 32% of vertebrates, and 17% of invertebrates are sister to Oriental lineages (Yoder & Nowak, 2006). This extant, unique biodiversity is, in the words of Ganzhorn et al. (2014), "rooted in the plate tectonics of the Mesozoic" (i.e., long isolation period), as well as the island's geography, climate, and late colonization by humans (Goodman & Benstead, 2003; Scales, 2014).

Madagascar was once part of Gondwana, but ~160 mya, the Gondwanan landmass began to split with Indo-Madagascar separating from Africa (Plummer & Belle, 1995; Gnos et al., 1997). By at least 80 mya, Madagascar separated from India and has been isolated ~400 km from Africa's southeastern coast since (Storey et al., 1995; Torsvik et al., 2000; Seward et al., 2004; Ali & Aitchison, 2008). Many plant and vertebrate studies have investigated historical biogeographic patterns for various Madagascan taxa. Although some systematic studies support influences of Gondwanan vicariance for the presence of some Madagascan lineages (e.g., ranid frogs [Bossuyt et al., 2006], boid snakes [Noonan & Chippindale, 2006], chameleons [Okajima & Kumazawa, 2010]), many recent studies based on divergence dating analyses support post-Gondwanan transoceanic dispersal from Afrotropical and Oriental regions (e.g., endemic mammalian lineages [Poux et al., 2005], Chrysophylloideae [Bartish et al., 2011], gerrhosaurid lizards [Raselimanana et al., 2009]). Comparatively fewer studies have investigated biogeographic histories of Madagascan insects. Several Madagascan insects have been hypothesized to be relicts of Gondwanan vicariance, e.g., Diplatyidae (Dermaptera) (Popham, 2000), Notonemourinae (Plecoptera) (Illies, 1965; Paulian & Viette, 2003), some Blephariceridae (Diptera) (Paulian & Viette, 2003), and Sialidae (Liu et al., 2015), but there is an increasing number of systematic studies that support Cenozoic transoceanic dispersal from the Afrotropical and Oriental regions. For example, allodapine bees (Fuller et al., 2005; Schwarz et al., 2006; Chenoweth & Schwarz, 2011) and scarabid beetles (Wirta et al., 2008; Wirta et al., 2010; Sole et al., 2011) colonized Madagascar multiple times in the last 65 my. Fungus-growing termites in Madagascar originated from a single colonization event ~7–11 mya (Nobre et al., 2010). Other studies on carpenter bees (Rehan et al., 2010), mayflies (Monaghan et al., 2005), pierid butterflies (Nazari et al., 2011), and dytiscid beetles (Bukontaite et al., 2015) have also supported Cenozoic colonization.

Millipede assassin bugs (Heteroptera: Reduviidae: Ectrichodiinae) are a diverse group of specialized millipede predators with 736 species in 121 genera that are distributed in circumtropical and some temperate regions (Maldonado, 1990; Dougherty, 1995; Carpintero & Maldonado, 1996; Forthman & Weirauch, 2012; Forthman et al., in press). Recently, Forthman et al. (in press) published a monograph of Madagascan millipede assassin bugs (excluding the genus

Distirogaster Horváth) in which 63 new species and three new genera were described, increasing the known Madagascan millipede assassin bug fauna by six-fold. All species and six of the eight genera found on Madagascar are endemic; of the 37 species of *Glymmatophora* Stål and 39 species of *Maraenaspis* Karsch, two and one, respectively, are endemic to Madagascar with the remainder distributed in Africa. This diverse Madagascan millipede assassin bug fauna thus presents an opportunity to investigate and contribute to a limited yet rapidly growing body of research exploring historical influences that have shaped Madagascar's terrestrial insect fauna. However, such an evolutionary investigation has been hindered by a lack of phylogenetic hypotheses; relationships between Ectrichodiinae genera have not been tested cladistically beyond a genus-level phylogeny of the New World fauna based on morphological data (Dougherty, 1995). A recent systematic study of the Reduviidae indicates that Ectrichodiinae originated 57–80 mya and, therefore, after the Madagascar-India split (Hwang & Weirauch, 2012). Thus, dispersal is likely responsible for the current distribution of millipede assassin bugs worldwide, but it is unknown what factors (e.g., ocean currents, land bridges, and stepping-stone islands) may have facilitated dispersal between Madagascar and other biogeographic regions.

Given the recent taxonomic treatment, Upper Cretaceous age, and worldwide distribution of the subfamily, as well as the general restriction of genera to particular biogeographic regions, millipede assassin bugs are an excellent model for biogeographic studies of the Madagascan fauna. Here, we present molecular phylogenetic results that include representatives of six of the eight Madagascan Ectrichodiinae genera and provide a framework for testing the number, timing, and origin of Madagascan lineages. Based on these results, we perform divergence dating and biogeographic analyses to investigate the geographic and oceanic influences that could have facilitated long-distance dispersal between Madagascar and other biogeographic areas. We also present results of a combined morphological and molecular phylogenetic analysis on a large sample of Madagascan Ectrichodiinae species that is used to formalize taxonomic decisions and inform diagnoses in Forthman et al.'s (in press) Madagascan Ectrichodiinae monograph.

Material and Methods

Taxon sampling, vouchering, and databasing

A total of 110 terminal taxa were examined, comprising 93 ingroup (Ectrichodiinae) and 17 outgroup taxa (seven Reduviidae subfamilies). Ingroup sampling comprised all eight genera and 67 species of Madagascan Ectrichodiinae. Due to the lack of DNA quality material, only 56 terminal taxa were sequenced (39 ingroups, including 14 Madagascan species in six genera; sequence data for the Madagascan genus *Toliarus* Forthman, Chłond, & Weirauch and the species *Maraenaspis bidens* [Reuter] are unavailable). Each taxon is represented by a mounted primary specimen voucher (molecular vouchers are listed in Table 3.1). For specimens sampled for molecular data, a hind leg was removed for DNA extraction; once extraction was completed, the leg was card mounted and associated with the pinned specimen. Each molecular voucher is associated with a unique specimen identifier (USI) label to connect it with specimen information and, where possible, images in the Planetary Biodiversity Inventory database (http://www.research.amnh.org/pbi/locality/index.php) and Heteroptera Species Pages (http://research.amnh.org/pbi/heteropteraspeciespage/) maintained by the American Museum of Natural History. All USI labels are comprised of the prefix AMNH_PBI or UCR_ENT followed by an 8-digit number. Sequenced specimens are also associated with an RCW number, which is the ethanol specimen collection number.

Specimens examined for this study are deposited in the following institutions: **AMNH**, American Museum of Natural History, New York, USA; **BMNH**, Natural History Museum, London, United Kingdom; **CAS**, California Academy of Sciences, California, USA; **FCAP**, Universidade Federal do Pará, Pará, Brazil; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MRAC**, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; **MTEC**, Montana State University, Montana, USA; **SU**, Department of Zoology, University of Silesia, Poland; **UCR**, University of California, Riverside Entomological Research Museum, California, USA; **USNM**, National Museum of Natural History, Washington D.C., USA.

Morphological methods, terminology, and abbreviations

Extreme sexual dimorphism (Fig. 3.1) is common among millipede assassin bugs and poses a significant problem when analyzing evolutionary relationships. As such, male ectrichodiine specimens were targeted for morphological character coding. However, two terminal taxa, *Maraenaspis coccinea* Horváth and *Racelda* sp., are represented by apterous females. The male of *Maraenaspis coccinea* has, to our knowledge, yet to be discovered and available specimens of *Racelda* were restricted to the one female at the time of this project. Despite the possibility of extreme dimorphism, some morphological features (e.g., antennal segmentation, relative lengths of labial segments, scutellar apical processes, etc.) remain similar among males and females within ectrichodiine species and genera. As such, these sexually static morphological features are inferred and coded in the analysis for taxa only represented by females.

External morphology and genitalic characters were examined using Nikon SMZ1000 and SMZ1500 dissecting microscopes. For males, genitalia (abdominal segment 8, pygophore, and phallus) were dissected, cleared in heated 10% potassium hydroxide (KOH) for 3–8 minutes, washed with distilled water and subsequently with 100% ethanol (EtOH), stained with Chlorazol Black E in 70% EtOH solution to give contrast to membranous areas, examined in glycerol, and permanently stored in genitalic capsules pinned to the specimen. A total of 145 morphological characters were coded in the Descriptive Language for Taxonomy (DELTA) program (Dallwitz, 1980; Dallwitz et al., 1999) using a modified morphological matrix from Weirauch (2008) and Weirauch (2010). In general, terminology follows a subset of terms used by Dougherty (1995), Weirauch (2008), and Forero & Weirauch (2012). Terminology for wing venation follows Hill (2014) and Weirauch (2008), although homology concepts are currently being reviewed across Paraneoptera (Dávid Rédei, pers. comm.). The morphological characters and character states used in this study are given in Table 3.2. The morphological matrix is provided in Supplementary Material (SM) 3.1 in nexus format.

Molecular markers, PCR, sequencing, and alignment

One mitochondrial (COI) and three nuclear (18S, 28S D2, and 28S D3–D5 rDNAs) gene regions were sampled. Sequences from Weirauch & Munro (2009) and Hwang & Weirauch (2012) were used for outgroup terminals and some Ectrichodiinae taxa (Table 3.1). To sequence remaining ectrichodiine taxa, primer sequences for 18S (18SF, 18SR) and 28S D3–D5 (D3Fa, D5Ra) were obtained from Weirauch & Munro (2009); 28S D2 (D2Fa, D2Ra) from Forero et al. (2013); and COI (C1-J-2183F) from Simon et al. (1994) and (C1-N-2609R) from Damgaard & Sperling (2001). DNA was extracted from a hind leg for each specimen using QIAGEN DNeasy Blood and Tissue Kit protocols. PCR was performed using either GE Healthcare Life Sciences PuReTaq-Ready-To-Go-PCR-Beads or EmeraldAmp GT PCR Master Mix and Fisher Scientific or BioRad T100 Thermal Cyclers. Gene regions were amplified following Weirauch & Munro (2009), except the initial denaturation was set at 5 minutes, and for the 28S gene regions, the annealing temperature was set to 50°C. Gel electrophoresis with SyberSafe gel stain and a UV illuminator were used to check amplification results. PCR products were cleaned using Bioline SureClean and sequenced on an Applied Biosystems 3730xl DNA Sequencer at UCR's Institute for Integrative Genome Biology. Sequences were assembled and edited using Sequencher v4.8

and are available on GenBank (Table 3.1). Each gene region was treated as a separate partition and aligned in MAFFT (Katoh & Standley, 2013) using the G-INS-i algorithm. Gene regions were concatenated in SequenceMatrix v1.7.8. (Vaidya et al., 2011) and exported with external gaps coded as question marks. The concatenated, aligned molecular matrix is provided in nexus format in SM 3.2.

Molecular phylogenetic analyses

A maximum likelihood (ML) analysis was performed using the molecular dataset and RAxML-HPC2 on XSEDE v8.0.24 (Stamatakis, 2014) on the Cyberinfrastructure for Phylogenetic Research Science Gateway v3.1 (CIPRES; http://www.phylo.org/sub_sections/portal/). Each gene partition was analyzed under a GTR+Γ+I model, which is the best fit model for each partition as determined by MEGA v6.06 (Tamura et al., 2013). Rapid bootstrap analysis (BS) was performed for 1,000 iterations and followed by a ML best tree search. Aside from estimating the proportion of invariable sites for each partition, default settings were used.

The molecular matrix was also subjected to parsimony analyses with New Technology search and equal (EW) and implied weights (IW) in TNT v.1.1 (Goloboff et al., 2008). Uninformative characters (1,990) were inactivated prior to analysis. For IW, three concavity constant values (*k*) were used: 3, 6, and 10. Internal gaps were treated as a fifth state, while external gaps were treated as missing. Default settings were used for sectorial search, drift, and tree fusing. The initial driven search level was set at 100 with level checked every 3 hits, initial addition sequences = 14, find minimum length 100 times, and random seed = 4,325. Standard BS resampling with absolute frequencies was performed using 500 replicates and New Technology search (initial driven search = 38, check level every 3 hits, initial addition sequences = 7, find minimum length 10 times).

Combined morphological and molecular phylogenetic analyses

Morphological and molecular datasets were concatenated using Mesquite v2.75 (Maddison & Maddison, 2011) and subjected to ML (RAxML-HPC v.8.1.15; Stamatakis, 2014) and EW parsimony analyses (New Technology search in TNT). For the ML analysis, each gene partition was analyzed under a GTR+Γ model, while the morphological partition was analyzed with a Mkv model (Lewis, 2001). Rapid BS was performed for 1,000 iterations and followed by a ML best tree search. Our equal weights parsimony analysis used the same search and bootstrap approaches applied to our molecular dataset (see previous section). Unambiguous character optimizations were examined on the strict consensus tree in WinClada v1.00.08 (Nixon, 2002) (SM 3.3).

Divergence dating estimation

Divergence dating estimates were generated on the molecular ML best tree using the CIPRES web server's BEAST2 on XSEDE (Bouckaert et al., 2014). Each gene region was assigned an unlinked site model (GTR+Γ+I) and linked to the same tree model (Yule). The number of gamma rate categories for each site model was set to 4 and the proportion of invariant sites set to 0.5, with the option to estimate the value of both parameters and the gamma shape. All other site model parameters and estimation options remained at default settings. Following Hwang & Weirauch (2012), a linked clock model was assigned to 28S D2 and 28S D3–D5 to reflect their single identity. As such, three unlinked relaxed lognormal clock models were assigned for 18S, 28S, and COI. Initially, all non-calibration priors were not modified from default settings, however low posterior, prior, and mutation rate effective sample size (ESS) values were extremely low (<50) after performing four independent runs in BEAST. To improve ESS values for these parameters, the default Jeffrey's prior was replaced with a log normal prior for the mutation rates (A. Rambaut & A. Drummond, https://groups.google.com/forum/#!forum/beast-users).

Given that there are no described Ectrichodiinae fossils, two outgroup fossils (*Triatoma dominicana* Poinar and *Apicrenus fossilis* Maldonado, Santiago-Blay, & Poinar) and two secondary calibrations (root node and Ectrichodiinae+Tribelocephalinae node) were used from a recent cladistic analysis of Reduviidae (Hwang & Weirauch, 2012). Fossils were assigned to nodes following Hwang & Weirauch (2012), using an apomorphy-based approach (Parham et al., 2011). For fossil-based node calibrations, a prior lognormal distribution was assigned with the minimum age corresponding to the minimum age of the fossil and with the 95% confidence interval encompassing the range of estimated dates recovered by Hwang & Weirauch (2012). For secondary calibrations, a prior normal distribution was assigned with the 95% confidence interval corresponding to the estimated 95% highest posterior density (HPD) credibility interval from Hwang & Weirauch (2012). Calibration nodes, means, standard deviations or sigma values, and offsets (in real space) are given in SM 3.4. Four Markov Chain Monte Carlo (MCMC) chains were ran for 200 million generations, with parameters and trees logged every 20,000 generations. Each chain was assessed for convergence in Tracer v1.6 and combined after discarding 5% burn-in. Combined ESS values for each parameter were ≥200. LogCombiner v2.1.3 was used to discard 5% of trees as burn-in and combine the remaining trees from each run. Median heights were annotated using TreeAnnotator v.2.1.2.

Biogeographic analyses

Ancestral ranges were reconstructed on the maximum clade credibility tree from the BEAST analysis using DIVA (Dispersal-Vicariance Analysis) in RASP v3.02 (Ronquist, 1997; Yu et al., 2010, 2015) and DEC (dispersal-extinction-cladogenesis) (Ree et al., 2005; Ree & Smith, 2008) and DEC+j (Matzke, 2014) models in the BioGeoBEARS v0.2.1 package (Matzke, 2013) in R v3.2.0 (R Core Team, 2015). Distribution ranges of Ectrichodiinae were divided into four areas: Neotropical, Afrotropical, Madagascar, and Oriental. Outgroup taxa were trimmed due to limited sampling of other assassin bug subfamilies.

The parsimony, event-based DIVA method was developed by Ronquist (1997) and reconstructs ancestral distributions based on a simple biogeographic model and a three-dimensional cost matrix. No penalty is allotted when speciation is the result of vicariance, but dispersal and extinction have a penalty of one per unit area added to or deleted from a distribution (Ronquist, 1997). To reduce the acquisition of multiple areas at nodes near the root, the maximum number of areas for each node was two.

The DEC models geographic range evolution by stochastic dispersal and local extinction events along branches and estimates the likelihood of ancestral ranges at cladogenesis (Ree et al, 2005; Ree & Smith, 2008). This model has two free parameters specifying the dispersal rate (*d*; range expansion) and extinction rate (*e*; range contraction) along branches (Ree et al., 2005; Ree & Smith, 2008; Matzke, 2014). The DEC model also has a fixed cladogenesis model that assumes that one daughter lineage will always inherit one subarea of a widespread ancestral range (Matzke, 2014). The DEC+j model has an additional free parameter *j* that enables one daughter lineage to disperse to a new range outside the ancestral range, thus modeling founder-event speciation events (Matzke, 2014). For both DEC and DEC+j models, the range constraint matrix was set at default with the maximum number of areas for each node set to two. Five time scales were constructed in the dispersal matrix to reflect changes in ocean currents in the Mozambique channel and the emergence of Indian Ocean islands: 1) 0–15 mya, 2) 15–23 mya, 3) 23–34 mya, 4) 34–56 mya, and 5) 56–66 mya. Dispersal rates between areas were assigned as 0.1 (very low; oppositely directed ocean circulation, lack of islands and land bridges, and areas not connected), 0.25 (low; ocean circulation in dispersal direction or presence of islands or land bridges), 0.5 (moderate; ocean circulation in dispersal direction and presence of islands or land bridges), 0.75 (high; areas closely adjacent or directly connected), and 1.0 (same area) based on paleoceanographic and paleogeographic reconstructions (Sanmartín et al., 2001; Heydt & Dijkstra, 2006; Ali & Huber, 2010; Lomolino, 2010; Pyron, 2014). Dispersal rates assigned for each time scale are given in SM 3.5. The DEC model is nested within the DEC+j model, and, as a result, we compare the two models using a Likelihood Ratio Test (LTR).

Results

Molecular phylogenetic analyses

The first published molecular ML best tree (Ln score = –25,426.19528) of millipede assassin bugs is shown in Fig. 3.2. Many nodes received moderate (BS = 70–89) to high support (BS = 90–100), but several deeper nodes were poorly supported (BS<70). Ectrichodiinae is monophyletic with high support and recovered as the sister group to Tribelocephalinae, which is congruent with previous morphological and molecular cladistic analyses (Weirauch, 2008; Weirauch & Munro, 2009; Hwang & Weirauch, 2012). Two major ectrichodiine clades are recovered with low support: a predominantly Neotropical clade (node 1), which includes the Afrotropical genus *Santosia* Stål, and an Old World clade (node 2) that includes Afrotropical, Oriental, and Madagascan taxa.

Four Madagascan Ectrichodiinae lineages are recovered with low to high support. A representative of the Madagascan genus *Gibbosella* Chłond is nested within a clade of Oriental taxa with moderate support, but relationships within this clade, especially the *Gibbosella* and *Caecina* Stål sister group relationship, are poorly supported. The genera *Tanindrazanus* Forthman, Chłond, & Weirauch, *Toxopus* Bergroth, and *Marojejycoris* Forthman, Chłond, & Weirauch is a poorly supported clade. Relationships within this clade are largely weakly supported. *Tanindrazanus* is recovered as the sister group of *Marojejycoris*, and together are closely related to *Toxopus*. *Distirogaster* also forms a clade, but is weakly supported as the sister group to a clade comprising Afrotropical, Madagascan, and Oriental taxa. The Madagascan species *Glymmatophora crassipes* Horváth is highly supported as the sister to the Afrotropical genus *Ectrichodia* Lepeletier & Serville.

A number of unresolved relationships are recovered throughout the EW parsimony phylogeny (SM 3.6), e.g., near the root of the phylogeny (i.e., most outgroups and Ectrichodiinae+Tribelocephalinae), between *Tanindrazanus*+*Marojejycoris* and two other clades (*Toxopus* and *Toxopus*+*Distirogaster*), among others. Ectrichodiinae is also rendered paraphyletic with respect to Tribelocephalinae. The ectrichodiine genus *Vilius* Stål is sister to Tribelocephalinae genera, which is a questionable result. Due to the lack of resolution in our EW phylogeny, we used IW under three concavity constant values that resulted in one (k = 6 or 10) or three (k = 3) most parsimonious trees (SM 3.6). Some of the relationships recovered from these IW analyses are similar with the molecular ML phylogeny. However, differences are observed (e.g., non-monophyly of *Toxopus* and Ectrichodiinae), some of which are questionable and unlikely based on morphology (e.g., *Vilius* nested with Tribelocephalinae, *Maraenaspis coccinea* sister to *Caecina* sp.). Some IW results consistently differed between weighting schemes, e.g., the phylogenetic positions of *Marojejycoris*, *Toxopus toamasina*, and *Toxopus griswoldi*. Despite topological differences between EW and IW parsimony trees, these results provide evidence for the non-monophyly of Madagascan Ectrichodiinae.

Combined morphological and molecular phylogenetic analyses

The TNT consensus tree of 938 parsimonious trees is shown in Fig. 3.3 (outgroups not shown but same as in Fig. 3.2) and was used to inform taxonomic decisions in Forthman et al. (in press). As in the molecular (SM 3.2) and combined ML analyses, Ectrichodiinae are monophyletic and recovered as the sister to Tribelocephalinae with high support (BS = 99). A predominantly Neotropical clade (node 1) is also recovered with low support, but unlike the ML analysis, this clade includes the Oriental genus *Vilius* along with *Santosia*. An Old World clade (node 2) is recovered with several topological differences from the ML tree. *Mendis* Stål+*Bannania* Hsiao+*Neolibavius* Miller is weakly supported as the sister to the remaining taxa, followed by a weakly supported *Microstemmatoides* Putschkov+*Synavecoris* Villiers+nr *Bannania* clade. A clade (node 3) comprised of *Ectrichodia*, *Glymmatophora*, *Cleptria* Stål, *Maraenaspis*, and *Ectrychotes* Burmeister is recovered as sister to a predominantly Madagascan clade (node 4) with low support. Relationships within the latter clade are supported with BS<50, with *Marojejycoris* sister to *Gibbosella*+*Caecina*, *Marojejycoris*+*Gibbosella*+*Caecina* sister to *Distirogaster*+*Toliarus*+*Tanindrazanus*+*Toxopus* (node 6), *Distirogaster* sister to *Toliarus*+*Tanindrazanus*+*Toxopus* (node 7), and *Toliarus* sister to *Tanindrazanus*+*Toxopus*. Character optimization results for the parsimony tree are given in SM 3.3.

Our combined ML result (SM 3.7) is largely congruent with the combined parsimony topology with the following exceptions: 1) *Maraenaspis bidens* is sister to *Racelda* sp., 2) *Gibbosella* is the sister to the *Caecina*+*Mendis*+*Neolibavius*+*Bannania*+nr *Bannania* clade, and 3) *Distirogaster* is the sister group to the *Glymmatophora*+*Ectrichodia*+*Centraspis*+

Ectrychotes+*Microstemmatoides*+*Cleptria*+*Maraenaspis coccinea* clade. The ML result supports the taxonomic decisions of Forthman et al. (in press) and produces minor character optimization differences in comparison to the parsimony tree for taxa and clades of interest (data not shown).

Divergence dating estimation

Results of the BEAST molecular divergence dating analysis are shown in Fig. 3.4, with HPD intervals shown in SM 3.8. Based on the analysis, Ectrichodiinae diverged from Tribelocephalinae approximately 68.53 mya (95% HPD = 57.61–79.39 mya), which is congruent with Hwang & Weirauch (2012). Within Ectrichodiinae, the Neotropical Ectrichodiinae+*Santosia* clade diverged from the Old World clade about 63.51 mya (95% HPD = 52.39–74.44 mya). Within the Old World clade, all Madagascan Ectrichodiinae lineages and genera diverged from their respective sister groups within the last 46 my: 1) *Gibbosella quadocris* Forthman, Chłond, & Weirauch (median = 27.33 mya, 95% HPD = 12.22–42.12 mya), 2) *Marojejycoris*+*Tanindrazanus*+*Toxopus* (median = 35.55 mya, 95% HPD = 25.34–45.60 mya), 3) *Distirogaster* (median = 32.86 mya, 95% HPD = 23.48–42.59 mya), and 4) *Glymmatophora crassipes* (median = 19.24 mya, 95% HPD = 11.46–27.85 mya).

Biogeographic analyses

Ancestral range reconstruction results based on the DEC and DEC+j models are reported and shown in Fig. 3.4. Results of the ancestral area reconstruction using the DIVA model are shown in SM 3.9 and are most similar to the highest probability ranges reconstructed by DEC+j. The likelihood, d, e, and j parameter values for the DEC and DEC+j models are as follows: (1) DEC: LnL = –39.09, $d = 0.0056$, $e = 0.0006$, $j = 0$ and (2) DEC+j: LnL = –27.10 $d = 1e^{-12}$, $e = 1e^{-12}$, $j = 0.1238$. The DEC+j model performed significantly better than the DEC (LRT $X^2 = 23.97$, df = 1,

$p = 9.80e^{-7}$), with the *j* parameter (or founder speciation effect) by far the most significant contributor to the current distribution.

In analyses with all three biogeographic models, a Neotropical and Oriental distribution is recovered for the ancestral node of Ectrichodiinae. The ancestral areas for the Neotropical Ectrichodiinae+*Santosia* clade and the Old World clade are inferred as Neotropical and Oriental, respectively, in all analyses. In the DEC+j analysis, the ancestral range of *Gibbosella quadocris* and *Caecina* sp. is recovered as Oriental with high probability, indicating the ancestor of *Gibbosella* dispersed to Madagascar from this region. An Oriental distribution is also reconstructed for the node that includes *Gibbosella* and *Ectrychotes* with subsequent dispersal to Madagascar for the node containing *Marojejycoris* and *Ectrychotes*. The ancestor of the clade containing *Centraspis* Schaum and *Ectrychotes* is reconstructed to have dispersed to the Afrotropical region from Madagascar, with a re-colonization from Africa to Madagascar by *Glymmatophora crassipes*. Results from DIVA are similar to DEC+j highest probability results, but differ in the following with respect to the Madagascan fauna: 1) the node containing *Gibbosella* and *Ectrychotes* is inferred as Madagascar+Oriental, 2) the ancestral range of *Gibbosella quadocris* and *Caecina* sp. is Madagascar+Oriental, 3) an Afrotropical+Madagascar distribution is recovered for the clade containing *Distirogaster* and *Ectrychotes*, and 4) the ancestral range of *Glymmatophora crassipes*+*Ectrichodia* is Afrotropical+Madagascar.

Reconstructions from the DEC analyses differ from DEC+j results for some nodes and by the presence of more widespread ancestral ranges. In the DEC analysis, a Madagascar+Oriental ancestral distribution is recovered for *Gibbosella quadocris*+*Caecina* sp. with high probability, as well as for the node containing *Marojejycoris* and *Ectrychotes* and the node containing *Distirogaster* and *Ectrychotes*. An Afrotropical+Oriental ancestral range is recovered for the clade including *Centraspis* and *Ectrychotes,* with the ancestral node of *Glymmatophora crassipes+Ectrichodia* having an Afrotropical+Madagascar distribution.

Discussion

Phylogeny of Madagascan Ectrichodiinae

Results of our molecular ML phylogeny are used to investigate the number of Madagascan Ectrichodiinae lineages, as well as to estimate temporal divergences and biogeographic history. Our combined morphological and molecular phylogeny was used by Forthman et al. (in press) to formalize taxonomic decisions and inform diagnostic features for Madagascan millipede assassin bugs. Both molecular ML and combined parsimony phylogenetic analyses recovered some similar relationships. Both phylogenetic hypotheses support a paraphyletic New World fauna, with respect to *Santosia* in the molecular ML phylogeny or *Santosia+Vilius* in the combined parsimony result. This predominately New World clade is recovered as sister to a larger clade of Afrotropical, Oriental, and Madagascan Ectrichodiinae with relatively weak support. Madagascan lineages are recovered with close relationships to Oriental and Afrotropical taxa in both analyses, which is congruent with Vences' (2004) and Yoder & Nowak's (2006) conclusions that a large proportion of the Madagascan biota exhibits relationships with Afrotropical and Oriental taxa. Species of *Glymmatophora* share a close relationship with *Ectrichodia* species. *Gibbosella* species are recovered as sister to *Caecina*, albeit with low support in both phylogenies. Although the molecular and combined phylogenies differ in their phylogenetic placement of *Marojejycoris*, the genera *Tanindrazanus* and *Toxopus* retain a close relationship in both analyses.

Despite recovering similar relationships, the two phylogenies show some degree of discordance in higher-level relationships within Ectrichodiinae, a result that may be due to the increase in missing molecular data in the combined analysis. Unlike the molecular phylogeny, most Madagascan taxa form a clade in the combined phylogeny (node 4, including *Caecina*) with low support. The phylogenetic placement of *Marojejycoris* and *Distirogaster* differ; in the ML phylogeny, *Marojejycoris* is recovered as sister to *Tanindrazanus* and *Distirogaster* as sister to a clade containing *Ectrichodia* and *Ectrychotes*, whereas the two genera are included within node 4 of the combined analysis. In general, more nodes are recovered with BS≥50 in the molecular phylogeny compared to the combined phylogeny. Regardless of the discordance between the two phylogenetic hypotheses, the combined phylogeny has permitted exploration of potential character support for taxa and been useful in determining diagnostic features for Forthman et al.'s (in press) taxonomic monograph.

Temporal divergence and biogeography

Based on our temporal divergence estimates and ancestral range reconstructions, millipede assassin bugs colonized Madagascar via transoceanic dispersal more than once within the last ~68 my. The DEC+j model outperformed the DEC model based on LRT and infers two colonization events from the Oriental region to Madagascar, once between 25–57 mya and once within the last 42 my. Subsequently, a single colonization event from Madagascar to the Afrotropical region is inferred to have occurred around the Eocene-Oligocene boundary (21–43 mya) with a back-colonization event (ancestral node of *Glymmatophora*+*Ectrichodia*) from the Afrotropical region to Madagascar within the last ~28 my. These results are congruent with the DIVA results (SM 3.9). Although the DEC results differ from the DEC+j in terms of the ancestral ranges reconstructed for several nodes, in general we find similar patterns: two dispersal events into Madagascar from the Oriental region and one dispersal from Africa to Madagascar. However, an out-of-Madagascar dispersal event to the Afrotropical region is not recovered in the DEC analysis; upon diverging from *Distirogaster*, the branch leading to the node containing *Centraspis* and *Ectrychotes* has an Oriental distribution, with a range expansion into the Afrotropical region at that node.

Several hypotheses have been proposed for dispersal events from the Oriental region to Madagascar and may explain the two colonization events reconstructed from the DEC+j model. While many researchers reconstruct an isolated India in the Late Cretaceous (~65 mya) (see Yoder & Nowak, 2006; Ali & Aitchison, 2008), Ali & Aitchison (2008) proposed a paleogeographic model in which India became progressively isolated but remained connected to Madagascar via the Seychelles-Mascarene Plateau. This connection was extended in the Palaeogene by the development of volcanic islands (Ali & Aitchison, 2008; Zhou et al., 2012) and would have facilitated dispersal as India moved north. Warren et al. (2010) reviewed geologic evidence and also proposed that the rise and fall of sea levels exposed islands between India and Madagascar over the last 65 my, thus reducing the distance of open ocean to traverse for potential colonizers. Warren et al. (2010) further proposed climatic influences that would facilitate long-distance dispersal (e.g., winter monsoon winds blowing from India towards Madagascar facilitating aerial dispersal).

Several studies have supported “out-of-Madagascar” dispersal events to surrounding islands and continents for plants and vertebrates (e.g., Jansa et al., 1999; Wikström et al., 2010; Harmon et al., 2008), as well as for several groups of insects. Torres et al. (2001) concluded that satyrine butterflies in the subtribe Mycalesina have a complex biogeographical history that involves dispersal from Madagascar to Africa. The mayfly genus *Cloeodes* Traver is inferred to have a Madagascan origin followed by dispersal into Africa (Monaghan et al., 2005). Zakharov et al. (2004) inferred out-of-Madagascar dispersal for species of the butterfly genus *Papilio* Linnaeus to Oriental and Afrotropical regions within the last 10 my. Recently, the out-of-Madagascar biogeographical hypothesis has been supported by systematic analyses of Madagascan diving beetles (Dytiscidae), with results indicating dispersal to Oriental and Afrotropical regions around the Oligocene and Miocene (Bukontaite et al., 2015).

Our DEC+j results support an out-of-Madagascar dispersal event to Afrotropical regions about 21–43 mya. Westward dispersal could not have been facilitated by ocean currents as these currents had an eastward movement during the Eocene and reversed direction only ~15 mya (Ali & Huber, 2010). McCall (1997) hypothesized that a land bridge known as the Davie Ridge once connected Africa and Madagascar during the mid-Eocene to early Miocene (i.e., 45–26 mya). However, this land bridge has not been supported by some studies (e.g., Leclaire et al., 1989; Bassias, 1992; Rogers et al., 2000), although some suggest that isolated islands may have been present (Rogers et al., 2000; de Wit, 2003). Thus, it is possible that islands in the Mozambique Channel have facilitated westward aerial dispersal during this time. Female specimens for extant Madagascan species of *Distirogaster* (5 spp.), *Toxopus* (2 spp.), and *Glymmatophora* (1 sp.) are apterous, which makes present-day aerial dispersal unlikely. However, it is unknown if the ancestors of these taxa were apterous or capable of flight, thus enabling long-distance aerial dispersal. Female specimens for the majority of Madagascan species, as well as many Afrotropical and Oriental taxa, remain unknown and hinder our ability to reconstruct ancestral states. Future discoveries of female specimens will allow us to to investigate the evolution of winglessness for each sex and to subsequently refine hypotheses on how ancestral species may have dispersed in and out of Madagascar.

Based on our DEC+j analysis, the presence of islands and the eastward ocean currents of the Mozambique Channel within the last ~28 my may have facilitated the re-colonization of Madagascar from Africa. The divergence time estimate of *Glymmatophora crassipes* (95% HPD = 11.46–27.85 mya) is consistent with this hypothesis. However, aerial dispersal cannot be ruled out as ocean currents reversed direction ~15 mya, which would hinder eastward dispersal via rafting. *Glymmatophora crassipes* is apterous in both sexes, but some African species in this genus are macropterous, and it is uncertain when and where the ancestor of *G. crassipes* has lost the capability of flight. Apterous and macropterous *Glymmatophora* species will need to be targeted for future analyses to determine if ocean currents or aerial dispersal are responsible for extant Madagascan *Glymmatophora*. Ancestral state reconstructions on the evolution of winglessness across *Glymmatophora* may provide further insight into possible avenues for the colonization of Madagascar.

Five Ectrichodiinae species in three genera — *Mascaregnasa* Distant, *Quinssyana* Distant, and *Rochonia* Distant — are known from another Indian Ocean island, the Seychelles (Maldonado, 1990). Each species is only known from the male holotype and, thus, were not included in our molecular or morphological analyses. We hypothesize, based on morphological similarities examined in habitus images of the holotypes, that *Quinssyana* is closely related to the Madagascan genus *Gibbosella* and the African genus *Synavecoris*, while *Toxopus* is closely related to *Rochonia*. *Mascaregnasa* is very different from other millipede assassin bug genera, and we are unable to hypothesize affinities with other taxa. Future inclusion of these taxa in systematic analyses will be critical for testing the role of the Seychelles as a stepping-stone island, which has been postulated for other taxa (e.g., *Tachycnemis* frogs [Vences et al., 2003a, b], *Nephilengys* hermit spiders [Kuntner & Agnarsson, 2011], and baetid mayflies [Monaghan et al., 2005]). Millipede assassin bugs from other Indian Ocean islands are currently unknown, but future taxonomic surveys on these islands may result in material that would also benefit future biogeographic investigations for Madagascan Ectrichodiinae.

Combined parsimony analysis to inform taxonomic diagnoses of Madagascan Ectrichodiinae

Character optimizations of the combined parsimony analysis were used as the basis for diagnoses in the taxonomic monograph of Madagascan Ectrichodiinae (Forthman at al., in press). A detailed discussion of important morphological characters for selected nodes shown in Fig. 3.3 is provided in SM 3.10. Here, we only discuss some examples of male diagnostic features for endemic Madagascan genera that are also included in Forthman and et al. (in press). Species of *Marojejycoris* are distinguished by features such as a complete pronotal transverse suture (57–1; Fig. 3.3H), the laterally visible MGE (71–1; Fig. 3.3K), and the fore wing lacking the distal part of M beyond the M+Cu junction (104–1; Fig. 3.3M). Diagnostic features for *Gibbosella* include the 8-segmented antennae (38–3; except 6-segmented in *G. pallidalata* Forthman, Chłond, & Weirauch), dorsally directed paramedian scutellar processes (62–1; except in *G. planiscutum* Forthman, Chłond, & Weirauch) (Fig. 3.3I), and transversely bicolored dorsal laterotergites (105–1) with posterior protuberances (107–1, 108–1, 109–1, 110–1; shared with *Caecina*). A number of features are diagnostic for *Distirogaster*, e.g., the metallic coloration (2–1), 8-segmented antennae (38–3), posterior tubercles on dorsal laterotergites III–VI (107–1, 108–1, 109–1, 110–1), and paramedian carinae on abdominal sternites (120–1; Fig. 3.3N). The small (1–0) red and black (2–2) body and a punctate posterior pronotal lobe (51–2) distinguish *Toliarus*. Although *Tanindrazanus* is not supported by any synapomorphic characters in our analysis, it is consistently recovered as a clade in molecular and combined analyses. An incomplete transverse suture between the meso- and metasterna (66–1), a laterally expanded dorsal laterotergite II (106–1), and the transversely bicolor dorsal laterotergites (105–1) are treated as diagnostic characters for *Toxopus*.

Conclusion

Madagascar's unique biodiversity is, at least partially, the result of long-term geologic isolation, transoceanic dispersal events followed by speciation, local geography, and climate change. The recently revised and diverse millipede assassin bug fauna of Madagascar have presented an opportunity to contribute to this growing knowledge of Madagascan invertebrates by investigating its historical biogeography. Phylogenetic hypotheses generated from molecular and combined morphological and molecular cladistic analyses are similar in some respects but discordant at higher-level relationships. Overall, the molecular phylogeny received higher BS support compared to the combined phylogeny. Regardless, results from the combined phylogeny have been important for informing taxonomic diagnoses in Forthman et al. (in press).

Based on our molecular dataset, millipede assassin bugs are shown to have colonized Madagascar within the last ~68 my. Given this relatively recent age, transoceanic dispersal rather than vicariance is responsible for the Madagascan Ectrichodiinae fauna we see today. Millipede assassin bugs colonized Madagascar twice from the Oriental region and once from the Afrotropical region. However, DEC+j and DIVA models reconstruct an out-of-Madagascan dispersal event to the Afrotropical region, whereas the DEC model does not. Temporal divergence estimates and biogeographic results indicate that dispersal from the Oriental region to Madagascar may have been facilitated by the Seychelles-Mascarene Plateau and volcanic islands in the Indian Ocean over the last ~65 my. Factors facilitating dispersal from the Afrotropical region to Madagascar are more difficult to determine, but aerial dispersal via stepping-stone islands in the Mozambique Channel is the most probable hypothesis when accounting for ancient oceanographic reconstructions (i.e., ocean currents had an eastward direction). Further testing of the geologic and oceanic factors facilitating dispersal will require a larger sample of Afrotropical millipede assassin bugs, as well as Seychellois species. Furthermore, apterous females are known for several Madagascan species, making aerial dispersal impossible. However, it remains to be investigated if the ancestors of these taxa possessed an apterous condition or were capable of flight. Our results are congruent with a small, yet, largely growing body of biogeographic studies for Madagascan invertebrates; Madagascan millipede assassin bugs have a complex biogeographic history, with Cenozoic transoceanic dispersal between Oriental, Afrotropical, and Madagascan regions solely responsible for the endemic fauna we currently find present on the island.

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Figure 3.1. Examples and criteria of limited (top) and extreme (bottom) sexual dimorphism in Ectrichodiinae. Arrows in top panel indicate distal margin of wings.

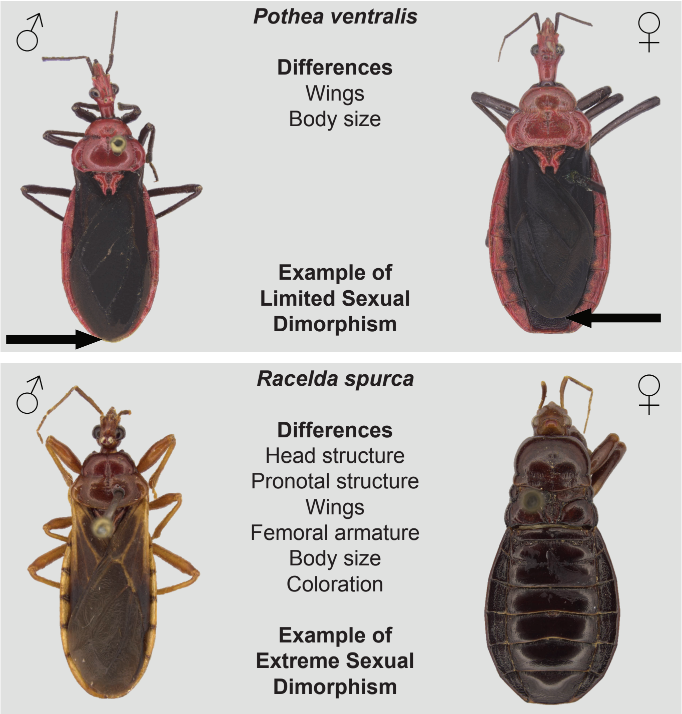
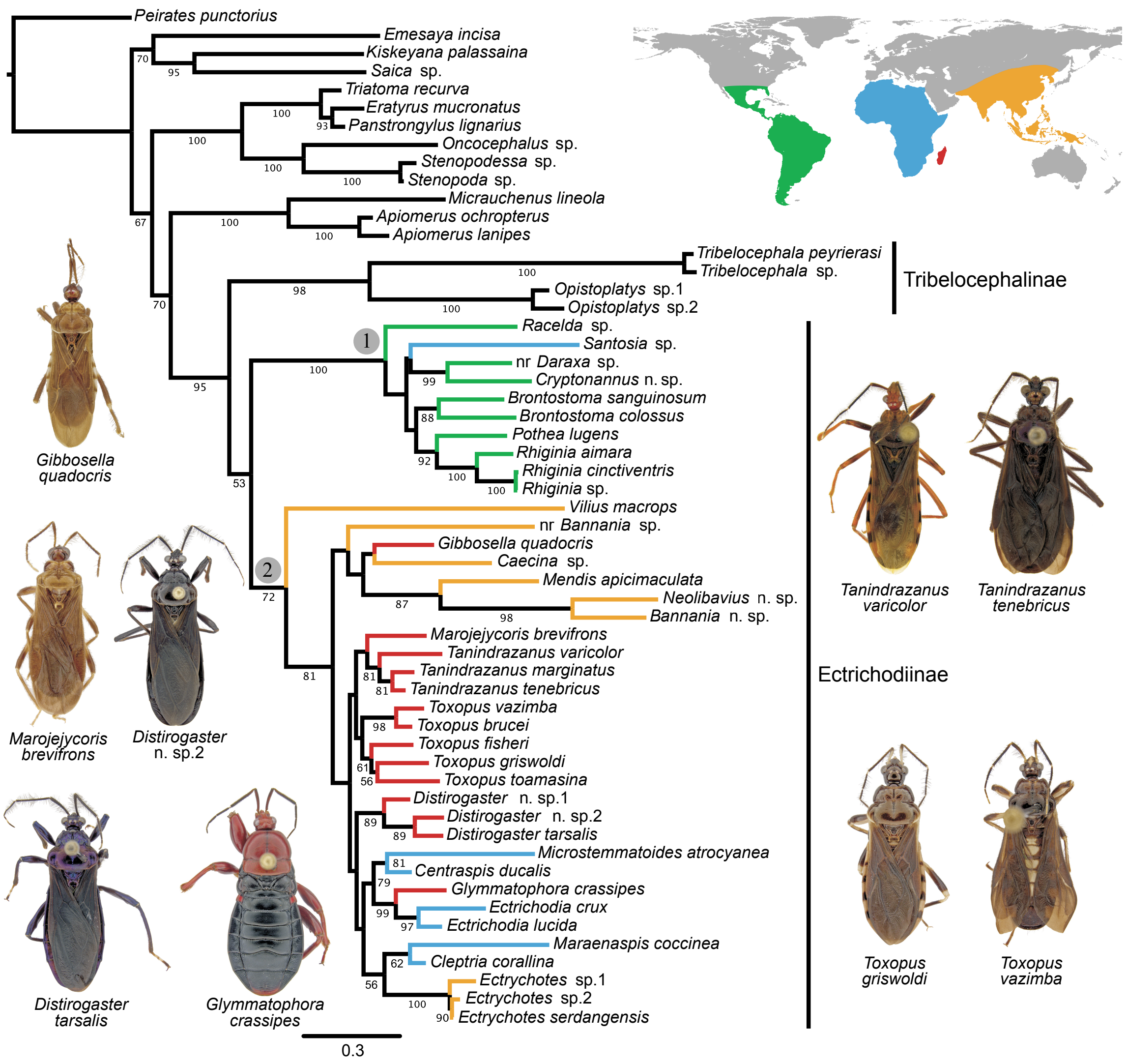

♂
Pothea ventralis
♀
Differences
Wings
Body size
Example of
Limited Sexual
Dimorphism
♂
Racelda spurca
♀
Differences
Head structure
Pronotal structure
Wings
Femoral armature
Body size
Coloration
Example of
Extreme Sexual
Dimorphism

Figure 3.2. Best tree based on ML analysis of 56 taxa, four G-INS-I aligned gene partitions (COI, 18S, 28S D2, 28S D3–D5), and GTR+Γ+I model of sequence evolution (final Ln = –25,426.19528). Terminal branches are colored by occurrence of a taxon in a given biogeographic region, which corresponds to the map legend. Numbers in gray circles refer to nodes discussed in the text. Bootstrap (BS) values ≥50 are reported below branches, with the exception that BS values are reported next to the node of *Microstemmatoides atrocyanea* and *Centraspis ducalis*, as well as the node of the clade containing *Microstemmatoides atrocyanea* and *Ectrichodia crux*.



Peirates punctorius
Emesaya incisa
Kiskeyana palassaina
Saica sp.
Triatoma recurva
Eratyrus mucronatus
Panstrongylus lignarius
Oncocephalus sp.
Stenopodessa sp.
Stenopoda sp.
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Tribelocephala peyrierasi
Tribelocephala sp.
Opistoplatys sp.1
Opistoplatys sp.2
Tribelocephalinae
Racelda sp.
Santosia sp.
nr Daraxa sp.
Cryptonannus n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Pothea lugens
Rhiginia aimara
Rhiginia cinctiventris
Rhiginia sp.
Vilius macrops
nr Bannania sp.
Gibbosella quadocris
Caecina sp.
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toxopus vazimba
Toxopus brucei
Toxopus fisheri
Toxopus griswoldi
Toxopus toamasina
Distirogaster n. sp.1
Distirogaster n. sp.2
Distirogaster tarsalis
Microstemmatoides atrocyanea
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia crux
Ectrichodia lucida
Maraenaspis coccinea
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Ectrichodiinae
1
2
70
95
100
93
100
100
100
67
100
100
70
100
98
100
95
100
99
88
92
100
100
53
72
87
98
81
81
81
98
61
56
89
89
81
79
99
97
62
56
100
90
0.3
Gibbosella quadocris
Marojejycoris brevifrons
Distirogaster n. sp.2
Distirogaster tarsalis
Glymmatophora crassipes
Tanindrazanus varicolor
Tanindrazanus tenebricus
Toxopus griswoldi
Toxopus vazimba

Figure 3.3. Strict consensus tree from 938 parsimonious trees from a TNT analysis of 110 taxa (outgroups removed from figure) and a combined morphological and molecular dataset (length = 7,250 steps; RI = 0.587; CI = 0.356). Terminal branches are colored by taxon distribution, which corresponds to the map legend. Numbers in gray circles refer to nodes discussed in the text and SM10. Bootstrap values ≥50 are reported below branches. Examples of morphological characters that are discussed in the text are given: A.–D. Dorsal (A., B.) and lateral (C., D.) head morphology: A. *Glymmatophora crassipes*, B. *Toxopus tibialis*, C. *Maraenaspis bidens*, D. *Tanindrazanus kathrynae*; E. Lateral antennal morphology of *Toxopus insignis*; Dorsal (F.–H.), lateral (I.), and ventral (J.): F. *Maraenaspis bidens*, G. *Toxopus italaviana*, H. *Marojejycoris notadichroa*, I. *Gibbosella conisimilis*, J. *Tanindrazanus irwini*; K. Metathoracic gland evaporatorium of *Tanindrazanus varicolor* in lateral view; L. Ventral mid leg morphology of *Glymmatophora crassipes*. M. Hemelytral morphology of *Gibbosella planiscutum*; N. Ventral abdominal morphology of *Distirogaster tarsalis*. A., C.–G., and I.–M. modified from Forthman et al. (in press). Character numbers and character state codings are listed in Table 3.2. Abbreviations used in figures: 1A, first anal vein; aa, antennal articulation; ain, antennal insertion site; ap, antennal pseudoarticulation; apl, anterior pronotal lobe; app, anterolateral pronotal projection; asp, anterior femoral subapical protuberance; bf, basiflagellomere; cl, clypeus; co, corium; cp, corial pterostigma; Cu, cubitus; df, distiflagellomere; e, compound eye; exM, extension of M beyond M+Cu distal junction; fmp, femoral medial protuberance; g, gula; is, interocular sulcus; L2, labial segment II (first visible segment); L3, labial segment III (second visible segment); M, media; mc, metacoxa; mf, mid femur; mge, metathoracic gland evaporatorium; mms, transverse suture between meso- and metasterna; mss, mesosternum; mt, mid trochanter; mts, metasternum; p, pedicel; pa, papillae; pc, sternal paramedian carinae; pcd, postclypeal depression; ppl, posterior pronotal lobe; psp, posterior femoral subapical protuberance; pts, pronotal transverse suture; R, radius; s, scape; s2, sternite II (fused sternites I and II); s3, sternite III; sc, scutellum; sis, sternal intersegmental suture; sl, synthlipsis; sld, sternal medial longitudinal depression.

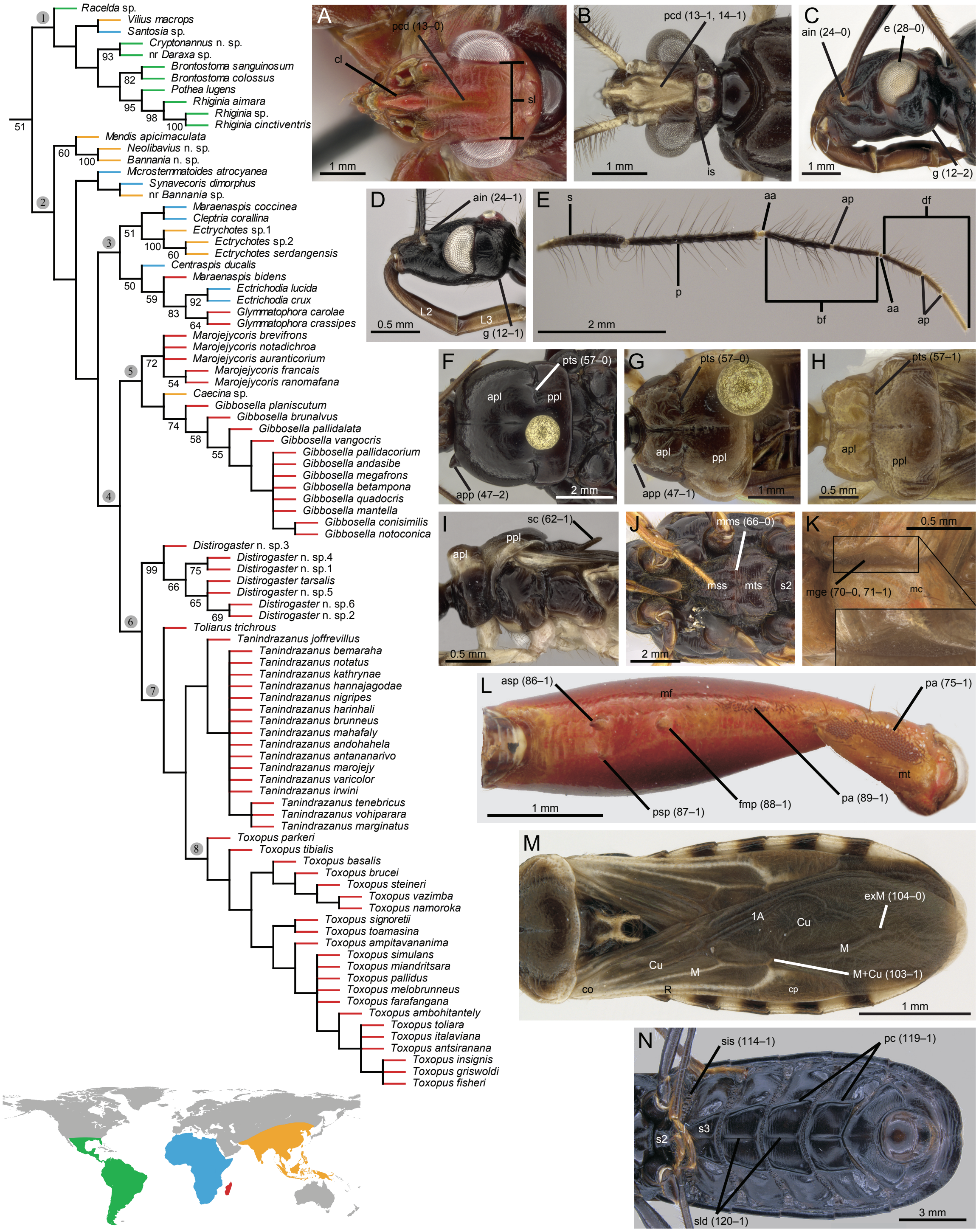

51
1
Racelda sp.
Vilius macrops
Santosia sp.
93
Cryptonannus n. sp.
nr Daraxa sp.
82
Brontostoma sanguinosum
Brontostoma colossus
95
Pothea lugens
98
Rhiginia aimara
100
Rhiginia sp.
Rhiginia cinctiventris
2
60
Mendis apicimaculata
100
Neolibavius n. sp.
Bannania n. sp.
Microstemmatoides atrocyanea
Synavecoris dimorphus
nr Bannania sp.
3
51
Maraenaspis coccinea
Cleptria corallina
100
Ectrychotes sp.1
60
Ectrychotes sp.2
Ectrychotes serdangensis
50
Centraspis ducalis
59
Maraenaspis bidens
92
Ectrichodia lucida
Ectrichodia crux
83
64
Glymmatophora carolae
Glymmatophora crassipes
5
72
Marojejycoris brevifrons
Marojejycoris notadichroa
Marojejycoris auranticorium
54
Marojejycoris francais
Marojejycoris ranomafana
Caecina sp.
74
Gibbosella planiscutum
Gibbosella brunalvus
58
Gibbosella pallidalata
55
Gibbosella vangocris
Gibbosella pallidacorium
Gibbosella andasibe
Gibbosella megafrons
Gibbosella betampona
Gibbosella quadocris
Gibbosella mantella
Gibbosella conisimilis
Gibbosella notoconica
4
99
Distirogaster n. sp.3
75
Distirogaster n. sp.4
66
Distirogaster n. sp.1
Distirogaster tarsalis
65
Distirogaster n. sp.5
69
Distirogaster n. sp.6
Distirogaster n. sp.2
6
Toliarus trichrous
7
Tanindrazanus joffrevillus
Tanindrazanus bemaraha
Tanindrazanus notatus
Tanindrazanus kathrynae
Tanindrazanus hannajagodae
Tanindrazanus nigripes
Tanindrazanus harinhali
Tanindrazanus brunneus
Tanindrazanus mahafaly
Tanindrazanus andohahela
Tanindrazanus antananarivo
Tanindrazanus marojejy
Tanindrazanus varicolor
Tanindrazanus irwini
Tanindrazanus tenebricus
Tanindrazanus vohiparara
Tanindrazanus marginatus
8
Toxopus parkeri
Toxopus tibialis
Toxopus basalis
Toxopus brucei
Toxopus steineri
Toxopus vazimba
Toxopus namoroka
Toxopus signoretii
Toxopus toamasina
Toxopus ampitavananima
Toxopus simulans
Toxopus miandritsara
Toxopus pallidus
Toxopus melobrunneus
Toxopus farafangana
Toxopus ambohitantely
Toxopus toliara
Toxopus italaviana
Toxopus antsiranana
Toxopus insignis
Toxopus griswoldi
Toxopus fisheri
A
pcd (13–0)
cl
sl
1 mm
B
pcd (13–1, 14–1)
is
1 mm
C
ain (24–0)
e (28–0)
g (12–2)
1 mm
D
ain (24–1)
L2
L3
g (12–1)
0.5 mm
E
s
aa
ap
df
p
bf
aa
ap
2 mm
F
pts (57–0)
apl
ppl
app (47–2)
2 mm
G
pts (57–0)
apl
ppl
app (47–1)
1 mm
H
pts (57–1)
apl
ppl
0.5 mm
I
sc (62–1)
ppl
apl
0.5 mm
J
mms (66–0)
mss
mts
s2
2 mm
K
0.5 mm
mge (70–0, 71–1)
mc
L
asp (86–1)
mf
pa (75–1)
mt
psp (87–1)
fmp (88–1)
pa (89–1)
1 mm
M
exM (104–0)
1A
Cu
M
Cu
M
M+Cu (103–1)
co
R
cp
1 mm
N
sis (114–1)
pc (119–1)
s3
s2
sld (120–1)
3 mm

Figure 3.4. Ancestral range reconstructions from DEC (left) and DEC+j (right) models for select nodes. Pie charts indicate the relative likelihoods of each reconstructed distribution, with geographical distributions color coded according to the legend at the top of the figure. The DEC+j model performed significantly better than the DEC: DEC+j LnL = –27.10; DEC LnL = –39.09; LRT p-value = $9.80e^{-7}$. Select dispersal events contributing to Madagascar's Ectrichodiinae diversity is shown for each model. Dispersal events unique to each model are indicated by dashed arrows.

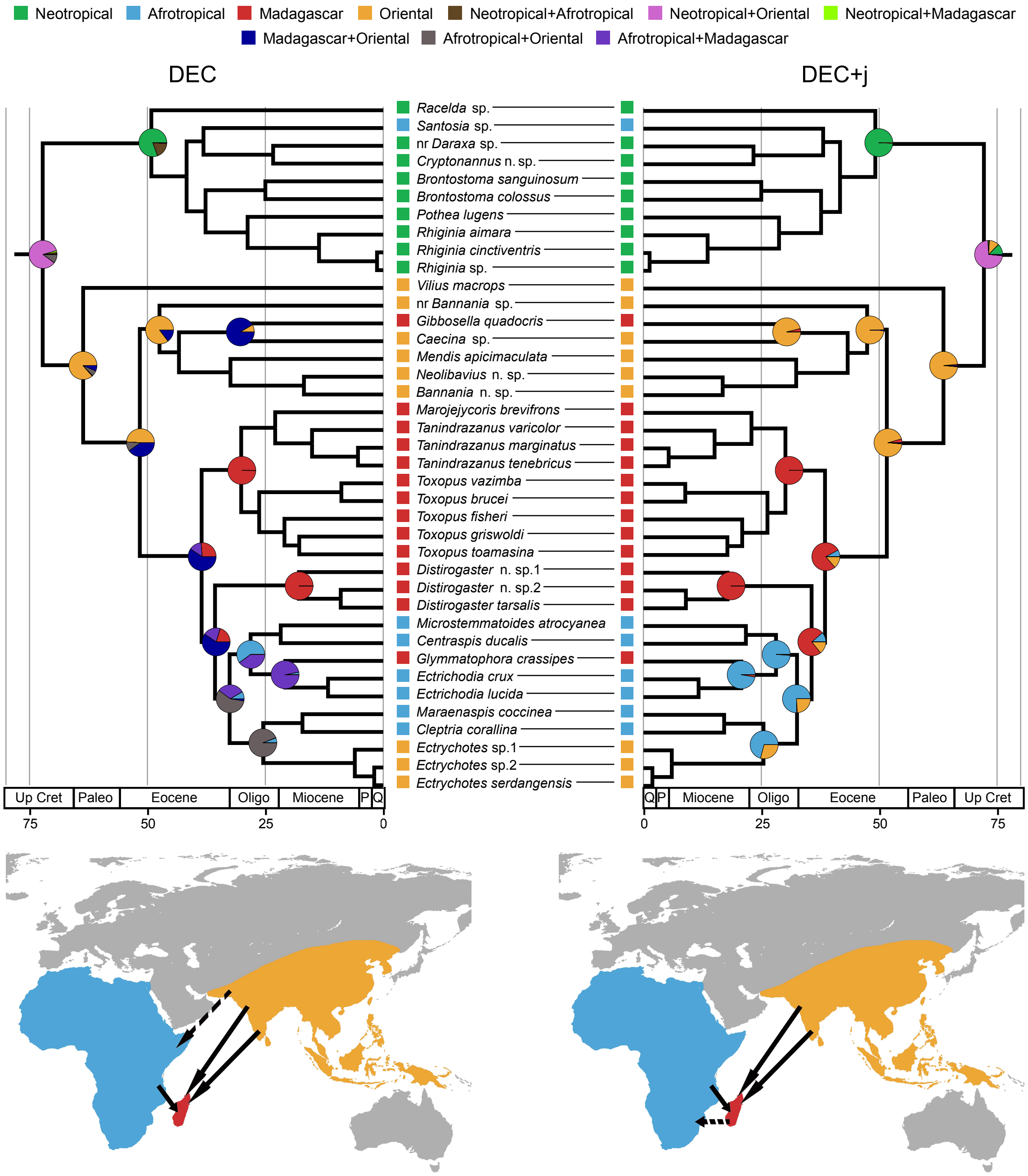

Neotropical
Afrotropical
Madagascar
Oriental
Neotropical+Afrotropical
Neotropical+Oriental
Neotropical+Madagascar
Madagascar+Oriental
Afrotropical+Oriental
Afrotropical+Madagascar
DEC
DEC+j
Racelda sp.
Santosia sp.
nr Daraxa sp.
Cryptonannus n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Pothea lugens
Rhiginia aimara
Rhiginia cinctiventris
Rhiginia sp.
Vilius macrops
nr Bannania sp.
Gibbosella quadocris
Caecina sp.
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toxopus vazimba
Toxopus brucei
Toxopus fisheri
Toxopus griswoldi
Toxopus toamasina
Distirogaster n. sp.1
Distirogaster n. sp.2
Distirogaster tarsalis
Microstemmatoides atrocyanea
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia crux
Ectrichodia lucida
Maraenaspis coccinea
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Up Cret
Paleo
Eocene
Oligo
Miocene
P
Q
75
50
25
0
Q
P
Miocene
Oligo
Eocene
Paleo
Up Cret
0
25
50
75

Table 3.1. Taxon sampling, USI codes, ethanol molecular specimen collection numbers (RCW), depositories, and GenBank accession numbers for sequenced specimens. Asterisks indicate sequences retrieved from GenBank.

					GenBank accession no.			
Subfamily	**Taxon**	**USI**	**RCW**	**Depository**	**COI**	**18S**	**28S D2**	**28D3–D5**
Ectrichodiinae	*Bannania* n. sp.	UCR_ENT 00119027	3064	UCR	KT221890	KT221910	KT221939	KT221968
	nr *Bannania* sp.	UCR_ENT 00004465	609	UCR	KT221908	KT221937	KT221966	KT221996
	Brontostoma colossus	UCR_ENT 00119017	3049	UCR	KT221891	KT221911	KT221940	KT221969
	Brontostoma sanguinosum	UCR_ENT 00002617	1243	UCR	KT221892	KT221912		KT221970
	Caecina sp.	UCR_ENT 00004440	2636	UCR	KT221893	KT221913	KT221941	KT221971
	Centraspis ducalis	UCR_ENT 00119021	3014	UCR	KT221894	KT221914	KT221942	KT221972
	Cleptria corallina	AMNH_PBI 00218770	14	UCR		FJ230462*	FJ230543*	FJ230621*, FJ230700*
	Cryptonannus n. sp.	UCR_ENT 00002757	1433	UCR	KT221895	KT221915		KT221973
	nr *Daraxa* sp.	UCR_ENT 00119016	3076	UCR	KT221909	KT221938	KT221967	KT221997
	Distirogaster tarsalis	UCR_ENT 00006366	2898	CAS	KR606396	KT221918	KT221945	KT221976
	Distirogaster n. sp.1	UCR_ENT 00007158	2881	UCR	KR606393	KT221916	KT221943	KT221974
	Distirogaster n. sp.2	UCR_ENT 00088090	3018	UCR	KR606395	KT221917	KT221944	KT221975
	Ectrichodia crux	UCR_ENT 00119022	3026	UCR	KT221896	KT221919	KT221946	KT221977
	Ectrichodia lucida	AMNH_PBI 00218769	13	UCR		FJ230461*	FJ230542*	FJ230620*, FJ230699*
	Ectrychotes serdangensis	AMNH_PBI 00218830	76	UCR		FJ230479*	FJ230560*	FJ230638*, FJ230717*
	Ectrychotes sp.1	UCR_ENT 00119028	571	UCR	KT221897	KT221920	KT221947	KT221978
	Ectrychotes sp.2	AMNH_PBI 00218932	188	UCR	JQ942322*	FJ230503*	FJ230584*	FJ230661*, FJ230740*
	Gibbosella quadocris	UCR_ENT 00044860	2938	UCR	KR606406			
	Glymmatophora crassipes	UCR_ENT 00088087	3020	UCR	KR606415	KT221921	KT221948	KT221979
	Maraenaspis coccinea	AMNH_PBI 00218772	16	UCR		FJ230463*	FJ230544*	
	Marojejycoris brevifrons	UCR_ENT 00006480	2923	CAS	KR606417	KT221922		KT221980

Table 3.1. (Continued).

Subfamily	**Taxon**	**USI**	**RCW**	**Depository**	**GenBank accession no.**			
					COI	**18S**	**28S D2**	**28D3–D5**
	Mendis apicimaculata	UCR_ENT 00119026	2647	UCR	KT221898	KT221923	KT221949	KT221981
	Microstemmatoides atrocyanea	UCR_ENT 00119029	3029	UCR	KT221899	KT221924	KT221950	KT221982
	Neolibavius n. sp.	UCR_ENT 00003965	1830	UCR	KT221900	KT221925	KT221951	KT221983
	Pothea lugens	UCR_ENT 00119018	3304	UCR	KT221902	KT221927	KT221953	
	Racelda sp.	AMNH_PBI 00218801	41	UCR		FJ230472*	FJ230553*	FJ230631*, FJ230710*
	Rhiginia aimara	UCR_ENT 00119019	3077	UCR	KT221903	KT221928	KT221954	
	Rhiginia cinctiventris	AMNH_PBI 00218891	139	UCR	JQ942333*	FJ230490*	FJ230571*	FJ230648*, FJ230727*
	Rhiginia sp.	UCR_ENT 00119020	3047	UCR	KT221904	KT221929	KT221955	KT221985
	Santosia sp.	UCR_ENT 00004138	2046	UCR	KT221905	KT221930	KT221956	KT221986
	Tanindrazanus marginatus	UCR_ENT 00006887	2902	CAS	KR606423	KT221931	KT221957	KT221987
	Tanindrazanus tenebricus	UCR_ENT 00006723	2931	CAS	KR606430	KT221932	KT221958	KT221988
	Tanindrazanus varicolor	UCR_ENT 00006482	2949	UCR	KR606433	KT221933	KT221959	KT221989
	Toxopus brucei	UCR_ENT 00045338	2901	UCR	KR606438		KT221960	KT221990
	Toxopus fisheri	UCR_ENT 00045431	2910	CAS	KR606446		KT221961	KT221991
	Toxopus griswoldi	UCR_ENT 00006435	2916	CAS	KR606448	KT221934	KT221962	KT221992
	Toxopus toamasina	UCR_ENT 00007056	2951	SU	KR606457		KT221963	
	Toxopus vazimba	UCR_ENT 00006472	2953	CAS	KR606462	KT221935	KT221964	KT221993
	Vilius macrops	UCR_ENT 00119025	3068	UCR	KT221907	KT221936		KT221995
Emesinae	*Emesaya incisa*	AMNH_PBI 00219017	282	UCR	JQ942323*	FJ230515*	FJ230598*	FJ230672*, FJ230751*
Harpactorinae	*Apiomerus lanipes*	AMNH_PBI 00219016	281	UCR	JQ942298*	FJ230514*	FJ230597*	FJ230671*, FJ230750*

Table 3.1. (Continued).

Subfamily	Taxon	USI	RCW	Depository	GenBank accession no.			
					COI	**18S**	**28S D2**	**28D3–D5**
	Apiomerus ochropterus	AMNH_PBI 00218777	22	UCR		FJ230466*	FJ230548*	FJ230625*, FJ230704*
	Micrauchenus lineola	AMNH_PBI 00218790	35	UCR	JQ942329*	FJ230471*	FJ230552*	FJ230630*, FJ230709*
Peiratinae	*Peirates punctorius*	AMNH_PBI 00218960	216	UCR		FJ230508*	FJ230590*	FJ230666*, FJ230745*
Saicinae	*Kiskeyana palassaina*	AMNH_PBI 00190561	10	USNM		FJ230460*	FJ230541*	FJ230619*, FJ230698*
	Saica sp.	AMNH_PBI 00218796	42	UCR		FJ230473*	FJ230554*	FJ230632*, FJ230711*
Stenopodainae	*Oncocephalus* sp.	UCR_ENT 00000182	79	UCR		FJ230481*	FJ230562*	FJ230640*, FJ230719*
	Stenopoda sp.	AMNH_PBI 00218904	154	UCR		FJ230493*	FJ230574*	FJ230651*, FJ230730*
	Stenopodessa sp.	UCR_ENT 00000078	398	FCAP		FJ230532*	FJ230611*	FJ230688*, FJ230767*
Triatominae	*Eratyrus mucronatus*	UCR_ENT 00052168	1811	UCR		JQ897555*	JQ897635*	JQ897711*
	Panstrongylus lignarius	UCR_ENT 00052166	1813	UCR		JQ897584*	JQ897656*	JQ897741*
	Triatoma recurva	AMNH_PBI 00218913	170	UCR		FJ230496*	FJ230577*	FJ230654*, FJ230733*
Tribelocephalinae	*Opistoplatys* sp.1	UCR_ENT 00119024	3056	UCR	KT221901	KT221926	KT221952	KT221984
	Opistoplatys sp.2	UCR_ENT 00052187	1592	UCR		JQ897612*	JQ897682*	JQ897767*
	Tribelocephala peyrierasi	AMNH_PBI 00219033	287	CAS		FJ230521*	FJ230601*	
	Tribelocephala sp.	UCR_ENT 00119023	3048	UCR	KT221906		KT221965	KT221994

Table 3.2. Morphological characters and character state codings.

Character no.	Character	Character states
GENERAL		
0	Wing form	(0) Macropterous; (1) Brachypterous; (2) Apterous; (3) Micropterous
1	Body length	(0) Small; (1) Medium; (2) Large
2	General coloration	(0) Dull, ranging from pale to dark brown/black; (1) Metallic; (2) Red and black, sometimes with yellow or white markings; (3) Red and dull; (4) Orange and black; (5) Red and metallic
3	Bulbous hairs on integument	(0) Present; (1) Absent
4	Vestiture	(0) Very dense; (1) Moderately dense; (2) Sparse; (3) Glabrous
HEAD		
5	Relative head length in dorsal view	(0) As long as wide; (1) Longer than wide; (2) Wider than long
6	Ventral surface of head	(0) Flat; (1) Anteromedially depressed; (2) Medially depressed; (3) Paramedially depressed
7	Depth of ventral head depression	(0) Shallow; (1) Deep
8	Ventral tubercles on head	(0) Absent; (1) Present
9	Ventrolateral tubercle on gula	(0) Absent; (1) Present
10	Anteocular length	(0) Shorter than postocular; (1) As long as postocular; (2) Longer than postocular
11	Postocular-neck constriction	(0) Absent, gradually transition; (1) Present, distinctly constricted
12	Gula shape in lateral view	(0) Flat, conforming to rounded head shape; (1) Moderately swollen ventrolaterally, not produced beyond ventral head margin; (2) Greatly swollen ventrolaterally, produced beyond ventral head margin
13	Postclypeal depression	(0) Flat; (1) Depressed
14	Width of postclypeal depression	(0) Narrow; (1) Broad
15	Depth of postclypeal depression	(0) Shallow; (1) Deep
16	Extension of postclypeal depression	(0) Posterior margin of clypeus to middle of synthlipsis; (1) Posterior margin of clypeus to interocular sulcus
17	Maxillary plate in lateral view	(0) Reaching or nearly reaching dorsal clypeal margin; (1) Not reaching dorsal clypeal margin
18	Clypeal process	(0) Absent; (1) Present

Table 3.2. (Continued).

Character no.	Character	Character states
19	Shape of clypeus	(0) Without dorsal projection; (1) With dorsal projection
20	Clypeal apex relative to labral base	(0) Not elevated; (1) Elevated
21	Antennifer armature	(0) Unarmed; (1) With dorsolateral tubercle
22	Antennal shield	(0) Absent, not expanded; (1) Present, expanded
23	Antennal insertion site in lateral view	(0) Not concealed by antennal shield; (1) Concealed by antennal shield
24	Point of antennal insertion	(0) Sublateral or lateral; (1) Dorsal
25	Presence of ocellar lens	(0) Present; (1) Absent
26	Orientation of ocellar lens	(0) Medially; (1) Laterally
27	Ocellar lens size	(0) Large; (1) Small
28	Eye height in lateral view	(0) Less than or half of head height; (1) More than half of head height
29	Eye shape	(0) Adpressed; (1) Globbose
30	Anterior eye margin	(0) Convex; (1) Concave
31	Posterior eye margin	(0) Concave; (1) Straight
32	Dorsal eye margin	(0) Not attaining dorsal head surface; (1) Attaining dorsal head surface
33	Ventral eye margin	(0) Not attaining ventral head surface; (1) Attaining ventral head surface
34	Synthlipsis width	(0) About width of eye; (1) About 1.5 times width of eye; (2) About 2 times width of eye; (3) About 2.5 times width of eye; (4) About 3 times or more width of eye
35	Scapus length	(0) Not surpassing clypeal apex; (1) Surpassing clypeal apex
36	Pedicel curvature	(0) Straight; (1) Curved
37	Scapo-pedicellar articulation	(0) Slightly bent; (1) Strongly bent, pedicel and flagellomeres point posteriad
38	Antennal segmentation	(0) 4-segmented; (1) 6-segmented; (2) 7-segmented; (3) 8-segmented; (4) >8 segments
39	Labrum structure	(0) Subdivided by transverse membrane; (1) Completely sclerotized
40	Ventral margin of labial segment III	(0) Straight; (1) Convex; (2) Concave

Table 3.2. (Continued).

Character no.	Character	Character states
41	Labial segment III length	(0) Longer than labial segment II; (1) Shorter than labial segment II; (2) Subequal to labial segment II
THORAX		
42	Pronotal length	(0) Wider than long; (1) As long as wide; (2) Longer than wide
43	Pronotal collar	(0) Distinct in dorsal view; (1) Indistinct in dorsal view
44	Anterior pronotal margin shape	(0) Medially concaved; (1) Straight or nearly straight
45	Anterior pronotal lobe shape	(0) Flat; (1) Dorsally elevated, conical
46	Anterior pronotal lobe structure	(0) Rugose; (1) Smooth; (2) Tuberculate
47	Anterolateral armature of pronotum	(0) Absent; (1) Small tubercle; (2) Strongly projecting process
48	Lateral carinae on anterior pronotal lobe	(0) Absent; (1) Present
49	Anterior pronotal lobe length	(0) Longer than posterior lobe; (1) Shorter than posterior lobe; (2) As long as posterior lobe
50	Anterior pronotal lobe width	(0) More than half as wide but not as wide as posterior lobe; (1) As wide as posterior lobe
51	Posterior pronotal lobe structure	(0) Striated; (1) Smooth; (2) Punctate; (3) Tuberculate; (4) Longitudinal ridges
52	Posterior pronotal lobe lateral depressions	(0) Present; (1) Absent
53	Posterior pronotal lobe lateral depression structure	(0) Not foveate; (1) Foveate
54	Extension of pronotal longitudinal depression on anterior lobe	(0) Reaching or nearly reaching anterior margin; (1) Not reaching anterior margin; (2) Absent
55	Presence of pronotal longitudinal depression on posterior lobe	(0) Absent; (1) Present
56	Structure of pronotal longitudinal depression on posterior lobe	(0) Not foveate; (1) Foveate
57	Pronotal transverse suture	(0) Incomplete, divided by paramedian ridges; (1) Complete, not divided by paramedian ridges
58	Pronotal transverse suture structure	(0) Not foveate; (1) Foveate

Table 3.2. (Continued).

Character no.	Character	Character states
59	Scutellar processes	(0) None, scutellum triangular; (1) Two paramedian apical processes; (2) Two paramedian and one medial apical processes; (3) Two paramedian and two lateral processes
60	Distance between paramedian scutellar processes	(0) Narrow; (1) Broad
61	Length of paramedian scutellar processes	(0) Short; (1) Long
62	Orientation of paramedian scutellar processes	(0) Horizontally directed; (1) Dorsally directed
63	Scutellar disc surface	(0) Medially depressed; (1) Flat
64	Prosternal stridulatory process length	(0) Short; (1) Long, surpassing posterior margin of fore coxal cavity
65	Shape of apex of prosternal stridulatory process	(0) Acute; (1) Rounded
66	Transverse suture between meso- and metasterna	(0) Complete; (1) Incomplete, at least partially
67	Mesosternal surface	(0) Medially and laterally depressed; (1) Medially depressed; (2) Flat
68	Metasternal surface	(0) Medially depressed; (1) Flat or convex
69	Presence of metathoracic gland	(0) Absent; (1) Present
70	Presence of metathoracic gland evaporatorium	(0) Present; (1) Absent
71	Metathoracic gland evaporatorium size	(0) Small, not visible in lateral view; (1) Large, visible in lateral view
LEG		
72	Shape of fore coxa	(0) Globular; (1) Elongate
73	Shape of fore femur	(0) Slender; (1) Incrassate
74	Presence of papillae on fore trochanter	(0) Absent; (1) Present
75	Presence of papillae on mid trochanter	(0) Absent; (1) Present
76	Presence of papillae on hind trochanter	(0) Absent; (1) Present
77	Presence of anteroventral row of spines/tubercles on fore femur	(0) Absent; (1) Present
78	Presence of posteroventral row of spines/tubercles on fore femur	(0) Absent; (1) Present
79	Presence of anterior subapical tubercle on fore femur	(0) Absent; (1) Present
80	Presence of posterior subapical tubercle on fore femur	(0) Absent; (1) Present
81	Presence of medial tubercle on fore femur	(0) Absent; (1) Present

Table 3.2. (Continued).

Character no.	Character	Character states
82	Presence of carina on fore femur	(0) Absent; (1) Ventrally entirely carinate; (2) Ventrally carinate basally
83	Presence of papillae on fore femur	(0) Absent; (1) Present
84	Presence of anteroventral row of spines/tubercles on mid femur	(0) Absent; (1) Present
85	Presence of posteroventral row of spines/tubercles on mid femur	(0) Absent; (1) Present
86	Presence of anterior subapical tubercle on mid femur	(0) Absent; (1) Present
87	Presence of posterior subapical tubercle on mid femur	(0) Absent; (1) Present
88	Presence of medial tubercle on mid femur	(0) Absent; (1) Present
89	Presence of papillae on mid femur	(0) Absent; (1) Present
90	Presence of anteroventral row of spines/tubercles on hind femur	(0) Absent; (1) Present
91	Presence of anterior subapical tubercle on hind femur	(0) Absent; (1) Present
92	Presence of posterior subapical tubercle on hind femur	(0) Absent; (1) Present
93	Presence of subapical medial tubercle on hind femur	(0) Absent; (1) Present
94	Presence of medial tubercle on hind femur	(0) Absent; (1) Present
95	Presence of fossula spongiosa on fore tibia	(0) Present; (1) Absent
96	Presence of fossula spongiosa on mid tibia	(0) Present; (1) Absent
97	Protibial groove	(0) Absent; (1) Present
FOREWING		
98	Extension of corium on fore wing	(0) Restricted to areas adjacent to basal wing veins and with pterostigma-like appearance; (1) Well-developed corium
99	Vestiture of corium on fore wing	(0) Long, simple setae; (1) Glabrous
100	Basal part of M and Cu on fore wing	(0) Separate veins; (1) Forming one vein, at least partially
101	Presence of cubital cell on fore wing	(0) Absent; (1) Present
102	Shape of cubital cell on fore wing	(0) Quadrate; (1) Hexagonal
103	Distal part of M and Cu on fore wing	(0) Separate veins; (1) Fused basally
104	Extension of distal part of M on fore wing	(0) Extends beyond distal M+Cu junction; (1) No extension beyond distal M+Cu junction

Table 3.2. (Continued).

Character no.	Character	Character states
ABDOMEN		
105	Color pattern of dorsal laterotergites	(0) Concolor; (1) Transversely bicolor; (2) Longitudinally bicolor
106	Expansion of dorsal laterotergite II	(0) Not expanded; (1) Laterally expanded; (2) Posterior tubercle
107	Dorsal laterotergite III armature	(0) Unarmed; (1) Posterior tubercle
108	Dorsal laterotergite IV armature	(0) Unarmed; (1) Posterior tubercle
109	Dorsal laterotergite V armature	(0) Unarmed; (1) Posterior tubercle
110	Dorsal laterotergite VI armature	(0) Unarmed; (1) Posterior tubercle
111	Connection of dorsal laterotergite and mediotergite	(0) Separated by membrane; (1) Sclerotized
112	Connection of ventral laterotergites and mediotergites III-VII	(0) Separated by membrane; (1) Sclerotized
113	Ventral connexival suture on sternite II	(0) Absent; (1) Present
114	Carinulation of intersegmental suture between abdominal sternites II and III	(0) Not carinulate; (1) Entirely carinulate
115	Carinulation of intersegmental suture between abdominal sternites III and IV	(0) Not carinulate; (1) Entirely carinulate; (2) Laterally carinulate
116	Carinulation of intersegmental suture between abdominal sternites IV and V	(0) Not carinulate; (1) Entirely carinulate; (2) Laterally carinulate
117	Carinulation of intersegmental suture between abdominal sternites V and VI	(0) Not carinulate; (1) Entirely carinulate; (2) Laterally carinulate
118	Carinulation of intersegmental suture between abdominal sternites VI and VII	(0) Not carinulate; (1) Entirely carinulate; (2) Laterally carinulate
119	Presence of paramedian carinae on abdominal sternites	(0) Absent; (1) Present
120	Abdominal sternite surface	(0) Flat; (1) Medially depressed; (2) Convex or keeled
121	Spiracle shape	(0) Ovoid or elliptical; (1) Circular
MALE GENITALIA		
122	Anteroposterior thickness of median pygophore process	(0) Flat; (1) Thickened, at least partially
123	Lateral thickness of median pygophore process	(0) Flat; (1) Thickened, at least partially
124	Lateral shape of median pygophore process	(0) Subtriangular; (1) Blade-like; (2) Hook-like; (3) Knob-like; (4) Rod-like
125	Shape of median pygophore process in caudal view	(0) Subtriangular; (1) Subquadrate; (2) Rod-like; (3) Spade-like

Table 3.2. (Continued).

Character no.	Character	Character states
126	Apex of median pygophore process	(0) Entire; (1) Medially notched, bifid
127	Process on ponticulus basilaris	(0) Absent; (1) Present
128	Median process on ductifer	(0) Absent; (1) Present
129	Length of basal plate extension	(0) Shorter than basal plate; (1) As long as basal plate; (2) Longer than basal plate
130	Posterior margin of dorsal phallothecal sclerite	(0) Rounded; (1) Medially notched
131	Armature of dorsal phallothecal sclerite	(0) Unarmed; (1) Armed with denticle-like processes
132	Presence of vesica on endosoma	(0) Absent; (1) Present
133	Sclerotization of posterior endosomal margin	(0) Membranous; (1) Entirely sclerotized; (2) Paramedian sclerites; (3) Slender sclerotized processes; (4) Sclerotized lateral margin; (5) Sclerotized lateral hooks adjacent to fan-like lobs and with a medial dorsally projecting spine
134	Medial sclerotization of posterior endosomal region	(0) Membranous; (1) Slightly sclerotized; (2) Distinctly sclerite
135	Lateral sclerotization of posterior endosomal region	(0) Membranous; (1) Sclerotized
136	Medial sclerotization of medial endosomal region	(0) Membranous; (1) Slightly sclerotized; (2) Paramedial sclerites
137	Lateral sclerotization of medial endosomal region	(0) Membranous; (1) Sclerotized
138	Medial sclerotization of anterior endosomal region	(0) Membranous; (1) Sclerotized
139	Lateral sclerotization of anterior endosomal region	(0) Membranous; (1) Sclerotized
GLANDS		
140	Presence of Brindley's gland	(0) Present; (1) Absent
141	Dorsal abdominal scent gland (DAG) I in adults	(0) Absent; (1) Present
142	DAG II in adults	(0) Absent; (1) Present
143	DAG III in adults	(0) Absent; (1) Present
144	Size of DAG III relative to DAGs I and II, external view	(0) Similar size; (1) Larger

Supplementary material 3.1. Morphological character matrix in nexus format for cladistic analysis.

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Cleptria_corallina Cryptonannus_n_sp Distirogaster_n_sp1 Distirogaster_n_sp2
Distirogaster_tarsalis Ectrichodia_crux Ectrichodia_lucida Ectrychotes_serdangensis
Ectrychotes_sp1 Ectrychotes_sp2 Emesaya_incisa Eratyrus_mucronatus Gibbosella_quadocris
Glymmatophora_crassipes Kiskeyana_palassaina Maraenaspis_coccinea
Marojejycoris_brevifrons Mendis_apicimaculata Micrauchenus_lineola
Microstemmatoides_atrocyanea Neolibavius_n_sp nr_Bannania_sp nr_Daraxa_sp
Oncocephalus_sp Opistoplatys_sp1 Opistoplatys_sp2 Panstrongylus_lignarius
Peirates_punctorius Pothea_lugens Racelda_sp Rhiginia_aimara Rhiginia_cinctiventris
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Tribelocephala_peyrierasi Tribelocephala_sp Vilius_macrops Synavecoris_dimorphus
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Toxopus_italaviana Toxopus_pallidus Toxopus_simulans Toxopus_insignis
Toxopus_ambohitantely Toxopus_antsiranana Toxopus_toliara Toxopus_farafangana
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0000000000000000-000000000001111001001100001000000100000111
          Tanindrazanus_irwini        0141110-
0021111100001010100011000011102000000010110000011001100011000101000000000000000
0000000000000000-00(0 1)00000000112200100100000100000010000011
          Tanindrazanus_marojejy      0121110-
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          Tanindrazanus_mahafaly
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          Tanindrazanus_harinhali     010111100021111000001010100011000011110(1
2)002000010010000011001100011000101010000000000000000000000000000-
00000000000111120100100000000000000100000111
          Tanindrazanus_hannajagodae  0221110-
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          Toxopus_parkeri
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Toxopus_basalis
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Toxopus_steineri
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Toxopus_namoroka
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Toxopus_ampitavananima
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Toxopus_italaviana
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Toxopus_pallidus
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Toxopus_simulans
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Toxopus_insignis 0101210-
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Toxopus_ambohitantely
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Toxopus_antsiranana
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Toxopus_toliara
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Toxopus_farafangana
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Toxopus_miandritsara
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Toxopus_melobrunneus
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Marojejycoris_auranticorium
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          Marojejycoris_ranomafana
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0000000000000000000000000-01000000000112200110 1???001000???????00111
          Gibbosella_vangocris
000121100011011001000010000111000011103011000011010100011101111011000100000000
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          Gibbosella_planiscutum
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0000000000000000000000000-10121111000111120110100000000000000100000111
          Gibbosella_pallidalata
0001211000111110001000010000111000021101011000010010100011101111011000100010000
00000000000000000000100000-101211110001111002101100000000000000100000111
          Gibbosella_brunalvus        00011110001110---
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          Gibbosella_conisimilis
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00012010001101010100001010001100000110301200001111010001110111??0111001000??00??
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          Gibbosella_betampona
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          Gibbosella_megafrons
00012110000101100100001010011100004110301200001101010001110111101 1?00100010000
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END;
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Supplementary material 3.2. Molecular character matrix in nexus format for cladistic analysis.

```
#NEXUS
BEGIN TAXA;
        TITLE Taxa;
        DIMENSIONS NTAX=56;
        TAXLABELS
                Apiomerus_lanipes Apiomerus_ochropterus Bannania_n_sp
Brontostoma_colossus Brontostoma_sanguinosum Caecina_sp Centraspis_ducalis
Cleptria_corallina Cryptonannus_n_sp Distirogaster_n_sp1 Distirogaster_n_sp2
Distirogaster_tarsalis Ectrichodia_crux Ectrichodia_lucida Ectrychotes_serdangensis
Ectrychotes_sp1 Ectrychotes_sp2 Emesaya_incisa Eratyrus_mucronatus Gibbosella_quadocris
Glymmatophora_crassipes Kiskeyana_palassaina Maraenaspis_coccinea
Marojejycoris_brevifrons Mendis_apicimaculata Micrauchenus_lineola
Microstemmatoides_atrocyanea Neolibavius_n_sp nr_Bannania_sp nr_Daraxa_sp
Oncocephalus_sp Opistoplatys_sp1 Opistoplatys_sp2 Panstrongylus_lignarius
Peirates_punctorius Pothea_lugens Racelda_sp Rhiginia_aimara Rhiginia_cinctiventris
Rhiginia_sp Saica_sp Santosia_sp Stenopoda_sp Stenopodessa_sp Tanindrazanus_marginatus
Tanindrazanus_tenebricus Tanindrazanus_varicolor Toxopus_brucei Toxopus_fisheri
Toxopus_griswoldi Toxopus_toamasina Toxopus_vazimba Triatoma_recurva
Tribelocephala_peyrierasi Tribelocephala_sp Vilius_macrops
        ;
END;

BEGIN CHARACTERS;
        TITLE  Character_Matrix;
        DIMENSIONS  NCHAR=3054;
        FORMAT DATATYPE = DNA GAP = - MISSING = ?;
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        Apiomerus_lanipes
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CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCACGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGTGGCATGTCCTGTCGGTGGTGAACAGAAT----------------------------------
----CCCCGGTA----C-GATGTAGGCTT-----TATTGCCGAAG-T-CTGTATCG----------TGC-
GTGATTCTGTTTGCCGA---
TCTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
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TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCTACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGG
AAGTATGGTTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCACCAGGAG
TGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCACCAGGCCAGGACATTG
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---TTGCTA---ATTTATTTAGTAATT-----GATAGTG-------------TTATTGTCC-GTTTACAA-
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AAAAAAA---------------------------ATTTTTTTTTA--------------
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TTGCGTGGCAATGCGCACCTAGAGCGTACACGCTGATACCCGAAAGATGGTGAACTA
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-
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Apiomerus_ochropterus

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TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
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TTAATGACTCGGCGGGGAGCTTCTACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGG
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AAAT------AATATTCTAAG-TA-----TAGTTAAAGTGCCTGTTT-AAAAGTATTT-------------
--------ACTGAAA-------------GGTA---TGCTTTTTACAGCTTTAA--CTA-ATAT------A--CT-
GGATATTT-------AT---ATTTTTAACAGT-AAAAAATGACGGTGTTGAGCCACTTAAAA--
--TTGCTA---ATTTATTTAGTAATT-----AATAGTG-------------TTATTGTCC-GTTTACAA-
GTGGGTTG-----TTTTTTTTTAGT-A-TAATCGTA--CTTAAGTCCGTTTAT-
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TGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGA
CGTGCAAATCGATCGTCGGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCT
AGTAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTTAGAT-------------------
---------AAAGAATCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAG-
ATCCCCGGCTTTCTTAAAA------------------
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CTGGCGCTGTGG??
??
??
??
??
????

Bannania_n_sp
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ATGTCTAA--CATCTGTTAGTCTAA-CTTTATCACCTA-CTGTTTGC-AAAA-TGTG--
CCTTGC-ATTAGTGCCT------
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TGTTTTAAAAG--------------------------CTTTTAG--------------------------------------
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CTGGAATTAAAATTTTCAGTTGATTAGCTACTCTTCACGGTAGCGTATTGAACCTTTC
CCCTAGATTATTATGAGCATTGGGATTCGTTTTCTTATTCACTATTGGAGGATTAACC
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TAGCCCATTTCC?????

Brontostoma_colossus

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ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGGAAT----------------------------------
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GGATGCCATTTGCCGA---
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CT-GAGTATTT-------TA--AACTTATGACAGT-
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CCTTA--GACTGTGCTT------
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Brontostoma_sanguinosum

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Caecina_sp

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Centraspis_ducalis

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Cleptria_corallina

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Cryptonannus_n_sp
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Ectrichodia_crux

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Emesaya_incisa
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Eratyrus_mucronatus

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Gibbosella_quadocris

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??ACC
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Glymmatophora_crassipes

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Kiskeyana_palassaina
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Maraenaspis_coccinea

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TCTTATCCGGTCCGT??
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Marojejycoris_brevifrons

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Mendis_apicimaculata

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Micrauchenus_lineola

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          nr_Daraxa_sp
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Opistoplatys_sp2

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Panstrongylus_lignarius

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Peirates_punctorius

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Rhiginia_aimara
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ATTAAAACCCAAAGGCGTAATAAAAGTAAAAAGTGATTTAAAAA--------------------------
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TAAAATT-------------------------------TTTACTACG-------AGTAAAAAAAAAT-------------TTT-
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CGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATC
GAACCATCTAGTAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCATT--

GAAGCGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
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AACCTCGGCTTTCTTAAAA-------------------
TGAAGCCGTAGGATTCGGATCAGAGGCAAGGG---------
CCTGGTAAGCAGAACTGGCGCTGTGG??????????TGAAGTCTACATTTTAATTCTACC
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CAGCAACAATAATTATTGCAGTACCCACAGGAATTAAAATTTTCAGTTGATTAGCCA
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Rhiginia_sp

???CCGTAA
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GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
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ACTGGCATGTCGCGGTATGTCCTGTCGGTGGTGAATGGGAT----------------------------------
----CCCCGGTG----C-TGCCTAGGCTT-TT---ATAGTCGAAG-C-ACGTGCCG----------TAC--
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CT-GAGTATTT-------T---ACTTTTTGATAGT-ATCAAATGATTGTGTTGAGCCACTTA-----
--TTATTT------------------------AAAGTG--------------TCTTTAGCC-GTTTACAA-GTAGGTT---
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CTGTTTGT-AAAC-TGTG--CCTTA--GACTGTGCTT------

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C??GGCGTAA
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Santosia_sp

??AT
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CCTTA--
GA???
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TAGCCCATTTT??????

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--TT-----------------------------AAGTGT-------------CTTATGGCT-ATTTGCAA-GTGAGTT----
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Stenopodessa_sp
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GACTGTGCTT------
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Tanindrazanus_marginatus

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A-ATGTCGAA--CTTTTGTTCGTCTAA-CTAAGCCGCCTA-CTGTTTGT-AAAC-TGTG--
CCTTA--GACAGTGCTT------
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AGGGTTTTACCGCTCGCATTTTATT----
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AGAT------AATACTCTAAG-TA-----TAGTTAAAGTGCCTGTCA-AAAGGTTATAAAATT--
----------------TATTT-------------TATA-AC---CATTTTACAGCTTTAA--CTAATTTT------A--
CT-GGGTATTT-------A----TTTTCTGACAGT-
AACGACTGATGGTGTAGAGCCACTTAAAA----ATTA-----------TTTATAATT----
TAAAAGTGTC----------TTTTGGTTGCC-GTTTACAA-GTGGGTT----TTTAGGTATTAGTT-
A-ATGTCGAA--CTTTTGTTCGTCTAA-CTAAGCCGCCTA-CTGTTTGT-AAAC-TGTG--
CCTTA--GACAGTGCTT------
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CGGACCAAGGAGA?????????????????????????????ACGCAAGTCATTGGGTG-
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--TATTT-----------ATATTAAG-TA---------------TA-TTTAAAATTTAGA-

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AGCACATTTTCAC???

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???GTTCGCCGCCTGTCGGT
GTTACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAAT----------------------------
----------CCCTGGTG----CTTACGTAGGCTT-TT--AATAGCTGAAG-T-TTGTGCCG----------
TGG--TGAATTCATTTGCCGA---
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GGGTATTT-------A----TTTTCTGACAGT-AACGAATGATGGTGTAGAGCCACTTAAAA---
-ATTA-----------TTTATAATT---TTATAAGTGTC---CAATTTTTTTTGATTGCC-
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TGGC-----
GA?????????CCAGAAGTTTACATTTTAATTTTACCAGGATTTGGAATTATTTCGCACAT
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-------------TATATTT-------------TATA-ACTTTATTTTTACAGCTTTAA--TTAATTTT------A--
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ACTTCCA????

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CAAACTCTAGAATTGATATTATTTTACATGATACTTATTATGTAGTTGCACACTTCCA
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??TTCCAGCTC
CAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGTTCTGCGTGCC
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CTGTTTGT-AAAC-TGTG--CCTTG--GACAGTTCTT------
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TGGC------
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GCCCACT????????

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CTCAGGGGTAAACGGAGAAGATCTGAA--
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TTAAAGTGTC-----CTAAATAATTTTTGCC-GTTTACAA-GTGGGTTTA-
AGGTATTAATTAGTT-A-ATGTCGAA--CTTTTGTTCGTCTAA-CTAAGCCGCCTA-
CTGTTTGT-AAAC-TGTG--CCTTG--GACAGTGCTT------
ACAACACCGGTCGGCA???
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????????????????????????TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTC
GCCGCCTGTCGGTGTTACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAAT-
--------------------------------------CCCCGGTG----C-TACGTAGGCTT-TT--ATTAGCTGAAG-T-
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-------------TATATTT-------------TATA-ACTTTATTTTTACAGCTTTAA--TTAATTTT------A--
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GGTGAACTATGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAG
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GAACCATCTAGTAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCACTCGGTT

GAGACGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAG-
ATCCCCGGCTTTCTTAAAA-----------------
GTGAAGCCGTGGGAATCGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAA
CTGGCGCTGTGG??
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Tribelocephala_peyrierasi
GCAGCAGGCACGCAAATTACCCACTCCCGGCACGGGGAGGTAGTGACAAAAAATAA
CGATCGGGGACTCTATTGAGGCCCCGTAATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCAATAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTTGCCGCCTGTCGGTGTA
ACTGGCATGTCTCGGCATGTCCTGTCGGTGGTGAATGTAATCTGGCCAATAGGTTTA
AGGGTTAGTAGTTCGATGTGCGCTAATGCG----C-TACACGGGCTT-TT--
CCCCTTCTAACTTGTTGGTTTT----------TTT--
TGATTATGTTTACCGATTTTTTTTCCTACTCCGGTGCTCTTAAACGAGTGTCGAAGTA
GGCCGACACGTTCACTTTGAACAAATTAGAGTGCTTAAAGCAGGCTGGAAATATCTG
CCTGAATAGTGGTGCATGGAATGATAAAATAGGACCTCGGTTCTATTTTATTGGTTTT
AGGAATATGAGGTAATGATCAATATGGACTGGCGGGGGCATTCGTATTGCGACGTTA
GAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCATTTGCCAAGTA
TGTCTTAATTGATCAAAAACGAAAGTTAGAGGTTCCAA-
GCGATCAGATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGA
TGTTCCTTTAATGACTCGGCGGGGAGCTTTTACCCGGGAAACCAAAGCTTTTGGGTTC
CGGGGGAAGTATGGTTGCAAAGCTGAAACTTAAAGGAATTGACGGAAGGGCACCAC
CAGGAGTGGAGCCTGCGGCTTAATTTGACTCAACACGGGAAACCTCA???????????????
???CGTGTTGCTTGATAGTGC
AGCCCTAAGTAGGTGGTAAACTCCATCTAAGGCTAAATAGTACCACGAGACCGATAG
CGAACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGT
ACG-TGAAACCG-CTCAGGGGTAAACGGAAAAGACCTGAA--
TATTCGAAAGGGGAGATTCACGTCTTACCGCAT---GTTTAACTTTTTATCTT----
TTATGAGATGATTTTTC-GCCCTGTCCAGTTTTTTTA--TACTG--
TGATGGTTGGGTTAAATCGCTCGTATATAATTA-----
GTAAAAACAGCGGTGGACCGCACTTCTCCCTTAGT-AGGACGTTGCGACTCGTG-
GGACAAT-ATATTATTCTAAG-CT-----ATATTAAAGTGTCTTTAT-ATATTGTATGTAGC-
----------------ATTGTTA-------------TTTA----TAATATATATAGCTATAA--TAAATAAA-----
TG--CT-GAATA---------------ATTTCCGACAGT-
AACGAATGATAGTGTTGAGCCGCTAATTT----TTTTCT------------------------TTAGCG-------
-------TTTTGACCA-ATTTACAA-GTGGGGTA-----KGAATAATTATT-A-ATGTCGAA--
CTTTTGTTCGTCTAA-TATGTTCTCCTA-CTGTTGGT-AAAT-TGTTTGTTTCA--
AACAAGGCTT------
ATAACACTGATCAGCAGCGATCCAGTTTCAGGCTCTTATCCGGTCCGT???????????????
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Tribelocephala_sp

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??TGCAGCCCAA
GTAGGTGGTAAACTCCATCTAAGGCTAAATAGTACCACGAGACCGATAGCGAACAA
GTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACG-
TGAAACCG-CTCAGGGGTAAACGGAAAAGACCTGAA--
TATTCGAAAGGGGAGATTCACGTCTTACCGCAT---GTTTAACTTTTTATCTT----
TTATGAGATGATTTTTC-GCCCTGTCCAGTTTTTTTA--TACTG--
TGATGGTTGGGTTAAATCGCTCGTATATAATTA-----
GTAAAAACAGCGGTGGACCGCACTTCTCCCTTAGT-AGGACGTTGCGATTTGTT-
GGACAAT-ATATTATTCTAAG-CT-----ATATTAAAGTGTCTTTAT-ATATTGTATGTAGC-
----------------ATTGTTA-------------TTTA----TAATATATATAGCTATAA--TAAATAAA-----
TG--CT-GAATA---------------ATTTCCGACAGT-
AACGAATGATAGTGTTGAGCCGCTAATTT----TTTTCT------------------------TTAGCG-------
-------TTTTGACCA-ATTTACAA-GTGGGGTA-----TGAATAATTATT-A-ATGTCGAA--
CTTTTGTTCGTCTAA-TATGTTCTCCTA-CTGTTGGT-AAAT-TGTTTGTTTCA--
AACAAGGCTT------
ATAACACTGATCAGCAGCGATCCAGTTTCAGGTACTTATCCGACCCGTCTTGAAA????
???????????????????????????????????????TGTACGCAAGTCATTGGGTAAATATTAAACCC
AAAGGCATAATAAAAGTAAATATAATGTAAAAAAAAA--------------GGAAAAAT---------
------------ACTTTTTTAATTTTTTTT---------------TTACATTACAAAGAGAAGATGG-----------
------------------------------TATATTGTTTTT----------TGTACT---------------------
CTTTGGTATAAAAGAT-
TGCCCGCATTCTCAGGGCGCTATTACTCTCGCTTTGCGAGTGTATGCGCACCCAGAGC
GTACACGATAATACCCGAAAGATGGTGAACTATGCCTGGCCAGGACGAAGCCAGGG
GAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGTGCAAATCGATCGTCAGAGCTGG
GTATAGGGGCGAAAGACCAATCGAACCATCTAGTAGCTGGTTCCCTCTGAAGTTTCC
CTCAGGATAGCTTGCGCTCGTGAT-------------------------
GTGATTAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAG-
AAGGCCGGCTTTCTTAAAA------------------TTGAAGCCG------------------
GTCAGATATATTTGTTTTGTTTTGGA------------
TAA??????????????AGTATATATTCTTATTCTACCGGGATTCGGACTCATTTCACATATT
ATTTCTATAGAAACAGGAAAAAATGAAGCTTTTGGAGTACTAGGAATAATTTATGCC
ATATTAGCTATTGGACTTCTGGGATTTATTGTTTGAGCACATCATATGTTCACAATCG
GAATGGACGTAGATACACGGGCCTATTTACATCAGCTACAATAATTATTGCTGTGC

CAACAGGTATTAAAATCTTCAGATGATTAGCCACATTGCATGGAAGAGTAATTATAT
ATAATCCAAGAATTTTATGAGCCTTAGGATTTGTATTCCTATTCACAATCGGGGGATT
AACAGGAGTTATTCTCGCTAATTCAAGAATTGACATTGTACTACACGACACCTATTAT
GTAGTAGCCCACTTCCA????

Vilius_macrops

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???????????????????GCGGTTAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGT
TCGCCGCCTGTCGGTGTTACTGACATGTCGCGGCATGTCCTGTCGGTGGTGAATGAA
AATTGCCAGTATTTAACTAAGGCTATTATTTTACT-----CCTCAATG----G-TATGTAG-----
TA--ATGGCTGTAAG-T-TTGTGCTG----------TAG--TAATTTAATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATTACTGCCTGAATAGTGGTGCATGGAATAATAGAATAGGACCTCGGTTCTATT
TTATTGGTTTTAGGAATATGAGGTAATGATCAATGTGGACTGGCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCTACCCGGGAAACCAAAGCTTTGGGTTCCGGGGG
AAGTATGGTTGCAAAGCTGAAACT???
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???GAGTTTCTTGTGTA
CGCAAGTCATTGGGTG--
ATTAAAACCTAAAGGCATAATGAAAGTAAATAGATATAAATGGGGTA--------------
GAGAA------------------------GTGATTCTTTTTCTTGTC---------------
TATATCTTTATAGGGAAGATGA--AAAATT-AATTTTAA----------------------------
TTCTTTTT----------CTTAAAAAG------------------AAAGATAAAATTAATT-
TTTCCGCATTCCTAGGGCGCTTG-
TTACTCGCATTGCGAGTTTATGCGCACCCAGAGCGTACACGATGATACCCGAAAGAT
GGTGAACTATGCCTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAG
CGATTCTGACGTGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATC
GAACCATCTAGTAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTTGTAT
TTAATTTAAATTAATAAAAAATTTTTAATTGAGTCTCATCCGGTAGAGCGAATGATT
AGAGGCATTGGGGTCG-AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAG-
AACCCTGGCTTTCTTGAAT---

AA?????????????AAGTATACATCCTAATTTTACCAGGATTCGGATTAATCTCCCATATT
ATTTCAATAGAAACAGGAAAAAATGAATCTTTTGGATCATTAGGAATGATTTATGCA
ATATTAGCCATCGGACTATTAGGATTCATTGTATGAGCACACCACATATTCACAGTA

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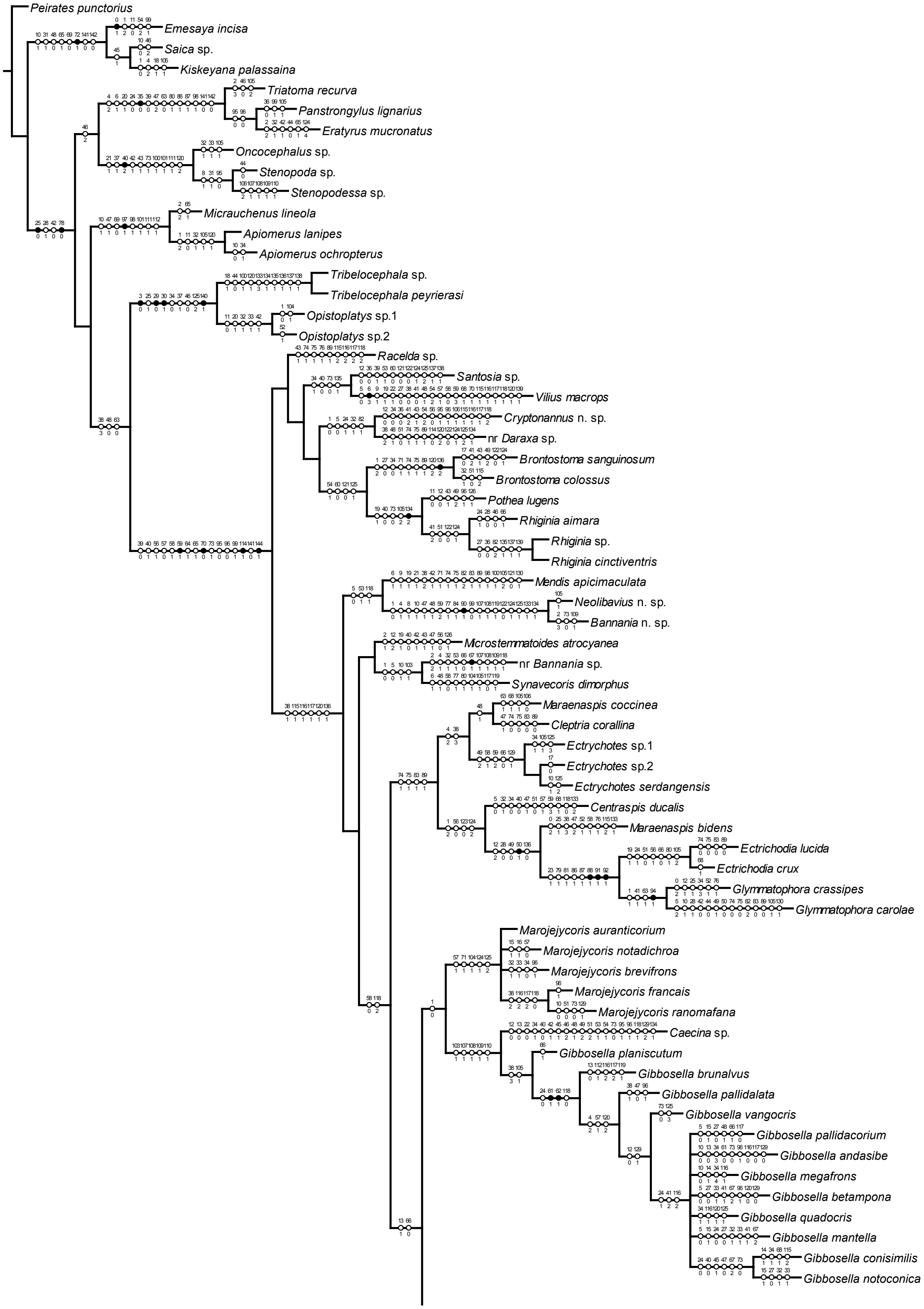
GGAATAGATGTAGATACCCGAGCTTACTTCACCTCTGCAACAATAATCATTGCTGTC
CCCACAGGTATTAAAATCTTCAGATGACTCGCCACCTTACACGGCAGTATAATTATA
CTTTCACCAAGAATTATATGAGCATTAGGATTCGTATTCCTATTCACCATAGGAGGAT
TAACTGGAGTAATTCTAGCTAATTCAAGAATCGACATTATCCTTCACGATACTTACTA
TGTCGTGGCACACTT???????
;
END;

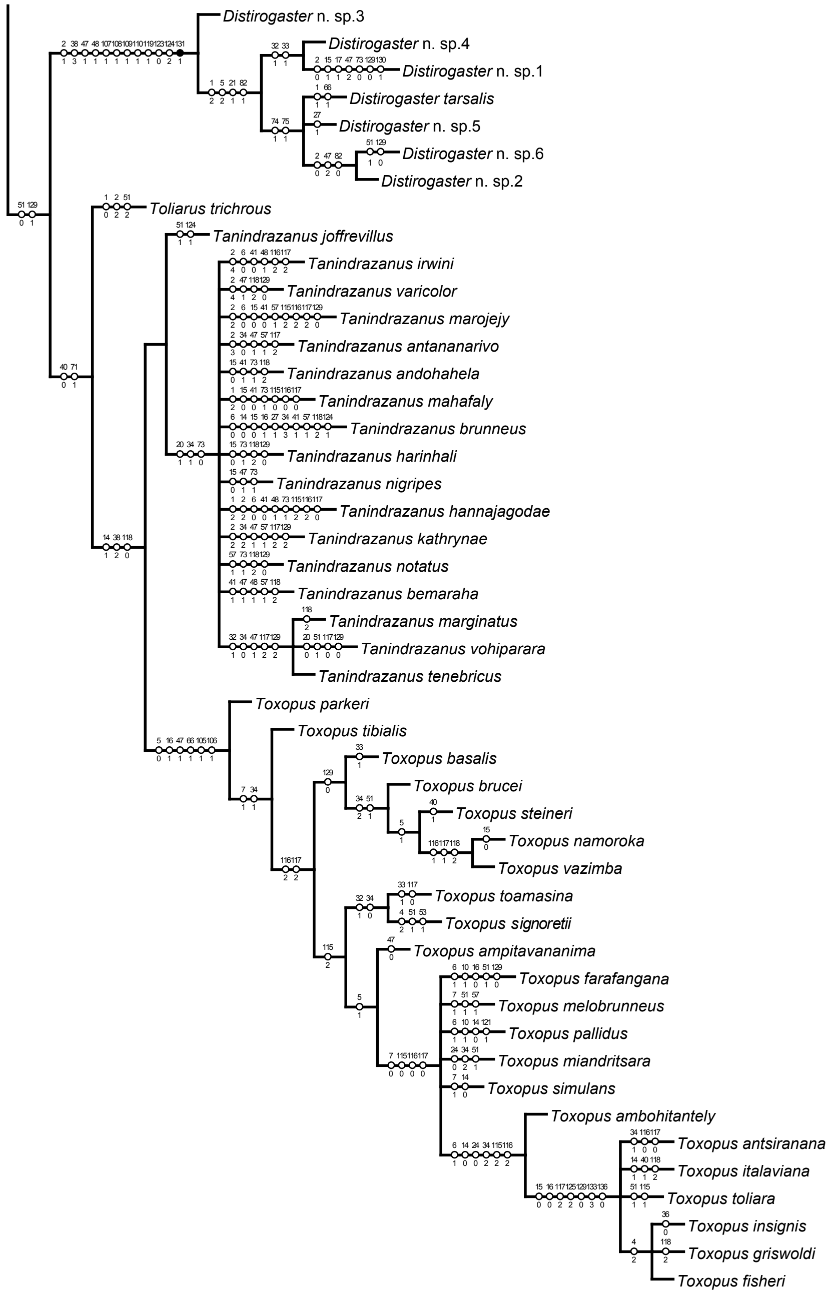
BEGIN SETS;
        CHARSET 18S_G_INS_i_aligned  =  1 -  1024;
        CHARSET 28S_D2_G_INS_i_aligned  =  1025 -  1855;
        CHARSET 28S_D3_5_G_INS_i_aligned  =  1856 -  2628;
        CHARSET COI_G_INS_i_aligned  =  2629 -  3054;

        TAXSET LENGTH_ATLEAST_400  =  1 -  56;
        TAXSET LENGTH_ATLEAST_600  =  1 -  19 21 -  56;
        TAXSET LENGTH_ATLEAST_800  =  1 -  19 21 -  56;
        TAXSET LENGTH_ATLEAST_1000  =  1 -  19 21 -  56;
        TAXSET LENGTH_ATLEAST_1200  =  1 -  19 21 -  50 52 -  56;
        TAXSET LENGTH_ATLEAST_1400  =  1 -  19 21 -  50 52 -  56;
        TAXSET LENGTH_ATLEAST_1600  =  1 -  19 21 -  23 25 -  50 52 -  56;
        TAXSET LENGTH_ATLEAST_2000  =  1 -  4 6 -  8 10 -  19 21 -  22 25 -  35 37 39 -
47 50 52 -  53;
        TAXSET LENGTH_ATLEAST_3000  =  1 17 -  18;
        TAXSET CHARSETS_ATLEAST_4  =  1 3 -  4 6 -  7 10 -  13 16 -  18 21 25 -  30 32 39
-  40 42 45 -  47 50 52;
        TAXSET CHARSETS_ATLEAST_3  =  1 -  19 21 -  22 25 -  50 52 -  53 55 -  56;
        TAXSET CHARSETS_ATLEAST_2  =  1 -  19 21 -  56;
        TAXSET TAXA_HAVING_18S_G_INS_i_aligned  =  1 -  19 21 -  47 50 52 -  54 56;
        TAXSET TAXA_HAVING_28S_D2_G_INS_i_aligned  =  1 -  4 6 -  8 10 -  19 21 -  23
25 -  55;
        TAXSET TAXA_HAVING_28S_D3_5_G_INS_i_aligned  =  1 -  19 21 -  22 24 -  35 37
39 -  50 52 -  53 55 -  56;
        TAXSET TAXA_HAVING_COI_G_INS_i_aligned  =  1 3 -  7 9 -  13 16 -  18 20 -  21
25 -  30 32 36 38 -  40 42 45 -  52 55 -  56;
END;
```

Supplementary material 3.3. Unambiguous character optimizations on the strict consensus tree from parsimony analysis of 110 taxa and a combined morphological and molecular dataset.


Peirates punctorius
Emesaya incisa
Saica sp.
Kiskeyana palassaina
Triatoma recurva
Panstrongylus lignarius
Eratyrus mucronatus
Oncocephalus sp.
Stenopoda sp.
Stenopodessa sp.
Micrauchenus lineola
Apiomerus lanipes
Apiomerus ochropterus
Tribelocephala sp.
Tribelocephala peyrierasi
Opistoplatys sp.1
Opistoplatys sp.2
Racelda sp.
Santosia sp.
Vilius macrops
Cryptonannus n. sp.
nr Daraxa sp.
Brontostoma sanguinosum
Brontostoma colossus
Pothea lugens
Rhiginia aimara
Rhiginia sp.
Rhiginia cinctiventris
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
Microstemmatoides atrocyanea
nr Bannania sp.
Synavecoris dimorphus
Maraenaspis coccinea
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Centraspis ducalis
Maraenaspis bidens
Ectrichodia lucida
Ectrichodia crux
Glymmatophora crassipes
Glymmatophora carolae
Marojejycoris auranticorium
Marojejycoris notadichroa
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Caecina sp.
Gibbosella planiscutum
Gibbosella brunalvus
Gibbosella pallidalata
Gibbosella vangocris
Gibbosella pallidacorium
Gibbosella andasibe
Gibbosella megafrons
Gibbosella betampona
Gibbosella quadocris
Gibbosella mantella
Gibbosella conisimilis
Gibbosella notoconica

Supplementary material 3.3. (Continued).


Distirogaster n. sp.3
Distirogaster n. sp.4
Distirogaster n. sp.1
Distirogaster tarsalis
Distirogaster n. sp.5
Distirogaster n. sp.6
Distirogaster n. sp.2
Toliarus trichrous
Tanindrazanus joffrevillus
Tanindrazanus irwini
Tanindrazanus varicolor
Tanindrazanus marojejy
Tanindrazanus antananarivo
Tanindrazanus andohahela
Tanindrazanus mahafaly
Tanindrazanus brunneus
Tanindrazanus harinhali
Tanindrazanus nigripes
Tanindrazanus hannajagodae
Tanindrazanus kathrynae
Tanindrazanus notatus
Tanindrazanus bemaraha
Tanindrazanus marginatus
Tanindrazanus vohiparara
Tanindrazanus tenebricus
Toxopus parkeri
Toxopus tibialis
Toxopus basalis
Toxopus brucei
Toxopus steineri
Toxopus namoroka
Toxopus vazimba
Toxopus toamasina
Toxopus signoretii
Toxopus ampitavananima
Toxopus farafangana
Toxopus melobrunneus
Toxopus pallidus
Toxopus miandritsara
Toxopus simulans
Toxopus ambohitantely
Toxopus antsiranana
Toxopus italaviana
Toxopus toliara
Toxopus insignis
Toxopus griswoldi
Toxopus fisheri

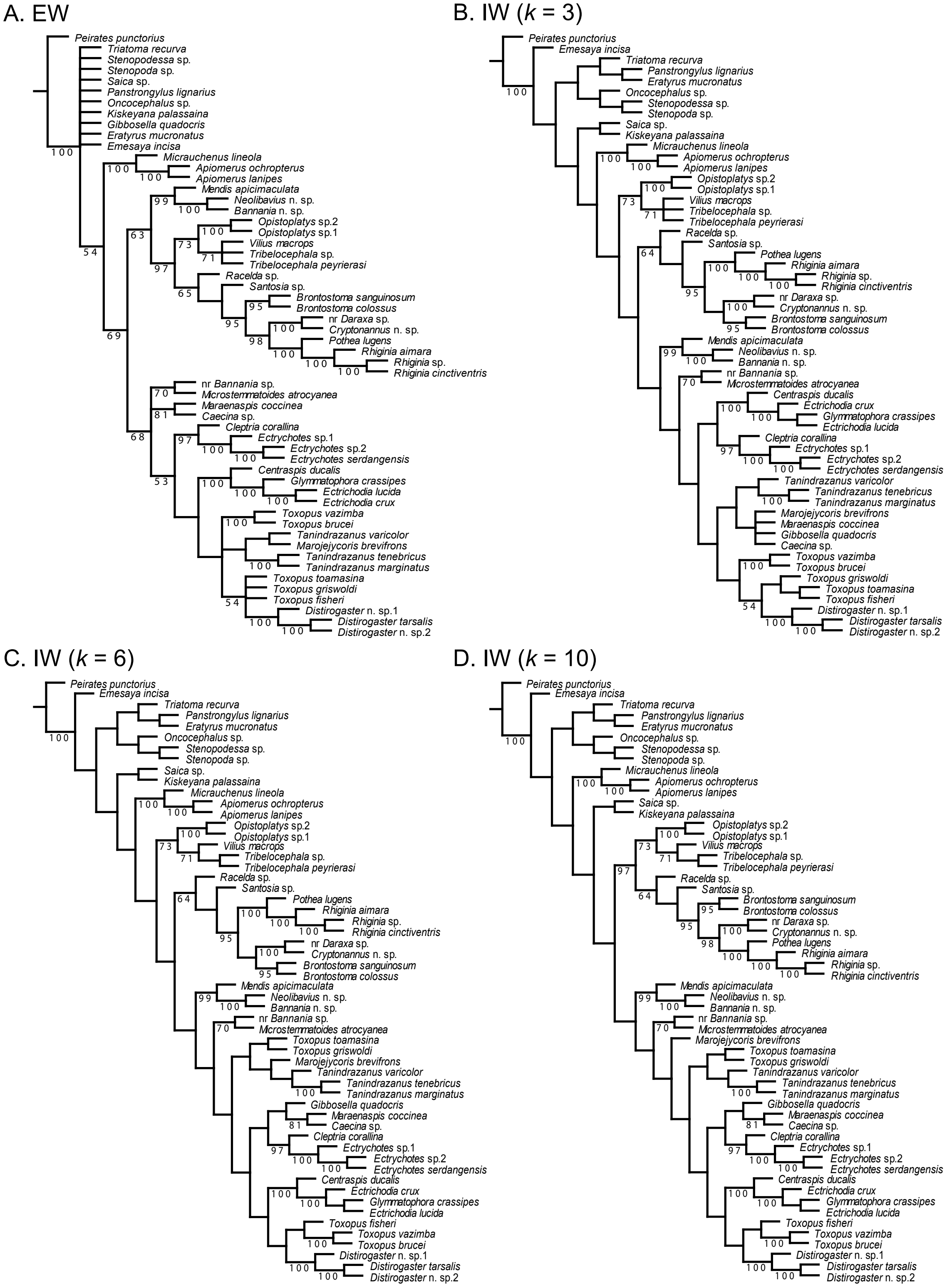
Supplementary Material 3.4. Fossil information and calibration nodes, means, standard deviations (SD) or sigma values, and offsets (in real space).

Fossil taxon	**Locality**	**Taphonomy**	**Age (mya)**	**References**	**Calibration node**	**Mean**	**SD**	**Sigma**	**Offset**
Apicrenus fossilis	Dominican	Amber	15–20	Maldonado et al. (1993); Iturralde-Vinent & MacPhee (1996)	Harpactorinae: Apiomerini	20	0.446		15
Triatoma dominicana	Dominican	Amber	15–20	Poinar (2005); Iturralde-Vinent & MacPhee (1996)	Triatominae	20	0.092		15
				Hwang & Weirauch (2012)	Root	96.85		9.39	
				Hwang & Weirauch (2012)	Ectrichodiinae + Tribelocephalinae	67.47		7.36	

Supplementary material 3.5. DEC and DEC+j time-stratified dispersal rate matrix. N = Neotropical, A = Afrotropical, M = Madagascar, O = Oriental.

Time constraint (mya)	**Rate matrix**				
0–15		N	A	M	O
	N	1.00	0.25	0.10	0.25
	A	0.25	1.00	0.10	0.75
	M	0.10	0.50	1.00	0.25
	O	0.25	0.75	0.50	1.00
15–23		N	A	M	O
	N	1.00	0.25	0.10	0.25
	A	0.25	1.00	0.50	0.75
	M	0.10	0.10	1.00	0.25
	O	0.25	0.75	0.50	1.00
23–34		N	A	M	O
	N	1.00	0.25	0.10	0.25
	A	0.25	1.00	0.50	0.50
	M	0.10	0.10	1.00	0.25
	O	0.25	0.50	0.50	1.00
34–56		N	A	M	O
	N	1.00	0.25	0.10	0.25
	A	0.25	1.00	0.50	0.10
	M	0.10	0.10	1.00	0.25
	O	0.25	0.25	0.50	1.00
56–66		N	A	M	O
	N	1.00	0.25	0.10	0.25
	A	0.25	1.00	0.50	0.25
	M	0.10	0.10	1.00	0.25
	O	0.25	0.25	0.50	1.00

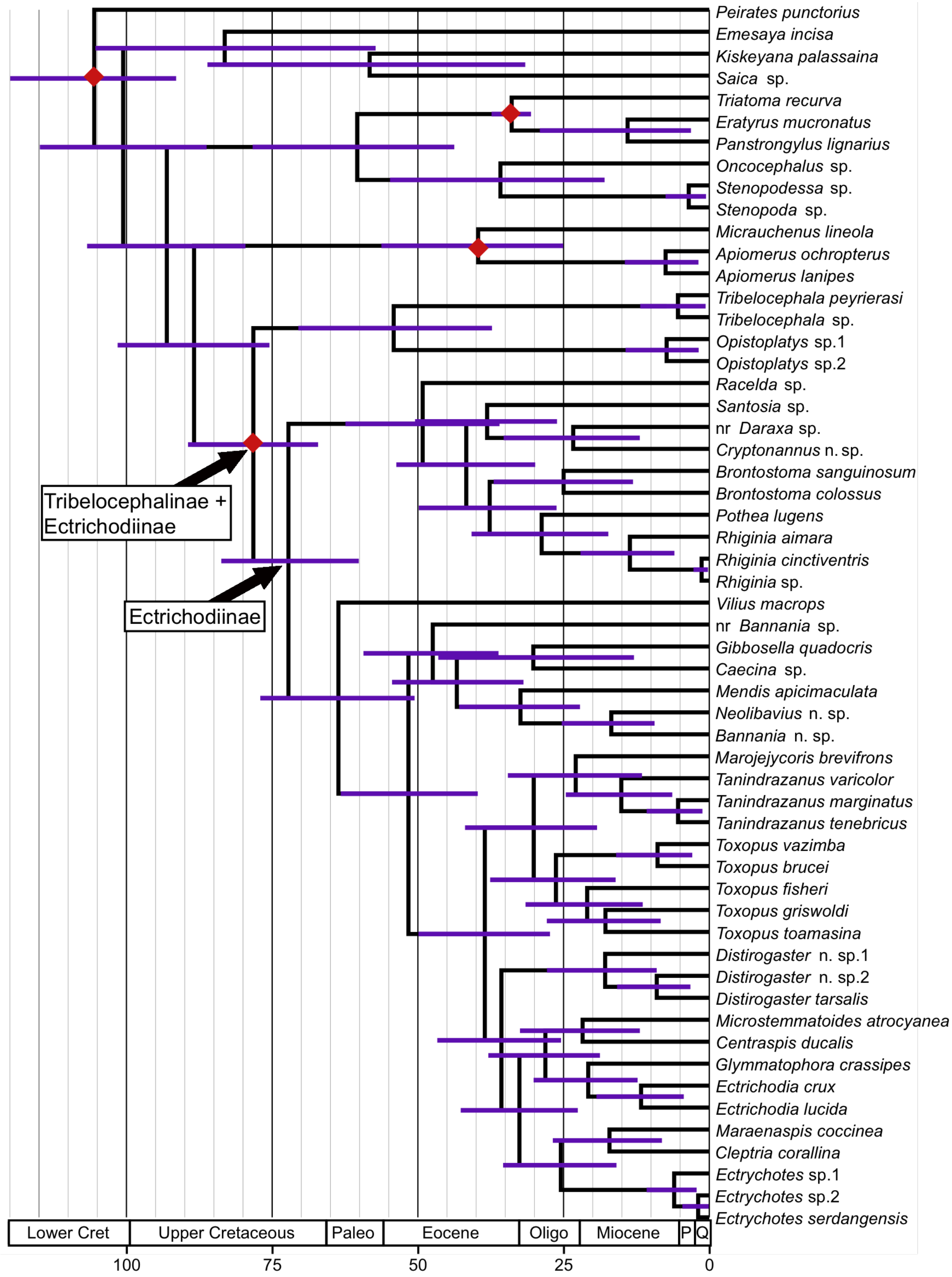
Supplementary material 3.6. Equal (EW) and implied weights (IW) molecular parsimony results for 56 taxa. A. Strict consensus tree from 147 parsimonious trees from an EW analysis (length = 6,232 steps; RI = 0.563; CI = 0.336). B. Strict consensus tree from 3 parsimonious trees from an IW analysis with *k* = 3 (length = 470.59899 steps; RI = 0.560; CI = 0.335). C. & D. Single parsimonious trees from IW analyses when *k* = 6 (C.) (length = 340.36981 steps; RI = 0.560; CI = 0.335) and *k* = 10 (D.) (length = 252.28554 steps; RI = 0.561; CI = 0.336). For A.–D., bootstrap values ≥50 are reported below branches.


A. EW
Peirates punctorius
Triatoma recurva
Stenopodessa sp.
Stenopoda sp.
Saica sp.
Panstrongylus lignarius
Oncocephalus sp.
Kiskeyana palassaina
Gibbosella quadocris
Eratyrus mucronatus
Emesaya incisa
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
Opistoplatys sp.2
Opistoplatys sp.1
Vilius macrops
Tribelocephala sp.
Tribelocephala peyrierasi
Racelda sp.
Santosia sp.
Brontostoma sanguinosum
Brontostoma colossus
nr Daraxa sp.
Cryptonannus n. sp.
Pothea lugens
Rhiginia aimara
Rhiginia sp.
Rhiginia cinctiventris
nr Bannania sp.
Microstemmatoides atrocyanea
Maraenaspis coccinea
Caecina sp.
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia lucida
Ectrichodia crux
Toxopus vazimba
Toxopus brucei
Tanindrazanus varicolor
Marojejycoris brevifrons
Tanindrazanus tenebricus
Tanindrazanus marginatus
Toxopus toamasina
Toxopus griswoldi
Toxopus fisheri
Distirogaster n. sp.1
Distirogaster tarsalis
Distirogaster n. sp.2
B. IW (k = 3)
Peirates punctorius
Emesaya incisa
Triatoma recurva
Panstrongylus lignarius
Eratyrus mucronatus
Oncocephalus sp.
Stenopodessa sp.
Stenopoda sp.
Saica sp.
Kiskeyana palassaina
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Opistoplatys sp.2
Opistoplatys sp.1
Vilius macrops
Tribelocephala sp.
Tribelocephala peyrierasi
Racelda sp.
Santosia sp.
Pothea lugens
Rhiginia aimara
Rhiginia sp.
Rhiginia cinctiventris
nr Daraxa sp.
Cryptonannus n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
nr Bannania sp.
Microstemmatoides atrocyanea
Centraspis ducalis
Ectrichodia crux
Glymmatophora crassipes
Ectrichodia lucida
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Tanindrazanus varicolor
Tanindrazanus tenebricus
Tanindrazanus marginatus
Marojejycoris brevifrons
Maraenaspis coccinea
Gibbosella quadocris
Caecina sp.
Toxopus vazimba
Toxopus brucei
Toxopus griswoldi
Toxopus toamasina
Toxopus fisheri
Distirogaster n. sp.1
Distirogaster tarsalis
Distirogaster n. sp.2
C. IW (k = 6)
Peirates punctorius
Emesaya incisa
Triatoma recurva
Panstrongylus lignarius
Eratyrus mucronatus
Oncocephalus sp.
Stenopodessa sp.
Stenopoda sp.
Saica sp.
Kiskeyana palassaina
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Opistoplatys sp.2
Opistoplatys sp.1
Vilius macrops
Tribelocephala sp.
Tribelocephala peyrierasi
Racelda sp.
Santosia sp.
Pothea lugens
Rhiginia aimara
Rhiginia sp.
Rhiginia cinctiventris
nr Daraxa sp.
Cryptonannus n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
nr Bannania sp.
Microstemmatoides atrocyanea
Toxopus toamasina
Toxopus griswoldi
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus tenebricus
Tanindrazanus marginatus
Gibbosella quadocris
Maraenaspis coccinea
Caecina sp.
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Centraspis ducalis
Ectrichodia crux
Glymmatophora crassipes
Ectrichodia lucida
Toxopus fisheri
Toxopus vazimba
Toxopus brucei
Distirogaster n. sp.1
Distirogaster tarsalis
Distirogaster n. sp.2
D. IW (k = 10)
Peirates punctorius
Emesaya incisa
Triatoma recurva
Panstrongylus lignarius
Eratyrus mucronatus
Oncocephalus sp.
Stenopodessa sp.
Stenopoda sp.
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Saica sp.
Kiskeyana palassaina
Opistoplatys sp.2
Opistoplatys sp.1
Vilius macrops
Tribelocephala sp.
Tribelocephala peyrierasi
Racelda sp.
Santosia sp.
Brontostoma sanguinosum
Brontostoma colossus
nr Daraxa sp.
Cryptonannus n. sp.
Pothea lugens
Rhiginia aimara
Rhiginia sp.
Rhiginia cinctiventris
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
nr Bannania sp.
Microstemmatoides atrocyanea
Marojejycoris brevifrons
Toxopus toamasina
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus tenebricus
Tanindrazanus marginatus
Gibbosella quadocris
Maraenaspis coccinea
Caecina sp.
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Centraspis ducalis
Ectrichodia crux
Glymmatophora crassipes
Ectrichodia lucida
Toxopus fisheri
Toxopus vazimba
Toxopus brucei
Distirogaster n. sp.1
Distirogaster tarsalis
Distirogaster n. sp.2

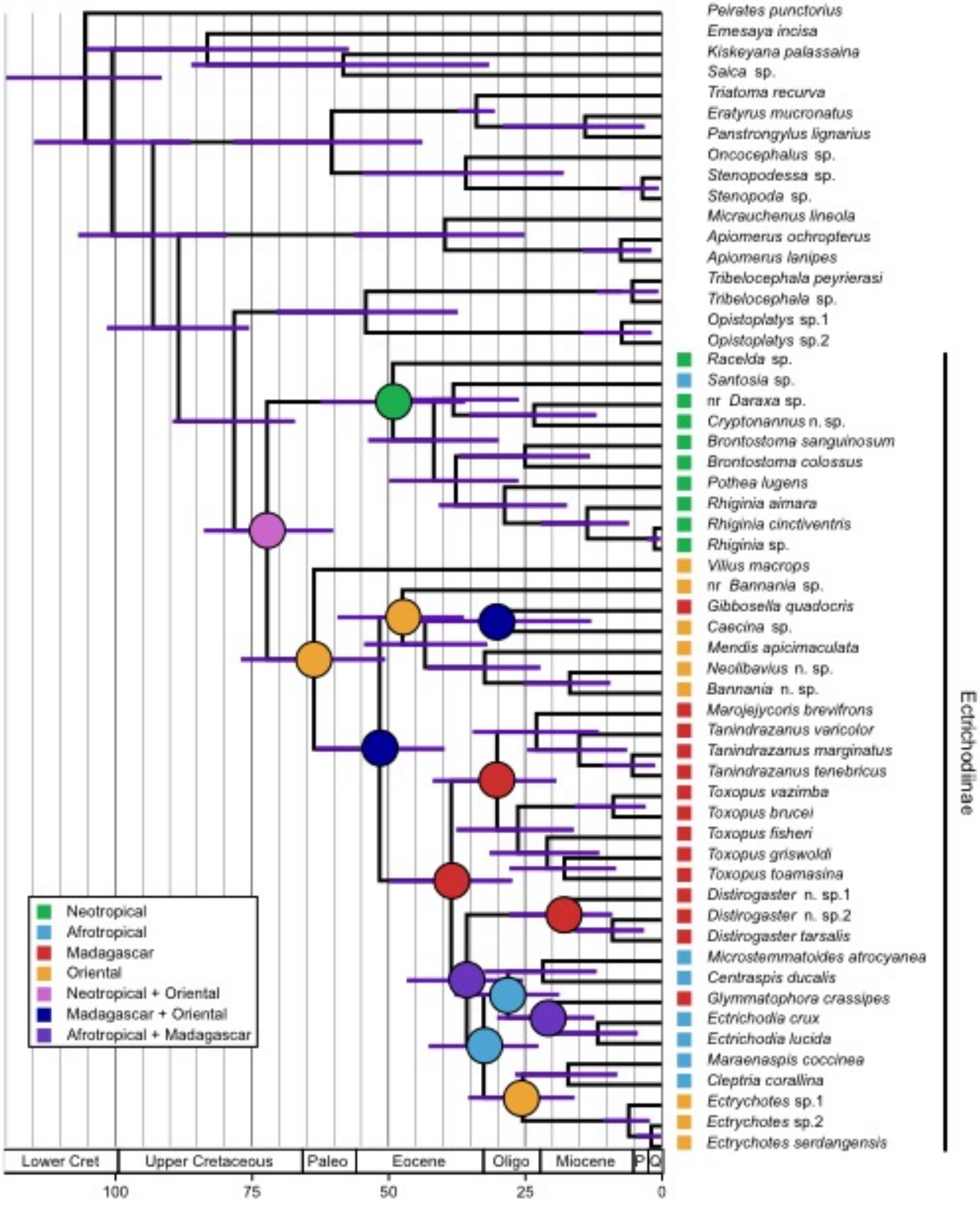
Supplementary material 3.7. Best tree based on ML analysis of 110 taxa, GTR+Γ+I model of sequence evolution for each G-INS-I aligned gene partitions (COI, 18S, 28S D2, 28S D3–D5), and Mkv model of morphological evolution (final Ln = –31,224.182191). Outgroups not shown. Bootstrap values ≥50 are reported below branches.


Maraenaspis bidens
Racelda sp.
nr Daraxa sp.
90
Cryptonannus n. sp.
Santosia sp.
63
72
Brontostoma sanguinosum
96
Brontostoma colossus
Pothea lugens
90
Rhiginia aimara
Rhiginia sp.
100
100
Rhiginia cinctiventris
100
Synavecoris dimorphus
Vilius macrops
Maraenaspis coccinea
51
Cleptria corallina
Ectrychotes sp.2
100
Ectrychotes serdangensis
64
Ectrychotes sp.1
Centraspis ducalis
Microstemmatoides atrocyanea
Glymmatophora carolae
70
Glymmatophora crassipes
91
Ectrichodia lucida
97
Ectrichodia crux
Distirogaster n. sp.3
Distirogaster n. sp.4
87
Distirogaster n. sp.1
100
81
Distirogaster n. sp.5
73
Distirogaster tarsalis
89
Distirogaster n. sp.2
95
Distirogaster n. sp.6
Marojejycoris auranticorium
88
Marojejycoris notadichroa
Marojejycoris brevifrons
Marojejycoris ranomafana
71
Marojejycoris francais
nr Bannania sp.
Caecina sp.
Mendis apicimaculata
68
Neolibavius n. sp.
100
Bannania n. sp.
Gibbosella planiscutum
91
Gibbosella brunalvus
79
Gibbosella pallidalata
67
Gibbosella vangocris
Gibbosella quadocris
Gibbosella megafrons
Gibbosella andasibe
Gibbosella conisimilis
53
Gibbosella notoconica
Gibbosella mantella
Gibbosella pallidacorium
Gibbosella betampona
Toliarus trichrous
Tanindrazanus joffrevillus
Tanindrazanus nigripes
Tanindrazanus bemaraha
Tanindrazanus antananarivo
Tanindrazanus kathrynae
Tanindrazanus tenebricus
Tanindrazanus vohiparara
Tanindrazanus marginatus
Tanindrazanus mahafaly
Tanindrazanus marojejy
51
Tanindrazanus hannajagodae
Tanindrazanus irwini
Tanindrazanus brunneus
Tanindrazanus andohahela
Tanindrazanus harinhali
Tanindrazanus varicolor
Tanindrazanus notatus
Toxopus vazimba
51
Toxopus namoroka
Toxopus steineri
Toxopus signoretii
Toxopus brucei
Toxopus basalis
70
Toxopus griswoldi
Toxopus toliara
Toxopus italaviana
Toxopus antsiranana
Toxopus insignis
58
Toxopus fisheri
Toxopus parkeri
Toxopus tibialis
Toxopus toamasina
Toxopus ampitavananima
Toxopus pallidus
Toxopus simulans
Toxopus melobrunneus
Toxopus farafangana
Toxopus miandritsara
Toxopus ambohitantely
0.2

Supplementary material 3.8. Divergence time estimates based on a BEAST analysis using the ML best tree (Fig. 3.2) and the same molecular dataset (COI, 18S, 28S D2, 28S D3–D5). Each gene partition was assigned an unlinked site model (GTR+Γ+I) and were linked to the same tree model. A linked clock model was assigned to 28S D2 and 28S D3–D5 to reflect their single identity. Three unlinked relaxed lognormal clock models were assigned for 18S, 28S, and COI. Placement of two outgroup fossil and two secondary calibrations are indicated by red diamonds. Purple node bars indicated 95% HPD credibility intervals.


Peirates punctorius
Emesaya incisa
Kiskeyana palassaina
Saica sp.
Triatoma recurva
Eratyrus mucronatus
Panstrongylus lignarius
Oncocephalus sp.
Stenopodessa sp.
Stenopoda sp.
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Tribelocephala peyrierasi
Tribelocephala sp.
Opistoplatys sp.1
Opistoplatys sp.2
Racelda sp.
Santosia sp.
nr Daraxa sp.
Cryptonannus n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Pothea lugens
Rhiginia aimara
Rhiginia cinctiventris
Rhiginia sp.
Vilius macrops
nr Bannania sp.
Gibbosella quadocris
Caecina sp.
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toxopus vazimba
Toxopus brucei
Toxopus fisheri
Toxopus griswoldi
Toxopus toamasina
Distirogaster n. sp.1
Distirogaster n. sp.2
Distirogaster tarsalis
Microstemmatoides atrocyanea
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia crux
Ectrichodia lucida
Maraenaspis coccinea
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Tribelocephalinae +
Ectrichodiinae
Ectrichodiinae
Lower Cret
Upper Cretaceous
Paleo
Eocene
Oligo
Miocene
P
Q
100
75
50
25
0

Supplementary material 3.9. Ancestral range reconstructions from the DIVA model for select nodes. Geographical distributions are color coded according to the legend.



Peirates punctorius
Emesaya incisa
Kiskeyana palassaina
Saica sp.
Triatoma recurva
Eratyrus mucronatus
Panstrongylus lignarius
Oncocephalus sp.
Stenopodessa sp.
Stenopoda sp.
Micrauchenus lineola
Apiomerus ochropterus
Apiomerus lanipes
Tribelocephala peyrierasi
Tribelocephala sp.
Opistoplatys sp.1
Opistoplatys sp.2
Racelda sp.
Santosia sp.
nr Daraxa sp.
Cryptonannus n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Pothea lugens
Rhiginia aimara
Rhiginia cinctiventris
Rhiginia sp.
Villus macrops
nr Bannania sp.
Gibbosella quadocris
Caecina sp.
Mendis apicimaculata
Neolibavius n. sp.
Bannania n. sp.
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toxopus vazimba
Toxopus brucei
Toxopus fisheri
Toxopus griswoldi
Toxopus foamasina
Distirogaster n. sp.1
Distirogaster n. sp.2
Distirogaster tarsalis
Microstemmatoides atrocyanea
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia crux
Ectrichodia lucida
Maraenaspis coccinea
Cleptria corallina
Ectrychotes sp.1
Ectrychotes sp.2
Ectrychotes serdangensis
Ectrichodiinae
Neotropical
Afrotropical
Madagascar
Oriental
Neotropical + Oriental
Madagascar + Oriental
Afrotropical + Madagascar
Lower Cret
Upper Cretaceous
Paleo
Eocene
Oligo
Miocene
P
Q
100
75
50
25
0

Supplementary material 3.10. Discussion of morphological support for major lineages recovered in the combined morphological and molecular phylogenetic analysis.

Phylogenetic hypotheses generated from the combined cladistic analysis are discussed in order of the node labels shown in Fig. 3.3 and with emphasis on Madagascan taxa. Important morphological characters are discussed for selected nodes, with character numbers and states shown in Table 3.2. Results of unambiguous character optimizations on the parsimony consensus tree are shown in SM 3.3. Character support for Madagascan genera has informed taxonomic diagnoses in Forthman et al.'s (in press) monograph.

Monophyly of Ectrichodiinae

The subfamily Ectrichodiinae is recovered as monophyletic and sister to the Tribelocephalinae with high support (BS = 99). Based on unambiguous character optimization, four synapomorphies support Ectrichodiinae monophyly: scutellum with two paramedian apical processes (59–1), metathoracic gland evaporatorium (MGE) present (70–0), carinulate intersegmental suture between sternites II and III (114–1; Fig. 3.3N), and the larger size of dorsal abdominal gland (DAG) III relative to DAGs I and II (144–1). The scutellum is further modified within Ectrichodiinae: an additional medial apical process (59–2) evolved twice independently in *Neolibavius*+*Bannania* (rudimentary in *Bannania*) and *Ectrychotes*, and four (59–3) evolved independently in *Vilius* and *Centraspis*. Twelve homoplasious characters further support the monophyly of millipede assassin bugs (SM 3.3).

Node 1: Neotropical Ectrichodiinae+*Santosia*+*Vilius* clade

A predominately Neotropical clade, including *Santosia* and *Vilius*, is recovered but not supported by any morphological synapomorphies. One terminal taxon, *Racelda* sp., is coded from an apterous female as a result of the inability to identify the species. Thus, the male representative of this taxon is unknown, resulting in some missing morphological data in the matrix. Dougherty (1995) investigated the phylogenetic relationships for 16 New World genera. Her analysis used a ground-plan approach with character polarity determined ad hoc through comparison with other reduviid taxa. Although that analysis excluded Old World Ectrichodiinae, Dougherty hypothesized a non-monophyletic New World based on shared features between Old World taxa and the New World genus *Ectrichodiella* Fracker and Bruner. Our results are congruent with Dougherty's hypothesis in that the New World fauna is not monophyletic in both molecular and combined analyses. However, our results should be tested further with a larger sample of Ectrichodiinae genera, including the genus *Ectrichodiella* from the Greater Antilles.

Node 2: Old World Ectrichodiinae clade

This clade of Afrotropical, Oriental, and Madagascan ectrichodiines receives weak support from six homoplastic characters, e.g., the carinulate intersegmental sutures between sternites III and VI (115–1, 116–1, 117–1) and the medially depressed abdominal sternites (120–1; Fig. 3.3N). In some taxa (e.g., *Tanindrazanus mahafaly* Forthman, Chłond, & Weirauch and *Maraenaspis bidens*), the intersegmental suture carinulation patterns are restricted to lateral areas or are entirely absent. In some species of *Gibbosella* and *Glymmatophora*, the sternites are convex or flat. This clade is further supported by the presence of 6-segmented antennae (38–1), which is further subdivided in many taxa (e.g., 7-segmented as in Fig. 3.3E). The medial region of the endosoma is slightly sclerotized (136–1) in most species, but is membranous (136–0) in some examined species of *Glymmatophora*, *Maraenaspis*, and *Toxopus*.

Node 3: *Maraenaspis+Cleptria+Ectrychotes+Centraspis+Ectrichodia+Glymmatophora* clade

This clade is supported by the presence of small papillae on the fore and mid trochanters (74–1, 75–1) and femora (83–1, 89–1; Fig. 3.3L). Within this clade, the Madagascan species *Maraenaspis bidens* does not form a sister relationship with the Afrotropical *Maraenaspis coccinea*, potentially an artifact of missing data. Sexually static morphological features were inferred from a female of *M. coccinea* since males are currently unknown. Furthermore, the genus may not be monophyletic and, to date, has not undergone thorough taxonomic revision. In our analysis, *M. bidens* is recovered as the sister to *Ectrichodia+Glymmatophora*. This relationship is supported by one synapomorphy: the anterior pronotal lobe is as wide as the posterior lobe (50–1; Fig. 3.3F). The *Maraenaspis bidens+Ectrichodia+Glymmatophora* clade is further supported by four homoplastic characters, such as the ventrolaterally swollen gula produced beyond the ventral head margin (12–2; Fig. 3.3C) (slightly reduced in *Glymmatophora crassipes*), the eye less than half of head height in lateral view (28–0; Fig. 3.3C), the anterior pronotal lobe longer than posterior lobe (59–0; Fig. 3.3F), and the membranous medial endosomal region (136–0). Madagascan species of *Glymmatophora* form a sister group relationship to the Afrotropical *Ectrichodia* species by several homoplastic features and the following synapomorphies: presence of a medial tubercle on the mid femur (88–1; Fig. 3.3L) and an anterior and posterior subapical tubercle on the hind femur (91–1, 92–1; Fig. 3.3L). The Madagascan *Glymmatophora* are recovered as closely related and are supported by one synapomorphic character: the presence of a medial tubercle on the hind femur (94–1; Fig. 3.3L). The medium body size (1–1), longer labial segment II relative to segment III (41–1; e.g., Fig. 3.3D), and flat scutellar disc (63–1) provide additional support for this relationship.

Node 4: *Marojejycoris+Caecina+Gibbosella+Distirogaster+Toliarus+Tanindrazanus+Toxopus* clade

The majority of Madagascan species, including a species of *Caecina* from Thailand, forms a weakly supported clade in our analysis. Two homoplastic characters support this large clade: the depressed postclypeus (13–1; Fig. 3.3B) and a complete transverse suture between the meso- and metasterna (66–0; Fig. 3.3J). Within this clade, the postclypeus is not depressed (13–0; Fig. 3.3A) in *Caecina* sp. and some *Gibbosella* species. Species of *Toxopus*, as well as some *Gibbosella* and *Distirogaster* species, have an incomplete transverse suture (66–1) between the meso- and metasterna.

Node 5: *Marojejycoris+Caecina+Gibbosella* clade

The *Marojejycoris+Caecina+Gibbosella* clade is weakly supported by one homoplasious character, the small body (1–0). The Madagascan genus *Marojejycoris* is highly supported by five homoplastic characters, such as a complete pronotal transverse suture (57–1; Fig. 3.3H), the MGE visible in lateral view (71–1; Fig. 3.3K), the distal part of M not extending beyond the M+Cu junction on the fore wing (104–1; see Fig. 3.3M for 104–0), and the shape of the medial pygophore process (124–1, 125–2). The Madagascan genus *Gibbosella* is recovered as sister to *Caecina* by the distal part of M and Cu basally fused on the fore wing (103–1; Fig. 3.3M) and presence of a posterior tubercle on dorsal laterotergites III–VI (107–1, 108–1, 109–1, 110–1). *Gibbosella* forms a clade supported by an 8-segmented antenna (38–3) (6-segmented in *G. pallidalata* Forthman, Chłond, & Weirauch) and the transversely bicolor dorsal laterotergites

(105–1). Two synapomorphic characters support *Gibbosella*, with the exclusion of *G. planiscutum* Forthman, Chłond, & Weirauch sister to the remaining *Gibbosella*: the long (61–1) and dorsally directed (62–1) paramedian scutellar processes (Fig. 3.3I). The sublateral antennal insertion (24–0; Fig. 3.3C) and lack of carinulae on the intersegmental suture between abdominal sternites VI and VII (118–0) are also optimized as homoplastic along this branch. Some species in *Gibbosella* exhibit a dorsal antennal insertion (24–1; Fig. 3.3D).

Node 6: *Distirogaster*+*Toliarus*+*Tanindrazanus*+*Toxopus* node

Two homoplasious characters are optimized on the branch of this clade: a striated posterior pronotal lobe (51–0) and the basal plate extension as long as the basal plate (129–1). Some taxa within this clade have smooth (51–1) or punctate (51–2) posterior pronotal lobes and a basal plate extension that is shorter (131–0) or longer (131–2) than the basal plate. Within this clade, the Madagascan genus *Distirogaster* is recovered as the sister group to other members of the clade. The presence of denticle-like processes on the dorsal phallothecal sclerite (131–1) is optimized as a synapomorphy of *Distirogaster*. *Distirogaster* is further supported by 11 homoplasious characters: the metallic coloration (2–1), 8-segmented antenna (38–3), relatively small anterolateral pronotal tubercles (47–1; Fig. 3.3G), laterally carinate anterior pronotal lobe (48–1), posterior tubercles on dorsal laterotergites III–VI (107–1, 108–1, 109–1, 110–1), paramedian carinae on abdominal sternites (120–1; Fig. 3.3N), and shape of the medial pygophore process (123–0, 124–2). One species of *Distirogaster* has a reversal to dull coloration (2–0), and large anterolateral projections on the pronotum (47–2; Fig. 3.3F) have evolved twice independently in the genus.

Node 7: *Toliarus+Tanindrazanus+Toxopus* clade

The straight ventral margin of labial segment III (40–0; Fig. 3.3D) and the laterally visible MGE (71–1; Fig. 3.3K) are homoplastic characters optimized on the branch of the Madagascan *Toliarus+Tanindrazanus+Toxopus* clade. However, the ventral margin of labial segment III is convex (42–1; Fig. 3.3C) rather than straight in some *Toxopus* species. The genus *Toliarus* is sister to *Tanindrazanus+Toxopus* and possesses the following homoplastic features: a small body (1–0), red and black coloration (2–2), and a punctate posterior pronotal lobe (51–2).

Node 8: *Tanindrazanus+Toxopus* clade

The broad postclypeal depression (14–1; Fig. 3.3B), 7-segmented antennae (38–2; Fig. 3.3E), and smooth intersegmental suture between sternites VI and VII (118–0) are homoplastic characters supporting this clade. The postclypeal depression is narrowed (14–0) in *Tanindrazanus brunneus* Forthman, Chłond, & Weirauch, *Toxopus namoroka* Forthman, Chłond, & Weirauch, and *Toxopus steineri* Forthman, Chłond, & Weirauch. Approximately half of the examined specimens of *Tanindrazanus harinhali* Forthman, Chłond, & Weirauch have 6-segmented antennae rather than 7; such polymorphism is also observed in individual specimens between the right and left antenna. Although the genus *Tanindrazanus* is not supported by any synapomorphic characters, it is consistently recovered as a clade both molecular and combined analyses. *Toxopus* is supported by six homoplastic features: a head as long as it is wide (5–0), a postclypeal depression extending from the posterior clypeal margin to the interocular sulcus (16–1) as in Fig. 3.3B, the small anterolateral tubercles on the pronotum (47–1; Fig. 3.3G), an incomplete transverse suture between the meso- and metasterna (66–1), the transversely bicolor dorsal laterotergites (105–1), and a laterally expanded dorsal laterotergite II (106–1). In 13 *Toxopus* species, i.e., the clade including *Toxopus ampitavananima* Forthman, Chłond, & Weirauch and

Toxopus fisheri Forthman, Chłond, & Weirauch, the head is longer than wide (5–1). The postclypeal depression only extends to the middle of the synthlipsis (16–0) in *Toxopus farafangana* Forthman, Chłond, & Weirauch and the clade including *Toxopus antsiranana* Forthman, Chłond, & Weirauch and *Toxopus fisheri*. The anteromedial pronotal tubercle is absent (47–0) in *Toxopus ampitavananima*.

Chapter 4: Millipede assassin bugs (Heteroptera: Reduviidae: Ectrichodiinae) show off: evolution of aposematic coloration and extreme sexual dimorphism

Abstract

Aposematic coloration has been shown to be positively association with body size in certain groups of organisms. Amongst the studies using insects as model systems (Lepidoptera; Hemiptera) to investigate this phenomenon, larval or adult gregariousness may have confounded body size. Millipede assassin bugs (Heteroptera: Reduviidae: Ectrichodiinae) display a diversity of color patterns across a range of body sizes, are typically solitary as adults, and are thus an excellent model for investigating a possible correlation. Some species also exhibit drastic sexual dimorphism with major changes in female morphology that has not been explored in a phylogenetic context. Here, a comprehensive phylogeny is constructed for 152 Ectrichodiinae and Tribelocephalinae taxa using morphological and molecular data. Based on the combined maximum likelihood phylogeny, ancestral states for coloration and sexual dimorphism were reconstructed, and phylogenetic logistic regression was employed to test for a coloration-body size correlation. The Ectrichodiinae+Tribelocephalinae ancestor is reconstructed as cryptically colored with limited sexual dimorphism. Multiple origins of aposematic and cryptic coloration and extreme sexual dimorphism are reconstructed. Prevalence of aposematic coloration is positively associated with male body length when regressions are performed on ultrametric trees but not on the phylogram. Thus, our results support the hypothesis that selection on Ectrichodiinae body size may influence evolutionary transitions between aposematic and cryptic coloration. Based on phylogenetic results, we synonymize Tribelocephalinae with Ectrichodiinae, describe three new tribes (Ectrichodiini, Tribelocodiini, and Abelocephalini) and two new subtribes (Opistoplatyina and Tribelocephalina), and revise Tribelocephalini.

Introduction

Scientists have long sought to understand the evolution and diverse functions of the astounding diversity of color patterns observed across the animal kingdom (Protas & Patel, 2008). Although many functions have been proposed, it is evident that coloration can be involved in environmental (e.g., thermoregulation), intraspecific (e.g., sexual selection), and interspecific interactions (e.g., predator evasion) (Areekul & Quicke, 2006; Protas & Patel, 2008). Widespread cryptic coloration allows individuals to conceal themselves in the environmental background. In contrast, some structurally or chemically defended species have evolved conspicuous colors that function as a warning, or aposematic, signal to deter potential predators (Poulton, 1890; Edmunds, 1987) and to enhance predator learning and memorization (see Ruxton et al., 2004; Exnerová et al., 2006). Such color patterns may also occur in undefended species but still afford protection against predators that might perceive the species as aposematic (Nilsson & Forsman, 2003) due to, e.g., Batesian mimicry (Bates, 1862) or innate or learned predator aversion (e.g., Smith, 1975; Guilford, 1988). Traditionally, aposematic coloration has been characterized by a combination of black with red, orange, yellow, or white (Cott, 1940; Fabricant et al., 2014). Some studies suggest that metallic or iridescent patterns may also function in aposematic signaling alone or by enhancing traditional aposematic colors (e.g., Arrow, 1951; Schultz, 2001; Fabricant et al., 2014).

Studies on aposematic coloration are prevalent but often restricted to a microevolutionary scale (Härlin & Härlin, 2003; Stevens, 2015). Comparably fewer investigations have studied aposematic coloration in a phylogenetic context, e.g., in poison dart frogs (Anura: Dendrobatidae) (e.g., Hagman & Forsman, 2003; Rudh, 2013), mammals (Stankowich et al., 2011), and holometabolous insects (e.g., Vogler & Kelley, 1998; Sagegami-Oba et al., 2007; Bocakova et al., 2016). Some of these microevolutionary and phylogenetic studies have suggested a positive relationship between the prevalence or conspicuousness of aposematic coloration and body size in poison dart frogs (Hagman & Forsman, 2003; Rudh, 2013), milkweed bugs (Insecta: Hemiptera: Lygaeidae) (Gamberale & Tullberg, 1996a, 1998), and butterflies and moths (Insecta: Lepidoptera) (Tullberg & Hunter, 1996). In insects, experimental studies by Gamberale & Tullberg (1996a, 1998) concluded that predator aversion increases with larger aposematically colored instars and larger aggregations of *Tropidothorax leucopterus* (Goeze), 1778 (Insecta: Hemiptera: Lygaeidae). Other experimental studies have also shown that nymphal aggregations of the aposematically colored *Spilostethus pandurus* (Scopoli), 1763, (Insecta: Hemiptera: Lygaeidae) result in higher predator aversion (Gamberale & Tullberg, 1996b). Only one phylogenetic comparative study based on independent contrasts concluded that larval gregariousness in Lepidoptera is correlated with aposematic coloration (Tullberg & Hunter, 1996). However, Nilsson & Forsman's (2003) comparative study of 578 moth species (Insecta: Lepidoptera) found no significant difference in larval body size between cryptic and aposematically colored species. Instead, they concluded that an association between coloration and gregarious lifestyles may have confounded their results since transitions to gregariousness were correlated with decreasing larval body length. A study on nudibranchs found a different trend: the prevalence of aposematic coloration decreases as body size increases and may be due to marine habitats (i.e., light environment and visual system of predators), diet, or habitat homogeneity (Cheney et al., 2014).

Insects are excellent models for studying aposematic coloration in an evolutionary context due to their morphological, behavioral, and ecological diversity. However, the two studies that have used phylogenetic comparative methods to explore the relationship between aposematic coloration and body size were restricted to Lepidoptera that exhibit larval gregariousness (Tullberg & Hunter, 1996; Nilsson & Forsman, 2003). These studies have employed phylogenetic independent contrasts (Felsenstein, 1985) to analyze correlations between characters, a method that is unable to adequately model categorical trait evolution without treating it as continuous "dummy" variables (Ives & Garland, 2010). Phylogenetic comparative studies on aposematic coloration and body size in insects have failed to embrace more recently developed approaches that resolves this issue, e.g., phylogenetic logistic regression (PLR; Ives & Garland, 2010).

The predominantly circumtropical millipede assassin bugs (Heteroptera: Reduviidae: Ectrichodiinae) are likely the largest group of specialized millipede predators with 736 species in 121 genera (Maldonado, 1990; Dougherty, 1995; Carpintero & Maldonado, 1996; Forthman & Weirauch, 2012; Gil-Santana, 2015; Forthman et al., in press). Although adult millipede assassin bugs are typically solitary, communal predatory behaviors occur in some species; out of 32 reports of adult predatory behavior, eight have documented an adult engaging in communal predation with conspecific nymphs and two with conspecific adults (see Forthman & Weirauch, 2012; unpublished data). Aside from communal predatory strategies, aggregations have not been observed, although immatures may be in close proximity to an adult female (pers. obs.). Furthermore, these insects show a remarkable diversity of color patterns: cryptic coloration, traditional aposematic coloration, uniform metallic colors, or a combination of aposematic and metallic patterns. The conspicuous color patterns observed in many millipede assassin bugs may serve an aposematic function. A study on a *Ectrichodia* sp. (Peschke et al., 2002) and our personal observations with *Centraspis ducalis* Distant, 1902, confirm that these brightly colored species emit chemical defenses from the metathoracic glands. In addition, Dougherty (1995) suggested that some species may belong to a Müllerian mimicry complex with species in other genera. Furthermore, Forthman & Weirauch (2012), as well as additional unpublished data, show that at least 20 species of Ectrichodiinae prey on chemically defended millipedes and suggest future investigations into the ability of this predatory group to sequester secondary metabolites from prey. However, no experimental study has been performed to confirm the hypothesis that conspicuous colors in millipede assassin bugs are an aposematic signal. Regardless, we have referred to these conspicuous patterns as aposematic coloration (i.e., red, yellow, orange, white, black, and/or metallic features).

Some of the smallest and largest species across Ectrichodiinae are either cryptically colored (e.g., *Ectrichodiella* Fracker & Bruner, 1924 [3–5 mm]; *Gibbosella* Chłond, 2010 [5–10 mm]; *Distirogaster* Horváth, 1914 [16–30 mm]; *Xenorhyncocoris* Miller, 1938 [32–37 mm]) or aposematic (e.g., *Antiopuloides* Miller, 1952 [10 mm]; *Schuhella* Dougherty, 1995 [6 mm]; *Centraspis* Schaum, 1862 [25–40 mm]; *Philodoxus* Horváth, 1914 [32–35 mm]). This preliminary observation suggests that coloration and body size may not be correlated in this clade, but this has not been tested in a phylogenetic comparative framework. Given the size of the group and diversity of color forms across a range of body sizes, millipede assassin bugs present an opportunity to explore, for the first time, the evolution of coloration and its association with body length in a non-holometabolous group of specialized predatory insects that are typically solitary as adults.

In addition to the diversity of color patterns, millipede assassin bugs exhibit sexual dimorphism (Fig. 4.1) that ranges from slight morphological differences between males and females in, e.g., body size, wing development, and eye and ocellar size, to extreme cases in which wing reduction is associated with drastic modifications to the female head, thoracic, and/or leg morphology. For species where data was available for both sexes from the literature and/or examined specimens (~200 spp.), females are always larger in size and have reduced antennal setation compared to males. Furthermore, approximately half of these species exhibit some wing reduction in the females when compared to males, which is variable within some species (i.e., pterygopolymorphism; e.g., some *Brontostoma* spp.) (Dougherty, 1995; pers. obs.).

Pterygopolymorphism may also be observed in both sexes in some Old World species (e.g., some *Glymmatophora* spp.), which can make associations between different morphs difficult. Other differences may be observed on the female's head, including reduced depressions and striations, a more pronounced gula, and a shorter scape, among other features. Thoracic morphology in females can include a shorter posterior pronotal lobe and/or a longer and wider anterior lobe, a reduction of sutures and depressions, or a weakly-developed scutellum. Females may further possess modified legs, e.g., stouter forefemora, a larger fossula spongiosa, and tubercles and papillae that may be absent in conspecific males. While any of these differences may occur in species that exhibit limited or extreme sexual dimorphism, a combination of the overall abundance and severity of morphological differences characterizes how extreme sexual dimorphism may appear. Approximately 80% of Ectrichodiinae species for which both sexes are known are, here, assigned to a limited condition, in which a few minor morphological differences are restricted to some structures or body regions (Fig. 4.1). The remainder of species are, here, considered to display extreme sexual dimorphism (e.g., *Racelda* spp., *Distirogaster* spp., *Rhysostethus glabellus* Hsiao, 1973) due to drastic morphological differences in almost every major body region (Fig. 4.1). Such extreme differences often pose significant difficulties in associating sexes when using morphology alone (Zhang & Weirauch, 2011; Forthman et al., in press) and males and females have sometimes been described as different species and even different genera (e.g., Rédei et al., 2012).

Extreme sexual dimorphism is also known to occur in a few other Reduviidae subfamilies: Harpactorinae (some *Zelus* spp.; Hart, 1972), Peiratinae (*Bekilya* genus group; Zhang & Weirauch, 2011), Emesinae (e.g., some *Bergemesa* spp., *Collartida oculata* Villiers, 1949; Wygodzinsky, 1966), and Stenopodainae (e.g., *Pseudobaebius* spp.; Villiers, 1948; Giacchi, 1987). With the possible exception of Emesinae, extreme sexual dimorphism in these subfamilies does not appear to be as prevalent as in Ectrichodiinae, and its origins have not been investigated using ancestral state reconstruction methods (ASRs). Extreme sexual dimorphism in other groups of insects (e.g., Coleoptera: Elateriformia; Bocakova et al., 2007; Kundrata & Bocak, 2011) has been shown to have evolved multiple times from a limited condition, with few or no reversals. Thus, extreme sexual dimorphism may result in convergent female morphology between unrelated taxa (Bocakova et al., 2007; Kundrata & Bocak, 2011). As such, evolutionary transitions between limited and extreme sexual dimorphism should be explored in Ectrichodiinae to determine if the extreme condition evolved more than once.

Comprehensive phylogenetic hypotheses using molecular and morphological data are currently unavailable for Ectrichodiinae, impeding evolutionary investigations of coloration and sexual dimorphism. Few Ectrichodiinae have been incorporated in recent phylogenic analyses of Reduviidae (Weirauch, 2008; Weirauch & Munro, 2009; Weirauch, 2010; Hwang & Weirauch, 2012; Zhang et al., 2016), with the exception of a larger analysis on Madagascan Ectrichodiinae (Forthman & Weirauch, in press). These studies support a clade formed by Ectrichodiinae and Tribelocephalinae, a small subfamily (~130 species, 16 genera; Maldonado, 1990; Weirauch, 2010) of mostly cryptically colored species that often display little sexual dimorphism. Although some of these studies support the monophyly of Ectrichodiinae, others found Ectrichodiinae to be paraphyletic with respect to Tribelocephalinae (Weirauch & Munro, 2009; Weirauch, 2010, Forthman & Weirauch, in press). Thus, relationships between Ectrichodiinae and Tribelocephalinae have remained unresolved. To investigate the evolution of coloration and sexual dimorphism, a resolved, well-supported phylogeny based on molecular and morphological data for a larger sample of Ectrichodiinae and Tribelocephalinae taxa is crucial.

Here, we reconstruct the most comprehensive phylogeny of Ectrichodiinae and Tribelocephalinae to date, using separate and combined morphological and molecular analyses to test the monophyly of both subfamilies. The resulting phylogenetic framework is used to investigate the evolution of coloration and sexual dimorphism with ASR methods. We predict that 1) the last common ancestor of Ectrichodiinae and Tribelocephalinae was cryptic and exhibited limited sexual dimorphism, 2) aposematic coloration evolved from cryptic coloration multiple times as seen in other groups of animals (e.g., Santos et al., 2003; Bocakova et al., 2016), and 3) extreme sexual dimorphism has evolved multiple times with very few reversals to a limited condition. A phylogenetic comparative analysis is also conducted to test our prediction that there is no significant relationship between the prevalence of aposematic coloration and male body length. Based on our phylogenetic results, we revise the Ectrichodiinae+Tribelocephalinae higher-level classification to reflect morphologically diagnosable clades recovered in the phylogeny.

Material and methods

Taxon sampling

To investigate the evolution of coloration and sexual dimorphism, taxa were selected to include all major color patterns and sexually dimorphic conditions across differently-sized species of Ectrichodiinae and Tribelocephalinae. In total, 156 terminal taxa were examined and comprise 138 Ectrichodiinae, 14 Tribelocephalinae, and four outgroup species belonging to other Reduviidae subfamilies. The morphological character matrix is based on male specimens, where possible, to minimize the effect of sexually dimorphic character states on phylogenetic reconstruction. However, 28 taxa are represented by females because: 1) some represent mono- or ditypic female-based genera (e.g., *Borgmeierina* Wygodzinsky, 1949, *Antiopuloides*) that may be females of male-based species classified in other genera (e.g., *Daraxa* Stål, 1859, *Caloundranius* Miller, 1957), 2) inclusion of female-based genera (e.g., *Schuhella*) permits assignment of undescribed males into existing genera for future taxonomic description, and 3) inclusion also permits assignment of undescribed females into existing genera (e.g., *Tribelocodia* Weirauch, 2010, *Neoscadra* Miller, 1941, *Katanga* Schouteden, 1903) for future taxonomic work. Of these 28 female-based terminal taxa, male morphology for 12 female-based terminals were coded based on taxonomic descriptions, digital images, and/or examination of specimens at the British Natural History Museum, London, United Kingdom and/or the American Museum of Natural History, New York, USA (see table in Supplementary Material [SM] 4.1). A total of 16 terminals lack information on male morphology because the males remain unknown or the species could not be determined. Despite the possibility for extreme sexual dimorphism in these 16 terminals, we follow Forthman & Weirauch (in press) and infer male morphological characters that are likely static among males and females (e.g., antennal segmentation, relative lengths of labial segments, scutellar apical processes, etc.) based on known patterns of sexual dimorphism among congenerics across Ectrichodiinae and Tribelocephalinae.

Specimens examined for this study are deposited in the following institutions: **AM**, Australian Museum, Sydney, Australia; **AMNH**, American Museum of Natural History, New York, USA; **ANIC**, Australian National Insect Collection, Canberra, Australia; **BMNH**, Natural History Museum, London, United Kingdom; **BPBM**, Bernice P. Bishop Museum, Hawaii, USA; **CAS**, California Academy of Sciences, California, USA; **CNC**, Canadian National Collection of Insects, Ontario, Canada; **DEI**, Deutsches Entomologisches Institute, Müncheberg, Germany; **FCAP**, Universidade Federal do Pará, Pará, Brazil; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **MRAC**, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; **MTEC**, Montana State University, Montana, USA; **QM**, Queensland Museum, Brisbane, Australia; **SAMC**, South Africa Museum, Cape Town, South Africa; **SU**, Department of Zoology, University of Silesia, Poland; **UCR**, University of California, Riverside Entomological

Research Museum, California, USA; **USNM**, National Museum of Natural History, Washington D.C., USA.

Morphological methods and data

External morphology was examined using Nikon SMZ1000 and SMZ1500 dissecting microscopes. Mandibular and maxillary stylets and genitalia were dissected from a subset of taxa and examined under a Zeiss Axioscope compound light microscope and Nikon SMZ1000 and SMZ 1500 microscopes, respectively. For phylogenetic analyses, 168 morphological characters were coded in the Descriptive Language for Taxonomy program (Dallwitz, 1980; Dallwitz et al., 1999) using morphological matrices modified from Weirauch (2008, 2010) and Forthman & Weirauch (in press). Additionally, 30 female characters were coded for species in which specimens of both sexes were available or described in taxonomic publications to investigate patterns of sexually dimorphic characters within terminal taxa. One sexual dimorphism and two coloration characters were also coded for ASR and male body lengths for phylogenetic comparative analyses. All morphological characters and character states used in this study are given in Table 4.1. The morphological matrix is provided in SM 4.2. Morphological terminology follows Dougherty (1995), Weirauch (2008), Forero & Weirauch (2012), Hill (2014), and Forthman & Weirauch (in press).

Molecular methods and data

Six gene regions (16S rDNA, 18S rDNA, 28S D2 rDNA, 28S D3–D5, rDNA, COI, Wingless [Wg]) were sampled for 59 taxa (47 Ectrichodiinae, nine Tribelocephalinae, three outgroups) (Table 4.2). For some taxa, sequence data were acquired from GenBank, which were contributed by Weirauch & Munro (2009), Hwang & Weirauch (2012), and Forthman &

Weirauch (in press). Molecular vouchers were associated with an ethanol specimen collection number (RCW prefix), as well as a unique specimen identifier (USI) label to link it with specimen information in the Planetary Biodiversity Inventory Arthropod Easy Capture database (http://www.research.amnh.org/pbi/locality/index.php) and Heteroptera Species Pages (http://research.amnh.org/pbi/heteropteraspeciespage/). All USI labels include an AMNH_PBI or UCR_ENT prefix followed by an 8-digit number.

DNA extraction was performed by removing a hind leg and following QIAGEN DNeasy Blood and Tissue Kit protocols. Extracted legs were card mounted and associated with their respective specimens. For new sequences, PCR was performed using either GE Healthcare Life Sciences PuReTaq-Ready-To-Go-PCR-Beads or EmeraldAmp GT PCR Master Mix and Fisher Scientific or BioRad T100 Thermal Cyclers with the protocols listed in SM 4.3. Primer sequences for 16S (16Sa, 16Sb), 18S (18SF, 18SR), and 28S D3–D5 (D3Fa, D5Ra) were taken from Weirauch & Munro (2009); 28S D2 (D2Fa, D2Ra) from Forero et al. (2013); COI (C1-J-2183F) from Simon et al. (1994) and (C1-N-2609R) from Damgaard & Sperling (2000); and Wg (Wg 1A) from Cryan et al. (2001) and (Wg DelR1) from Urban & Cryan (2007). Amplification was assessed using gel electrophoresis with SyberSafe gel stain and a UV illuminator. PCR products were cleaned using Bioline SureClean and sequenced at Macrogen USA (Sanger sequencing) or on an Applied Biosystems 3730xl DNA Sequencer at UCR’s Institute for Integrative Genome Biology. Sequences were assembled and edited in Sequencher v4.8 and are available on GenBank (Table 4.2).

Each gene region was independently aligned in MAFFT (Katoh & Standley, 2013) using the G-INS-i algorithm. Gene regions were concatenated in SequenceMatrix v1.7.8. (Vaidya et al., 2011) and exported with external gaps coded as question marks (matrix provided in SM 4.4). The best partition scheme and models of sequence evolution were determined using the greedy algorithm and Bayesian information criterion for model selection in PartitionFinder v1.1.1 (Lanfear et al., 2012). Each ribosomal gene was treated as a separate subset in the data blocks, while COI and Wg were subdivided into separate codon positions. The resulting partition scheme and models are: *Partition 1*: 16S, 28S D2, and 28S D3–D5 (GTR+Γ+I); *Partition 2*: 18S, COI codon positions 1 and 2, Wg (GTR+Γ+I); and *Partition 3*: COI codon position 3 (HKY+Γ+I).

Phylogenetic analyses

Morphological and molecular datasets were concatenated using Mesquite v3.04 (Maddison & Maddison, 2015). Separate and combined morphological and molecular phylogenetic analyses were performed using parsimony (TNT v1.1; Goloboff et al., 2008), maximum likelihood (ML) (GARLI v2.01; Zwickl, 2006), and Bayesian inference (MrBayes v3.2.6; Ronquist et al., 2012) optimality criteria. For the morphological and combined phylogenetic analyses, the first 168 morphological characters in Table 4.1 were used. Unless otherwise stated, parameter settings for a given program were used for all three datasets.

All datasets were subjected to equal weights (EW) parsimony analysis using New Technology search, but the combined dataset was also analyzed using implied weights (IW) due to poor phylogenetic resolution from the EW analysis. Internal gaps in the molecular data were treated as fifth state and external gaps as missing data. Prior to analysis, 2,661 uninformative molecular characters were inactivated. Although there is no clear criterion for choosing a particular *k*-value and the optimal *k*-value is probably matrix dependent, we used three concavity constant (*k*) values for IW analysis (3.000000 [default], 4.266835, and 18.980060) with the latter two based on calculations for average character fit at 58% and 86%. We selected these average character fit values because they encompass a range of *k*-values shown to produce results with the highest similarity to the preferred tree based on various measures of performance (see Reemer &

Ståhls, 2013). Default settings for sectorial search, drift, and tree fusing were used, the initial driven search level was set at 100 and checked every 3 hits, the initial addition sequences set to 14, find minimum length set to 100 times, and the random seed set to 4,325. Standard bootstrap resampling with absolute frequencies was conducted with 500 replicates and New Technology search (initial driven search = 38, check level every 3 hits, initial addition sequences = 7, find minimum length 10 times).

The ML analyses were conducted using the best partition scheme and models of molecular evolution determined by PartitionFinder and the Mkv model of morphological evolution (Lewis, 2001). A total of 50 search replicates were performed using random starting trees for each dataset. Non-parametric BS analyses were performed for 500 iterations with the termination condition reduced from 20,000 to 10,000 as recommended in the GARLI manual (Zwickl, 2008).

Bayesian analyses used the same partition scheme and models of molecular and morphological evolution as in our ML analyses. Two simultaneous runs of 20 million generations were carried out with four Markov Chain Monte Carlo (MCMC) chains each. Parameters and trees were sampled every 20,000 generations with the first 25% discarded as burn-in. Stationarity was assessed by the average standard deviation of split frequencies (<0.01 for molecular and morphology only datasets; <0.03 for combined dataset) and the potential scale reduction factor (~1.0 for all datasets). Each chain was also assessed for convergence in Tracer v1.6 (Rambaut et al., 2014) and possessed combined ESS values >200 in for each parameter after burn-in. The majority-rule consensus tree was generated from the sample of post-burn-in trees.

Ancestral state reconstructions: aposematic coloration and extreme sexual dimorphism

For ASR analyses, the combined ML phylogram was used for the following reasons: 1) a phylogeny with branch lengths is needed for the statistical approaches used, 2) is more resolved than the Bayesian majority rule consensus tree, and 3) all three phylogenetic approaches recovered similar higher-level relationships. Traditionally, ultrametric trees have been preferred for ASRs as phenotypic change is expected to be related to the amount of time elapsed rather than molecular rates of change along a branch (Bromham et al., 2002; Litsios & Salamin, 2012; Cusimano & Renner, 2014). However, some studies have shown correlations between molecular branch lengths and phenotypic evolution (e.g., Omland, 1997; Smith & Donoghue, 2008); if this is the case, then inferring ASRs on time-calibrated phylogenies could produce inaccurate results as it may not appropriately represent the evolution of the species traits (Litsios & Salamin, 2012). Recently, Litsios & Salamin (2012) and Cusimano & Renner (2014) have studied the effects of time-calibrated versus molecular branch lengths on ASRs of continuous and discrete characters, respectively. Based on these studies, there is no consensus regarding whether ultrametric trees or phylograms produce greater accuracy in ASRs.

Given the potential for branch-length effects on ASRs, we estimated ancestral states on our combined ML phylogram and ultrametric trees. We followed a similar approach to the one implemented by Litsios & Salamin (2012) to transform the phylogram into three ultrametric trees using penalized likelihood in r8s v1.70 (Sanderson, 2002, 2003) under the Powell algorithm and different penalties: parametric estimation (penalty = 0), penalty on rate change (penalty = 10), and global molecular clock (penalty = 10,000). Ultrametric trees had a fixed length of 13.53 to match the length of the phylogram. Outgroup taxa were subsequently pruned from all trees in Mesquite. Although the ML phylogram is completely resolved, the r8s program collapsed eight of the very small, non-zero branch lengths in the generated ultrametric trees. Despite this, we used these trees as generated for ASR since 1) most were near the terminals, 2) all but one were within clades in which terminals had the same state, and 3) we did not expect major differences with regards to the reconstructions of these nodes on the phylogram.

Coloration was treated as categorical data based on the rankings made by five observers independent of the project: cryptic, traditional aposematic, uniform metallic, and aposematic and metallic. Each observer was presented with the same insect specimens, habitus images, and when available, images of individuals in natural habitat. In four cases where a majority opinion was not achieved, ties were broken by the senior author's assignments made prior to surveying the observers. In our first ASR dataset, coloration was coded as (0) cryptic or (1) aposematic, uniform metallic, or aposematic and metallic (character 198). Since some studies suggest uniform metallic appearances may serve a cryptic function (e.g., Parker, 1998; Thomas et al., 2007), we alternatively coded coloration as (0) cryptic or uniform metallic or (1) aposematic or aposematic and metallic (character 199). Sexual dimorphism (character 200) was also investigated, and was coded as either (0) limited or (1) extreme based on the severity and number of differences (≥6 for extreme condition) observed between sexes. Some taxa, e.g., *Glymmatophora aeniceps* Horváth, 1914, and *G. dejoncki* Schouteden, 1919, exhibit different morphs within males and/or females; when paired with similar morphs, this species will appear to have little sexual dimorphism, but will appear extremely sexually dimorphic when paired with different morphs. As such, we code these terminals as polymorphic for both conditions.

Mesquite was used for parsimony ASR by tracing characters on the combined ML phylogram, while BayesTraits v2 (Pagel et al., 2004) MultiState was used with ML and MCMC approaches on the phylogram and ultrametric trees. For the ML approach, 1,000 iterations were performed with rate parameters free or equal, followed by likelihood ratio tests (LTR) to compare the two models; we report ASR results based on restricted rates ($p > 0.09$, $df = 1$). Under the Bayesian framework, a hyperprior on an exponential distribution drawn from a uniform distribution (interval between 0 and 10) was used. Twenty million generations were conducted with sampling every 2,000 generations and the first 25% of generations discarded as burn-in under a free rates and equal rates model. Acceptance rates were between 0.2–0.4. Bayes Factors (BF) were calculated to compare results under the free and equal rates models; we report ASR results based on restricted rates (BF < 2). Tracer v1.6 was used to obtain the mean state value for each node, with ESS values >200 for all nodes reconstructed.

Phylogenetic comparative approaches: aposematic coloration and male body length

To examine the relationship between a binary dependent trait (i.e., coloration) and a continuous independent trait (i.e., body length) in a phylogenetic context, PLR with Firth correction was implemented using PLogReg.m (Ives & Garland, 2010) in MATLAB R2015b. This approach uses a two-state Markov process to model the evolution of the dependent trait along a phylogeny and estimate the strength of phylogenetic signal. Subsequently, the independent trait influences the dependent trait, with the evolutionary rate no longer dependent on phylogenetic signal but on the independent trait's regression coefficient (Ives & Garland, 2010).

The combined ML phylogram and ultrametric trees discussed in the previous section were pruned to exclude 23 terminals lacking male body length data and converted to phylogenetic variance-covariance matrices using the PDAP package in Mesquite (Midford et al., 2009). The two coloration datasets for ASR analyses were used to test if increases in male body length were associated with increased prevalence of aposematic coloration. When possible, average male body lengths were measured from the clypeal apex to the posterior margin of the abdomen for up to five specimens per species following Forthman & Weirauch (in press). When male specimens were not available, male body length was determined from taxonomic descriptions; if a range of lengths was provided, the average of the minimum and maximum lengths was used. Prior to analysis, log-transformed male body length was standardized to have a mean equal to zero and standard deviation equal to one following the recommendation of Ives & Garland (2010). A BS procedure was used for 2,500 replicates to generate confidence intervals and test for statistical significance of the regressions. In all but one case, some replicates failed to converge. Removal of non-converged replicates resulted in slightly different parameter and confidence interval values, which are reported with estimates based on converged and non-converged replicates together.

Results

Ectrichodiinae+Tribelocephalinae phylogenetics

Results of the separate molecular and morphological analyses are given in SM 4.5–4.7. We report the ML best tree for our combined dataset in Fig. 4.2, with parsimony and Bayesian results in SM 4.8–4.10. Tribelocephalinae monophyly is not supported in all of our phylogenetic analyses, with the phylogenetic position of *Xenocaucus* China & Usinger, 1949, among the recovered Tribelocephalinae lineages being uncertain. Ectrichodiinae monophyly is also not supported, except in the molecular ML and Bayesian analyses (BS <50 and 92, SM 4.5B and C, respectively).

Molecular analyses (SM 4.5) recovered at least three Tribelocephalinae lineages with low to high support: *Tribelocephala+Opistoplatys*, *Afrodecius+Abelocephala*, and *Tribelocodia*. In our molecular parsimony analysis (SM 4.5A), *Tribelocephala+Opistoplatys* is the sister group to an Old World+New World clade ("Green clade") of Ectrichodiinae with moderate support, while molecular ML and Bayesian analyses (SM 4.5B and C, respectively) recover *Tribelocephala+Opistoplatys* as sister to Ectrichodiinae with weak to high support. In the latter analyses, two major Ectrichodiinae clades are recovered with moderate to high support: the Green clade and an Old World clade ("Orange clade").

Our morphological parsimony result (SM 4.6) is congruent with our molecular results with respect to the Tribelocephalinae lineages recovered: *Tribelocephala+Centrogastocoris+*

Opistoplatys, *Megapocaucus+Apocaucus+Afrodecius +Abelocephala*, and *Tribelocodia*. However, ML and Bayesian analyses (SM 4.7A and B, respectively) support a paraphyletic Tribelocephalinae with respect to the Ectrichodiinae genus *Ectrichodiella*. *Ectrichodiella* is recovered as the sister group to *Tribelocodia* in all morphological analyses with moderate to high support. The Green and Orange clades are not supported in our morphological analyses, with the exception of a monophyletic Green clade that is weakly supported in our ML phylogeny; our Bayesian analysis recovered a large polytomy near the base of the remaining Ectrichodiinae.

Higher-level relationships between our combined EW and IW (k = 18.980060) parsimony (SM 4.8A and 4.9B, respectively), ML (Fig. 4.2), and Bayesian (SM 4.10) phylogenetic results are largely congruent. The same Tribelocephalinae lineages from the morphological parsimony and molecular results are recovered, with *Ectrichodiella* as the sister group to *Tribelocodia*. The *Tribelocephala+Centrogastocoris+Opistoplatys* clade is weakly supported as the sister group to the remaining Ectrichodiinae, with the exception of our Bayesian phylogeny (unresolved polytomy at the root). In our other IW parsimony analyses (SM 4.8B, 4.9A), *Tribelocodia* is not monophyletic; *Tribelocodia* sp. is sister to *Xenocaucus*, while *T. ashei* Weirauch, 2010, is sister to *Ectrichodiella*. In the IW (k = 3.000000) parsimony tree (SM 4.8B), *Tribelocephala+ Centrogastocoris+Opistoplatys* is sister to *Megapocaucus+Apocaucus+Abelocephala* with poor support, while *Afrodecius* is weakly supported as the sister group to Ectrichodiinae+*Tribelocodia ashei*. In contrast, *Afrodecius+Abelocephala* is poorly supported as the sister group to *Tribelocephala+ Centrogastocoris+Opistoplatys* in the IW (k = 4.266835) analysis, which together are sister to *Megapocaucus+Apocaucus*. This larger Tribelocephalinae clade is weakly supported as the sister group to Ectrichodiinae+*Tribelocodia ashei*. With the exclusion of *Ectrichodiella*, the remaining Ectrichodiinae form a monophyletic group with weak to high support in all combined phylogenies. The Orange clade was recovered in all phylogenetic analyses with low to high support, while the Green clade was recovered in all but the IW phylogenies (paraphyletic with respect to the Orange clade).

Evolution of aposematic coloration: ASR and phylogenetic comparative analyses

We report the result of our ML ASR based on the phylogram when treating cryptic coloration as a separate character from all other color patterns (color character 198; Fig. 4.3). The Ectrichodiinae+Tribelocephalinae ancestor is reconstructed as cryptically colored, with aposematic coloration evolving early in the phylogeny (clade including *Tribelocephala* sp. and *Glymmatophora aeniceps*). There are at least 15 reversals to cryptic coloration, as well as seven additional gains of aposematic coloration (eight total independent origins). In general, parsimony reconstructions (SM 4.11) are highly congruent with the highest probability reconstructions on the phylogram near the tips but are more ambiguous at deeper nodes (at least five gains of aposematic coloration, at least eight reversals to cryptic coloration). Our ML reconstructions on ultrametric trees (SM 4.12) are similar to those based on our phylogram with several exceptions. First, while there is no change with respect to the highest probable state for many nodes, some show significantly more or less probability in their reconstructions than reported in our phylogram (clades indicated by pair of taxa contained within): *Katanga–Cimbus*, *Synavecoris–Cimbus*, *Microstemmatoides–Cimbus*, *Tanindrazanus varicolor–Tanindrazanus tenebricus*, *Tanindrazanus–Marojejycoris*, *Distirogaster–Glymmatophora*, *Cryptonannus–Schottus*, and *Afrodecius–Glymmatophora*. At three nodes, the highest probable state is opposite of that in ML phylogram reconstruction: *Toliarus–Marojejycoris*, *Adrania gracilis–Adrania cylindrica*, and *Scadra–Neoscadra*. Five additional nodes have ambiguous reconstructions in our ultrametric trees compared to the phylogram: *Distirogaster* n. sp.–*Distirogaster tarsalis*, nr. *Neolibavius–Bannania*, *Pseudopothea–Jorgcoris*, *Daraxa ambrosettii–Daraxa* sp., and *Neoscadra ornata–*

Neoscadra annulicornis. The MCMC reconstructions on the phylogram and ultrametric trees are highly similar to ML reconstructions (SM 4.12). Results of our PLRs on ultrametric trees indicate that prevalence of aposematic coloration is associated with larger male body length ($p<0.05$; Table 4.3). However, while the regression coefficient is significantly different from zero for PLR on the phylogram ($p=0.0005$), the bootstrap mean is not ($p=0.4456$).

Results of ASRs when treating cryptic coloration and uniform metallic coloration as one character, with all other color patterns as a second state (color character 199), are given in SM 4.13–4.15. All analyses reconstruct a cryptically colored ancestor and support the early evolution of aposematic coloration. Parsimony reconstructions (SM 4.13) are also congruent with ML reconstructions near the tips of the phylogram (SM 4.14) but are more ambiguous at deeper nodes; at least five gains of aposematic coloration and six reversals to cryptic coloration are reconstructed. Based on ML reconstructions on the phylogram, there are at least seven independent origins of aposematic coloration and 18 reversals to cryptic coloration. ML reconstructions on ultrametric trees (SM 4.15) are largely similar to those of the phylogram. We observed similar patterns for some, but not all, of the nodes in which differences are observed between the phylogram and ultrametric trees in our ASR analysis on color character 198. Additionally, one node is ambiguous (*Haematorrhophus linnaei–Haematorrhophus pedestris*), and three have the same highest probability state but show significant changes in probability (*Centraspis–Philodoxus*, *Centraspis–Glymmatophora*, *Microstemmatoides–Glymmatophora*). The MCMC reconstructions are similar to ML reconstructions (SM 4.15). The PLRs on the phylogram and ultrametric trees for this color character resulted in the same trends observed in with the other color character (SM 4.16).

Evolution of extreme sexual dimorphism

Despite the amount of missing data, ML ASR reconstructs limited sexual dimorphism as the ancestral state of Ectrichodiinae+ Tribelocephalinae based on the phylogram (Fig. 4.4). At least seven independent transitions of extreme sexual dimorphism from a limited condition is supported. Only one reversal to limited sexual dimorphism is reconstructed at the node containing *Xenocaucus* and *Ectrichodiella*. These results are supported by parsimony-based ASR (with exception of no reversals; SM 4.17), ML reconstructions on ultrametric trees (SM 4.18), and MCMC reconstructions (SM 4.18).

Plotting sexually dimorphic characters at the terminals reveals that taxa exhibiting only limited sexual dimorphism are generally characterized by one to three minor changes. These morphological differences often include a reduction in the female's eye, wing development (brachypterous, micropterous, or apterous), and associated changes in pronotal lobe lengths. Other taxa may exhibit minor differences in other pronotal features, as well as leg and abdominal features. However, in all cases, the presence or absence of the ocellar lens, postclypeal surface, presence or absence of the antennal shield, anterior pronotal width, scapus length, and presence or absence of paramedian abdominal sternal carinae do not differ between sexes. One species, *Haematorrhophus linnaei* (Stål), 1859, was coded as having a limited condition despite the fact that five morphological differences were observed. Females of this species can be easily associated to males despite aptery and an enlarged anterior pronotal lobe. Color patterns are not reduced between sexes in *Haematorrhophus* species, and head and abdominal structures in *H. linnaei* are similar in males and females. Males of this species also possess a relatively large anterior pronotal lobe that is nearly subequal to the posterior lobe, and the pronotal depression and sutures are retained in the females.

Taxa exhibiting only extreme sexual dimorphism tend to have at least six drastic differences between sexes. In these species, the extreme condition is often characterized by apterous females, with drastic changes in pronotal dimensions, or more often, the dimensions of the pronotal lobes. Eyes are generally reduced or completely lacking (e.g., *Xenocaucus*). If ocelli are present in males, these are drastically reduced or absent in the females. In a number of taxa, males have a depressed postclypeus and well-developed paramedian scutellar processes (e.g., *Distirogaster*), but females exhibit a flat postclypeus and weakly-developed scutellar processes. Females may also have increased leg armature (tubercles and/or papillae) and reduced abdominal features.

Two of the four *Glymmatophora* species we included have data on dimorphic males and/or dimorphic females. Based on a survey of the literature for *Glymmatophora* species exhibiting dimorphism within a sex, macropterous morphs have ocelli, small eyes, a flat postclypeus, an antennal shield, a scapus surpassing the apex of the head, an anterior pronotal lobe that is slightly shorter than or subequal to the posterior lobe, a wider posterior pronotal lobe relative to the anterior lobe, thoracic depressions and sutures, well-developed scutellar processes, no small tubercles on the legs but may have papillae, and no paramedian carinae on the abdominal sternites. Micropterous morphs have no or small ocelli, small eyes, a flat postclypeus, an antennal shield, a scapus surpassing the apex of the head, an anterior pronotal lobe that is longer than and as wide as the posterior lobe, reduced thoracic depressions and sutures, weakly-developed scutellar processes, no small tubercles on the legs but often with papillae, and no paramedian carinae on the abdominal sternites. Despite these morphological patterns, we did not code for all of these structures for *G. dejoncki* and *G. aeniceps*, as one representative for each species was available and the taxonomic descriptions sparse in detail (particularly for *G. aeniceps*). However, we still coded both taxa as polymorphic for limited and extreme conditions based on known patterns observed in *Glymmatophora*: males and females of the same morph are very similar patterns observed in *Glymmatophora*: males and females of the same morph are very similar morphologically, but drastic differences between morphs can make associations between sexes of a species difficult.

Discussion

Evolution of aposematic coloration and its association with body length

Based on our results, the ancestor of Ectrichodiinae+Tribelocephalinae exhibited cryptic coloration, with aposematic coloration evolving in the ancestor of *Tribelocephala*+ *Centrogastocoris*+*Opistoplatys*+Ectrichodiinae (excluding *Ectrichodiella*). Our results also support multiple subsequent origins of aposematic coloration from cryptically colored ancestors within this clade, which is an evolutionary pattern observed in other insect groups (e.g., Lepidoptera, Tullberg & Hunter, 1996; Cleroidea, Bocakova et al. 2016) and vertebrates (e.g., Dendrobatidae, Santos et al., 2003; Vences et al., 2003). Our PLR analyses using ultrametric trees for both coloration datasets support the hypothesis that increasing prevalence of aposematic coloration is associated with increasing body size, which is congruent with other phylogenetic comparative studies in poison dart frogs (Hagman & Forsman, 2003; Rudh, 2013). Only one phylogenetic comparative study concluded that larval gregariousness in Lepidoptera is correlated with aposematic coloration (Tullberg & Hunter, 1996). Thus, these studies have suggested an interplay between body size or size of the signal (i.e., aggregation size) and aposematic coloration. Based on these and other experimental studies, it has been hypothesized that species that recently acquired aposematic coloration are under selection for a larger body size (Forsman & Merilaita, 1999; Hagman & Forsman, 2003). Alternatively, a large body size may impair the effectiveness of cryptic coloration, and, thus, aposematic coloration may evolve more easily in already large species (Hagman & Forsman, 2003). While we did not test for either hypothesis, our positive coloration-body size relationship is congruent with both of them.

Although PLR results based on our phylogram estimated regression coefficients significantly different from zero, parametric bootstrapping resulted in non-significance. For this approach, the parametric bootstrap procedure is currently the best approach to assess the quality of the parameter estimates (Ives & Garland, 2010, 2014), and studies employing this method base their conclusions from the significance of the bootstrap mean. Thus, in our case, there is no association between aposematic coloration and male body length when PLRs are performed on our phylogram. This result may be an artifact of the methodological approach of PLR on phylogenies with non-contemporaneous tips. The PLC approach of Ives & Garland (2010) standardizes tip-to-tip distances for non-contemporaneous trees. However, even if two tips are phylogenetically related (e.g., species A and species B), the standardization procedure may result in one tip being nearest to another less closely related tip (species A and species C) (Ives & Garland, 2010). Only one other phylogenetic comparative study on Lepidoptera larvae has failed to find support for a coloration-body size relationship (Nilsson & Forsman, 2003), which may have been confounded by the association between gregariousness and smaller larval body size and adult wing span.

Other phylogenetic comparative studies in poison dart frogs have shown associations between the prevalence or conspicuousness of aposematic coloration and other traits. Santos et al. (2003) found support for an apparent association with diet specialization (ants, termites, and mites) despite a lack of dietary information for most species. Summers & Clough (2001) found that a positive relationship with toxicity, which is supported by some microevolutionary studies at the species scale (e.g., Maan & Cummings, 2012). Such associations may also occur in millipede assassin bugs given their apparent predatory specialization and chemical defensiveness. However, a lack of dietary and toxicity data for a significant number of species currently hinders any testing of these hypotheses, although many of the identified millipede-feeding species and genera in Forthman & Weirauch (2012), as well as unpublished images, display aposematic coloration.

Multiple transitions from limited to extreme sexual dimorphism

Our study confirms that extreme sexual dimorphism has evolved multiple times from a limited condition throughout the Tribelocephalinae+Ectrichodiinae phylogeny. Based on our results and observations of other species, extreme sexual dimorphism is apparent in taxa that have macropterous males and apterous or some micropterous females (e.g., *Xenocaucus*, *Toxopus*, *Distirogaster*). Compared to males, females generally show drastic reductions in a number of head, thoracic, and abdominal features, while anterior pronotal lobe enlargement and additional leg armature is observed. Given the convergence of these characters in distantly related taxa, we caution the use of female characters in phylogenetic reconstruction and taxonomic decisions, especially for known or potentially extremely dimorphic species. Other phylogenetic studies on cantharoid and elateroid beetles (Bocakova et al., 2007; Bocak et al., 2008; Kundrata & Bocak, 2011) have reached the same conclusions; previous higher-level classifications in these groups were primarily based on characters that are shown to be highly homoplasious among lineages with neotenic females (Bocakova et al., 2007; Kundrata & Bocak, 2011).

Although there is missing data for many species, we are aware of genera in which described or putative macropterous male-based and micropterous or apterous female-based species are observed. For example, both described species of *Apocaucus* Distant, 1909, are known from macropterous males. We have examined apterous females of this genus that exhibit morphological reductions in the head and thorax, which suggests the possibility of extreme sexual dimorphism in these species. These females may be individuals belonging to one of the described species, but we are unable to assign them based on morphology alone. Thus, other sources of data, e.g., molecular and distributional data, would be needed to confirm conspecificity. Similar situations have been personally observed in, e.g., *Tribelocodia*, *Lyramna* Breddin, 1900, and many other species of *Gibbosella*. Previous taxonomic works have also demonstrated the difficulty of extreme sexual dimorphism in associating males and females; e.g., *Parascadra breuningi* Kerzhner & Günther, 2004, was described from a micropterous female specimen that was later shown to be a female of *Rhysostehus glabellus* males (Rédei et al., 2012). We suspect that similar taxonomic issues are more widespread in Ectrichodiinae given that over half of the genera are monotypic and based on one or few individuals of a single sex; this may even extend to many species within genera.

Wing reduction and/or extreme sexual dimorphism in females has been observed in many other insect orders (e.g., Diptera, Disney, 1996; Phasmatodea, Whiting et al., 2003; Strepsiptera, Kathirithamby, 1989), and hypotheses have been proposed to explain the evolution of this phenomenon. One hypothesis posits that a reduction in wings and other morphological features permits reallocation of resources to increased fecundity in females and/or reduce the age of first reproduction (Darwin, 1859; Roff, 1986; Denno et al., 1989; Roff & Fairbairn, 1991). A second, compatible hypothesis is that these species are under less selection pressure to maintain dispersive flight capabilities in stable environments (Slater, 1977; see Roff, 1990). Non-macropterous morphs of millipede assassin bugs are commonly observed in stable leaf litter microhabitats compared to macropterous morphs that fly in open vegetation (Dougherty, 1995; pers. obs.). However, experimental evidence on allocation trade-offs between flight and reproduction are lacking in this group. Regardless, trade-offs between the production of morphological features for dispersive flight and increased reproduction and the role of stable habitats are plausible hypotheses to explain the evolution of wing reduction and extreme sexual dimorphism in Ectrichodiinae and Tribelocephalinae. Another hypothesis states that flight capabilities are reduced in taxa that occupy isolated habitats (e.g., oceanic islands, caves, mountaintops), since dispersers are likely to experience higher risks of mortality (Darwin, 1859; Wagner & Leibherr, 1992). Under this hypothesis, we would expect both sexes in a species to exhibit the same wing and associated morphological reductions (i.e., limited sexual dimorphism), which is observed in some Ectrichodiinae species (e.g., *Maraenaspis* Karsch, 1892, *Haematorrhophus* Stål, 1874). However, for species in which only brachypterous to apterous forms are known, it is possible that macropterous forms exist (e.g., *Glymmatophora*) but remain to be discovered. With respect to other species, the isolation hypothesis would not explain why there is sex-specific morphological reductions.

Phylogenetics and reclassification of Ectrichodiinae and Tribelocephalinae

Previous Reduviidae systematic investigations support a close relationship of Ectrichodiinae with Tribelocephalinae. Although these two subfamilies have drastically distinct habitus, Weirauch (2008, 2010) recovered several synapomorphies supporting this clade: e.g., numerous transverse ridges on the mandibular stylets, lamellate processes on the right maxillary stylet, subdivision of the antennal flagellomeres, and extremely short female external genitalia, among others. However, the monophyly of neither subfamily has been firmly established from previous studies. Weirauch & Munro's (2009) molecular cladistic analyses recovered a monophyletic Ectrichodiinae, with the exception of one analysis supporting paraphyly with respect to the single included Tribelocephalinae representative. Weirauch's (2010) morphological parsimony analysis supported Ectrichodiinae monophyly in half of the parsimonious trees, but *Ectrichodiella minima* (Valdés), 1910 was recovered as the sister group to the Tribelocephalinae in the remaining trees.

Our separate and combined morphological and molecular phylogenetic results based on a larger sample of Ectrichodiinae and Tribelocephalinae taxa supports the non-monophyly of both analyses, with some discordance with our morphology only results. As such, we use the results of our combined morphological and molecular ML phylogenetic results to reclassify the Ectrichodiinae+Tribelocephalinae higher-level relationships into diagnosable monophyletic groups (Fig. 4.5). We refrain from revising the tribe Xenocaucini or re-assigning *Xenocaucus* to another tribe due to the uncertain phylogenetic position of this genus in on our analyses. Unambiguous character optimizations were examined on the combined ML topology in WinClada v1.00.08 (Nixon, 2002) to inform diagnoses (Fig. 4.5). Diagnoses and descriptions are primarily based on male characters.

Taxonomy

Ectrichodiinae Amyot & Serville, 1843

Fig. 4.5A–T

Ectrichodiinae Amyot & Serville, 1843, 1: 342.

Tribelocephalinae Stål, 1865, 3: 44. New synonymy.

Type genus: *Ectrichodia* Lepeletier & Serville, 1825

REVISED DIAGNOSIS: This subfamily is recognized by the subdivided antennal basi- and/or distiflagellomeres making the antennae appear 5–8-segmented (Fig. 4.5D) (4-segmented in *Schottus* Distant, 1902, *Schuhella* Dougherty, 1995, *Tribelocodia*, *Vilius* Stål, 1863, and *Zirta* Stål, 1859), longer and denser vestiture on the scapus and pedicellus in males (Fig. 4.5D), more than 35 external transverse ridges on the mandibular stylet (47–1; Fig. 4.5F), lamellate ventral processes on the right maxillary stylet interiorly (49–0; Fig. 4.5G) (toothlike in *Vilius*), a medially depressed scutellar disc (83–1; Fig. 4.5K) (flat in some genera, e.g., *Abelocephala* Maldonado, 1996, *Glymmatophora*, and *Haematorrhophus*), and a globular forecoxa (94–0; Fig. 4.5L). Females have short, platelike external genitalia.

REDESCRIPTION: **MALE:** STRUCTURE: HEAD: Short or elongate, variably shaped; scapus and pedicellus with long, dense, erect to semi-erect setae; antennal flagellomeres 5- to 8-segmented with the exception of 4-segmented antenna in *Schottus*, *Schuhella*, *Tribelocodia*, *Vilius*, and *Zirta*; labium with three visible segments (segments II–IV; segment I reduced); mandibular stylet with more than 35 transverse ridges on external surface; right maxillary stylet with interior lamellate ventral processes (toothlike in *Vilius*). THORAX: Scutellar disc medially depressed; globular coxae; tarsi 3-segmented (2-segmented in *Xenocaucus*; 1-segmented and fused to tibia in *Tribelocodia*); hemelytron with two to three membranal cells (one in *Quinssyana funeralis* Distant, 1913). ABDOMEN: Dorsal laterotergites separated from mediotergites by membrane; ventral laterotergites separated from mediosternites by membrane (except segment II in Ectrichodiini, new tribe); mediosternites fused.

DISCUSSION: A taxonomic history of Ectrichodiinae prior to our study is provided by Dougherty (1995). No tribal classification has been previously proposed for this subfamily. Prior to our phylogenetic results and reclassification, Ectrichodiinae was diagnosed by the following features: subdivided basi- and/or distiflagellomeres, making the antennae appear more than 4-segmented; presence of ventral and dorsal processes on the left maxillary stylet; bifurcated scutellum; hemelytral membrane with two or three cells; fossula spongiosa on foretibia, as well as midtibia in many species; absence of the ventral connexival suture on abdominal sternite II; Brindley's gland and associated evaporatorium present, and three dorsal abdominal glands (DAGs) with DAG III ostioles larger than those of DAGs I and II.

The Tribelocephalinae was first recognized as a subfamily of Reduviidae by Stål (1865) and was subsequently divided by Villiers (1943) into two tribes based on venation patterns of the hemelytron: Opistoplatyini and Tribelocephalini. A third tribe, Xenocaucini, was later erected by Maldonado (1996) for the female-based genus *Xenocaucus* characterized by a number of unique features among Tribelocephalinae. Species of Tribelocephalinae have been characterized by less globular eyes, a long first visible labial segment, the strongly bent scapo-pedicellar articulation, the very small corium compared to the large membranous area of the hemelytron, and the presence of dense vestiture that included trichomes with a bulbous base and thin, curved apex. All species of the subfamily lack ocelli, with the exception of *Tribelocodia*.

As mentioned, previous phylogenetic results have provided consistent support for the Ectrichodiinae+Tribelocephalinae clade, with some of the morphological synapomorphies from these studies (Weirauch 2008, 2010) supported by our results. However, the monophyly of both subfamilies remained doubtful, and our phylogenetic results confirm their non-monophyly. As such, we synonymize Tribelocephalinae with Ectrichodiinae, erect three new tribes and two subtribes, and revise the tribe Tribelocephalini. We also include Xenocaucini as a tribe in Ectrichodiinae. In addition to the characters listed in the diagnosis, our character optimizations recovered additional synapomorphies: very dense vestiture with bulbous hairs present on the integument (absent in the Ectrichodiini), eye more than one-half of the head height (reduced in many apterous species or in females), pedicellus ventrally inserted on scapus so that pedicellus and flagellomeres point posteriorly (absent in the Ectrichodiini), pronotum wider than long (exceptions observed in a number of taxa), anterior pronotal lobe shorter than the posterior lobe (exceptions observed in a number of taxa, particularly in individuals with reduced wings), and lateral depression present on the posterior pronotal lobe (absent in some apterous individuals).

Tribelocodiini, new tribe

Fig. 4.5I, N, Q, S

Type genus: *Tribelocodia* Weirauch, 2010

DIAGNOSIS: This tribe is diagnosed by the narrow postocular shape in dorsal view (14–0); presence of ocelli (22–1; Fig. 4.5B); pedicellus ventrally inserted on scapus so that pedicellus and flagellomeres point posteriorly (38–1; Fig. 4.5C); pronotal transverse furrow laterally divided by elevated cuticle (69–1; Fig. 4.5I), which is distinctly ridgelike in some *Ectrichodiella* species; posteriolateral margin of pronotum surpassing medial pronotal margin (71–1; Fig. 4.5I); scutellum with paramedian scutellar processes and a well-developed medial process (75–1, 80–1; Fig. 4.5I); small tubercles uniformly covering the trochanters, femora, and tibiae (97–1, 101–1, 108–1, 113–1, 117–1, 124–1, 129–1, 131–1, 138–1; Fig. 4.5Q); tibiae lacking fossula spongiosa; and proximal parts of M and Cu of forewing forming one vein (143–1; Fig. 4.5N).

DESCRIPTION: **MALE:** STRUCTURE: HEAD: Clypeus without anterior process; postocular narrow in dorsal view; eye reniform with concave posterior margin; ocelli present; pedicellus ventrally inserted on scapus so that pedicellus and flagellomeres point posteriorly; pedicellus moderately to strongly curved; basiflagellomere 1-segmented; constriction between postocular region and neck; labrum sclerotized. THORAX: Pronotum with transverse furrow subdivided by laterally elevated cuticle, ridgelike in *Ectrichodiella*; posteriolateral pronotal margin surpassing medial pronotal margin; metepisternal supracoxal lobe of mesocoxal cavity present; scutellum with well-developed paramedian processes and a well-developed medial process; trochanters, femora, and tibiae with small, uniformly distributed setigerous tubercles; tibiae lacking fossula spongiosa; proximal parts of M and Cu of forewing forming one vein. ABDOMEN: DAGs I–III ostioles present in adults (except I absent in *Tribelocodia*) and of similar sizes.

DISCUSSION: This tribe includes the Neotropical genera *Ectrichodiella* and *Tribelocodia*.

Abelocephalini, new tribe

Fig. 4.5E

Type genus: *Abelocephala* Maldonado, 1996

DIAGNOSIS: Abelocephalini may be diagnosed by the following characters: bulbous trichomes present (2–1; Fig. 4.5A), eye reniform with concave posterior margin, ocelli absent, antennal shield present (32–1; Fig. 4.5B, E), scapus with ventroposterior apical lobe (37–1; Fig. 4.5E) (absent in *Abelocephala*), pedicellus ventrally inserted on scapus so that pedicellus and flagellomeres point posteriorly (38–1; Fig. 4.5C), posteriolateral margin of pronotum surpassing medial pronotal margin (71–1; Fig. 4.5I), scutellum with well-developed medial process (80–1; Fig. 4.5I, J) (paramedian process also present in *Afrodecius* Jeannel, 1919), tibiae lacking fossula spongiosa, tarsi 2-segmented, hemelytron greatly surpassing abdominal apex, proximal part of M and Cu of hemelytron forming one vein (143–1; Fig. 4.5N, O).

DESCRIPTION: **MALE:** VESTITURE: Dense vestiture on parts of the head, anterior to lateral margins of the pronotum, and near the thoracic-abdominal articulation; bulbous trichomes present. STRUCTURE: HEAD: Clypeus without anterior process; ocelli absent; antennal shield present; scapus with ventroposterior apical lobe (except in *Abelocephala*), pedicellus ventrally inserted on scapus so that pedicellus and flagellomeres point posteriorly; pedicellus strongly curved; distinct constriction between postocular region and neck; labrum completely sclerotized. THORAX: Posteriolateral margin of pronotum surpassing medial pronotal margin; scutellum with well-developed medial process (paramedian process also present in *Afrodecius* Jeannel, 1919); tibiae lacking fossula spongiosa; tarsi 2-segmented; hemelytron greatly surpassing abdominal apex; proximal part of M and Cu of hemelytron forming one vein. ABDOMEN: DAGs II and III ostioles only present and of similar size in adults.

DISCUSSION: *Abelocephala*, *Afrodecius*, *Apocaucus*, and *Megapocaucus* Miller, 1954 are included within this tribe based on our phylogenetic results. Based on our diagnosis, we also include *Enigmocephala* Rédei, 2007, *Gastrogyrus* Bergroth, 1921, *Homognetus* Bergroth, 1923, and *Mantangocoris* Miller, 1940. Rédei (2007) highlight the morphological similarities between *Enigmocephala* with *Gastrogyrus*, *Mantangocoris*, and *Afrodecius*, particularly with head morphology (e.g., the anteriorly declivent head, pubescent postocular and gular regions, robust labium, and/or apical processes on ultimate labial segment). *Homognetus* is also similar to these genera in the pubescent postocular and gular regions. It is worth noting that an undescribed male specimen of *Xenocaucus* was observed for our analysis and also exhibits many of the same diagnostic features of this tribe (e.g., 2-segmented tarsus; hemelytron greatly surpassing abdominal apex), as well as other morphological features (fringe of hairs on postocular and gular areas; DAGs II and III ostioles of similar size). Thus, it is possible that this genus may be a member of Abelocephalini and was recovered as sister to or nested within this tribe in some of our phylogenetic results; however, further phylogenetic testing is needed with more representatives of this tribe for both molecular and morphological data.

Tribelocephalini Villiers, 1943

Fig. 4.5C, J, O, P

Tribelocephalini Villiers, 1943, 10: 9.

Type genus: *Tribelocephala* Stål, 1853

REVISED DIAGNOSIS: Species of this tribe are distinguished by the dense, tomentose vestiture throughout the body (especially the entire head) (Fig. 4.5C), head longer than pronotum (except little shorter than pronotum in *Tomolus* Stål, 1874), clypeus with anterior process (20–1; Fig. 4.5C) (absent in *Opistoplatys* Westwood, 1834 and *Tomolus*), eye adpressed closely to the head surface and with concave anterior and posterior eye margin (26–0, 27–1; Fig. 4.5C) (concavity slight in *Tomolus*), ventral margin of second visible labial segment (appears dorsal when retracted under the head) is straight or concave (45–0), apex of short prosternal stridulatory process acute (86–0), and DAG I–III ostioles present in adults and of similar sizes (164–1; Fig. 4.5S).

REDESCRIPTION: **MALE:** VESTITURE: Dense tomentose vestiture throughout the entire body, bulbous trichomes present. STRUCTURE: HEAD: Head longer than pronotum (little shorter than pronotum in *Tomolus*); clypeus with anterior process (absent in *Opistoplatys* and *Tomolus*); eye adpressed closely to the head surface and with concave anterior and posterior eye margin; ocelli absent; antennal shield absent; pedicellus slightly to moderately curved; pedicellus ventrally inserted on scapus so that pedicellus and flagellomeres point posteriorly; pedicellus strongly curved; labrum completely sclerotized; ventral margin of second visible labial segment straight or concave. THORAX: Posteriolateral margin of pronotum surpassing or slightly surpassing medial pronotal margin; scutellum with well-developed medial process only; apex of short prosternal stridulatory process acute; tibiae lacking fossula spongiosa; tarsi 3-segmented, hemelytron reaching or extending a little beyond abdominal apex. ABDOMEN: DAG I–III ostioles present in adults and of similar sizes.

DISCUSSION: Villiers (1943) erected the tribe as a member of the Tribelocephalinae and included all of the genera in our new tribe Abelocephalini, as well as *Tomolus* and *Tribelocephala* Stål, 1853. The tribe was once diagnosed by the absence of the proximal m-cu cross vein in the hemelytra. *Acanthorhinocoris* Miller, 1940, was initially assigned to the Tribelocephalinae, but Rédei (2007) transferred the genus to the Opistoplatyini based on the presence of the m-cu cross vein. Based on our results, we revise the Tribelocephalini and establish two subtribes, the Opistoplatyina and Tribelocephalina. Based on our diagnostic features and other morphological characters, we include *Acanthorhinocoris*, *Centrogastocoris* Miller, 1958, *Distantus* Villiers, 1943, *Opistoplatys*, *Plectrophorocoris* Miller, 1958, *Tribelocephala*, and *Tomolus*.

Opistoplatyina, new subtribe

Fig. 4.5J, P

Type genus: *Opistoplatys* Westwood, 1834

DIAGNOSIS: In addition to the tribal diagnosis, this subtribe is diagnosed by the eyes reaching or nearly reaching the dorsal and ventral surfaces of the head (29–1, 30–1), antennal insertion laterally concealing suture between maxillary and mandibular plates (34–1), scapus without apical lobes, a prominent postscutum (84–1; Fig. 4.5J), and the proximal parts of M and Cu forming separate veins in the hemelytron (143–0; Fig. 4.5P).

DESCRIPTION: **MALE:** as in diagnosis.

DISCUSSION: This subtribe retains the same generic composition as the previously recognized Opistoplatyini: *Acanthorhinocoris*, *Centrogastocoris*, *Distantus*, *Opistoplatys*, and *Plectrophorocoris*.

Tribelocephalina, new subtribe

Fig. 4.5C, O

Type genus: *Tribelocephala* Stål, 1853

DIAGNOSIS: Species of this subtribe are characterized by the antennal insertion ventral to the suture between the maxillary and mandibular plates (34–2; Fig. 4.5C), scapus with ventroanterior and ventroposterior apical lobes (36–1, 37–1; Fig. 4.5E), a reduced or absent postscutum (84–0), and the proximal parts of M and Cu forming a fused vein in the hemelytron (143–1; Fig. 4.5O).

DESCRIPTION: **MALE:** as in diagnosis.

DISCUSSION: We include *Tribelocephala* and *Tomolus* in this subtribe based on the diagnosis.

Ectrichodiini, new tribe

Fig. 4.5A, D, F–H, K–M, R, T

Type genus: *Ectrichodia* Lepeletier & Serville, 1825

DIAGNOSIS: This large tribe is diagnosed by the absence of bulbous trichomes; the distally or slightly ventrally inserted pedicellus (38–0; Fig. 4.5D); basiflagellomere subdivided into two pseudosegments (42–1; Fig. 4.5D) (not subdivided in *Schottus*, *Schuhella*, *Vilius*, and *Zirta*); a subdivided labrum (44–0; Fig. 4.5B) (not subdivided in *Schuhella*); the ventral, internal row of processes on the left maxillary stylet (51–1; Fig. 4.5H); paramedian scutellar processes present (75–1; Fig. 4.5K); a long prosternal stridulatory process that surpasses the posterior margin of the forecoxal cavity (85–1; Fig. 4.5L); the metathoracic gland evaporatorium as modified cuticle (91–1; Fig. 4.5M); and the absence of the ventral connexival suture on abdominal sternites II (154–0; Fig. 4.5T).

DESCRIPTION: **MALE:** VESTITURE: Glabrous to dense, erect to semi-erect vestiture without bulbous trichomes. STRUCTURE: HEAD: Ocellar lens in, at least, macropterous individuals; pedicellus distally or slightly ventrally inserted in scapus; basiflagellomere typically subdivided into two pseudosegments (one-segmented in *Schottus*, *Schuhella*, *Vilius*, and *Zirta*); labrum subdivided by transverse membrane (completely sclerotized in *Schuhella*); left maxillary stylet with ventral, internal row of processes. THORAX: Macropterous forms, at least, with a distinct longitudinal depression on the posterior pronotal lobe; posteriolateral margin of pronotum not or barely surpassing medial pronotal margin; paramedian scutellar processes present; prosternal stridulatory process long, surpassing posterior margin of forecoxal cavity; metathoracic gland evaporatorium present as modified cuticle; tarsi 3-segmented. ABDOMEN: ventral connexival suture on abdominal sternites II absent; DAGs II and III ostioles present in adults (DAG II ostioles absent in some species; see discussion), with DAG III larger than DAG II.

DISCUSSION: All genera recognized in the previous classification of Ectrichodiinae, with the exception of *Ectrichodiella*, are included in the Ectrichodiini. Several other synapomorphies of the nominal tribe were recovered in our optimizations, but show reversals or future modifications in some of the included taxa. The absence of a single medial scutellar process (79–0) is optimized on our phylogeny, however some genera (e.g., *Ectrychotes* Burmeister, 1835) have very small medial processes. Many genera and species are characterized by more incrassate forefemora compared to the mid femora (95–1), but a number of other genera and species have slender legs (e.g., *Tanindrazanus* Forthman, Chłond, & Weirauch, [in press]; *Pothea* Amyot & Serville, 1843). A fossula spongiosa is commonly observed on the fore- and mid tibiae (111–1, 127–1), but there are several instances of reversals on one or both legs. Although DAGs II and III ostioles are present in many of the species we have observed (Fig. 4.5R), as well as by Weirauch (2006), some species in *Scadra* Stål, 1859, *Pseudopothea* Wygodzinsky, 1951, *Microsanta* Breddin, 1903, and *Adrania* Stål, 1863, lack DAG II ostioles.

Conclusion

The evolution of aposematic coloration in animals has been largely explored outside a phylogenetic context. This is especially true for insects other than Lepidoptera and Coleoptera. While a few vertebrate and invertebrate studies have shown a positive association of body size and prevalence or conspicuousness of aposematic coloration, others have provided evidence of negative or no associations. However, results indicating no coloration-body size associations in Lepidoptera are likely confounded by the gregarious lifestyles of many species. The typically solitary millipede assassin bugs presented an opportunity to contribute to a limited body of research that has sought to understand the evolution of coloration and its association with body size. We also had the opportunity to explore the evolution of extreme sexual dimorphism in this group, which is a phenomenon that has not been explored in a phylogenetic framework for other Reduviidae subfamilies. Lastly, we were able to test conflicting phylogenetic hypotheses regarding relationships between Ectrichodiinae and Tribelocephalinae. Phylogenetic hypotheses were generated from separate and combined morphological and molecular cladistic analyses under different optimality criteria, all of which confirmed non-monophyly of both subfamilies. Furthermore, most phylogenetic results recovered similar higher-level clades, which we have recognized in our new classification of Ectrichodiinae.

Based on our phylogenetic hypothesis, aposematic coloration is shown to have evolved from a cryptic ancestor early in the evolutionary history of millipede assassin bugs. Subsequent reversals to cryptic coloration and regains of aposematic coloration are reconstructed. Our PLRs support a positive association between aposematic coloration and body length when performed on ultrametric trees. However, this association is not supported when estimated on phylograms, which may be an artifact of the method used. Due to a lack of data, we were unable to investigate other hypotheses regarding the prevalence of aposematic coloration and toxicity or diet specialization. Thus, characterizing the defense compounds and collecting more natural history observations are critically needed. Future studies should also investigate the role of aposematic coloration and metallic features in aposematic signaling within Ectrichodiinae. Extreme sexual dimorphism is also shown to evolve multiple times from a more limited condition despite the lack of data on both sexes for many species. This gap in knowledge may be, in part, the result of taxonomic decisions based on one sex. Thus, careful consideration must be given to the use of female morphology in phylogenetic investigations and taxonomic decisions, especially in cases were extreme sexual dimorphism may be apparent based on patterns recovered from our study.

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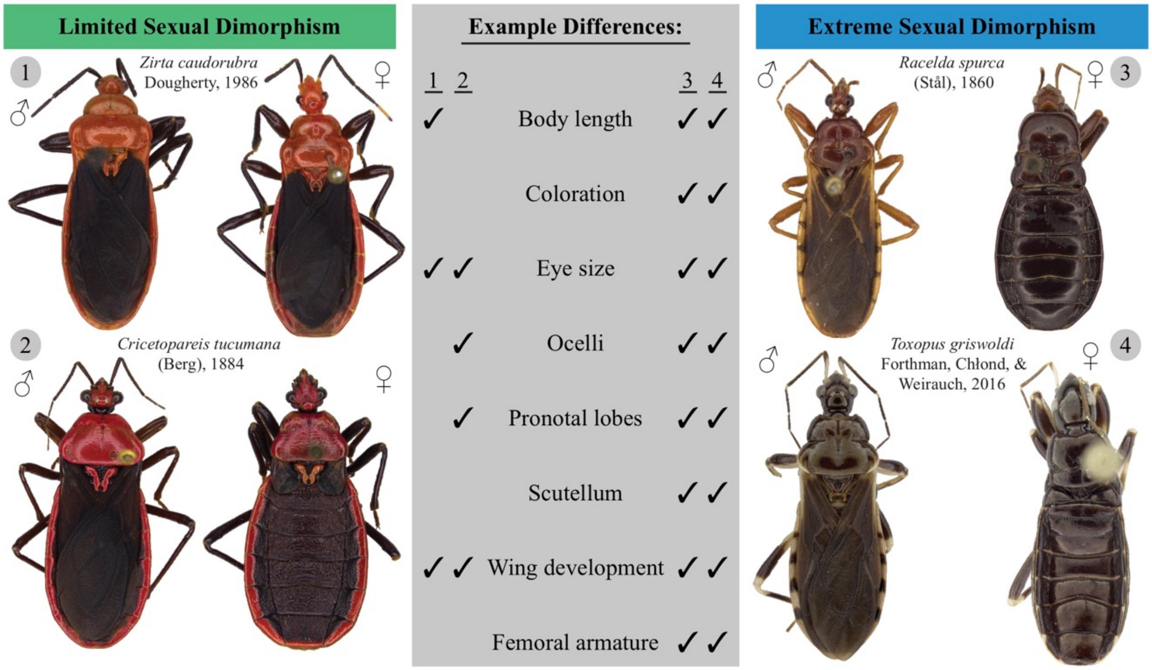
Figure 4.1. Examples of limited and extreme sexual dimorphism in Ectrichodiinae species. Headers correspond to the color code for the right panel of Fig. 4.3. Numbers in circles correspond to numbers highlighting examples of general morphological differences observed between sexes of the indicated species, but do not reflect how exaggerated the difference may be. Images are not scaled to size.



Example Differences:

1	2		3	4
✓		Body length	✓	✓
		Coloration	✓	✓
✓	✓	Eye size	✓	✓
	✓	Ocelli	✓	✓
	✓	Pronotal lobes	✓	✓
		Scutellum	✓	✓
✓	✓	Wing development	✓	✓
		Femoral armature	✓	✓

Figure 4.2. ML best tree (final Ln = –44,072.4153) based on 156 taxa (outgroups removed from figure) and a combined morphological and molecular dataset. Molecular data were divided into three partitions and models of sequence evolution: 16S, 28S D2, 28S D3–D5 (GTR+Γ+I); 18S, COI codon positions 1 and 2, Wg (GTR+Γ+I); COI codon position 3 (HKY+Γ+I). Morphological data were analyzed under Lewis' (2001) Mkv model of morphological evolution. Bootstrap values ≥50 are reported. Branch colors correspond to select clades mentioned in the discussion and serves as a reference to compare with all other molecular and/or morphological phylogenies in the supplementary materials.

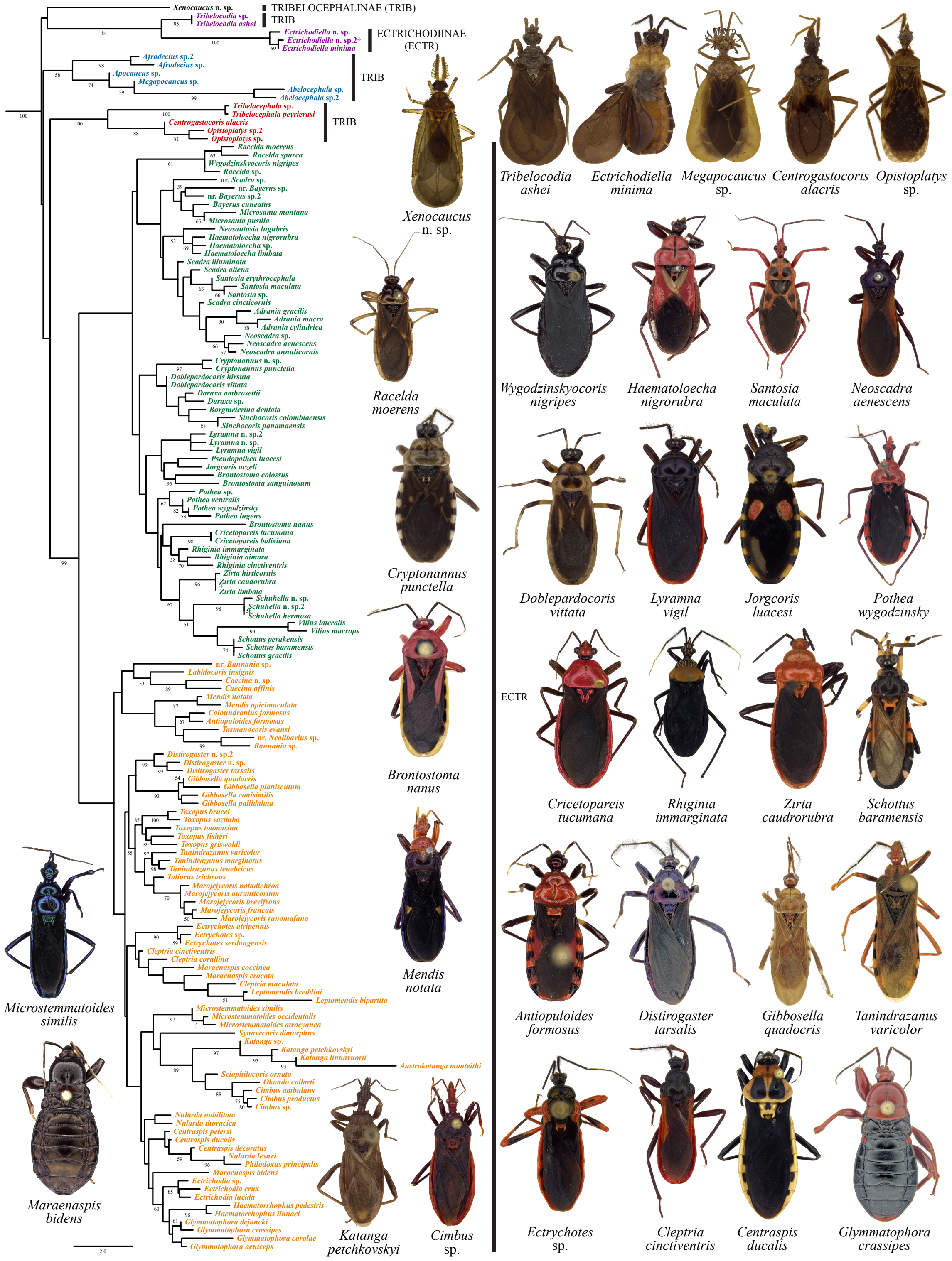

Xenocaucus n. sp.
TRIBELOCEPHALINAE (TRIB)
Tribelocodia sp.
TRIB
95
Tribelocodia ashei
84
Ectrichodiella n. sp.
ECTRICHODIINAE (ECTR)
100
Ectrichodiella n. sp.2†
69
Ectrichodiella minima
Afrodecius sp.2
98
Afrodecius sp.
58
Apocaucus sp.
TRIB
74
Megapocaucus sp.
59
Abelocephala sp.
99
Abelocephala sp.2
Tribelocephala sp.
100
100
Tribelocephala peyrierasi
100
Centrogastocoris alacris
TRIB
Opistoplatys sp.2
88
81
Opistoplatys sp.
Racelda moerens
63
Racelda spurca
61
Wygodzinskyocoris nigripes
Racelda sp.
nr. Scadra sp.
59
nr. Bayerus sp.
nr. Bayerus sp.2
Bayerus cuneatus
Microsanta montana
65
Microsanta pusilla
Neosantosia lugubris
52
Haematoloecha nigrorubra
69
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
63
Santosia maculata
66
Santosia sp.
Scadra cincticornis
Adrania gracilis
90
Adrania macra
88
Adrania cylindrica
Neoscadra sp.
66
Neoscadra aenescens
57
Neoscadra annulicornis
Cryptonannus n. sp.
97
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
84
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
95
Brontostoma sanguinosum
Pothea sp.
62
Pothea ventralis
82
Pothea wygodzinsky
53
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
98
Cricetopareis boliviana
Rhiginia immarginata
58
Rhiginia aimara
70
Rhiginia cinctiventris
99
Zirta hirticornis
96
Zirta caudorubra
51
Zirta limbata
67
Schuhella n. sp.
98
Schuhella n. sp.2
58
Schuhella hermosa
51
Vilius lateralis
99
Vilius macrops
Schottus perakensis
74
Schottus baramensis
Schottus gracilis
nr. Bannania sp.
Labidocoris insignis
53
Caecina n. sp.
89
Caecina affinis
Mendis notata
87
Mendis apicimaculata
Caloundranius formosus
67
Antiopuloides formosus
Tasmanocoris evansi
nr. Neolibavius sp.
99
Bannania sp.
Distirogaster n. sp.2
99
Distirogaster n. sp.
99
Distirogaster tarsalis
54
Gibbosella quadocris
Gibbosella planiscutum
93
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
85
100
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
89
Toxopus griswoldi
55
97
Tanindrazanus varicolor
Tanindrazanus marginatus
98
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
70
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
50
Marojejycoris ranomafana
Ectrychotes atripennis
90
Ectrychotes sp.
59
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
81
Leptomendis bipartita
Microstemmatoides similis
97
Microstemmatoides occidentalis
51
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
97
Katanga petchkovskyi
95
Katanga linnavuorii
93
Austrokatanga monteithi
89
Sciaphilocoris ornata
Okondo collarti
88
Cimbus ambulans
75
Cimbus productus
80
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
59
Nularda lesnei
96
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
85
Ectrichodia crux
Ectrichodia lucida
60
Haematorrhophus pedestris
98
Haematorrhophus linnaei
61
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
2.0
Xenocaucus n. sp.
Racelda moerens
Cryptonannus punctella
Brontostoma nanus
Mendis notata
Microstemmatoides similis
Maraenaspis bidens
Katanga petchkovskyi
Cimbus sp.
Tribelocodia ashei
Ectrichodiella minima
Megapocaucus sp.
Centrogastocoris alacris
Opistoplatys sp.
Wygodzinskyocoris nigripes
Haematoloecha nigrorubra
Santosia maculata
Neoscadra aenescens
Doblepardocoris vittata
Lyramna vigil
Jorgcoris luacesi
Pothea wygodzinsky
ECTR
Cricetopareis tucumana
Rhiginia immarginata
Zirta caudrorubra
Schottus baramensis
Antiopuloides formosus
Distirogaster tarsalis
Gibbosella quadocris
Tanindrazanus varicolor
Ectrychotes sp.
Cleptria cinctiventris
Centraspis ducalis
Glymmatophora crassipes

Figure 4.3. BayesTraits Multistate ML ancestral state reconstruction of color character 198 on the ML phylogram (Fig. 4.2) for Tribelocephalinae and Ectrichodiinae taxa (tree converted to cladogram for visual). Terminal taxa coded as cryptic (black) or either aposematic, metallic, or aposematic and metallic (blue). Pie charts at select nodes show probability values from the ML analysis and are used to visualize transitions between states; branches are colored to reflect the highest probability of a color state at that branch.

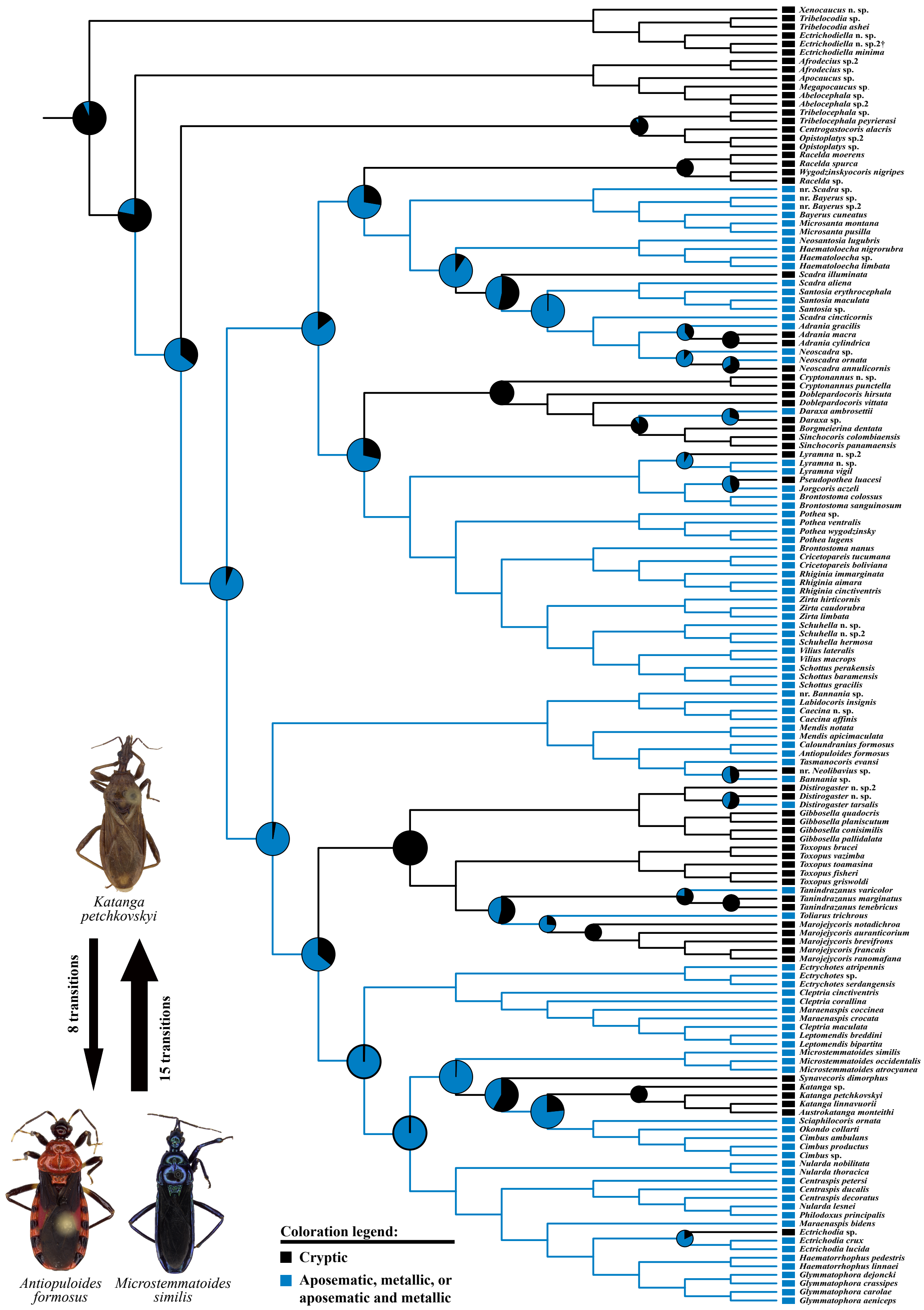

Xenocaucus n. sp.
Tribelocodia sp.
Tribelocodia ashei
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
Afrodecius sp.2
Afrodecius sp.
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
Racelda moerens
Racelda spurca
Wygodzinskyocoris nigripes
Racelda sp.
nr. Scadra sp.
nr. Bayerus sp.
nr. Bayerus sp.2
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Neoscadra sp.
Neoscadra ornata
Neoscadra annulicornis
Cryptonannus n. sp.
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
Brontostoma sanguinosum
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Mendis notata
Mendis apicimaculata
Caloundranius formosus
Antiopuloides formosus
Tasmanocoris evansi
nr. Neolibavius sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
Leptomendis bipartita
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia crux
Ectrichodia lucida
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Katanga petchkovskyi
8 transitions
15 transitions
Antiopuloides formosus
Microstemmatoides similis
Coloration legend:
Cryptic
Aposematic, metallic, or aposematic and metallic

Figure 4.4. BayesTraits MultiState ML reconstruction of ancestral sexual dimorphism states on the ML phylogram (Fig. 4.2) for Tribelocephalinae and Ectrichodiinae taxa (tree converted to cladogram for visual). On the left, sexual dimorphism for terminal taxa is coded as limited (black), extreme (blue), polymorphic (gradient blue and black), or missing data (gray). Pie charts at select nodes show probability values from the ML reconstructions; branches are colored to reflect the highest probability of a color state at that branch; gray internal branches indicate ambiguity in reconstructions. On the right, color codes correspond to Fig. 4.1, with characters that exhibit no differences (black), differences in limited sexual dimorphism (green) or differences in extreme sexual dimorphism (blue) between males and females shown for species in which data on both sexes are known. For taxa that exhibit limited sexual dimorphism, individuals of a sex that exhibit no or minor differences (i.e., polymorphic) are coded gradient black and green. For taxa exhibiting both limited and extreme sexual dimorphism (i.e., males and/or females have different morphs), differences are indicated with gradient green and blue. Missing data indicated in gray.

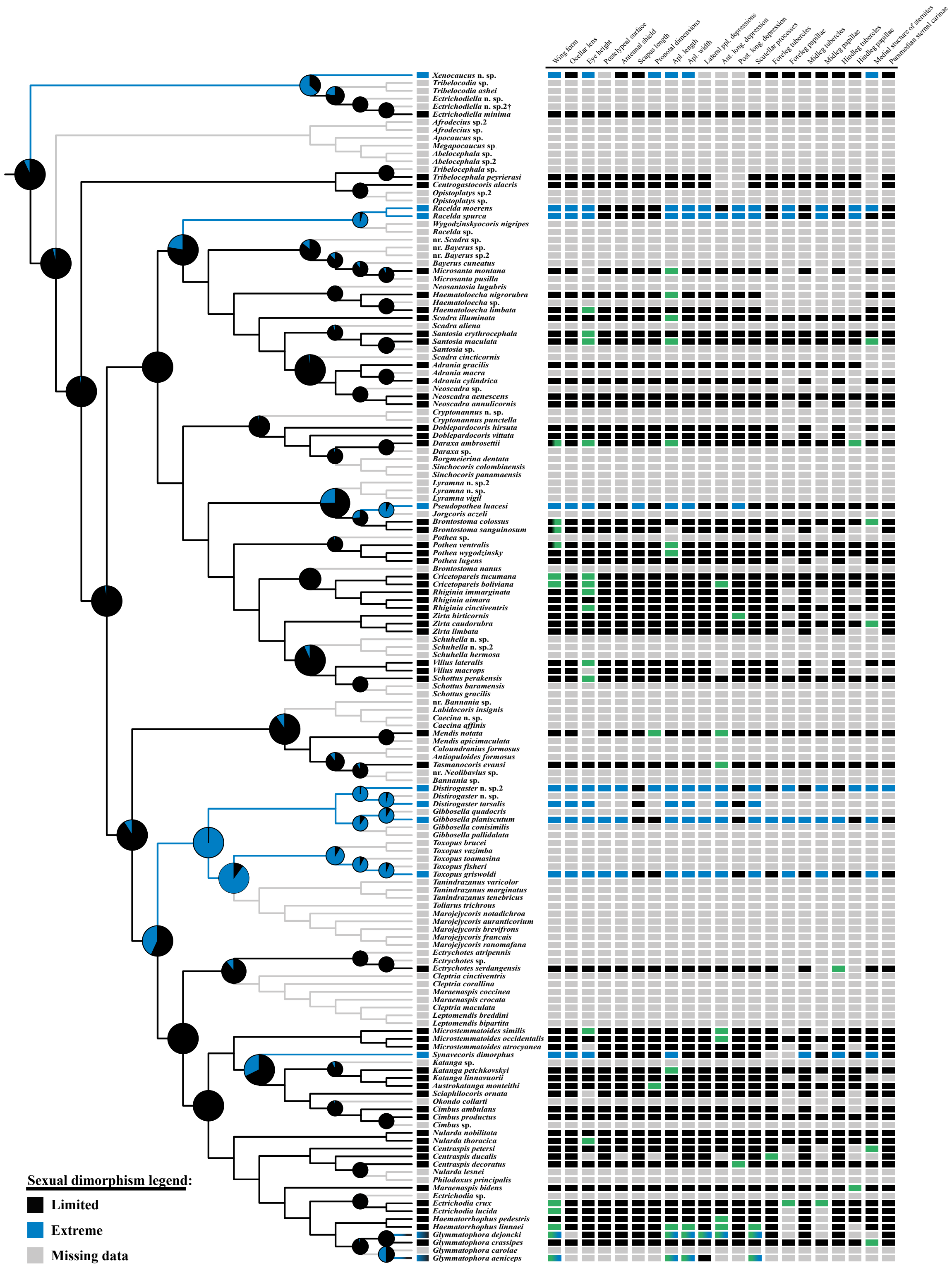

Wing form
Ocellar lens
Eye height
Postclypeal surface
Antennal shield
Scapus length
Pronotal dimensions
Apl. length
Apl. width
Lateral ppl. depressions
Ant. long. depression
Post. long. depression
Scutellar processes
Foreleg tubercles
Foreleg papillae
Midleg tubercles
Midleg papillae
Hindleg tubercles
Hindleg papillae
Medial stucture of sternites
Paramedian sternal carinae
Xenocaucus n. sp.
Tribelocodia sp.
Tribelocodia ashei
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
Afrodecius sp.2
Afrodecius sp.
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
Racelda moerens
Racelda spurca
Wygodzinskyocoris nigripes
Racelda sp.
nr. *Scadra* sp.
nr. *Bayerus* sp.
nr. *Bayerus* sp.2
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Cryptonannus n. sp.
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
Brontostoma sanguinosum
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
nr. *Bannania* sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Mendis notata
Mendis apicimaculata
Caloundranius formosus
Antiopuloides formosus
Tasmanocoris evansi
nr. *Neolibavius* sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
Leptomendis bipartita
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia crux
Ectrichodia lucida
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Sexual dimorphism legend:
■ Limited
■ Extreme
■ Missing data

Figure 4.5. Combined morphological and molecular ML phylogram (converted to cladorgram) showing new classification of Ectrichodiinae (see Fig. 4.2 for comparison to old classification). Unambiguous character optimizations are shown. A. Bulbous trichome of *Tribelocephala* sp. B. Rostral view of *Distriogaster tarsalis* head. C. Lateral view of *Tribelocephala* sp. head. D. Lateral antennal morphology of *Toxopus insignis* (modified from Forthman et al., in press). E. Dorsolateral-rostral view of *Afrodecius* sp. head and scapus. F. Apex of mandibular stylet in *Rhiginia cinctiventris*. G. Apex of right maxillary stylet in *Centraspis ducalis*. H. Apex of left maxillary stylet in *Rhiginia cinctiventris*. I. Thoracic morphology of *Ectrichodiella* n. sp., in dorsal view. J. Scutellum and postscutum of *Centrogastocoris alacris*. K. Thoracic morphology of nr. *Bannania* sp., in dorsal view. L. Thoracic sternal morphology in *Tanindraanus* sp. (modified from Forthman et al., in press). M. Metathoracic gland evaporatorium of *Tanindrazanus varicolor*, in lateral view. N.–P. Hemelytral morphology of *Ectrichodiella minima* (N.), *Tribelocephala* sp. (O.), and *Centrogastocoris alacris* (P.). Q. Foreleg morphology of *Ectrichodiella minima*. R. Dorsal abdominal glands of *Cricetopareis tucumana* female. S. Dorsal abdominal glands of *Ectrichodiella minima*. T. Ventral connexival suture and ventral abomdinal morphology of *Tanindrazanus varicolor*. Character numbers and character state codings are listed in Table 4.1. Abbreviations used in figures: 1A, first anal vien, bf, basiflagellomere; cs, ventral connexival suture; Cu, cubitus; DAG I, dorsal abdominal gland I; DAG II, dosal abdominal gland II; DAG III, dorsal abdominal gland III; df, distiflagellomere; M, media; mms, suture separating mandibular and maxillary plates; R, radius; s2, abdominal sternite II (fused sternites I and II); s3, abdominal sternite III; vlt, ventral laterotergites III.

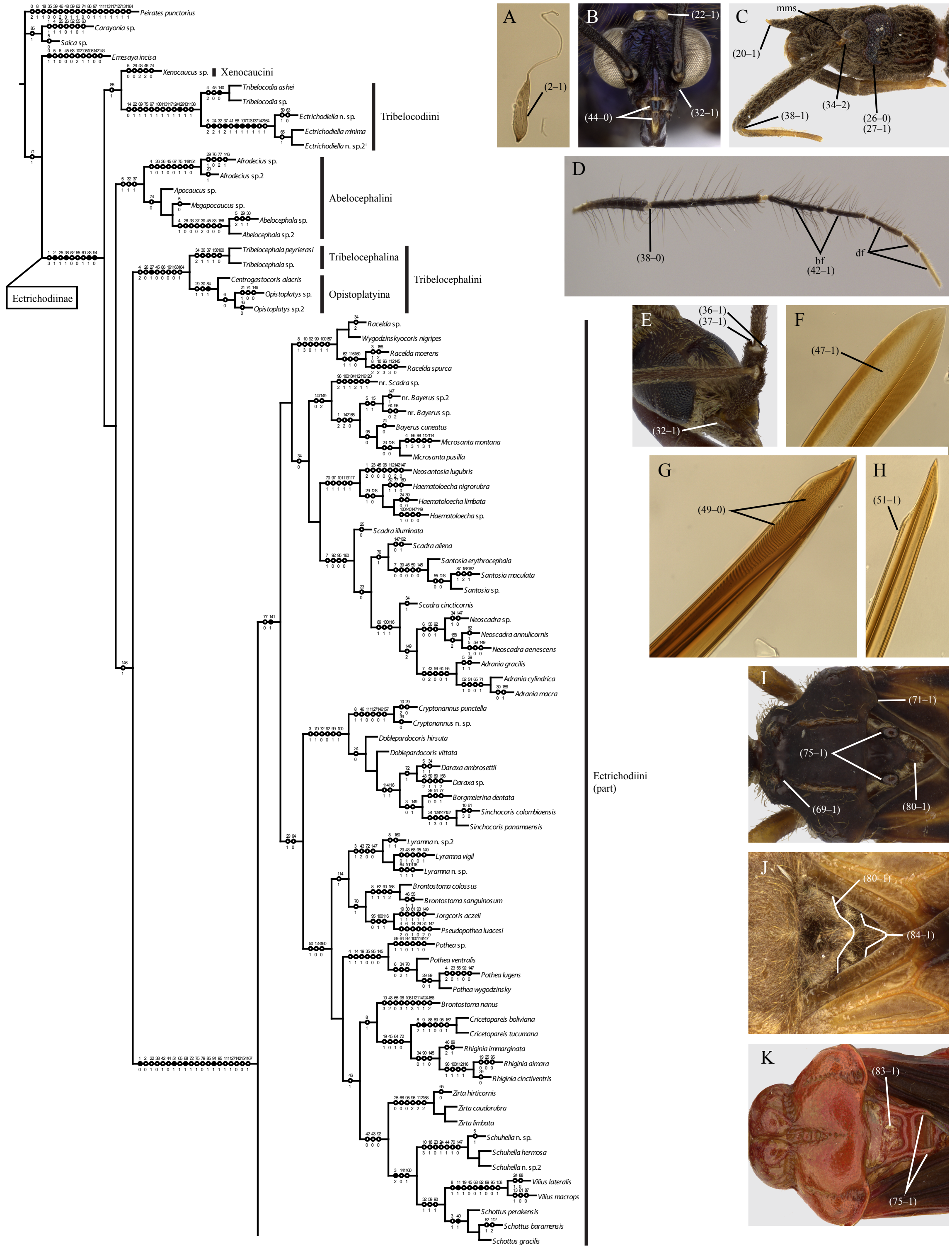
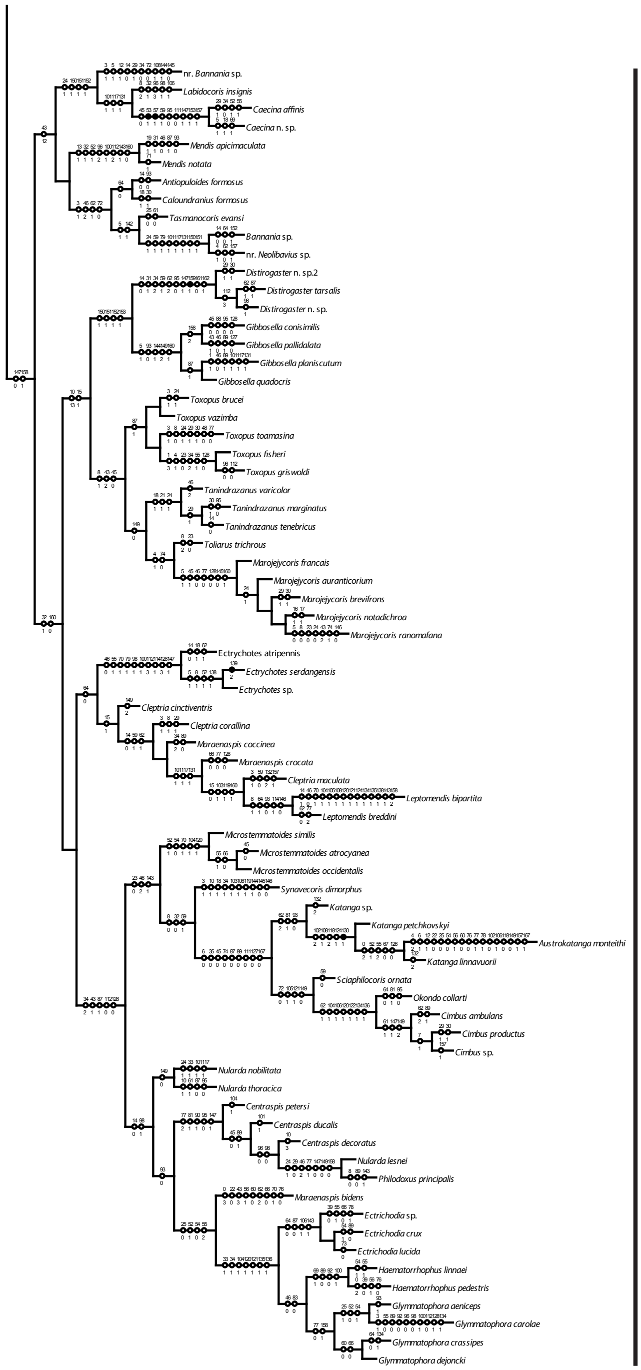

Peirates punctorius
Carayonia sp.
Saica sp.
Emesaya incisa
Xenocaucus sp.
Xenocaucini
Tribelocodia ashei
Tribelocodia sp.
Ectrichodiella n. sp.
Ectrichodiella minima
Ectrichodiella n. sp.2
Tribelocodiini
Afrodecius sp.
Afrodecius sp.2
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Abelocephalini
Tribelocephala peyrierasi
Tribelocephala sp.
Tribelocephalina
Centrogastocoris alacris
Opistoplatys sp.
Opistoplatys sp.2
Opistoplatyina
Tribelocephalini
Ectrichodiinae
Racelda sp.
Wygodzinskyocoris nigripes
Racelda moerens
Racelda spurca
nr. Scadra sp.
nr. Bayerus sp.2
nr. Bayerus sp.
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha limbata
Haematoloecha sp.
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Neoscadra sp.
Neoscadra annulicornis
Neoscadra aenescens
Adrania gracilis
Adrania cylindrica
Adrania macra
Cryptonannus punctella
Cryptonannus n. sp.
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramma n. sp.2
Lyramma vigil
Lyramma n. sp.
Brontostoma colossus
Brontostoma sanguinosum
Jorgcoris aczeli
Pseudopothea luacesi
Pothea sp.
Pothea ventralis
Pothea lugens
Pothea wygodzinsky
Brontostoma nanus
Cricetopareis boliviana
Cricetopareis tucumana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cincticentris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella hermosa
Schuhella n. sp.2
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
Ectrichodiini (part)
A
(2–1)
B
(22–1)
(44–0)
(32–1)
C
mms
(20–1)
(38–1)
(34–2)
(26–0)
(27–1)
D
(38–0)
bf
(42–1)
df
E
(36–1)
(37–1)
(32–1)
F
(47–1)
G
(49–0)
H
(51–1)
I
(71–1)
(75–1)
(69–1)
(80–1)
J
(80–1)
(84–1)
K
(83–1)
(75–1)

Figure 4.5. (Continued).



Ectrichodiini
(part)

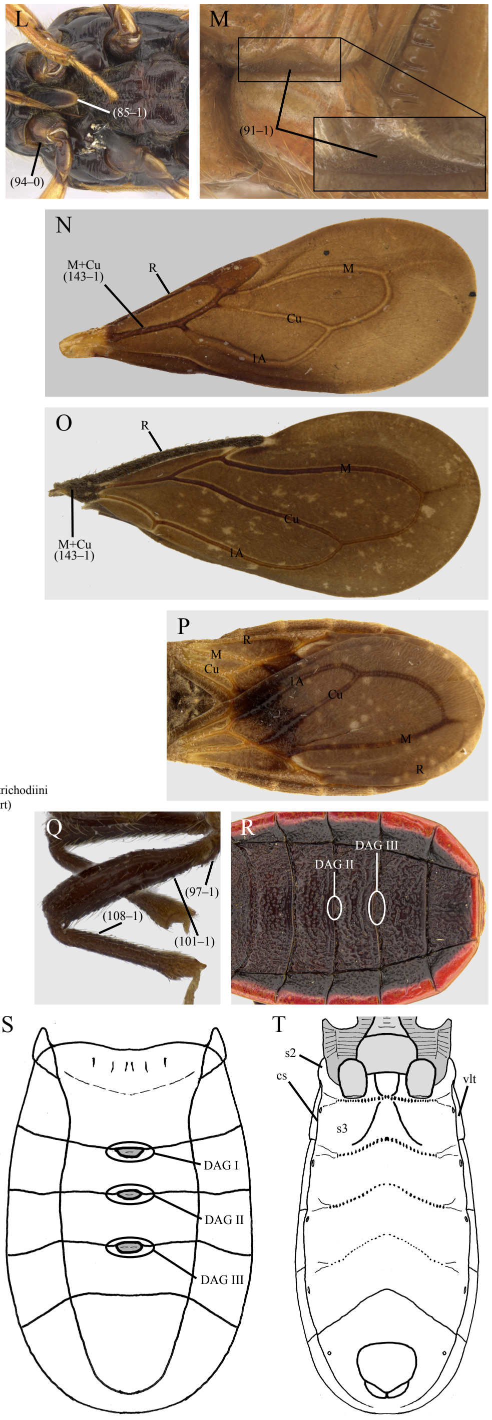


Table 4.1. Morphological characters and character state codings.

Character no.	Character	Character states
GENERAL		
0	Wing form	(0) Macropterous (reaches/surpasses tergite VII); (1) Brachypterous (reaches/surpasses tergite VI but not VII); (2) Micropterous (minute leathery wing pads covering, at most, base of abdomen); (3) Apterous
1	General vestiture, excluding hemelytra and legs	(0) Glabrous to sparse; (1) Moderately dense; (2) Dense; (3) Very dense, conspicuously thick pubescence obscuring integument on all or part of the body
2	Basally bulbous trichomes	(0) Absent; (1) Present
HEAD		
3	Head length (clypeal apex to anterior neck margin) relative to head width in dorsal view	(0) Longer than wide; (1) About as long as wide; (2) Wider than long
4	Head length relative to greatest pronotal length in dorsal view	(0) Shorter than pronotum; (1) About as long as pronotum; (2) Longer than pronotum
5	Anteocular length (clypeal apex to anterior eye margin) relative to postocular length (hind eye margin to anterior neck margin or, if postocular-neck constriction obsolete, halfway to anterior pronotal margin)	(0) Shorter than postocular; (1) About as long as postocular; (2) Longer than postocular
6	Postocular-neck constriction	(0) Absent, gradually transitioning; (1) Present, distinctly constricted
7	Shape of anterolateral neck area	(0) Flat; (1) Bulbous
8	Shape of posterolateral gula area in lateral view	(0) Flat to slightly swollen, conforming to rounded head shape; (1) Moderately swollen; (2) Very swollen
9	Extension of posterolateral gula area relative to ventral head margin	(0) Not or barely surpassing ventral head margin; (1) Distinctly surpassing ventral head margin
10	Ventral medial longitudinal depression	(0) Absent; (1) Restricted to anteocular region; (2) Restricted to postocular region; (3) Present along entire ventral length
11	Ventral paramedial longitudinal depression	(0) Absent; (1) Present
12	Small tubercles on ventromedial region of gula	(0) Absent; (1) Present
13	Ventrolateral tubercle on gula	(0) Absent; (1) Present
14	Postocular shape in dorsal view	(0) Narrow; (1) Broad
15	Postclypeal surface	(0) Flat or convex; at most a thin medial line visible but not distinctly depressed; (1) Distinctly depressed

Table 4.1. (Continued).

Character no.	Character	Character states
16	Extension of postclypeal depression	(0) Posterior clypeal margin to middle of synthlipsis; (1) Posterior clypeal margin to interocular sulcus
17	Width of postclypeal depression	(0) Narrow to slightly wide; (1) Very wide
18	Maxillary plate in lateral view	(0) Not reaching dorsal clypeal margin; (1) Reaching dorsal clypeal margin
19	Dorsal subtriangular elevation of clypeus	(0) Absent, clypeus rounded, sometimes with dorsally swollen area; (1) Present
20	Anterior clypeal process	(0) Absent; (1) Present
21	Clypeal apex relative to labral base	(0) Not elevated; (1) Elevated
22	Ocellar lens	(0) Absent; (1) Present
23	Location of ocelli	(0) On flat to shallowly elevated tubercle; (1) On moderately to extremely elevated cuticle
24	Shape of ocellar tubercle	(0) Convex; (1) Medially concaved, but ocelli appear on one tubercle; (2) Medially concaved, but ocelli appearing on separate tubercles
25	Eye height in lateral view	(0) Less than or half of head height; (1) More than half of head height
26	Eye shape	(0) Adpressed; (1) Globbose
27	Anterior eye margin in lateral view	(0) Convex; (1) Concave
28	Posterior eye margin in lateral view	(0) Concave; (1) Straight
29	Dorsal eye margin in lateral view	(0) Not attaining dorsal head surface; (1) Attaining dorsal head surface
30	Ventral eye margin in lateral view	(0) Not attaining dorsal head surface; (1) Attaining dorsal head surface
31	Antennifer armature	(0) Unarmed; (1) With dorsolateral tubercle
32	Antennal shield	(0) Absent, not expanded; (1) Present, expanded
33	Antennal insertion site in lateral view	(0) Not concealed by antennal shield; (1) Concealed by antennal shield
34	Point of antennal insertion relative to suture between mandibular and maxillary plates in lateral view	(0) Dorsal, ventrally exposing suture between mandibular and maxillary plates; (1) Lateral, largely obscuring suture between mandibular and maxillary plates; (2) Ventral, dorsally exposing suture between mandibular and maxillary plates
35	Scapus length	(0) Not surpassing or barely surpassing clypeal apex; (1) Surpassing clypeal apex
36	Ventroanterior apical lobe of scapus	(0) Absent; (1) Present

Table 4.1. (Continued).

Character no.	Character	Character states
37	Ventroposterior apical armature of scapus	(0) Absent; (1) Lobed; (2) Toothlike
38	Scapo-pedicellar articulation	(0) Pedicellus distally or, at most, slightly ventrally inserted on scape; (1) Pedicellus ventrally inserted on scape, so that pedicellus and flagellomeres point posteriorly
39	Curvature of pedicellus	(0) Straight; (1) Slightly to moderately curved; (2) Very curved
40	Shape of pedicellus	(0) Cylindrical; (1) Laterally flattened
41	Diameter of flagellomeres	(0) Similar to diameter of pedicellus; (1) More slender than diameter of pedicellus
42	Basiflagellomere segmentation	(0) 1-segmented; (1) 2-segmented
43	Distiflagellomere segmentation	(0) 1-segmented; (1) 2-segmented; (2) 3-segmented; (3) 4-segmented; (4) 5-segmented
44	Labrum structural	(0) Subdivided by transverse membrane; (1) Completely sclerotized
45	Ventral margin (appears dorsal when reflexed) of labial segment III (second visible segment)	(0) Straight or concave; (1) Convex
46	Labial segment III length	(0) Shorter than labial segment II; (1) Subequal to labial segment II; (2) Longer than labial segment II
47	Number of transverse ridges on mandibular stylets in external view	(0) Up to 35; (1) More than 35
48	Dorsal row of processes on right maxillary stylet in internal view	(0) Absent; (1) Present
49	Structure of ventral processes of right maxillary stylet in internal view	(0) Lamellate; (1) Hairlike; (2) Tootlike
50	Dorsal row of processes on left maxillary stylet in internal view	(0) Absent; (1) Present
51	Ventral row of processes on left maxillary stylet in internal view	(0) Absent; (1) Present
THORAX		
52	Greatest length of pronotum relative to greatest width	(0) Wider than long; (1) About as long as wide; (2) Longer than wide
53	Pronotal structure	(0) Smooth, striated, rugose, punctate, or any combination of; (1) entirely tuberculate/spinulose
54	Pronotal collar	(0) Absent; (1) Present
55	Anterior pronotal lobe greatest length relative to posterior pronotal lobe	(0) Shorter than posterior lobe; (1) About as long as posterior lobe; (2) Longer than posterior lobe

Table 4.1. (Continued).

Character no.	Character	Character states
56	Anterior pronotal lobe greatest width relative to posterior pronotal lobe	(0) Less than width of posterior lobe; (1) About as wide as posterior lobe
57	Medial expansion of anterior pronotal lobe	(0) Not medially expanded; (1) Medially expanded anteriorly
58	Medial discal tubercles on anterior paramedial pronotal lobes	(0) Absent; (1) Present
59	Lateral carinae on anterior pronotal lobe	(0) Absent; (1) Present
60	Lateral depressions on posterior pronotal lobe	(0) Absent; (1) Present
61	Structure of lateral depressions on posterior pronotal lobe	(0) Not foveate; (1) Foveate
62	Anterolateral armature of pronotum	(0) Absent; (1) Small tubercle; (2) Strong projecting process
63	Presence of pronotal longitudinal depression on anterior lobe	(0) Absent; (1) Present
64	Extension of pronotal longitudinal depression on anterior lobe	(0) Not reaching anterior margin; (1) Reaching or nearly reaching anterior margin
65	Presence of pronotal longitudinal depression on posterior lobe	(0) Absent; (1) Present
66	Structure of pronotal longitudinal depression on posterior lobe	(0) Not foveate; (1) Foveate
67	Pronotal transverse suture development	(0) Absent or weakly developed, anterior and posterior pronotal lobes at most weakly delimited; (1) Well-developed, anterior and posterior pronotal lobes distinctly delimited
68	Paramedial division of pronotal transverse suture	(0) Absent; (1) Present
69	Lateral division of pronotal transverse suture	(0) Absent; (1) Present
70	Pronotal transverse suture structure	(0) Not foveate; (1) Foveate
71	Posteriolateral margin of pronotum	(0) Not or slightly surpassing medial posterior margin of pronotum; (1) Distinctly surpassing medial posterior margin of pronotum
72	Expansion of mesopleuron	(0) Not expanded anterodorsally onto lateral side of pronotum; (1) Expanded anterodorsally onto lateral side of pronotum, overlapping pronotum
73	Shape of mesopleural expansion	(0) Knoblike; (1) Broad, sinuate
74	Metepisternal supracoxal lobe of mesocoxal cavity	(0) Absent; (1) Present
75	Paramedian scutellar processes	(0) Absent; (1) Present

Table 4.1. (Continued).

Character no.	Character	Character states
76	Development of paramedian scutellar processes	(0) Weakly developed; (1) Well developed
77	Distance between paramedian scutellar processes	(0) Extremely narrow, apices nearly contiguous, less than one-tenth of posterior pronotal lobe width; (1) Moderately broad, between one-tenth to one-fourth posterior pronotal lobe width; (2) Very broad, more than one-fourth posterior pronotal lobe width
78	Orientation of paramedian scutellar processes	(0) Horizontally directed; (1) Dorsally directed
79	Presence of single medial scutellar process	(0) Absent; (1) Present
80	Development of medial scutellar process	(0) Weakly developed; (1) Well developed
81	Presence of two medial scutellar processes	(0) Absent; (1) Present
82	Presence of lateral scutellar processes	(0) Absent; (1) Present
83	Scutellar disc surface	(0) Flat; (1) Medially depressed
84	Postscutum development	(0) Absent or reduced, not prominently projecting posteriorly; (1) Present, prominently projecting posteriorly
85	Prosternal stridulatory process length	(0) Short, not reaching or surpassing posterior margin of procoxal cavity; (1) Long, surpassing posterior margin of procoxal cavity
86	Apical shape of prosternal stridulatory process	(0) Acute; (1) Rounded, blunt
87	Transverse suture between meso- and metasterna	(0) Complete; (1) Incomplete, at least partially
88	Medial surface of mesosternum	(0) Flat or convex; (1) Anteriorly depressed; (2) Depressed along entire length
89	Medial surface of metasternum	(0) Flat or convex; (1) Posteriorly depressed; (2) Depressed along entire length
90	Metathoracic gland callus in lateral view	(0) Absent; (1) Present
91	Metathoracic gland evaporatorium	(0) Absent, cuticle along metaxocal rim not modified into ridges or meshlike structures; (1) Present, cuticle along metaxocal rim modified into ridges or meshlike structures
92	Cuticular structure of metathoracic gland evaporatorium	(0) Faint to distinct ridges without meshlike structure; (1) Meshlike structure
93	Metathoracic gland evaporatorium size	(0) Small, not visible in lateral view; (1) Large, visible in lateral view
LEG		
94	Shape of forecoxa	(0) Globular; (1) Elongate

Table 4.1. (Continued).

Character no.	Character	Character states
95	Width of forefemur relative to mid femur	(0) About as wide as mid femur; (1) Wider than mid femur
96	Ventral vestiture of foretrochanter	(0) Glabrous; (1) Long, slender setae; (2) Short, thick setae; (3) Round to rodlike papillae
97	Presence of small tubercles on foretrochanter	(0) Absent; (1) Present
98	Presence of ventral papillae on forefemur	(0) Absent; (1) Present
99	Distribution of papillae on forefemur	(0) Basally; (1) Longitudinally along at least half the length of the femur
100	Presence of ventral longitudinal carinae on forefemur	(0) Absent; (1) Present
101	Presence of small tubercles on forefemur	(0) Absent; (1) Present
102	Distribution of small tubercles on forefemur	(0) Entirely throughout femur; (1) Throughout ventral femoral surface; (2) Restricted to ventroapical half of femur
103	Vestiture of small tubercles on forefemur	(0) Glabrous; (1) With setae
104	Medial projection of forefemur	(0) Absent; (1) Present
105	Anterior subapical projection on forefemur	(0) Absent; (1) Present
106	Posterior subapical projection on forefemur	(0) Absent; (1) Present
107	Paired ventroapical projections on forefemur	(0) Absent; (1) Present
108	Presence of small tubercles on foretibia	(0) Absent; (1) Present
109	Distribution of small tubercles on foretibia	(0) Entirely throughout tibia; (1) Throughout ventral tibial surface; (2) Restricted to ventroapical half of tibia
110	Vestiture of small tubercles on foretibia	(0) Glabrous; (1) With setae
111	Presence of fossula spongiosa on foretibia	(0) Absent or reduced; (1) Present
112	Ventral vestiture of mid trochanter	(0) Glabrous; (1) Long, slender setae; (2) Short, thick setae; (3) Round to rodlike papillae
113	Presence of small tubercles on mid trochanter	(0) Absent; (1) Present
114	Presence of ventral papillae on mid femur	(0) Absent; (1) Present
115	Distribution of papillae on mid femur	(0) Basally; (1) Longitudinally along at least half the length of the femur
116	Presence of ventral longitudinal carinae on mid femur	(0) Absent; (1) Present
117	Presence of small tubercles on mid femur	(0) Absent; (1) Present

Table 4.1. (Continued).

Character no.	Character	Character states
118	Distribution of small tubercles on mid femur	(0) Entirely throughout femur; (1) Throughout ventral femoral surface; (2) Restricted to ventroapical half of femur
119	Vestiture of small tubercles on mid femur	(0) Glabrous; (1) With setae
120	Medial projection of mid femur	(0) Absent; (1) Present
121	Anterior subapical projection on mid femur	(0) Absent; (1) Present
122	Posterior subapical projection on mid femur	(0) Absent; (1) Present
123	Paired ventroapical projections on mid femur	(0) Absent; (1) Present
124	Presence of small tubercles on mid tibia	(0) Absent; (1) Present
125	Distribution of small tubercles on mid tibia	(0) Entirely throughout tibia; (1) Throughout ventral tibial surface; (2) Restricted to ventroapical half of tibia
126	Vestiture of small tubercles on mid tibia	(0) Glabrous; (1) With setae
127	Presence of fossula spongiosa on mid tibia	(0) Absent or reduced; (1) Present
128	Ventral vestiture of hind trochanter	(0) Glabrous; (1) Long, slender setae; (2) Short, thick setae; (3) Round to rodlike papillae
129	Presence of small tubercles on hind trochanter	(0) Absent; (1) Present
130	Basal curvature of hind femur	(0) Not curved or slightly curved posteriorad; (1) Extremely curved posteriorad, almost from 45 to 90 degree angle
131	Presence of small tubercles on hind femur	(0) Absent; (1) Present
132	Distribution of small tubercles on hind femur	(0) Entirely throughout femur; (1) Throughout ventral femoral surface; (2) Restricted to ventroapical half of femur
133	Vestiture of small tubercles on hind femur	(0) Glabrous; (1) With setae
134	Medial projection of hind femur	(0) Absent; (1) Present
135	Anterior subapical projection on hind femur	(0) Absent; (1) Present
136	Posterior subapical projection on hind femur	(0) Absent; (1) Present
137	Paired ventroapical projections on hind femur	(0) Absent; (1) Present
138	Presence of small tubercles on hind tibia	(0) Absent; (1) Present
139	Distribution of small tubercles on hind tibia	(0) Entirely throughout tibia; (1) Throughout ventral tibial surface; (2) Restricted to ventroapical half of tibia
140	Tarsal segmentation	(0) 1-segmented; (1) 2-segmented; (2) 3-segmented

Table 4.1. (Continued).

Character no.	Character	Character states
FOREWING		
141	Extension of corium	(0) Restricted to areas adjacent to basal wing veins and with pterostigmalike appearance; (1) Well-developed corium
142	Vestiture of corium	(0) Long, simple setae absent; (1) Long, simple setae sparse; (2) Long, simple setae dense
143	Proximal part of M and Cu	(0) Separate veins; (1) Forming one vein, at least partially
144	Distal part of M and Cu	(0) Separate veins; (1) Fused basally
145	Extension of distal part of M	(0) Absent; (1) Present
146	Distal part of R	(0) Absent; (1) Present
147	Development of distal R cell	(0) Incomplete; (1) Complete, although may appear faint apically
ABDOMEN		
148	Division of dorsal synlaterotergite I+II	(0) Not divided; (1) Divided
149	Expansion of dorsal synlaterotergite I+II	(0) Not expanded; (1) Laterally expanded; (2) Posterior tubercle
150	Dorsal laterotergite III armature	(0) Unarmed; (1) Posterior tubercle
151	Dorsal laterotergite IV armature	(0) Unarmed; (1) Posterior tubercle
152	Dorsal laterotergite V armature	(0) Unarmed; (1) Posterior tubercle
153	Dorsal laterotergite VI armature	(0) Unarmed; (1) Posterior tubercle
154	Ventral connexival suture on sternite II	(0) Absent; (1) Present
155	Carinulation of intersegmental suture between sternites II and III	(0) Not carinulate; (1) Carinulate
156	Development of intersegmental sutures between III and VI	(0) Absent or reduced; (1) Well-developed
157	Sternal surface	(0) Smooth or slightly wrinkled; (1) Punctate, at least laterally
158	Medial structure of sternites	(0) Flat; (1) Medially depressed, at least partially; (2) Convex or keeled, at least partially
159	Paramedian sternal carinae	(0) Absent; (1) Present
160	Spiracle shape	(0) Ovoid or elliptical; (1) Circular
MALE GENITALIA		
161	Anteroposterior thickness of median pygophore process	(0) Flattened; (1) Thickened, at least partially

Table 4.1. (Continued).

Character no.	Character	Character states
162	Lateral thickness of median pygophore process	(0) Flattened; (1) Thickened, at least partially
GLANDS		
163	Presence of meshlike Brindley's gland evaporatorium	(0) Absent; (1) Present
164	Dorsal abdominal scent gland (DAG) I ostioles in adults	(0) Absent; (1) Present
165	DAG II ostioles in adults	(0) Absent; (1) Present
166	DAG III ostioles in adults	(0) Absent; (1) Present
167	Size of DAG III ostioles relative to DAGs I and II ostioles in adults	(0) Similar size; (1) Larger
FEMALE		
168	Wing form	(0) Macropterous (reaches/surpasses tergite VII); (1) Brachypterous (reaches/surpasses tergite VI but not VII); (2) Micropterous (minute leathery wing pads covering, at most, base of abdomen); (3) Apterous
169	Ocellar lens	(0) Absent; (1) Present
170	Eye height in lateral view	(0) Less than or half of head height; (1) More than half of head height; (2) Absent
171	Postclypeal surface	(0) Flat or convex; at most a thin medial line visible but not distinctly depressed; (1) Distinctly depressed
172	Antennal shield	(0) Absent, not expanded; (1) Present, expanded
173	Scapus length	(0) Not surpassing or barely surpassing clypeal apex; (1) Surpassing clypeal apex
174	Greatest length of pronotum relative to greatest width	(0) Wider than long; (1) About as long as wide; (2) Longer than wide
175	Anterior pronotal lobe greatest length relative to posterior pronotal lobe	(0) Shorter than posterior lobe; (1) About as long as posterior lobe; (2) Longer than posterior lobe
176	Anterior pronotal lobe greatest width relative to posterior pronotal lobe	(0) Less than width of posterior lobe; (1) About as wide as posterior lobe
177	Lateral depressions on posterior pronotal lobe	(0) Absent; (1) Present
178	Extension of pronotal longitudinal depression on anterior lobe	(0) Not reaching anterior margin; (1) Reaching or nearly reaching anterior margin; (2) Absent or reduce
179	Presence of pronotal longitudinal depression on posterior lobe	(0) Absent; (1) Present

Table 4.1. (Continued).

Character no.	Character	Character states
180	Development of paramedian scutellar processes	(0) Weakly developed; (1) Well developed; (2) Absent
181	Ventral vestiture of foretrochanter	(0) Glabrous; (1) Long, slender setae; (2) Short, thick setae; (3) Round to rodlike papillae
182	Presence of small tubercles on forefemur	(0) Absent; (1) Present
183	Presence of ventral papillae on forefemur	(0) Absent; (1) Present
184	Presence of small tubercles on foretibia	(0) Absent; (1) Present
185	Presence of ventral papillae on fore tibia	(0) Absent; (1) Present
186	Ventral vestiture of mid trochanter	(0) Glabrous; (1) Long, slender setae; (2) Short, thick setae; (3) Round to rodlike papillae
187	Presence of small tubercles on mid femur	(0) Absent; (1) Present
188	Presence of ventral papillae on mid femur	(0) Absent; (1) Present
189	Presence of small tubercles on mid tibia	(0) Absent; (1) Present
190	Presence of ventral papillae on mid tibia	(0) Absent; (1) Present
191	Ventral vestiture of hind trochanter	(0) Glabrous; (1) Long, slender setae; (2) Short, thick setae; (3) Round to rodlike papillae
192	Presence of small tubercles on hind femur	(0) Absent; (1) Present
193	Presence of ventral papillae on hind femur	(0) Absent; (1) Present
194	Presence of small tubercles on hind tibia	(0) Absent; (1) Present
195	Presence of ventral papillae on hind tibia	(0) Absent; (1) Present
196	Medial structure of sternites	(0) Flat; (1) Medially depressed, at least partially; (2) Convex or keeled, at least partially
197	Paramedian sternal carinae	(0) Absent; (1) Present
COLORATION		
198	Coloration coding 1	(0) Cryptic; (1) Aposematic, uniform metallic, or aposematic and metallic
199	Coloration coding 2	(0) Cryptic and uniform metallic; (1) Aposematic or aposematic and metallic
SEXUAL DIMORPHISM		
200	Sexual dimorphism	(0) Limited; (1) Extreme
MALE BODY LENGTH		
201	Male body length from clypeal apex to posterior abdominal margin	Continuous values

Table 4.2. Taxon sampling, USI codes, ethanol molecular specimen collection numbers (RCW), depositories (Dep.), and GenBank accession numbers for sequenced specimens. Asterisks indicate sequences retrieved from GenBank.

					GenBank accession no.					
Subfamily	**Taxon**	**USI**	**RCW**	**Dep.**	**16S**	**18S**	**28S D2**	**28S D3–D5**	**COI**	**Wg**
Ectrichodiinae	*Bannania* sp.	UCR_ENT 00119027	3064	UCR	KU764537	KT221910*	KT221939*	KT221968*	KT221890*	
	nr *Bannania* sp.	UCR_ENT 00004465	609	UCR		KT221937*	KT221966*	KT221996*	KT221908*	
	nr *Bayerus* sp.	UCR_ENT 00004096	2001	UCR			KU764586	KU764601	KU764610	
	nr *Bayerus* sp.2	UCR_ENT 00004102	1969	UCR			KU764585	KU764600		
	Brontostoma colossus	UCR_ENT 00119017	3049	UCR	KU764538	KT221911*	KT221940*	KT221969*	KT221891*	KU764611
	Brontostoma nanus	UCR_ENT 00123508	4030	UCR	KU764539		KU764574	KU764589	KU764603	KU764612
	Brontostoma sanguinosum	UCR_ENT 00002617	1243	UCR	KU764540	KT221912*		KT221970*	KT221892*	KU764613
	Caecina affinis	UCR_ENT 00004440	2636	UCR	KU764541	KT221913*	KT221941*	KT221971*	KT221893*	
	Ceacina n. sp.	UCR_ENT 00123509	3959	UCR	KU764542		KU764575	KU764590		
	Centraspis ducalis	UCR_ENT 00119021	3014	UCR	KU764543	KT221914*	KT221942*	KT221972*	KT221894*	KU764614
	Cimbus sp.	UCR_ENT 00123510	4722	UCR		KU764569	KU764576	KU764591	KU764604	KU764615
	Cleptria corallina	AMNH_PBI 00218770	14	UCR	FJ230388*	FJ230462*	FJ230543*	FJ230621*, FJ230700*		JQ897871*
	Cryptonannus n. sp.	UCR_ENT 00002757	1433	UCR	KU764544	KT221915*		KT221973*	KT221895*	KU764616
	Daraxa sp.	UCR_ENT 00119016	3076	UCR	KU764564	KT221938*	KT221967*	KT221997*	KT221909*	

Table 4.2. (Continued).

Subfamily	Taxon	USI	RCW	Dep.	GenBank accession no.					
					16S	18S	28S D2	28S D3–D5	COI	Wg
	Distirogaster tarsalis	UCR_ENT 00006366	2898	CAS		KT221918*	KT221945*	KT221976*	KR606396*	
	Distirogaster n. sp.	UCR_ENT 00088090	3018	UCR		KT221917*	KT221944*	KT221975*	KR606395*	
	Distirogaster n. sp.2	UCR_ENT 00007158	2881	UCR		KT221916*	KT221943*	KT221974*	KR606393*	
	Ectrichodia crux	UCR_ENT 00119022	3026	UCR		KT221919*	KT221946*	KT221977*	KT221896*	KU764617
	Ectrichodia lucida	AMNH_PBI 00218769	13	UCR	FJ230387*	FJ230461*	FJ230542*	FJ230620*, FJ230699*		JQ897878*
	Ectrichodia sp.	UCR_ENT 00123511	3715	UCR	KU764545		KU764577	KU764592	KU764605	KU764618
	Ectrychotes atripennis	AMNH_PBI 00218932	188	UCR	FJ230424*	FJ230503*	FJ230584*	FJ230661*, FJ230740*	JQ942322*	JQ897879*
	Ectrychotes serdangensis	AMNH_PBI 00218830	76	UCR		FJ230479*	FJ230560*	FJ230638*, FJ230717*		
	Ectrychotes sp.	UCR_ENT 00119028	571	UCR	KU764546	KT221920*	KT221947*	KT221978*	KT221897*	KU764619
	Glymmatophora crassipes	UCR_ENT 00088087	3020	UCR	KU764547	KT221921*	KT221948*	KT221979*	KR606415*	KU764620
	Haematoloecha sp.	UCR_ENT 00123512	3956	UCR	KU764548		KU764578	KU764593	KU764606	KU764621
	Katanga sp.	UCR_ENT 00123513	4029	UCR	KU764549		KU764579	KU764594	KU764607	KU764622
	Maraenaspis coccinea	AMNH_PBI 00218772	16	UCR	FJ230389*	FJ230463*	FJ230544*			JQ897889*
	Marojejycoris brevifrons	UCR_ENT 00006480	2923	CAS	KU764550	KT221922*	KU764580	KT221980*	KR606417*	KU764623

Table 4.2. (Continued).

Subfamily	Taxon	USI	RCW	Dep.	GenBank accession no.					
					16S	18S	28S D2	28S D3–D5	COI	Wg
	Mendis apicimaculata	UCR_ENT 00119026	2647	UCR	KU764551	KT221923*	KT221949*	KT221981*	KT221898*	KU764624
	Microstemmatoides atrocyanea	UCR_ENT 00119029	3029	UCR	KU764552	KT221924*	KT221950*	KT221982*	KT221899*	
	nr *Neolibavius* sp.	UCR_ENT 00003965	1830	UCR	KU764565	KT221925*	KT221951*	KT221983*	KT221900*	
	Neoscadra sp.	UCR_ENT 00004990	2139	UCR	KU764553		KU764581	KU764595	KU764608	KU764625
	Pothea lugens	UCR_ENT 00119018	3304	UCR	KU764554	KT221927*	KT221953*		KT221902*	KU764626
	Pothea sp.	UCR_ENT 00123514	4028	UCR	KU764555		KU764582	KU764596	KU764609	
	Racelda sp.	AMNH_PBI 00218801	41	UCR	FJ230398*	FJ230472*	FJ230553*	FJ230631*, FJ230710*		JQ897915*
	Rhiginia aimara	UCR_ENT 00119019	3077	UCR	KU764556	KT221928*	KT221954*		KT221903*	KU764627
	Rhiginia cinctiventris	AMNH_PBI 00218891	139	UCR	FJ230410*	FJ230490*	FJ230571*	FJ230648*, FJ230727*	JQ942333*	JQ897917*
	nr *Scadra* sp.	UCR_ENT 00052213	699	UCR	JQ897793*		JQ897634*	JQ897710*		JQ897880*
	Santosia sp.	UCR_ENT 00004138	2046	UCR	KU764557	KT221930*	KT221956*	KT221986*	KT221905*	KU764628
	Tanindrazanus marginatus	UCR_ENT 00006887	2902	CAS	KU764558	KT221931*	KT221957*	KT221987*	KR606423*	
	Tanindrazanus tenebricus	UCR_ENT 00006723	2931	CAS	KU764559	KT221932*	KT221958*	KT221988*	KR606430*	
	Tanindrazanus varicolor	UCR_ENT 00006482	2949	UCR		KT221933*	KT221959*	KT221989*	KR606433*	

Table 4.2. (Continued).

Subfamily	Taxon	USI	RCW	Dep.	GenBank accession no.					
					16S	18S	28S D2	28S D3–D5	COI	Wg
	Toxopus brucei	UCR_ENT 00045338	2901	UCR			KT221960*	KT221990*	KR606438*	
	Toxopus fisheri	UCR_ENT 00045431	2910	CAS	KU764560		KT221961*	KT221991*	KR606446*	
	Toxopus griswoldi	UCR_ENT 00006435	2916	CAS		KT221934*	KT221962*	KT221992*	KR606448*	
	Toxopus toamasina	UCR_ENT 00007056	2951	SU			KT221963*	KU764597	KR606457*	
	Toxopus vazimba	UCR_ENT 00006472	2953	CAS	KU764561	KT221935*	KT221964*	KT221993*	KR606462*	
Emesinae	*Emesaya incisa*	AMNH_PBI 00219017	282	UCR	FJ230436*	FJ230515*	FJ230598*	FJ230672*, FJ230751*	JQ942323*	
Peiratinae	*Peirates punctorius*	AMNH_PBI 00218960	216	UCR	FJ230430*	FJ230508*	FJ230590*	FJ230666*, FJ230745*		
Saicinae	*Saica* sp.	AMNH_PBI 00218796	42	UCR	FJ230399*	FJ230473*	FJ230554*	FJ230632*, FJ230711*		
Tribelocephalinae	*Abelocephala* sp.	UCR_ENT 00106432	3308	UCR	KU764536	KU764567	KU764572	KU764588	KU764602	
	Abelocephala sp.2	UCR_ENT 00107032	3963	UCR		KU764566	KU764571	KU764587		
	Afrodecius sp.	UCR_ENT 00092725	4711	SAMC		KU764568	KU764573			
	Opistoplatys sp.	UCR_ENT 00119024	3056	UCR		KT221926*		KT221984*		
	Opistoplatys sp.2	UCR_ENT 00052187	1592	UCR	JQ897851*	JQ897612*	JQ897682*	JQ897767*		
	Tribelocephala peyrierasi	AMNH_PBI 00219033	287	CAS	FJ230440*	FJ230521*	FJ230601*			

Table 4.2. (Continued).

Subfamily	Taxon	USI	RCW	Dep.	GenBank accession no.					
					16S	18S	28S D2	28S D3–D5	COI	Wg
	Tribelocephala sp.	UCR_ENT 00119023	3048	UCR	KU764562		KT221965*	KT221994*	KT221906*	
	Tribelocodia sp.	UCR_ENT 00122389	4721	UCR		KU764570	KU764583	KU764598		
	Xenocaucus n. sp.	UCR_ENT 00020656	4707	CNC	KU764563		KU764584	KU764599		

Table 4.3. Phylogenetic logistic regression parameter estimates for the effects of log-transformed male body length on coloration in 133 Ectrichodiinae and Tribelocephalinae species. Aposematic, uniform metallic, and aposematic and metallic color patterns are treated as one state with cryptic coloration as a separate state. Parameters are phylogenetic signal (*a*), intercept (b_0), and the regression coefficient (b_1), and p-values ≤0.05 are indicated in bold. Abbreviations: Phylo, phylogram; Ultra0, ultrametric tree generated with penalty set to 0; Ultra10, ultrametric tree generated with penalty set to 10; Ultra10000, ultrametric tree generated with penalty set to 10000; Par, parameter; SE, standard error; BS, bootstrap; C, converged; NC, non-converged.

Tree/dataset	**Par**	**Estimate**	**SE**	***p*-value**	**BS mean (C and NC)**[a]	**BS confidence interval (C and NC)**[a]	**BS *p*-value (C and NC)**[a]	**BS mean (C only)**	**BS confidence interval (C only)**
Phylo TA+UM									
	a	–1.1535			–1.5274	(–2.8656, –0.3581)	**0.0088**	–1.4888	(–2.8745, –0.2869)
	*b*0	0.3058	0.4420	0.4902	0.1196	(–2.2624, 2.3698)	0.8072	0.0866	(–2.2315, 2.0630)
	*b*1	0.8857	0.2498	**0.0005**	0.4773	(–2.5222, 2.7345)	0.4456	0.4658	(–2.3864, 2.3871)
Ultra0 TA+UM									
	a	–0.6208			–0.0933	(–3.4576, –0.4597)	**0.0180**	–0.9365	(–3.4482, –0.4129)
	*b*0	–0.2458	0.5559	0.6592	–0.2911	(–1.5741, 1.0498)	0.6160	–0.2907	(–1.5610, 1.0496)
	*b*1	0.7983	0.2325	**0.0008**	0.8945	(–0.3999, 1.6021)	**0.0008**	0.8944	(–0.4014, 1.6000)
Ultra10 TA+UM									
	a	–0.0238			–0.5099	(–3.9681, 1.0646)	**0.0240**	–0.5153	(–3.8989, 1.0510)
	*b*0	–0.1197	0.6771	0.8598	–0.1841	(–1.5967, 1.3802)	0.7960	–0.1840	(–1.5876, 1.3802)
	*b*1	0.7557	0.2309	**0.0014**	0.8776	(0.3657, 1.5349)	**<0.0001**	0.8774	(0.3666, 1.5349)
Ultra10000 TA+UM									
	a	–0.0233			–0.4881	(–2.9396, 0.9724)	**0.0168**	–0.4949	(–2.9080, 0.9357)
	*b*0	–0.1195	0.6772	0.8598	–0.1738	(–1.5637, 1.3268)	0.7976	–0.1741	(–1.5596, 1.3268)
	*b*1	0.7557	0.2308	**0.0014**	0.8779	(0.3791, 1.5382)	**0.0008**	0.8786	(0.3798, 1.5382)

[a] Parametric bootstrapping was performed to obtain means and confidence intervals, as well as test the null hypotheses that there is no phylogenetic signal in the residuals, (H_0: $a = -4$, 1-tailed test) and that the regression coefficient equals 0 (H_0: $b_1 = 0$, 2-tailed test).

Supplementary material 4.1. Twenty-eight female-based terminal taxa, with sources of male morphological data indicated. Abbreviations: I, digital images; T, taxonomic descriptions; M, direct examination of specimens at the British Natural History Museum, London, United Kingdom and/or the American Museum of Natural History, New York, USA.

Female-based terminal taxa	Male morphological source	Taxonomic reference
Adrania gracilis	I, T, M	Miller (1955)
Afrodecius sp.2		
Antiopuloides formosus		
Apocaucus sp.		
nr *Bayerus* sp.		
nr *Bayerus* sp.2		
Borgmeierina dentata		
Centraspis decoratus	I, T, M	Villiers (1951)
Centraspis petersi	M	
Cimbus productus	M	
Ectrichodia lucida	I, T, M	Lepeletier & Serville (1825); Stål (1865); Villiers (1948)
Ectrichodiella minima	T	Gil-Santana et al. (2013)
Glymmatophora dejoncki	T	Villiers (1948)
Haematorrhophus pedestris	I, T, M	Distant (1904)
Katanga sp.		
Maraenaspis coccinea		
Mendis notata	M	
Microstemmatoides occidentalis	T, M	Villiers (1973)
Microstemmatoides similis	T	Schouteden (1952); Villiers (1973)
Neoscadra sp.		
Okondo collarti		
Opistoplatys sp.2		
Pothea sp.		
Racelda sp.		
nr *Scadra* sp.		
Schottus perakensis	I, T	Miller (1941)
Schuhella hermosa		
Tribelocodia sp.		

Supplementary material 4.2. Morphological character matrix in nexus format for cladistic analysis.

```
#NEXUS
BEGIN TAXA;
          TITLE Taxa;
          DIMENSIONS NTAX=156;
          TAXLABELS
                    Adrania_cylindrica Adrania_gracilis Adrania_macra Antiopuloides_formosus
Austrokatanga_monteithi Bannania_sp nr_Bannania_sp Bayerus_cuneatus Borgmeierina_dentata
Brontostoma_colossus Brontostoma_nanus Brontostoma_sanguinosum Caecina_affinis
Caecina_n_sp Caloundranius_formosus Centraspis_decoratus Centraspis_ducalis
Centraspis_petersi Cimbus_ambulans Cimbus_productus Cimbus_sp Cleptria_cinctiventris
Cleptria_corallina Cleptria_maculata Cricetopareis_boliviana Cricetopareis_tucumana
Cryptonannus_punctella Cryptonannus_n_sp Daraxa_ambrosettii Daraxa_sp
Distirogaster_tarsalis Distirogaster_n_sp Distirogaster_n_sp2 Doblepardocoris_hirsuta
Doblepardocoris_vittata Ectrichodia_crux Ectrichodia_lucida Ectrichodia_sp
Ectrichodiella_minima Ectrichodiella_n_sp Ectrichodiella_n_sp2 nr_Bayerus_sp2 nr_Bayerus_sp
Ectrychotes_serdangensis Ectrychotes_sp Ectrychotes_atripennis Gibbosella_conisimilis
Gibbosella_pallidalata Gibbosella_planiscutum Gibbosella_quadocris Glymmatophora_aeniceps
Glymmatophora_carolae Glymmatophora_crassipes Glymmatophora_dejoncki
Haematoloecha_limbata Haematoloecha_nigrorubra Haematoloecha_sp
Haematorrhophus_linnaei Haematorrhophus_pedestris Jorgcoris_aczeli Katanga_linnavuorii
Katanga_petchkovskyi Katanga_sp Labidocoris_insignis Leptomendis_bipartita
Leptomendis_breddini Lyramna_vigil Lyramna_n_sp Lyramna_n_sp2 Maraenaspis_bidens
Maraenaspis_coccinea Maraenaspis_crocata Marojejycoris_auranticorium
Marojejycoris_brevifrons Marojejycoris_francais Marojejycoris_notadichroa
Marojejycoris_ranomafana Mendis_apicimaculata Mendis_notata Microsanta_montana
Microsanta_pusilla Microstemmatoides_atrocyanea Microstemmatoides_occidentalis
Microstemmatoides_similis nr_Neolibavius_sp Neosantosia_lugubris Neoscadra_annulicornis
Neoscadra_ornata Neoscadra_sp Nularda_lesnei Nularda_nobilitata Nularda_thoracica
Okondo_collarti Philodoxus_principalis Pothea_lugens Pothea_ventralis Pothea_wygodzinsky
Pothea_sp Pseudopothea_luacesi Racelda_moerens Racelda_spurca Racelda_sp Rhiginia_aimara
Rhiginia_cinctiventris Rhiginia_immarginata Santosia_erythrocephala Santosia_maculata
Santosia_sp Scadra_aliena Scadra_cincticornis Scadra_illuminata nr_Scadra_sp
Schottus_baramensis Schottus_gracilis Schottus_perakensis Schuhella_hermosa Schuhella_n_sp
Schuhella_n_sp2 Sciaphilocoris_ornata Sinchocoris_colombiaensis Sinchocoris_panamaensis
Synavecoris_dimorphus Tanindrazanus_marginatus Tanindrazanus_tenebricus
Tanindrazanus_varicolor Tasmanocoris_evansi Toliarus_trichrous Toxopus_brucei
Toxopus_fisheri Toxopus_griswoldi Toxopus_toamasina Toxopus_vazimba Vilius_lateralis
Vilius_macrops Wygodzinskyocoris_nigripes Zirta_caudorubrum Zirta_hirticornis Zirta_limbata
Abelocephala_sp Abelocephala_sp2 Afrodecius_sp Afrodecius_sp2 Apocaucus_sp
Centrogastocoris_alacris Megapocaucus_sp Opistoplatys_sp Opistoplatys_sp2
Tribelocephala_peyrierasi Tribelocephala_sp Tribelocodia_ashei Tribelocodia_sp Xenocaucus_sp
Emesaya_incisa Carayonia_sp Saica_sp Peirates_punctorius
          ;
END;
```

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BEGIN CHARACTERS;
	TITLE  Character_Matrix;
	DIMENSIONS  NCHAR=201;
	FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = "  1 2 3 4
5";
	MATRIX
	Adrania_cylindrica           111113211-111121--111121112111111-
12111211??121????2112111221211-2211221222211-1121221?2121112211-21--11111--2211-
21--11111--22111--11111-
321?12221311111221211212????1211122212112?1?1??1?1??1?1?11111
	Adrania_gracilis            111112211-111121--111121112112111-
121112112312 1????11221111221212222121212222 11-112122132121112211-21--11111--
2211-21--11111--21111--11111-321?12221311111221111??2112-
1211121212122211112111111111??221
	Adrania_macra              111113211-111121--111121112111111-
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2211-21--11111--22111--11111-
321?12221311111221211??2?????????????????????????????????11?
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311112211311111221212??2?????????????????????????????????22?
	Austrokatanga_monteithi      311133211-112121--11111--12111111-
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	Bannania_sp                121212211-112111--111122222111111-
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3121122113222112212122121222?????????????????????????????22?
	nr_Bannania_sp              121212211-112111--111122222112111-
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3111212113222112212122121222?????????????????????????????22?
	Bayerus_cuneatus            131113211-111121--111122222111111-
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323??1??1311111221112??2?????????????????????????????????22?
	Borgmeierina_dentata         111113211-111111--11112??22111111-
12111211??121????111?1111221212222 1211-222211-112122?3?1???12?1??2??11111--
2?1??21--11111--22111--11111-
321?112212111112?1??2???????????????????????????????????11?
	Brontostoma_colossus         11111321211111111--111122122112111-
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2)2211211121224121141211111111221
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Brontostoma_sanguinosum 1111132121111111--111122122112111-2211121124122221221122111121221222212121222111-112122133222112412111--11111--2412111--11111--21111--11111-3211122211111112213112121222(1 2 3)221121?12122?1?1??1?1??1?1??1221

Caecina_affinis 131113211-111121--111122222112111-1211121122112?????22?2121222322222211122122311-112122133122211211-122111111--1211-122111111--121122111111-3131122213222212222122121222????????????????????????????????22?

Caecina_n_sp 131112211-111121--211122222111111-2211121123112?????12?1121222322222221122122311-112122133122211211-122111111--1211-122111111--121122111111-3131122213222212222122121222????????????????????????????????22?

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Centraspis_decoratus 11121321??411111--11112212211211213211121122112?????11211111211222?2211122222311-212122232222111111-11--11111--2111-11--11111--21111--11111-311112221211111221211??2????12212211122121111111111111111121221

Centraspis_ducalis 1112132121111111--11112212211211213211121122112221121121111121122222211121222311-2121222322221114121123111111--2412111--11111--21111--11111-311112221211111221211122122212?1?2?112?22?1?1??1?1??1?1??1221

Centraspis_petersi 11121321??111111--11112212211211213211121122122?????1121111121122222211121222311-212122233222111?1??11--21111--2?1??11--11111--21111--11111-311112221211111221211??2????122122111222241211?1?1?111111211

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Cimbus_productus 111133121-111121--111122122112211-3111121124113?????112111122222222221111-122311-1121221?1122212111-11--22211--1111-11--22211--11111--22211-311212221311111221212??2????122111111222211111111111111121221

Cimbus_sp 111133121-111121--111122122111111-3111121124113?????112111122222222221111-122311-112122111122212111-11--22211--1111-11--22211--11111--22211-311212221311111222212??21221????????????????????????????????22?

Cleptria_cinctiventris 111113213111112211?1112212211111212211121124122?????1121111121121222211122222211-112122?3?122212211-11--11111--2211-11--11111--22111--11111-311112211311111221?11112?????????????????????????????????????22?

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          Cleptria_maculata          111213213111111--
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3)2111211121221111111111111111221
          Cricetopareis_tucumana       111213213211111--121122122111111-
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3)2111211122222111111111111111221
          Cryptonannus_punctella       111213212131111 1--111122122111111-
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          Cryptonannus_n_sp          111213212111111--111122122112111-
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          Daraxa_ambrosettii          111212211-111111--111122122112111-
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2)2111213121224121141211411111221
          Daraxa_sp                111213211-111111--111122122112111-
121112112312 12?1?2112111122212122221212122211 1-1121222321211124122 21--11111--
2412221--11111--22111--11111-
321?1222111111122131221212 22?????????????????????????????11?
          Distirogaster_tarsalis
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2???2111???23?1-
2???2111???22?1???1111??32111221131111122 1?12??21222??????????????????????????????2
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          Schottus_baramensis         111213211-111111--
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          Schottus_gracilis           111213211-111111--
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311112221211111221111 2212 1222??????????????????????????????22?
          Schottus_perakensis         111213211-111111--
11112212211211212211122111121?????11211112221212222111222222 11-
11212223322111 2?11-11--11111--2?11-11--11111--21111--11111-
31111222121111122111 2??2????1211221112122311113111111111111221
          Schuhella_hermosa           1113132 1??411111--21112??2211??11-
221112111 1222?????112?1111221222222 1211-222111-11212223312?112111-11--11111--2111-
11--11111--21111--11111-3111122112111112221 12??2???????????????????????????????????22?
          Schuhella_n_sp              111312211-411111--211121222111111-
2211121111223?????1121111122122222221211-222111-1121222 3312?112111-11--11111--
2111-11--11111--21111--11111-
311112211211111222112 2121222??????????????????????????????22?
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Schuhella_n_sp2 111313211----111--211121222111111-
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Sciaphilocoris_ornata 111132111----121--111121122111111-
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Sinchocoris_colombiaensis 111113211-411111--111121122112111-
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Synavecoris_dimorphus 111212211-211121--211121122111111-
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2111-122211111--211122211111-3112211-
121111122121 2??2122231111212122 22?2???121211212111112
Tanindrazanus_marginatus
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Tanindrazanus_varicolor
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Tasmanocoris_evansi 1312122131111121--111121112111111-
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2211-11--11111--22111--11111-
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Toliarus_trichrous
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Toxopus_brucei
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          Toxopus_toamasina          121213211-
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          Toxopus_vazimba
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          Vilius_lateralis          1113132121121111--
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12212221122111111 1-11--11111--2111-11--11111--21111--11111-
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          Vilius_macrops          111313212112121 1--
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          Wygodzinskyocoris_nigripes    1111132121411111--111122222111111-
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          Zirta_caudorubrum          111113211-111111--111122112111111-
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          Zirta_hirticornis          111113211-111111--111122112111111-
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          Zirta_limbata          111113211-111111--111122112111111-
22111211111222212211211111211212221111212221 11-112122233121111311-11--11111--
2311-11--11111--21111--11111-
32111222111111221311??21222121112111212 2?1?1??1?1??1?1??1221
          Abelocephala_sp          142123211----121--11111--
21112212112112312242 11?????11?1111?211??1-2???21-11---2211111 2???1???11211-11--
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          Abelocephala_sp2          142122211----121---1111--
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          Afrodecius_sp          142122211----12??11111--
211121122122222122421 2?????11?11111211??1-112121-221322211211 2???1???11211-11--
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        Afrodecius_sp2            142122211-----2???11111--
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11111??1??2??21221????????????????????????????????11?
        Apocaucus_sp              142?1221????????????1?1--
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        Centrogastocoris_alacris      142133211----121--11211--21212211-
2211221???212????11?1111211????2???11-21---22112211??????11211-11--11111--1211-
11--11111--12111--11111-3131122??11112?21112???2221112112111 2??-
21111211112111 1?1111
        Megapocaucus_sp           142?11211----1??????1?1--
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        Opistoplatys_sp           142133111----121--11121--21212211-
2211221???21222111111111 11211221-211111-11---22112211??11--11211-11--11111--1211-
11--11111--12111--11111-3131121-111111 2?2111212 12221????????????-??????????????????11?
        Opistoplatys_sp2          142133111----121--11111--21212211-
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11--11111--12111--11111-31311221111112?21112??12221????????????-
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        Tribelocephala_peyrierasi     142133211---1121--11211--21211111-
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11--11111--12111--11111-31321???111112?212111 1?2221112112111 2??-
21111211112111 1?1111
        Tribelocephala_sp         142133211---1121--11211--21211111-
322222111521222111111111 11211221-211121-21---22112111??11--11211-11--11111--1211-
11--11111--12111--11111-31321?2211111 12?21211111 2221????????????-
??????????????????11?
        Tribelocodia_ashei        14?133211-41?111---11?22122111211-
221123111111?????11111111211??1-112121-222111-1121221111??11221-
121211112121221-
121211112121221212111 1211132122211111??21212???1221?????????????????????????????
11?
        Tribelocodia_sp           ???13?211-
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2??????????221111??11221-1???1111???12?1-
1???1111???12?1???1111??1???????111111??21?12???1221??????????????????????????????11
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        Xenocaucus_sp             142211211----121---1111--21112211-
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11--11111--12111--11111-2132121-111111 2?2131????1221413?12232???-
21111211112111 11112
        Emesaya_incisa            231112111-111121--11111--12121111-
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11--11111--1?111--11111-31111?1-11111121211 12??2111---------------------------------
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          Carayonia_sp               121123211-111121--11111--21121111-
12111211112211221121211111211212121211111-21---22111?22???11--21211-11--11111--1211-
11--11111--12111--11111-31?21?1-1111112?21112???111----------------------------------
          Saica_sp                   131111211-111121--11111--12121111-
1211121111221?????311311111-1211-211111-21---22111?2221111--21211-11--11111--1211-
11--11111--12111--11111-31321???1111112121112???111----------------------------------
          Peirates_punctorius        3311132121111121--21111--12111111-
111111111122311211312321121-22121211111-11---2211111121111--22221-122111111--2221-
122111111--221122111111-3-------1111112121112??22221---------------------------------
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END;

BEGIN CHARACTERS;
          TITLE  Character_Matrix2;
          DIMENSIONS  NCHAR=1;
          FORMAT DATATYPE = CONTINUOUS GAP = - MISSING = ?;
          MATRIX
          Adrania_cylindrica          12.62
          Adrania_gracilis            11.00
          Adrania_macra               12.95
          Antiopuloides_formosus          ?
          Austrokatanga_monteithi     10.80
          Bannania_sp                  5.92
          nr_Bannania_sp               6.64
          Bayerus_cuneatus             8.68
          Borgmeierina_dentata            ?
          Brontostoma_colossus        25.11
          Brontostoma_nanus           12.48
          Brontostoma_sanguinosum     25.87
          Caecina_affinis              8.71
          Caecina_n_sp                10.89
          Caloundranius_formosus       9.03
          Centraspis_decoratus        36.00
          Centraspis_ducalis          24.56
          Centraspis_petersi              ?
          Cimbus_ambulans             21.00
          Cimbus_productus            21.00
          Cimbus_sp                   19.12
          Cleptria_cinctiventris      11.72
          Cleptria_corallina          13.97
          Cleptria_maculata            7.87
          Cricetopareis_boliviana     15.75
          Cricetopareis_tucumana      19.65
          Cryptonannus_punctella       5.75
          Cryptonannus_n_sp            6.44
          Daraxa_ambrosettii           8.41
          Daraxa_sp                    7.97
          Distirogaster_tarsalis      15.93
```

Distirogaster_n_sp	21.48
Distirogaster_n_sp2	29.20
Doblepardocoris_hirsuta	9.56
Doblepardocoris_vittata	9.38
Ectrichodia_crux	?
Ectrichodia_lucida	23.00
Ectrichodia_sp	21.83
Ectrichodiella_minima	3.79
Ectrichodiella_n_sp	4.82
Ectrichodiella_n_sp2	3.30
nr_Bayerus_sp2	?
nr_Bayerus_sp	?
Ectrychotes_serdangensis	10.23
Ectrychotes_sp	12.51
Ectrychotes_atripennis	10.91
Gibbosella_conisimilis	8.07
Gibbosella_pallidalata	5.18
Gibbosella_planiscutum	5.32
Gibbosella_quadocris	5.57
Glymmatophora_aeniceps	17.93
Glymmatophora_carolae	15.77
Glymmatophora_crassipes	17.94
Glymmatophora_dejoncki	21.00
Haematoloecha_limbata	10.23
Haematoloecha_nigrorubra	14.98
Haematoloecha_sp	11.13
Haematorrhophus_linnaei	23.61
Haematorrhophus_pedestris	22.00
Jorgcoris_aczeli	16.75
Katanga_linnavuorii	12.07
Katanga_petchkovskyi	11.64
Katanga_sp	?
Labidocoris_insignis	10.86
Leptomendis_bipartita	8.98
Leptomendis_breddini	8.09
Lyramna_vigil	11.58
Lyramna_n_sp	13.69
Lyramna_n_sp2	15.60
Maraenaspis_bidens	21.85
Maraenaspis_coccinea	?
Maraenaspis_crocata	17.67
Marojejycoris_auranticorium	8.96
Marojejycoris_brevifrons	6.58
Marojejycoris_francais	6.50
Marojejycoris_notadichroa	7.94
Marojejycoris_ranomafana	5.46
Mendis_apicimaculata	14.91
Mendis_notata	?

Microsanta_montana	11.32
Microsanta_pusilla	8.61
Microstemmatoides_atrocyanea	13.03
Microstemmatoides_occidentalis	12.25
Microstemmatoides_similis	17.50
nr_Neolibavius_sp	4.51
Neosantosia_lugubris	12.25
Neoscadra_annulicornis	19.16
Neoscadra_ornata	16.92
Neoscadra_sp	?
Nularda_lesnei	31.30
Nularda_nobilitata	26.58
Nularda_thoracica	16.66
Okondo_collarti	?
Philodoxus_principalis	34.35
Pothea_lugens	13.93
Pothea_ventralis	19.85
Pothea_wygodzinsky	16.95
Pothea_sp	?
Pseudopothea_luacesi	11.37
Racelda_moerens	13.51
Racelda_spurca	16.16
Racelda_sp	?
Rhiginia_aimara	15.59
Rhiginia_cinctiventris	17.84
Rhiginia_immarginata	17.37
Santosia_erythrocephala	15.49
Santosia_maculata	13.27
Santosia_sp	13.49
Scadra_aliena	11.33
Scadra_cincticornis	12.88
Scadra_illuminata	11.27
nr_Scadra_sp	?
Schottus_baramensis	11.52
Schottus_gracilis	9.50
Schottus_perakensis	11.50
Schuhella_hermosa	?
Schuhella_n_sp	5.92
Schuhella_n_sp2	6.05
Sciaphilocoris_ornata	7.33
Sinchocoris_colombiaensis	7.65
Sinchocoris_panamaensis	9.85
Synavecoris_dimorphus	5.76
Tanindrazanus_marginatus	15.33
Tanindrazanus_tenebricus	16.12
Tanindrazanus_varicolor	16.00
Tasmanocoris_evansi	7.68
Toliarus_trichrous	8.22

```
          Toxopus_brucei              11.84
          Toxopus_fisheri             10.29
          Toxopus_griswoldi            9.39
          Toxopus_toamasina            12.02
          Toxopus_vazimba              11.99
          Vilius_lateralis           17.45
          Vilius_macrops              20.16
          Wygodzinskyocoris_nigripes    16.38
          Zirta_caudorubrum            14.21
          Zirta_hirticornis           14.29
          Zirta_limbata               17.95
          Abelocephala_sp              3.25
          Abelocephala_sp2              2.53
          Afrodecius_sp               7.98
          Afrodecius_sp2               ?
          Apocaucus_sp                 ?
          Centrogastocoris_alacris      6.59
          Megapocaucus_sp              4.24
          Opistoplatys_sp             7.54
          Opistoplatys_sp2             ?
          Tribelocephala_peyrierasi     ?
          Tribelocephala_sp           12.50
          Tribelocodia_ashei          2.27
          Tribelocodia_sp             ?
          Xenocaucus_sp                3.40
          Emesaya_incisa               -
          Carayonia_sp                -
          Saica_sp                  -
          Peirates_punctorius          -
;
END;
```

Supplementary material 4.3. PCR protocols for each targeted gene region. Denaturation, annealing, and extension were conducted for 35 cycles for all gene regions sampled.

Gene region	**PCR step**	**Temperature (°C)**	**Time**
16S, 18S rDNAs	Initial denaturation	94	5 min
	Denaturation	94	30 sec
	Annealing	48	30 sec
	Extension	72	45 sec
	Final extension	72	7 min
28S D2, 28S D3–D5 rDNAs	Initial denaturation	94	5 min
	Denaturation	94	30 sec
	Annealing	50	30 sec
	Extension	72	45 sec
	Final extension	72	7 min
COI mtDNA	Initial denaturation	94	10 min
	Denaturation	94	45 sec
	Annealing	43	45 sec
	Extension	72	1 min
	Final extension	72	7 min
Wg npcDNA	Initial denaturation	94	5 min
	Denaturation	94	30 sec
	Annealing	54	1 min
	Extension	72	1 min
	Final extension	72	7 min

Supplementary material 4.4. Molecular character matrix in nexus format for cladistic analysis.

```
#NEXUS
BEGIN TAXA;
	TITLE Taxa;
	DIMENSIONS NTAX=59;
	TAXLABELS
		Abelocephala_sp Abelocephala_sp2 Afrodecius_sp Bannania_sp
nr_Bannania_sp nr_Bayerus_sp nr_Bayerus_sp2 Brontostoma_colossus Brontostoma_nanus
Brontostoma_sanguinosum Caecina_affinis Caecina_n_sp Centraspis_ducalis Cimbus_sp
Cleptria_corallina Cryptonannus_n_sp Daraxa_sp Distirogaster_n_sp Distirogaster_n_sp2
Distirogaster_tarsalis Ectrichodia_crux Ectrichodia_lucida Ectrichodia_sp Ectrychotes_atripennis
Ectrychotes_serdangensis Ectrychotes_sp Emesaya_incisa Glymmatophora_crassipes
Haematoloecha_sp Katanga_sp Maraenaspis_coccinea Marojejycoris_brevifrons
Mendis_apicimaculata Microstemmatoides_atrocyanea Neoscadra_sp nr_Neolibavius_sp
Opistoplatys_sp Opistoplatys_sp2 Peirates_punctorius Pothea_lugens Pothea_sp Racelda_sp
Rhiginia_aimara Rhiginia_cinctiventris Saica_sp Santosia_sp nr_Scadra_sp
Tanindrazanus_marginatus Tanindrazanus_tenebricus Tanindrazanus_varicolor Toxopus_brucei
Toxopus_fisheri Toxopus_griswoldi Toxopus_toamasina Toxopus_vazimba
Tribelocephala_peyrierasi Tribelocephala_sp Tribelocodia_sp Xenocaucus_n_sp
	;
END;

BEGIN CHARACTERS;
	TITLE  Character_Matrix;
	DIMENSIONS  NCHAR=4055;
	FORMAT DATATYPE = DNA GAP = - MISSING = ?;
	MATRIX
Abelocephala_sp 	??????????????????ATCTTTTTTG----------TTATTATATA-
AAATTTGGCCTGCCCTATGA---
AAATGATTAAATGGCCGCAGTATTTTAACTGCGCTAAGGTAGCATAATAAATTGTCT
TTTAATTAAGGGCTTGTATGAATGGTTGGACGAAATAAAAACTATTTTG--TTTTAT--
TTTTTGAATTTAATTTTTTAGTTAAAAGGCTAA-
GATTTTATTAAGGGACGAGAAGACCCTATAAAGCTTTATACGTGA-GGTA--
GGCACCCAATTTTAG-ATTTTTAAT-
AAATTGGGTGCTTTATTTGTGGCGTATTAAATTGGGGTGATTGGGGAATTC-
TTTTAACTTCTGA--ATA-CTGATTTCGTTAATAT--TCGAT--TTAATTGATCCAGT---
TTTATTGATTATAAGATTAAGTTACTTTAGGGATAACA-
GCGTAATTTTCTCAGAGAGTTCAAATTGATGAGATAGTTTGCGACCTCGATGTTGGAT
TAAAA-TTAGCC-GTTGGTGCAGCAATTA-ATTGG-
CTTGGTCTGTTCGACCATTGAAAT-
TTTACATGAT??????????????????????????????????????????????????????????????????????????????
??????????????????????????????????????????????????????????????????CGAGGATCCA-
TTGGAGGGCAAGCCT--
GGTGCCAGCAGCTGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAACCAAATTC-------------------------------
--------TTGGTAT----AAACTAAGCT---TAAATGCTGAAT-T-TGTAT-CCA----------TA-G-
```

TAATTTT--GTTTGCCGA---
TTTCTCCTATTTCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
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TATAATGACTCGGCGGGGAGCTTCT-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAA???
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AGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGA
AACCGCTCAGGGGTAAACGGAAAAGAACTGAA-
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TTTGAGATGGTCATTTC-GCCCTATCCAG----TGCAA--ACTGTG--TTAG-
TGGGTTTGATTACTCGCATTTT-ATAA--
GATGTCAAGGCAGCGGTGGACCGCACTTCTTCCTTAGT-
AGGACGTTGCGACTTGTCACTA-GAAT-----ACTTTAAGT--AT-A-----GTTAA---
AGTGCCTGTAT-T-TAACAA--TTAGACTTT---------ACTATTTAATTA--------
TAGTAATTTCATTTTTATTTACAGC-TTTAA--CAT--AAAA------ATACCGAGTATAT------
----
ACTTGTGACAATAACGATCGATGGTTGTTGAGCCGCTAAAAATTATAAATAATTTTT
ATTTATA-----G------TTATAAGCGTT------------TATTGGCCT-TTATACAA-
GTGGTTGTCAAGTTCAAGTGTTAATT-A-
TTGTCAATATGTCCTTTTTATGTTCAGTCATG-TTA-ATCTTACTA-CTGTTGGTA---
TAAT-TG--TG-CCTTT--AACAG--TGCTTA--
CAACACTGGTCGGCAGCGATCAAG???
???
???ATTATCAA
GGGAAGATGG--AAAT-----------ATTATACAAGTAAC--------------------------------
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TTCCCGCATTCCCAGGGCGTTTG-TTACTCTCA---TG-
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GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
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CCTATTATGTAGTTGCTCAT??
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??ATGAGTACA
CTTTAAGT-CCTTTAACGAGGATCCA-TTGGAGGGCAAGCCT--
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TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAACAAAATTC----------------------------
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TGGGTGTGATTACTCGCATTTT-ATA----
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AGGACGTTGCGACTTGTCAATA-GAAT-----ACTTTAAGT--AT-A-----GTTAA---
AGTGCCTGTAT-T-TAATAA--TAAGACTTT---------ACTATTTAATTA--------
TAGTAATTTCATTTTTATTTACAGC-TTTAA--CAT--ATAA------ATACTGAGTATAT-------
---ATTTTTGACAATAACGATCAATGGTTGTTGAGCCGCTAAAAATTATAAATTAGTT---
TTTATA-----A------TTATTAGCGTT-------------TATTGCCT-TTATACAA-GTGGTTTT-------
AGGTATTAGTT-A-ATGTCGAAACTTTT--------TTCCGTCTAG-CTA-ATCCTACTA-
CTGTTGGTATAATAAT-TG--TG-CCTTT--GACAG--TGCTTA--
CAACACCGGTCGGCAGCGATCAAG???AGA
GAGGTAAGAAAAGAATGGTTAAATATTTGTTTCTTACACTTTTTTTT-------
TCCCCCTTTTTCAAGACCTTAAACAAGAAATGAGGTGGGG-------------

GGGGGGAAAAAAG--------ACTCTTCTTTTTTT------------------TTT-
TTTTTTTAAGGGAAGATGG--AAAT-----------GTTAATTAATTAAC----------------------------
----AACTTTT----------------------------GTT-AATTTCTAATAAT-
TTCCCGCATTCCCAGGGCGTTTG-TTACTCTCA---AG-
TGAGTCTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
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AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGAT------------T-----
TTAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCTATGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCC???
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TTACCCACTCCCGGCACGGGGAGGTAGTGACAAAAAATAACGATACGGGACTCTATT
GAGGCCCCGTAATCGGAATGAGTACACTTTAAAT-CCTTTAACAAGGATCCA-
TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGGAATCC-----------------------------
--------CTGGTTC----AGACTAGGCT-TTA--CTGCCGAAG-T-TTGTT-CCG----------TG-G-
TGATACC--GTTTGCCGA---
TTTCTCCTACTTCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
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TAAAGGAATTGACG???
???AGT

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GTACGTGAAACCGCTCAGGGGTAAACGGAAAAGACCTGAA--
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AGGGTTTTGCCGCTCGCATTTT-TTT-----
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AGGACGTTGCGACCTGTTAAAT--AAT-----ATTCTAAGT--AT-A-----GTTAA---
AGTGTCTGTAT-TTTAGGTT--ATACTGAAA---------------------------------
GGTTTACCTTTTTTTACAGC-TTTAA--CAAT-------TAC-ATACCGAATA-------------
TTAATTAACAGTATCGATTGGTGG-TGTTGAGCCACTTTTAAAATTTATATA--
TTTATATATA-----GT-----TTAAAAGTGTC--------------TTTGGTC-GTCTGCAA-GTGGGT---
------AGATATTAATT-A-ATGTCGGGCTT-TT--------GTCCGTCTAG-TTA-AATCTCTTA-
CTGTTGGTA----GAT-AG--TG-CCTCA--GACCG--TGCTTA--
CAACACCGTTCGGCAGCGATCCAGGTTCAGGCTCTTATCCGACCCGTCTTGAAACAC?
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TTTAATTTTA-AGGTTTAACCTGCCCAATGA-----
TTTATTTAATGGCCGCAGTATATTAACTGTGCTAAGGTAGCATAATCATTTGTCTTTT
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AATTTTTTTATGGGACGAGAAGACCCTATAGATCTTTATATTTAT-ATTT--
ATTTATTAATTTTAGGATTGA-------
TGATTTTTTTAAGTGAATTAATTATTTAATTGGGGTGATTGAAGAATTT-
TGTGAACTTCTTT--TTTGTTGTTTTCATAATTT---TATGT--
ATATTTGATCCA??
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??????????????????????CCGTAATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--

GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAATTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTTTCGCACTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGAATGTCCTGTCGGTGGTGAATAAAATTC------------------------------
--------CTGGTGC----TAACCTAGGC-TTTTATAGCTGAAG-T-CGGTG-CCG----------TG-
GTTGATTTT--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAAGTAGGCCGACACATTTACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
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TG-CCTTGC-ATTAG--TGCCTA--
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AAAGTAAAGGATAAAAAGATAAAAG-------------------AAGTTAAG--------
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TCTAAACATAGAT-CTCCCGCATTCCCAGGGCGCTTG--CACTTGCTT--TG-
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TCAAGAATTGATATTGTACTTCATGATACATACTATGTTGTAGCCCATTTCC??????????
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??GTAATTCCAGCTCCAATAGCGT
ATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGG
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T-ATGTG-CCG----------CG-G-TGAGTTC--ATTCGCCGA---
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??AAA
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TAAACGGAGAAGACCTGAA--TATTCGAAAGAGGAGATTCACGTCTTACCAC----
TGCCCGACATTGAAGTAC-----ACTGAGATGGTAA-TTT-GCCCTGTCCAG----TTTAT--
ACTGTT--GCAG-AGGGTTTTGCCGCTCGTATTTC-ATTT--
AAGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGCA--AAT-----ACTCTAAAT--AT-G-----ATTAA---
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TTTACTGACAGTAACGACTGATGG-TGTCGAGCCGCTTCTGTAAA----------------------------
-----AGGAAGCGTC---------CTTTACAAAGCC-GTTTACAA-GTGGGCTAG-------
GTACTTGGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-GGCCTCCTA-
CTGTTTGTA----AAC-TG--TG-CCCTG--GACAG--TGCTTA--
TACCGCCGGTCGGCAGCGATTCAGGTTCAGGCTC???????????????????????????????????
????????????????????????????????ACGCAAGTCATTGGGTGAT-

AAAAAACCCAAAGGCGTAATGAAAGTAAAGAGTTTGAGAGATAAAGGA----------------
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TTCGCTCAAGGGAAGATGG--ATAT-----------
CTTTATTTTTTCTTTTATTAACAATCGGTT----------GTGTTTTAATATTT-
TTAATATTATACACAATTGTTGTTTTTTTTT-TGGAAAATATAGA-
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AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GTGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAG-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGCGGGATTCGGATCAGAGTGCC??
????????????????????????????AAGTTTATATTCTCATTTTACCTGGATTTGGATTAATTTC
CCATATTGTATCCATAGAAACAGGTAAAACAGAAGCCTTCGGTTCTTTAGGAATAAT
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GTTAACAGGAATTATTCTAGCAAATTCAAGAATTGATATTGTACTTCACGACACCTA
CTATGTAGTAGCCCATTTTCATT??
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???GTGCAGCCCTAAGTAGGTGGT
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GGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAG

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TTGTTTAACTTATAAATGTA---TTAAGAGATGTTTA-TAC-GCCCTATTTAG----TGCAA--
ACTGTA--ATAG-TGGGTTTATTCGCTCGCATTTATATT----
TAGTAAGAACAATGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGATCTGTCAGAT--AAT-----ACTCTAAGT--AT-G----CATTAA---
AGTGTCTGTAT-T-TAAATGTGGTTGAAATTGAA--ATTTTTTTTTGTTTTG---------------
CTATATTTTTTTTACAGC-TTTAA--TCA--AT----TATAATACTGAGTATTT----------
TATACTGATAGTAACAAATGATAG-TGTTGAGCCACTTGCT--------------------------------T--
-TTTAAAAAGTG--------------TCTAGCC-GTTTACAA-GTAGGTATTTAGG-----
CTTAAGCT-A-ATTTCGGGCTT-GT------TAGTCCGTATAG-CTG-GGCCACTTA-
CTGTTGGTA----AACGTGTTCATTCTTA--
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??GCGT
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CGAGTATATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
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GTTGTGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
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CCTCGGCTT???
???????????????????????????????????????TTGGACATCCGGAAGTTTATATTCTAATTTTA
CCAGGATTTGGTATTATCTCCCATGTAATTGCAATAGAAACTGGAAAAAATGAAGCA
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GATATTATTCTACACGATACATACTATGTAGTAGCCCACT???????????????????????????
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???GTGCAGCCCTAAGTAGGTGGT
AAACTCCATCTAAGGCTAAATACAACTACGAGTCCGATAGCGAACAAGTACCGTGA
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GGGTAAACGGAGAAGATCTGAA--TTTTCGAAAGGGGAGATTCACGTCTTACCATA--
TTGTTTAACTTTTAAATGTA---TTAAGAGATGTTTA-TTC-GCCCTATTCAG----TGCAA--
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AGGACGTTGCGATCTGTCAGAT--AAT-----ACTCGAAGT--AT-G-----TTTAA---
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TATACTGATAGTAACAATTGATAG-TGTTGAGCCACTTATT-----------------------------------
TAATATAGTG--------------TCTAGCC-GTTTACAA-GTAGGTATTAGGC---TTATTTAGCT-
A-ATTTCGGGCTT-TT------TAGTCCGTATAG-CTA-GGCCACTTA-CTGTTGGTA----
GGCGTG--CT-TCTTG--GACAGATTGCTTA--
AAACACTGATCAGCAGCGATTCAG???
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???????????????????????????AATGAAA-ATCTTGCATTCCTAGGGCGCTTG-
TCTCTCGCAT--TG-
CGAGTATATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCATT---TTTT-----T---
TAGTTGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCTCGGCT??
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AATTTATTTG-AAGTTTAACCTGCCCAATGAA-

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AATTAATTTTAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCAATTGTCT
TTTAATTGAAGGCTTGTATGAAAGGTTGAATGAAACATATACTTTCTTT-ATATTGT-
AATTTTGAATTTAATTTGTTAGTTAAAAGGCTAA-
CATTTTTTTATGGGACGAGAAGACCCTATAGATCTTTATATTAAT-AGTT--
TATATTTAAATTG---TTTTA-------
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TATTAACTTCTAG--TTT--TTATTTCATTAATA---TATGT--TTAATTGATCCAAT---
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GCGTAATTTCTTCGGAGAGTTCATATTGATGAAGGAGATTGCGACCTCGATGTTGGA
TTAAAA-TAAGTT-TTAGGCGTAGAAGTTG-AATTA-
CTAGGTCTGTTCGACCTTTAATAT-
TTTACATGATCTGAGTTCAAACCGG??????????????????????????????????????????????????
???????????????????????????????CCGTAATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGGAATCC------------------------------
--------CCGGTGC----TTCTTGGGCT-TCT-TTAGCCTAAG-T-ATGTG-CCG----------TA-C-
GGATGCC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
GAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
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TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
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ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAATTGACGGAAGG??????????????????????????????????????????????????????????
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AGTGCAGCCCTAAGTAGGTGGTAAACTCCATCTAAGGCTAAATACAACTACGAGTCC
GATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCA
AGAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGAACTGAA--
TTTTCGAAAGGGGAGATTCACGTCTTACCATA--TTGTTTAGCTTTTAAATGT----
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AGGGTTTATTCGCTCGCATTTA-ATA----
TAGTAAAAACAATGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGATCTGTCAGTT--AAT-----ACTCTAAGT--AT-G-----GTTAA---
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TTTTTTCTTTTTACAGC-TTTAA--TCAT-------TTT-ATACTGAGTATTT-------
TAAACTTATGACAGTATCAATTGATGG-TGTTGAGCCACTTTATAACTT--------------------
-----TT---TCTAAAGTGTC--------------TTTAGCCGGTTTACAA-GTAGGTTT-----------
AGTAGTT-A-ATTTCGGGCTT-TT------CGGTCCGTATAA-CTA-GGCCACTTA-
CTGTTAGTA----AAC-TG--TG-CCTTA--GACTG--TGCTTA--
TAACACTGATCAGCAGCGATCCAG???????????????????????????????????????????????????
??????????????????????????????????????????????????ACCCAAAGGCATAATAAAAGTAAA
GAGTAATTTAATTATAA-------------------AAG-----------TGTTAGTACTTTTTTT----------------
TATTA-AATTCTTAAAGGAAGATAG--ATTT-----------
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AATTTCTTTAATAGAAAAAGAGTGAT--------------ATTTTTTATTTCTC-TT----------TT-----
----------TT-TTTTTTTAGAAAT-ATCTTTCATTCCTAGGGCGCTTG-TTTCTCGCAT--TG-
CGAGTATATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCAAT----------------
GAAACGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCTCGGCT??
???TATATATTTTAATCTTACCCGGA
TTTGGTATTATTTCACACTCTATCAGTATAGAGACCGGAAAAAATGAAACCTTTGGA
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TGTCTGGCTTYTGTACAGTTAAAACATGCTGGATGCGTTTACCACCATTTCGTCTTGT
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GTAATCCTAGATTAGGTATACAAGGAACACACGGACGCCAGTGTAACGCTACATCAC
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Brontostoma_nanus ??????????????????CATGTCCTTTTGT--TT-----
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AATTGGGGGCTAGGATGAACGGGTTTATGAAGCACTTTCTTTCTTT-TTATTAT-
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TATTTTATTAAAGGACGAGAAGACCCTATAGAGCTTTATATTTAA-TTAT--
TTGTTTAATTTTT---GTTAATAT-----
TTTTTATACAATTGAGTTAATTATTTGATTGGGGTGATTTTGGTATTT-
TTATAACTACTTT--TTA--AAGTTTCATTTATG---AATGT--TTTTATGATCCATT---
ATTTATGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTTATTTTCTTGGAGAGTTCTTATTGATAAGGAAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAGTA-ATGGGCGTAGCAGTTC-ATTTA-
CTGGGTCTGTTCGACCTTTAAAGT-
TTTACA???
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GAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGAACTGAA--
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AGTGTCTGTAT-A-AGAAGA--ATAGT--------------TTTATTTTAT--------
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-T--TATATTGATAGTATCAAATGATAG-TGTTGAGCCACATTTT-----------------------------
AA---ATAAATGTGTT-------------TTAAGCC-GTTTACAA-GTAGGTTT-----------
AGTAGTT-A-ACTTCGGACTT-TT------CGGTCCGTATAA-CTATCACCACTTA-
CTGTTAGTA----AAC-TG--TG-CCTTT--AACTG--TGCTTA--
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??AGGCATAATGAAAGT
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--TA--------------TT-AAAGGAAAAAATT-
ATCTTGCATTCCTAGGGCGCTTG-TAACTCGCAT--
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CCTCGGCTT??
?????????????????????????????????????TTGGCCACCCTGAAGTATATATCCTAATTCTA
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Brontostoma_sanguinosum ????????????AAAAACATGTCTTCTTGT--T------
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GCGTTATTTCTTCGGAGAGTTCATATCGATGAAGGAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAGTC-
TTGGATGTAGTG??
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GGACGCC--ATTTGCCGA---
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ATAATGACTCGGCGGGGAGCTTCT-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAG????????????
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???TACGCAAGTCATTGGGTAA
T--TAAAACCCAAAGGCGCAATAAAAGTAAAGAGCAATTTAAATAAGT-------------------
ATTAGTAC------------------TTTTT----------------TTTTA-AATTCTTAAAGGAAGACAG--
ATTT-----------TTAACTGCTTTAAT--AAGAAAATTC-----
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AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCAAT----------------
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AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCTCGGCTTTCTTAAAA------------------
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A---
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Caecina_affinis ????????????AAAAACATGTCCTTTAGT---------
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TTTA??
???GGATCCA-
TTGGAGGGCAAGTCT--
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ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAATTC------------------------------
--------CTGGTAC----TGCGTAGGCT-TTAAATAGCTGAAG-T-TTGTG-CCG----------TG-G-
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ACCCGGGAAACCAAAGCTTTTGGGTTCC???
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??????????AAATACAACCACGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGTTGA
AAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGA

GAAGATCTGAA--TGTTCGAAAGAGGAGATTCACGTCTTACCAG---
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ACTGTG--GTGG-TGGGTTTTGCCGCTCGTATTTC-ATT----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTATCAGAC--AAT-----ACTCTAAGT-TTT-A-----ATTAA---
AGCGCCTGTGT-A-TTGGTT--GTATATT--------------TATTTATA-----------------
TAATCTTTATACAGC-TTTAA--TAA--AT----TTT---ACTGGGTATTTA---------
TTTTCTGATAGTAACGACTGATGG-TGTAGAGCCACTTTAC----------------TATATA-----
ATG-----TAAAAGTGTCC--------GATTTTTTGGGC-GTTTACAA-GTGAGTTTAG-----
GCTTTTTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-TGCCGCTTA-
CTGTTTGTA----AAC-TG--CG-CCTTG--GACAG--TGCTTA--
CAACACCGGTCGGCAGCGATTCAGGT???
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????????????????????????????????????TTTTTTTTAATCTTTGAT--------------TCT-
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-------------TT-TAATTAAG-----------------GA-AAAAAAGTTTTGA-
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???????????????????????AGTTTATATTTTAATTTTACCCGGATTTGGATTAATTTCCCAT
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CGATATTAACTATTGGATTATTGGGATTTATTGTATGAGCCCATCATATATTTACAGT
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Caecina_n_sp ???????????????ACATGTCCTTAAGT---------
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ATTAATTTAGGTCTGTTCGACCTATAAAAT-
TTTACATGA???
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?????????????GAGTGCAGCCCTAAGTAGGTGGTAAACTCCATCTAAGGCTAAATACAA
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TGTTCGAAAGAGGAGATTCACGTCTTACCAG---TTGCTCTACTTTGAGATAC----
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TAATCTTTATACAGC-TTTAA--TAA--AT----TTT---ACTGGGTATTTA---------
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----ATG-----TGAAAGTGTTT---------TTTCTTAGGC-GTTTACAA-GTGAGTTA--------
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TTGTTTGTA----AAC-TG--CG-CCTTA--GACAG--TGCTTA--
CAACACCGGTCGGCAGCGATTCAGGTTCAGGCTCTTATCCGACCCGTCTTGAA???????
??????????????????????CAAGGAGTTTATCGTGTACGCAAGTCATTGGGTGAT--
AAAAACTCAAAGGCGAAATGAAAGTAAAGAATGCAAGATAGAGAG------------------
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---------------------------------------TT-AGAAAAATTTTGA-
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AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT-----------T---
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AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCCGGCTTTCTTAAAA-----------------
TTGAAGCCGTGGGATTCTGATCAGAGTGCCAAGTGGGCCAATTTTGGTA?????????????
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Centraspis_ducalis ????????TATCAAAAACATGTCCTTTAGT--TG-----
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TAA???
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GGTATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-AGCCGCCTA-
CTGTTTGTA----AAC-TG--TGCCCTTG--AACAG--TGCTTA--

CAACACCGGTCGGCAGCGATC??
??AGTAAAGAGTAGA
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-----------------------TAT---TT-ATATTAAG-TAA-------------GTA-TTTAAAATATAGA-
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Daraxa_sp ????????????????ACATGTCCTTTAGT--TT-----TATTTATTA-
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----ATG-----TAAAAGTGTT-------------CATTTGCC-GTTTACAA-GTGGGTTAGGT----
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ATCCGCCTA-CTGTTTGTA----AAC-TG--TG-CCTTG--AACAG--TGCTTA--
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TG???
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TTTATATTTTTTTT---GTTTA--------
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CTGTTTGTA----AAC-TG--TG-CCTTG--AACAG--TGCTTA--
CAACACCGGTCAGCAGCGATCCAGGTTCAGGCTCTTATCCGGTCCGT????????????????
??????CTTGAAACACGGACCAAGGAGTTTATTGTGTACGCAAGTCATTGGGTGAT-
ACAAAACCTAAAGGCGAAATGAAAGTAAAGAGTAGTAAGATAGAGG-------------------
AAGAAATT--------TATTTTTCATCCTTGAT---------------TCT-

TGCTCTCAAGGGAAGATGG--TTAT-----------CTTATTTTAAATTA-----------------------------
-----TAT---T---TAATTAT-AT---------------TA-TTTAAGATGTAGA-
TTCCCGCATTCCCAGGGCGCTTG-TTTCTCGCTT--TG-
CGAGTTTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCTCTCAGGATAGCTTGCGCTCGAT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGGATTCGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAAC
TGGCGCTGTGG???????????????????????????????????????CATTTAATCCTTCCGGGATT
TGGTTTAATTTCCCATATTATTTCAATAGAAACAGGAAAAAGAGAAGCATTTGGTCC
TTTAGGTATAATTTATGCAATAATTACTATCGGACTTTTAGGATTTATTGTATGGGCA
CACCATATATTCACTGTAGGTATAGATGTTGATACACGAGCATATTTTACCTCAGCTA
CTATAATTATTGCAGTTCCTACAGGAATTAAAATTTTTAGATGATTAGCAACTTTACA
TGGAAGAATATTAACTTTCTCTCCTAGACTTTTATGAGCATTAGGCTTCGTATTCCTTT
TTACTATTGGAGGATTAACAGGAGTAATTTTAGCAAATTCAAGTATTGATATTGTACT
ACACGATACTTACTATGTAGTAGCACATTT?????????????????????????????????ATGTCT
GGATCATGTACAGTAAAAACATGTTGGATGCGTTTACCACCGTTTYGTGTCGTCGGA
GATAATTTAAAAGATCGTTTCGACGGCGCATCACGCGTTATGGTAAGCAATTCTGGT
TCATTACGCGGCA---
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AGCCACCAGGCGTTAAAGATCTAGTATATTTAGAACCATCGCCATTATTCTGCGAAC
GTAATCCAAAGCTTGGCATACAGGGTACACATGGA??????????????????????????????????
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???GCAGCAGGCAC
GCAAATTACCCACTCCCGGCACGGAGAGGTAGTGACAAAAAATAACGATACGGGAC
TCTATTGAGGCCCCGTAATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCCAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAGTCC-----------------------------
--------CCGGTAC----TGCGTAGGCT-TTTATTAGCTGAAG-TTGTTTA-TCG----------TG-G-
TGACTTC--ATTTGCCGA---
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TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAAAGCGAAAGCA
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GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
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ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
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CAACACGGGAAACCTCACCAGGCCAGGACATTGGAAGGATTGACAGATTGATAGCT
CTTTCTTGATTCAGTGGGTAGTGGTGCATGGCCGTTC?CGTGTTGCTTGATAGTGCAG
CCCTAAGTAGGTGGTAAACTCCATCTAAGGCTAAATACAACCACGAGTCCGATAGCG
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TATTCGAAAGAGGAGATTCACGTCTTACCAC---TTGCTCGACTTTAAAGTGC----
TCTTGAGATGGTAA-TTC-GCCCTATTCAG----TATTT--ACTGTG--GTAG-
AGGGTTTTACCGCTCGCATTTT-ATA----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAAT--AT-G-----ATTAA---
AGTGACTGTCT-A-GAGGTT--ATAGAAT---------------TTATTTTA------------------
TAATCTTTTTACAGC-TTTAA--TTA--AT----TTT---ATTGAGTATTTA---------
TTTTCTGACAGTAACGACTGATGG-TGTAGAGCCACTTTA-----------------------------ATT---
--TTAAAGTGTTC--------ATTTGTATTGCC-GTTTACAA-GTGGGTTTT-------
GATATTAGTT-A-ATGTTGAACTT-TT--------GTTCGTCTAACCTA-AGTCGCCTA-
CTGTTTGTA----AAC-TG--TG-CCTTG--AACAG--TGCTTA--
CAACACCGGTCAGCAGCGATCCAGGTTCAGGCTCTTATCCGGTCCGT????????????????
??????CTTGAAACACGGACCAAGGAGTTTATTGTGTACGCAAGTCATTGGGTGAT-
ACAAAACCTAAAGGCGAAATGAAAGTAAAGAGTAGTAAGATAGAGG-------------------
AAGAAATT--------TATTTTTCATCCTTGAT---------------TCT-
TGCTCTCAAGGGAAGATGG--TTAT-----------CTTATTTTA--
-----------AATTAT-AT---------------TA-TTTAAGATGTAGA-
TTCCCGCATTCCCAGGGCGCTTG-TTTCTCGCTT--TG-
CGAGTTTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
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GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCTCTCAGGATAGCTTGCGCTCGAT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGGATTCGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAAC
TGGCGCTGTGG??
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Ectrychotes_sp ???????????????AACATGTCCTTATGG--T------
TATATATTTA-AGGTTTAACCTGCCCAATGA---
AAATTTTTTAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCAATTGTCTT

TTAATTAAGGGCTTGAATGAATGGTTGGACAAAATATTAACTTTCTTT-TTATTAA--
TTAATGAATTTAATTTTTAAGTGAAAAAGCTTA-
AATATATTTAAGGGACGAGAAGACCCTATAGAGCTTTATATTTAT-ATTT--
ATTTAATGAATTT---GTTTA--------
TGTATTTTATAATATTTTGTGTATTTTGTTGGGGTGACAGTAAAATTT-
TATTAACTTTTAT--TTT-TTATTATCATTTATT---TATGT--TACTTTGATCCATT---
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GCGTAATTTATTCGAAGAGTTCATATTGATGAATAAGTTTGCGACCTCGATGTTGGAT
TAAAA-TTAGAT-TTAGGCGCAGAAGTTT-ATTAT-CTAGGTCTGTTCGACCTTTAATTT-
TTTACATGATCTGA???
?????????????????????????CCGTAATCGGAATGAGTACACTTTAAAT-
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TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATAAAGTCC------------------------------
--------CCGGTAC----TGCGTAGGCT-ATTATTAGCTGAAGTT-GTTTA-TCG----------TG-G-
TGACTTT--ATTTGCCGA---
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TTAATGACTCGGCGGGGAGCTTCT-
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TAAAGGAATTGACGGAAGG??
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????????????????????AAACTCCATCTAAGGCTAAATACAACCACGAGTCCGATAGCGAA
CAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGT
GAAACCGCTCAGGGGTAAACGGAGAAGAACTGAA--
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TTTTGAGATGGTAA-TTC-GCCCTATTCAG----TATTT--ACTGTG--GTAG-
AGGGTTTTACCGCTCGCATTTT-ATA----
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AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAAT--AT-G-----ATTAA---
AGTGACTGTCT-A-GAGGTT--ATAGAAT---------------TTATTTA------------------
TAATCTTTTTACAGC-TTTAA--TTA--AT----TTT---ATTGAGTATTTA---------
TTTTCTGACAGTAACGACTGATGG-TGTAGAGCCACTTTA-----------------------------ATT---
--TTAAAGTGTTC--------ATTTGTATTGCC-GTTTACAA-GTGGGTTTA-------
GATATTAGTT-A-ATGTTGAACTT-TT--------GTTCGTCTAA-CTA-AGTCGCCTA-
CTGTTTGTA----AAC-TG--TG-CCTTG--AACAG--TGCTTA--
CAACACCGGTCAGCAGCGATCCAGGTTCAGTCTC????????????????????????????????????
???????????????????????????TGTACGCAAGTCATTGGGTGAT-
ACAAAACCTAAAGGCGAAATGAAAGTAAAGAGTAGTAAGATAGAGG-------------------
AAGAAATT--------TATTTTTCATCCTTGAT---------------TCT-
TACTCTCAAGGGAAGATGG--TTAT-----------CTTATTTTAAATTA------------------------------
-----TAT---T---TAATTAT-AT---------------TA-TTTAAGATGTAGA-

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CGAGTTTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
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GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCTCTCAGGATAGCTTGCGCTCGAT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGGATTCGGATCAGAGTGCCAA-----------------------------------
G????????????????????????????????AAGTGTATATTTTAATTCTTCCCGGATTTGGATTAA
TTTCTCATATTATTTCTATAGAAACAGGAAAGAGAGAAGCTTTTGGACCTTTAGGTAT
AATTTATGCAATAATTACTATTGGTCTTTTAGGGTTTATTGTATGAGCACATCATATA
TTTACTGTAGGTATAGATGTTGATACACGGGCTTATTTTACCTCTGCTACTATAATTA
TTGCAGTACCTACTGGTATTAAGATTTTTAGATGATTAGCTACATTACATGGAAGAAT
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TTACTATGTAGTAGCACATTTTCA??????????????????????????????ATGTCTGGATCATG
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AAAGATCGTTTCGACGGCGCATCACGCGTTATGGTAAGCAATTCTGGTTCATTACGC
GGCA---
ATGGAGGACGTAAGAGTCGTTATAATTTACAATTGAAACCATACAATCCAGATCATA
AACCACCAGGTGTTAAAGATCTAGTATATTTAGAGCCATCGCCATTATTCTGCGAAC
GTAATCCAAAGCTTGGTATACAGGGTACACATGGACGTCAATGTAATGCTACATCGC
AGGGTGTTGAAGGTTGTGATTTAATGTGTTGTGG

Emesaya_incisa CGCCTGTTTATCAAAAACATGTCCTTTTGA--TT----
TTTAAAATTTT-AGGTCTAACCTGCTCTATGA-----
TTTATTAAATGGCCGCGGTATTCTAACTGTGCTAAGGTAGCATAATTATTTGTCTTTT
AATTGAAGGCTGGAATGAATGGTTGGACAAATAACTTTCTTTCTTT-ATTTTAA-
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AATTTTTTTGTAGGACGAGAAGACCCTATAGATCTTTATATAAGC-TTTA--
ATAATAATATTTT---GGTAAGTG----
TAATTTTTATTATTATGGTTTGTATTTTGTTGGGGTGATGTCAGAATCT-
AACTAACTTCTGT--TAC-ATTATTACATTAATT---TATGT--TTATATGATCCATT---
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CGGAATGAGTACACTTTAAAT-CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAACGGGATCC----------------------------
---------CCGGTGC----TAACTGAGAC-TTC--TTGTCAAAG-TAATGTG-CCG----------TGTG-
TGATGTC--GTTTGCCGA---
TCTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
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TTGCGACG-
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TATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCAGATACCGCC
CTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCTATAATGACT
CGGCGGGGAGCTTCT-
ACTCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
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TTAAGAGATGGCAA-GTC-GCCCTATCCAG----TGCAA--ACTGTG--GTAG-
AGGGTCTGGTCGCTCGCATATT----A--
AAGGTTTTGGTAGTGGTGGACCGCACTTCTCCCTCAGT-
AGGACGTTGCGACCTGTCATTT--TAC-----ATTCTAAGT--GC-GTTTGTGTTAA---
AGTGCCTGTAT-T-TAGATA--ATGTCGCAA------------------------------------
GATATTATCTTTTACAGC-TTTAA--CAA--TA----TGC---ACCGAGTGTTAA--------
TTTTTATGACAGTAACAAATGATGG-TGTTGAGCCACTTAAAATTGTTGTCAT----
TATTGATG-----ATAA---TGGAGAGTGTC--------------TTAGGCCGGTTTGCAA-
GTGGGCTG--------TTTTATAGTT-A-TATTCGGACTT-TT--------GTCCGTCTTG-CTA-
TTGCTCTCA-CTGTTGGTA----GAC-TG--TG-CCTCT--GACAG--TGCTTA--
CAACATCAGTCAGCAGCGATCAAGGTTCAGATTCTTATCCGGTCCGT????????????????
??????CTTGAAACACGGACCAAGGAGTTTATCGTGTACGCGAGTCATTGGGTAAA--
GAAAACCCAAAGGCGAAATGAAAGTAAATAGTGGGAAATTGATTT------------------------
-----------TATTTCTATATTATCAG---------------TTT-CCCCTATAAGGGAAGATGG--AAAA-
----------CTATATCAGTAATG--------------------------GTGTGATAATATCA-TA----------TT------
---------GT-TGTTGATACAAGT-TTCCCGCACTCCCGGGGCGCTTG-TTTCTCGCTT--TG-
CGAGTCACTGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCGGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
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AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAACCCCCGGCTTTCTTAA
AA------------------
ATGAAGCCCGTGGGATTCGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAAC
TGGCGCTGTGG???
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Glymmatophora_crassipes ??????????????AACATGTCCTTTAGT---------
TTTAAATTTA-AGGTTTGACCTGCCCAATGA--
TGAATAATTTAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCAGTTGTCT
TTTAATTGAGGGCTGGAATGAAGGGTCGGACGAGGAATAGTCTTTCTTT-TTAGTAA--
TTAATAAATTTGACTTTTTAGTTAAAAGGCTAA-
AATTTTTTTGTGGGACGAGAAGACCCTATAGATCTTTATATTTAT-ATAT-
AATTTAAGTTTTTA---GTACA--------
TGAATAATTGAATTTATTAGGTATTTTGTTGGGGTGATACGAGAATTT-
TTTTAACTTCTTG--TTATTTTAATTCATTTATT---TATGT--TTTTATGATCCATT----
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GCGTAATTTTTTCGGAGAGTTCATATCGATGAAGAAGTTTGCGACCTCGATGTTGGAT
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TTTACATGATCT??
??????????????????????CCGTAATCGGAATGAGTACACTTTAAAT-
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GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
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ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAATTC-----------------------------
--------CCGGTGC----TACGTAGGCT-TTTATTAGCTGAAG-T-ATGTG-CCG----------TG-G-
TGATTTC--ATTTGCCGA---
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AACAAATTAGAGTGCTTAAAGCAGGCT-
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???GCGAACAAGTACCGTGAGGGAAAGT
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ACTGTG--GTAG-AGGGTTTTATTGCTCGCATTTT-ATT---
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AGTGTCTATCT-A-AAGGTT--ATAAATTTA-----------TCTAAGTTTA-----------------
TTACCTTTTTATAGC-TTTAA--TCA--AT----TAT-ACACTGGGTGTTTG--------
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TTTTATTATA-----ATG-----TAAAAGTGTC---------CATGTGTTTGCC-GTTTACAA-
GTGGGTTTA-------GGTATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-
AGCCGCCTA-CTGTTTGTA----AAC-TG--TG--

C???GTAATGAAAGTAA
AGAGAGTGTAGAGGAGGGGAAAGAAAA-----AGGATAAAAGTTTT------
TATACTTTTAACTTTGATTTCTCTCTGTCTCTCTCT-CTCTCTCAAGGGAAGATGG--

AAAT-----------CTTATTTTAAGTGA-TGT--TA----------
-----AA-TTTAAAATGTTGA-TTCCCGCATTCCCAGGGCGCTTG-TTTCTCGCTT--TG-
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AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
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CCCCGGCTTTCTTAAAA-----------------
TTGAAGCCGTGGGATTCTGATCAGAGTGCCAAGTGGGCCAATTTTGGTAA??????????
???TTATATTTAATTTTACCAGGATTTGGTTT
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GACACTTACTATGTAGTAGCCCACTTCCA???????????????????????????ATGTCTGGA
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ACGCGGTA---
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GTAATCCAAGGCTAGGTATACAGGGTACGCATGGACGACAGTGTAACGCAACAT????
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Haematoloecha_sp ????????????AAAAACATGTCCTTTTGA--------
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TTCTTGAATTTAATTTATCGATTAAAAAGTTGA-
TATAAAATTAAGGGACGAGAAGACCCTATAGATCTTTATAATTAA-
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CTAGGTCTGTTCGACCTTTAAAAT-
TTTACATGATCTG??
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?????????????GAGAGTGCAGCCCTAAGTAGGTGGTAAACTCCATCTAAGGCTAAATAT
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CGAGTATATGCGCACCTAAAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
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AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCATT----TTT-----T---
TAGTTGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCTCGGCTTTCTTAAAA-------------------
TGAAGCCGTAGGATTTGGATCAGAGTGCAAAGTGGGCCAATTTTGGTAAGC?????????
?????????????????????GATTTTTGGACATCCCGAAGTTTATATTTAATTTTACCAGGAT
TTGGAATTATTTCTCACGTAATTGCTATAGAAACAGGAAAAAATGAAGCCTTCGGTA
CTTTAGGGATAATTTATGCTATACTTGCTATTGGACTTTTAGGATTTATTGTATGAGC
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AACTATAATCATTGCAGTTCCAACAGGAATTAAAATTTTCAGTTGATTAGCAACACTT
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TTATTTACCATTGGGGGATTAACGGGAGTTATTTTAGCCAACTCAAGTATTGATATTA
TTTTACATGATACTTATTATGTAGTAGCACACTTCCATTATGTATTATCAATA?????????
??????????TGGATCATGTACAGTGAAAACCTGTTGGATGAGGTTACCACCATTTCGTAT
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TGCAGGTTCAATACGTGCAA---
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Katanga_sp ????????????AAAAACATGTCTTTAAGT----------
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?????????????ACCACGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAG
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GTCTGAA--TATCCGAAAAAAGAGATTCACGTCCTACCGC---
TAGCTCTACTTTGAAGTGC----ATTTGAGATGATAA-TTC-GCCCTATCCAG----
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CCCCGGCT??

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Maraenaspis_coccinea CGCCTGTTTATCAAAAACATGTCCTTTTGA--T------
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ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAATCC-----------------------------
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CAACACCGGTCGGCAGCGATCCAGG------
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Marojejycoris_brevifrons ??????????????AACATGTCTTATATGAAT------
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TATTAACTTCTAT--TTT--ATTTATCATTGATT---AATGT--TTTTTTGATCCATA-
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TAA??
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????TGAGTTACACTTTAAATCCCTTTAACAAGGATCCATTTGGAGGGCAAGTTCTGGT

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TGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAATCC--------------------------------
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TGACTTC--ATTTGCCGA---
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---ATA-----TAAAAGTGTGTA---ATTGTTTTTGTTGCC-GTTTACAA-GTGGGTTTTTA----
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CTGTTTGTA----AAC-TG--TG-CCTTA--GACAG--TGCTTA--
CAACACCGGTCGGCAGCGATCCAGGTTCAGGC??
?????????????????????????????TACGCAAGTCATTGGGTGAT-
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----------------------TA---------------TA-TTTAAAATTTAGA-
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CCCCGGCTTTCTTAAAA------------------
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GTA---
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???????????CCATCTAAGGCTAAATACAACCACGAGTCCGATAGCGAACAAGTACCGT
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A??

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CCCCGGCTTTCT??
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GGATTTGGGTTAATCTCACATATTATTTCAATAGAAACTGGCAAAAGAGAAGCCTTT

GGCTCCTTAGGAATAATTTATGCAATGTTAACTATTGGACTACTAGGATTCATCGTTT
GAGCTCACCATATATTTACAGTAGGAATAGATGTTGATACACGAGCTTATTTACTTC
TGCAACAATAATTATTGCAGTACCTACAGGGATTAAAATCTTTAGATGATTAGCCAC
CTTACATGGCAGACCTTTATCTTTCTCCCCTAGTCTTTTATGAAGATTAGGATTCGTAT
TTTTATTTACAATTGGAGGATTAACTGGAATTATTTTAGCTAATTCAAGAATTGATAT
TATTCTTCATGATACTTATTATGTTGTTGCCCA??????????????????????????????????????
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Neoscadra_sp ?????????????AAAACATGTCCTCTTTG--T------
TATTTATATG-AGGTCTGACCTGCCCGATGA-----
TGTTTTCAATGGCCGCAGTATACTGACTGTGCTAAGGTAGCATAATCATTTGTCTTTT
AATTGAAGGCTGGAATGAAGGGTTGGACGAGATATTAGCTTTCTTT-TTATTAC--
ATTCTAAATTTAACTTTTAGGTTAAAAGGCCTA-
TATTATATTAAGGGACGAGAAGACCCTATAGATCTTTATATTTAT-
TATTATTTATCATCCTTTA---GTTAGATA-----
ATTGATGGTATATTTAATATATATTTAATTGGGGTGATTACAGAATTA-
CTATAACTTCTGT--TTT--AGCTTGCATTGATT---TATGT--TTTAGTGATCCATT---
ATTATTGATTGTAAGATTAAGTTACCTTAGGGATAACA-
GCGTTATTCTTTCAGAAAGTTCTTATTAATGAAAGAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAGTT-TTGGGCGCAAAAGTCT-AATTA-
CTTGGTCTGTTCGACCATTAAATT-
TTTACATGATCTGA???
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??ATATAACTACGAGTCCGAT
AGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGA
GTACGTGAAACCGCTCAGGGGTAAACGGAGAAGATCTGAA--
TTTTCGAAAGGGGAGATTCACGTCTTACCATA--TTGTTTAACTTATAAATGTA---
TTAAGAGATGTTTA-TTC-GCCCTATTCAG----TGCAA--ACTGTA--ATAG-
AGGGTTTATTCGCTCGCATTTATTTT----
TAGTAAAAACAATGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGATCTATCAATT--AAT-----ACTCTAAGT--AT-G-----TTTAA---
AGTGACTGTAT-T-AATGTA--ATT-------------------TTTTTTTA---------------
AATTATATTTTTTACAGC-TTTAA--GCA--AT----TATAATACTGAGTATTT-------T--
AATATTGATAGTAACAATTGATAG-TGTTGAGCCACTTTAA---------------------------------
TTATAAAAGTG--------------TCTAGCC-GTTTACAA-TTAAGTAATAGGC--
TTATTTTAGCT-A-ATTTCGGGCTT-TA------TGGTCCGTATAG-TTA-TGCCACTTA-

ATGTTTGTA----AACGTG--CT-CCTTA--GACAGATTGCTAA--
TAACACTGATCAGCAGCGATCCAGGTTCAGTCTCTTATCCGACCCGTCTTGA?????????
??GTA
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AATTA-AATTCTTGAAGGAAGAAAG--ATTA-----------
ATTTATTTCATTAAAAAAAAAAAAA---------------------------TTTT-TT----------TT-------------
TT-TTTTATTAATGAA-GTCTTGCATTCCTAGGGCGCTTG-TCTCTCGCAT--TG-
CGAGTATATGCGCACCTAAAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
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AGCTGGTTCCCTCTGAAGTTTCTCTCAGGATAGCTTGCGCTCATT---TTTTATAAAT---
TATTTGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCTCGGCTT??
?????????????????????????????????????TTGGACATCCTGAAGTTTACATTTTAATTCTGC
CGGGATTTGGGATCATTTCCCATGTTATCGCCATAGAAACAGGTAAAAATGAAGCCT
TTGGGACACTAGGTATAATTTATGCAATACTAGCAATTGGATTATTAGGATTTATCGT
ATGAGCCCATCATATATTCACAGTCGGAATAGACGTTGATACTCGAGCCTATTTTACC
TCCGCTACCATAATTATTGCTGTTCCTACTGGTATTAAAATCTTCAGATGACTAGCAA
CCTTACATGGAAGTAAGATCACATTCACGCCAAGAATAATATGAGCATTAGGATTTG
TATTTTTATTCACCATTGGAGGATTAACCGGAGTGATTCTAGCTAATTCAAGAATTGA
CATTGTATTACATGATACTTATTATGTAGTCGCACA?????????????????????????????????
??ATGTCTGGCTCATGTACAGTTAAAACCTGCTGGATGCGTTTACCACCGTTTCGTATT
GTCGGTGATAATTTAAAAGATAGATTTGATGGTGCCTCACGTGTAATGGTTAGCAAT
GCAGGCTCAATACGTGCAA---
CAGGCGGACGTAAGAATCGTTATAATTTACAATTAAAACCATTTAATCCAGATCATA
AACCGCCGGGTGTAAAAGATCTTGTTTATCTTGAACCATCGCCAGTATTTTGTGAACG
TAATCCAAGATTAGGTATACAAGGTACACACGGACGTCAGTGTA????????????????????
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nr_Neolibavius_sp ????????????????ACATGTCCTTTATG--T------
GTTAATTTTA-AGGTTTGACCTGCCCAATGA-----
TTAATTTAATGGCCGCAGTATATTAACTGTGCTAAGGTAGCATAATCATTTGTCTTTT
AATTGTAGGCTAGTATGAAAGGTTGGACGAGAAATTGACTTTCTTT-TATATAA--
TAATTGAATTTAATTTTTAAGTTAAAGAGCTTA-
AATTTTTTTATGGGACGAGAAGACCCTATAGATCTTTATAATTAT-ATTT--
TTTTATTTATTTTAGAGTTGA-------
TTATTTTTTTTAGTGAATTAATTATTTGATTGGGGTGATTGAAGAATTT-
AAATAACTTCTTT--TGT-TTTTTTTCATAATTT---TATGT--ATTTTTGATCTTTT---
ATTAAGGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTAATTTTTTTGGAGAGTTCTTATCGATAAAGAAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAGTT-TCGGGTGCAGTAATTT-GATTA-CTAGGTCTGTTCGACCTTTAAATT-
TTTACATGATCT???
????????????????????????????ATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAATTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTTCCGCACTGTCGGTTCACCGCCTGTCGGTGTT
ACTGGCATGTCGCGGAATGTCCTGTCGGTGGTGAATAAAGTTC------------------------------
--------CTGGTGC----TACCTAGGCT-TTTTATAGCTGAAG-T-GTGTG-CCG----------TG-G-

TGACTTT--ATTTGCCGA---
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AACAAATTAGAGTGCTTAAAGCAGGCT-
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ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAT???
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??????????TGGTAAACTCCATCTAAGGCTAAATATAACCACGAGTCCGATAGTAAACA
AGTACCGTGAGGAAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAATAGTACGTGA
AACCGCTCAGGGGTAAACGGAGAAGATCTGAA-
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GAAGTTTTGCCGCTCGTACTTT-ATTTT-
AAGTAAGCTGTAATGCTGGACCGCACTTCTCTTTTAGTAAGGACGTTGCAACCTGTC
AGAT--AAT-----ACTCTAAGT--AT-G-----ATTAA---AGTGTCTCTGT-A-AATGTA--
ATTTAAAAC-------------TTGTTTTA-------------ATATTATATCTTGCAGTAGC-TTTTA--
TCA--AT----TTTACTACTGGGTGTTTA---------TATTCTGACAGTATCAACT-ATGG-
TGTAGAGCCACTAAAAATTA--------------------------------AGTAAGCATCCG-------------------
-TTTTACAA-GTTTGGTA--------ATTATAAGTT-A-ACGTCTAACTT-TT--------
GTTAGTCTAA-CTT-TATTACCTA-CTGTTTGTA----AAA-TG--TA-ACTTGCTTTTAG--
TGCTCA--
TCACACCGGTTGGCAGCGATTCAGGTTCAGATTCTTATCCG??????????????????????????
??AGGCGTAATGAAAGT
AAAGGATAAAAAGATAGAAG-------------------AAGTTAAG--------
CAATTTTCATCTTTGAT---------------TCT-TTTATCCTAGGGAAGATGG--ATAT-----------
CTTGTTTTAAAAAA--------------------------------AAATTTTT-TT----------TT---------------TT-
TTTAAACATAGAT-CTCCCGCATTCCCAGGGCGCTTG--GACTTGCTT--TG-
CAAGTCTATGCGCACCTAGAGGGTACACGATGACACCCGAAAGATGGTGAACTATG
CCTGGCCAGGCCGAAGCCAGGGGAAACCCTGGGGGAGGTCCGCAGCGATTCTGACG
TGCAAATCGATCGTTAGAGCTGGGTATAGGGGGGAAAGACCAATCGAACCATCTAG
TAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGAT------------T---
TTAAAGAGTTTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCAGGCTTTCTTAAAGAGAGAAAAAAGAAAATTTTTAA????????????????????????????
??TTTGGGCACCCAGAGGTCTAT
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AAAATGAAGCCTTTGGTTCCTTGGGAATAATTTATGCTATGCTAACCATTGGCCTTTT
AGGATTTATTGTATGAGCACATCATATATTTACTGTAGGAATAGATGTAGATACACG
AGCCTACTTTACTTCAGCAACAATAATTATTGCTGTACCCACCGGAATTAAAATTTTT
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GCCCTGGGATTCGTTTTCTTATTCACTATTGGAGGGTTGACTGGAGTTATTTAGCAA
ATTCAAGAATTGATATTGTTCTCCATGATACATACTATGTAGTTGCCCATTTT????????
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??CCGTAATCGGAATGAGT
ACACTTTAAAT-CCTTTAACAAGGATCTA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTTGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGTATGTCCTGTCGGTGGTGAATGTAATGG----------------------------
--------CAACGG-----TGCCAGGGTA-TGCTTTATCAAAAG-T-ATACG-
CGGGTTAACTTGTTGTT-CAATTAC--ATTTGCCGT---
TTTTTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
GAAATATCTGCCTGAATAGTGGTGCATGGAATGATAGAATAGGACCTCGGTTCTATT
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TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCT-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAATTGACGGAAGG??
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???????????????????GCATAATAAAAGTAAAAAGGTGTTTTGGATGAT--------------
GGGGGAAGATTATTTTTTTTTTTTTTTCTTCATTTAT---------------CCT-
TAATCCTAAGGGAAGATGA--TAAT-----------TACTTTTTTCTCAA-----------------------------
-----TTTTT----TTTTTGAG------------------TAAAAAGATAAACAAT-
TGTCCGCATTCCCGGGGCGCTTG--TTCTTGCTT--TG-
CAAGTCTATGCGCACCTAGAGCGTACACGATAATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT

AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGACGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCT??
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Opistoplatys_sp2 ???????????CAAAAACATGTCTTTTTGT---------
AATTTATTTA-ATGTTGGTCCTGCTCAATGA--
TTTTATATTTAATAGCCGCAGTATATTAACTGTGCTAAGGTAGCATAATCAATTGTCT
TTTAATTAAAGGCTGGAATGAAAGGTTTGACGAGGTAATAGCTTTCTTT-AATTTAA-
TTAATTGAATTTAATTTTTAGGTTAAAAAGCTTA-
AATTAAATTAAGGGACGAGAAGACCCTATAGATTTTAATATTTTG-TTTA--
ATTTTATTGATTTA--GTTTA-------
TTATTAATAAAATTGATTTATTTATTTAATTGGGGCGATTTAGAAATTT-
ATTGAACTTTTTA--TTT--ATTTTTCATTAATT---TATGT--TTTATTGATCCGTT---
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GCGTAATTTTTCCAGAGAGTTCTTATTGATGGATAA?????????????????????????????????
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???CGTAATCGGAAT
GAGTACACTTTAAAT-CCTTTAACAAGGATCTA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
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ACTGGCATGTCGCGGTATGTCCTGTCGGTGGTGAATGTAATGG-----------------------------
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CGGGTTAACTTGTTGTT-CAATTAC--ATTTGCCGT---
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AACAAATTAGAGTGCTTAAAGCAGGCT-
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TTAATGACTCGGCGGGGAGCTTCT-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
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?????????????????????????????????ACCACGAGACCGATAGCGAACAAGTACCGTGAGGG
AAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGTTCAGGGG
TAAACGGAAAAGACCTGAA--TATTCGAAAGGGGAGATTCACGTCTTACCGC---
CTGTTTAACTATTGAATGTTATTCATTGAGATGTTTC-TTC-GCCCTGTCCAG--

TTTATAT--ACTGTG--ATGG-TGGGTTGAAACGCTCGCATTTA-ATT-----
AGTAAAAACAGCGGTGGACCGCACTTCTCCCTCAGT-
AGGACGTTGCGATTTGTCAAAA-AAAT-----ATTCTAAGC--ATCC-----GTTAA---
AGTGTCTGTAT-T-TGTGAA--AGGTGTAGGGGA-----ATTTTTTCTTTTA-----------
CATTTTTTTTCCCTATACAGC-TTTAA--TAA--ATAA------ATGCTGAATA-------------
TATTTTAACAGTAACAAATGATGG-TGTTGAGCCACTTTA-----------------------------------
CAAAAAGTGTC--------------TTGGCCA-ATTTACAA-GTGGGGTATG------AACATTAGTT-
A-ATGTCGGTCTTAAT--------GTCCGTCTAA-CTG-GTTCTCCTA-CTGTTGGTA----AAT-
TGTATG-CTTTG--GACAG--CGCTAA--
CAGCACCGATCGGCAGCGATCAAGGTTCAGGCTCTTATCCGACCCGTCTTGAAAC???
???AAA
AGTAAAAAGGTGTTTTGGATGAT--------------GGGGGGGAAAAAT-----
TTTTTTTYTTCTTCATTTAT---------------CCT-TAATCCTAAGGGAAGATGA--TAAT--------
---TACTTTTTTTTTCC----------------------------------CCTGA----TAAAGGGG-----------------
AGAGAAAAGAAAACGAT-TGTCCGCATTCCCGGGGCGCTTG--TTCTTGCTT--TG-
CAAGTCTATGCGCACCTAGAGCGTACACGATAATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGACGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCTTAAAA------------------
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Peirates_punctorius CGCCTGTTTATCAAAAACATGTCCCTTTTG--TT-----
TATTTATTTA-AGGTCTGTCCTGCCCAATGA-----
GTGTTTTAATGGCCGCGGTATATTAACCGTGCTAAGGTAGCGTAATCATTTGTCTTTT
AATTGTGGGCTTGTATGAAGGGTCGAACGAGGCACATTCTTTCTTT-ATCTTGA--
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AATTTATCTGTGGGACGAGAAGACCCTATAGATCTTTATATTACT-TTTT--
ATTGAGCTTGTTT---AGCAAAAT-----
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CAGCAACCTCTGT--TTT-AGTATTTCGTTTATG---GGCGT--TTTAATGATCCATT---
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GCGTAATCTTTCCGGAGAGTTCCTATCGATGGAGGGGTTTGCGACCTCGATGTTGGA
TTAAAA-TAAGTA-TTGGGTG-AGCGATTT-AATTA-
CTGGGTCTGTTCGACCCTTAATTT-
TTTACATGATCTGAGTTCAAACCGGAGGCAGCAGGCACGCAAATTACCCACTCCCGG
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CGGAATGAGTACACTTTAAAT-CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAACGGGATCC-----------------------------
---------CCGGTGC----TGTTGAGGCC-GTC--AGGTCAAAG-C-ATGTA-CCG----------TGTG-
TGTTTCC--GTTTGCCGA---
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AACAAATTAGAGTGCTTAAAGCAGGCT-
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CAACACGGGAAACCTCACCAGGCCAGGACATTGGAAGGATTGACAGATTGATAGCT
CTTTCTTGATTCAGTGGGTAGTGGTGCATGGCCGTTC?CGTGTTGCTTGATAGTGCAG
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TGGGTTTGTTCGCTCGTATTTA--TT----
ATGCAAGGGTGGTGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGACCCGTCAAAC--AAT-----GCTCTAAGT--ATTT-----GTTTT---
AGTGTCTGTAT-A-AGTGTA------------------------TACCGTTA------------
GGTATATTTATCTTGTACAGC-TTTAA--CAA--TT----TAT-ATACTGGGTATTTG------------
TTAGACGGTAACAAACGATGG-TGTCGAGCCACTTTAATTTT--------------------------------
TTTAAAGTGTC-------------CACCGGCT-GTTTGCAA-GTGAGTTTG-------GTTAATAAAT-
T-AGTCGGGCTTT-TG--------GTCCGTCTAA-TTA-TTCCACTTA-CTGTTGGCG----GAC-
AT--AG-CCTCG--GACAG--TGCTTA--
CAACACCAGTCGGCAGCGATCCAGGTTCAGGCTCTTATCCGGTCCGT????????????????
??????CTTGAAACACGGACCAAGGAGTTTATCGTGTACGCAAGTCATTGGGTTAG--
CTAAACCCAAAGGCGAAATGAAAGTAAATAGTGTTTAATAGTGGT------------------------
---------------TTTTCCATTT------------------TTT-TACACTTAAGGGAAGATAG--AATC---------
--TATTTGTAGATTTT---------------------------------AAATTTTT-TTTATAAAAAATTT-----------
----AG-TTTACAAAATAGT-TTCTCGCACTCCCTGGGCGCTTG-TTCTCGTTTT--TG-
CGAGTCAATGCGCACCCAGAGCGTACACGCTGATACCCGAAAGATGGTGAACTATG
CCTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACG
TGCAAATCGATCGTCGGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAG
TAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGA------------
TAAAGAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCTTAAAA------------------
CTGAAGCCGTGGGACTCGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAA
CTGGCGCTGTGG??
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Pothea_lugens ?????????????AAAACATGTCCTTTAGT--AT-----
TAATTATTTA-AGGTTTGCCCTGCCCAATGA-----
TTTATTTAATGGCCGCAGTATATTAACTGTGCTAAGGTAGCATAATAAATTGTCTTTT
AATTGAAGGCTGGAATGAAGGGGTGAATGAGATATCAGCTTTCTTT-TTATTAA-
TCTTTTTAATTTAATTTATTAGTCAAAAAGCTAA-
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TAAATTTTATTTA---TATAATTT-----
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TTTTAACTACTAT--CT---ATTTTTCATTGATG---GATGT--TTAATTGAGCCAAT---
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GCGTAATTTCTTTGGAGAGTTCATATCAATAAGGGAGTTTGCGACCTCGATGTTGGAT
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TTTACATGATCT??
????????????????????????CCGTAATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
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TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGGGATCT----------------------------
--------CCGGTGC----TGCCTAGGCT-TC--ACAGCTGAAG-T-ACGTG-CCG----------TT-T-
TGATGCC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
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ATAATGACTCGGCGGGGAGCTTCT-
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TAAAGGAATTGACGGAAGG??
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??????????????GGTGGTAAACTCCATCTAAGGCTAAATACAACTACGAGTCCGATAGCG
AACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTAC
GTGAAACCGCTCAGGGGTAAACGGAGAAGAACTGAA--
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ACAAGAGATGTTTA-TTC-GCCCTATTCRG----TGCAA--ACTGTT--ATAG-
AGGGTTTATTCGCTCGCATTTA-ATT----
TAGTAAAAACAATGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGATCTATCAGAT--AAT-----ACTCTAAGT--AT-G-----GTTAA---

AGTGTCTGTAT-A-AAAATA--ATTGG--------------TTTCGGCT-----------------
AATTTTTTTTTTACAGC-TTTAA--TCA--AT----TAT-ATACTGAGTATAA-------C-
ATTCTCTGATAGTATCAAATGATGG-TGTTGAGCCACTTGTT----------------TTTTTA------
-AT---TAAAAAGTGTC-------------TTTAGCC-GTTTACAA-GTAGGTTT-----------
AGTAGTT-A-ATTTCGGGCTT-TT------CGGTCCGTATAA-CTA-TGCCATTTA-
CTGTTTGTA----AAC-TG--TG-CCTTT--GACTG--TGCTTA--
TAACACTGATCAGCAGCGAT???
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AAGTCTACATTCTAATTTTACCAGGATTTGGGCTTATTTCCCATATTATCGCAATAGA
GACAGGAAAAAACGAAGCTTTTGGAGCTCTGGGTATAATTTATGCAATAATCGCCAT
TGGAATTTTGGGATTTATTGTATGAGCCCATCATATATTTACAGTAGGAATAGATGTT
GACACACGGGCCTACTTTACTTCCGCAACTATAATTATTGCTGTACCTACAGGAATTA
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Pothea_sp ???????????????AACATGTCCTTTTGT--TT-----AATTTATTTA-
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Racelda_sp CGCCTGTTTATCAAAAACATGTCCTTTTGG---------
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Rhiginia_cinctiventris CGCCTGTTTATCAAAAACATGTCCTTTTGT--TT----
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TTAATTTAAGGCTGGAATGAAGGGTTGGACGAGATATTATCTTTCTTTATTTTTAA--
AATTTTAATTTAACTTGTGAGTTAAAAGGCTCA-
TTTAATTTTAAGGGACGAGAAGACCCTATAGATCTTTATATTTAT-ATTT--
TTGTTTTTTTGTA---GCTAAATA-----
AAAATTTATAAAAGCAGTATTTATTTAATTGGGGTGATTTCAGAATTT-
TAAAAACTTCTGT--AT---TTTTAACATTGATG---GATGT---TTTGTGATCCAAT---
ATTATTGATTATTAGATTAAGTTACCTTAGGGATAACA-
GCGTAATTCTTTTGGAGAGTTCTTATCGATAAAAGAGTTTGCGACCTCGATGTTGGAT
TAAAA-TGAGTT-TTGGGTGCAAAAGTTC-AATTA-
CTTGGTCTGTTCGACCATTAAAGT-
TTTACATGATCTGA???
??????????????????????????????ATCGGAATGAGTACACTTTAAAT-
CCTTTAACCAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGTCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGGATGGAATCC------------------------------
--------ACGTTAC----TGCTTTAGTTTACTATAAGCTGAAG-T-ATGTA-TCG----------TT-C-
GGGCGCC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
GAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
TTATTGGTTTTAGGAATATGAGGTAATGATCAATGTGGACTGGCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCA
ATAATGACTCGGCGGGGAGCTTCC-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAAT??
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??GTTGAAA
AGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGATCAGGGGTAAACGGAGA
AGATCTGAA--TTTTCGAAAGGGGAGATTCACGTCTTACCATA--
TTGTTTAACTTATAAATGTA---TTAAGAGATGTTTA-TTC-GCCCTATTTAG----TGCAA--
ACTGTA--ATAG-AGGGTTTATTCGCTCGCATTTATTTT----
TAGTAAAAACAATGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGATCTGTCAGTT--AAT-----ACTCGAAGT--AT-G-----ATTAA---
AATGTCTGTAT-T-TATGTA--ATTTT---------------TTTTTTTTTA---------------
AATTATATTTTTTACAGC-TTTAA--TCA--AT----TTTAATACTGAGTATTT-------T--
AATATTGATAGTAACAAATGATAG-TGTTGAGCCCCTTTAA-----------------------------------
--AAAAAAGTG-------------TCTAGCC-GTTTACAA-GTATGTTTTTAGG--CTTATTTAGCT-
A-ATTTCGGGTTT-TA------TGATCCGTATAG-CAA-GGCCACATA-CTGTTGGTA----
GATGTG--CT-CCTTA--

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???AGTAAAGAGTA
ATTTAATTTAGT-------------------------------------AGTAATACTTTT----------------AATTA-
ACTTCTTAAAGGAAGAAAG--ATTT-----------TAATTTTTTTTTTTTCATTAAAAAG--------
----------------------TT----------TT---------------AT-ACTTTTAATGAAA-
GTCTTGCATTCCTAGGGCGCTTG-TCTCTCGCGT--TG-
CGAGTATATGCGCACCTAAAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCATT------------T------
TTGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA?????????????????????????
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?????????????????????????GTATATATTTTAATTTTACCAGGATTCGGAATTATCTCCCAT
GTAATTGCAATAGAAACAGGAAAAAATGAAGCATTTGGGGCTTTAGGTATAATTTAT
GCAATGCTATCTATTGGTCTTTTAGGATTCATTGTTTGAGCTCATCACATATTTACAA
TCGGAATAGATGTAGATACTCGAGCTTATTTTACATCTGCTACTATGATTATTGCTGT
CCCAACAGGAATTAAAATTTTTAGTTGACTTGCTACTCTTCATGGAAGTAAAATTATA
TTCACCCCAAGTATAATATGGGCTTTAGGTTTTGTTTTTTTGTTCACTGTTGGCGGTTT
AACAGGCGTAATTTTAGCAAATTCAAGAATTGATATTATTTTACATGACACCTATTAT
GTAGTAGCCCATTTT????????????????????????????????ATGTCTGGATCGTGTACAGTAA
AAACTTGCTGGATGAGATTACCACCGTTTCGTGTTGTTGGTGATAATTTAAAAGATCG
CTTTGACGGCGCCTCACGTGTAATGGTCAGCAATGCAGGCTCAATACGTGCAA---
CTGGCGGACGTAGAAATCGTTATAATTTCCAATTAAAACCATACAATCCTGATCATA
AACCGCCAGGTGTTAAAGATCTTGTCTATCTTGAACCATCGCCTGTTTTTTGTGAACG
TAATCCAAGATTAGGTATACAAGGTACACACGGACGTCAGTGTAATGCAACATCACA
GGGTGTTGAAGGTTGTGATTTAATGTGTTGTGG

nr_Scadra_sp ???????????CAAAAACATGTCCTTAAGT---------
TTATTTTTTA-AGGTTTGACCTGCTCAATGA---
TTTTTATTTAATGGCCGCAGTATATTAACTGTGCTAAGGTAGCATAATCAATTGTCTT
TTAATTGAAGGCTAGCATGAAGGGTTGGACGAAATATTAGCTTTCTTT-TTATTAA--
AGTTTAAATTTAATTTGCTGGTTAAAAAGCTAG-
CATTATTTTAAGGGACGAGAAGACCCTATAGATCTTTATATATCG-TGAT--
TTATATTATTTTT---GTTTA--------
TATTTTATTTATGTTTCTATTTATTTGATTGGGGTGATCTTAGAATTT-
TATTAACTTTTTT--TTGTTATTATTCATAAATT---AGTGT--AAATTTGATCCATT---
ATTATTGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTTATTTTTTTGGAGAGTTCATATTGATAAAAAAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAATA-TTAGATGCAGGAGTTT-AATAA-
TTAGGTCTGTTCGACCTTTGAAAT-
TTTACATGATCTGAGTTCA???
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?????????????????????GTGCAGCCCTAAGTAGGTGGTAAACTCCATCTAAGGCTAAATA
CAATTACGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTG
AAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGATCTGAA
--TTTTCGAAAGGGGAGATTCACGTCTTACCATA--TTGTTTAACTTATAAATGTA---
TTAAGAGATGTTTA-TTC-GCCCTATTCAG----TGCAA--ACTGTA--ATAG-
AGGGTTTATTCGCTCGCATTTATATT----
TAGTAAGAACAATGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGATCTGTCAGAT--AAT-----ACTCTAAGT--AT-G----TTTTAA---
AGTGTCTGTAT-T-AATGTA--ATTAAAAAGGTT--TTTATTAATTTTTTTA---------------
ATCTATATTTTTACAGCTTTTTA--ACA--AT----TAT-ATACTGAGTATTT----------
TATACTGATAGTAACAATTGATAG-TGTTGAGCCACTTAAAAATTTA----------------------
-AA---AACAAAAAGTG--------------TCTAGCC-GTTTGCAA-GTAAATATTTAGG--
CTTTTTTAGCT-A-ATTTCGGGCTT-TT------TGGTCCGTATAG-CTA-GGCCACTTA-
CTGTTGGTG----AACGTGTTTT-TCTTA--GACAGATTGCTTA--
AAACACTGATCAGCAGCGATTCAGGTTCAGTCTCTTATCC??????????????????????????
???TTGGGTAAT--
TAAAACCCAAAGGGGTAATAAAAGTAAAGRGTAATTTAATTTCTA------------------
AAAATTTTTT---TAATTAAAACTTTTAAG---------------AATTA-
AATTCTTAAAGGAAGAAAG--ATTT-----------AATTTTTTTTCATT---------------------------
AAAAGAATTTTT-TT----------TT--------------TT-TTTTTTAATGGAA-
ATCTTGCATTCCTAGGGCGCTTG-TCTCTCGCAT--TG-
CGAGTATATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CGGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCATTAAATTTT-----T---
TTATTGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCTCGGCTTTCTTAAAA-----------------
TTGAAGCCGCAGGATTTGGA???
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??????????????????????ATGTCTGGATCATGTACAGTGAAAACCTGCTGGATGAGATTAC
CGCCATTCCGTGTTGTTGGTGATAATTTAAAGGATCGTTTCGACGGTGCATCACGTGT
AATGGTCACCAATGCAGGCTCAATACGTGCAA---
CTGGTGGACGCAGAAATCGTTATAATTTTCAATTAAAACCATACAATCCTGATCATA
AACCGCCAGGTGTTAAAGATCTTGTTTATCTTGAGCCATCGCCAGTATTTTGTGAGCG
TAATCCAAAATTAGGTATACAGGGTACACATGGACGACAGTGTAATGCAACATCACA
GGGAGTTGAAGGGTGCGATTTAATGTGTTGTGG

Tanindrazanus_marginatus ?????????????AAAACATGTCCTCTAGG--T------
TTTAAATTTG-AGGTCTAACCTGCCCAATGA--
TTATTAATTTAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCAATTGTCT

TTTAATTAAAGGCTTGAATGAACGGTTGGACGAGGTGTTATCTTTCTTT-TAATTAT--
TTGATTAATTTAATTTTTAAGTTAAAAAGCTTA-
AATTTTTTTATGGGACGAGAAGACCCTATAGATCTTTATATTTAT-AGGG--
ATTAAATTTTTTG---GTTTGAT------
ATTTTATTTGATTTTTTTATGTATTAAATTGGGGTGATTGAAGAATTT-
TTTTGACTTCTAT--TGTTTATTATTCATTTATT---TATGT--TTTATTGATCCATT----
TTATTGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTAATTCTTTTGGAGAGTTCTTATCGATAAATGAGTTTGCGACCTCGATGTTGGAT
TAAAT-TAAGTT-TTAGGTGTAGTGGCTT-ATTAA-CTAGGTCTGTTCGACCTTTAAAAT-
TTTACATGATCTGA??
?????????????????????????CCGTAATCGGAATGAGTACACTTTAAAT-
CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAATCC------------------------------
--------CTGGTGC---TTACGTAGGCT-TTTATTAGCTGAAG-T-TTGTG-CCG----------TG-G-
TGACTTC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
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TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCC-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAATTGACG???
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??????????????????????????CTAAGGCTAAATACAACCACGAGTCCGATAGCGAACAAGT
ACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAAC
CGCTCAGGGGTAAACGGAGAAGATCTGAA--
TATCCGAAAGGGGAGATTCACGTCTTACCGC---TTGCACGACTTTGAAGTGC----
TTTTGAGATGGTAA-TTC-GCCCTATCCAG----TGAAT--ACTGTG--GTAG-
AGGGTTTTACCGCTCGCATTTT-ATT----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGCCTGTCA-A-AAGGTT--ATAAAAT---------------TTATTTTA------------------
TAACCATTTTACAGC-TTTAA--CTA--AT----TTT---ACTGGGTATTTA---------
TTTTCTGACAGTAACGACTGATGG-TGTAGAGCCACTTAAAAATT------------ATTTATA-
----ATT-----TAAAAGTGTC----------TTTTGGTTGCC-GTTTACAA-GTGGGTTTTT-----
AGGTATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-AGCCGCCTA-
CTGTTTGTA----AAC-TG--TG-CCTTA--GACAG--TGCTTA--
CAACACCGGTCGGCAGCGATCCAGG???
????????????????????????GTACGCAAGTCATTGGGTGAT-
ATAAAACCCAAAGGCGTAATGAAAGTAAAGAGTAGAAGGATAGAAG-------------------
AAGAAAAT--------TAATTTTCATCTTTGAT-------------TCT-
TTCTCTCAAGGGAAGATGGATATAT-----------CTTATTTTAAATAA-TATTTAG-------------
--------------TAT---TT-ATATTAAG-TA---------------TA-TTTAAAATTTAGA-

TTCCCGCATTCCCAGGGCGCTTG-TATCTCGCTC--TG-
CGAGATTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGGATTAGGATCAGAGTGCCAA??????????????????????????????????????
???????????????????????????????AGTATATATTCTAATTCTACCAGGATTTGGATTAATTT
CACACATTATTGCAACAGAAACTGGCAAGAGAGAAGCATTTGGATCATTGGGTATAA
TTTACGCTATAATTACTATCGGACTTCTTGGATTTATTGTATGAGCTCACCATATGTTC
ACTGTTGGGATAGATGTTGACACTCGAGCCTACTTCACCTCAGCAACTATAATTATTG
CCGTACCCACAGGAATTAAAATCTTCAGATGACTAGCAACATTACATGGAAGAGTAA
TAACCTTTTCTCCTAGAATACTATGAGCCTTAGGATTTGTGTTCCTGTTCACTATTGG
AGGCTTAACAGGAGTCATGCTAGCTAATTCCAGAATTGATATTATCTTACACGATAC
ATACTATGTAGTAGCACATTTC???
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?????????????????????AGGTAGCATAATCAATTGTCTTTTAATTAAAGGCTTGAATGAAC
GGTTGGACGAGGTATTGACTTTCTTT-TAATTAT--
TTAATTAATTTAATTTTTAAGTTAAAAAGCTTA-
ATTTTTTTTATGGGACGAGAAGACCCTATAGATCTTTATATTTAT-AAAG--
TTTAAATTTTTTA---GTTTTA-------
TTTTTTGTTTGATCTTTTATGTATTTAATTGGGGTGATTGAAGAATTT-
TTTTAACTTCTAA--TGTTTTTTTTTCATTTATT---TATGT--TTTATTGATCCATA----
TTAATGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTAATTCTTTTGGAGAGTTCTTATCGATAAATGAGTTTGCGACCTCGATGTTGGAT
TAAAT-TAAGTT-TTAGGTGTAGTGGCTT-ATTAA-CTGGGTCTGTTCGACCTTTAAAAT-
TTTACATGATCTGAGT???
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?????GCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTT
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAATCC------------------------------
--------CCGGTGC---TTACGTAGGCT-TTTATTAGCTGAAG-T-TTGTG-CCG----------TG-G-
TGACTTC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
TTATTGGTTTTAGGAATATGAGGTAATGATCAATGTGGACTGGCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCC-

ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAG??
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???AGTCCGATAGCGAACAAGTACCGTGAGGG
AAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGG
TAAACGGAGAAGATCTGAA--TATCCGAAAGGGGAGATTCACGTCTTACCGC---
TTGCACGACTTTGAAGTGC----TTTTGAGATGGTAA-TTC-GTCCTATCCAG----TGAAT--
ACTGTG--GTAG-AGGGTTTTACCGCTCGCATTTT-ATT----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGCCTGTCA-A-AAGGTT--ATAAAAT---------------TTATTTTA------------------
TAACCATTTTACAGC-TTTAA--CTA--AT----TTT---ACTGGGTATTTA---------
TTTTCTGACAGTAACGACTGATGG-TGTAGAGCCACTTAAAAATT------------ATTTATA-
----ATT-----TAAAAGTGTC----------TTTTGGTTGCC-GTTTACAA-GTGGGTTTTT-----
AGGTATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-AGCCGCCTA-
CTGTTTGTA----AAC-TG--TG-CCTTA--GACAG--TGCTTA--
CAACACCGGTCGGCAGCGATCCAGGTTCAGGCTCTTATCCGACCCGTCTTGAAACAC
GGACCAAGGAGA??????????????????????????????ACGCAAGTCATTGGGTGAT-
ATAAAACCCAAAGGCGTAATGAAAGTAAAGAGTAGAAGGATAGAAG-------------------
AAGAAAAT--------TAATTTTCATCTTTGAT---------------TCT-
TTCTCTCAAGGGAAGATGGATATAT-----------CTTATTTTAAATAA-TATTTAG------------
--------------TAT---TT-ATATTAAG-TA---------------TA-TTTAAAATTTAGA-
TTCCCGCATTCCCAGGGCGCTTT-TATCTCGCTC--TG-
CGAGATTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CCCCGGCTTTCTTAAAA-----------------
TTGAAGCCGTGGGATTAGGATCAGAGTGCCAA?????????????????????????????????????
???????????????????????????????GTATATATTCTGATTTTACCAGGATTTGGACTCATTT
CACATATTATTGCTACAGAAACCGGTAAAAGAGAAGCGTTTGGGTCACTAGGAATAA
TTTATGCAATAATTACTATTGGACTTTTAGGATTCATTGTCTGAGCTCATCATATATTC
ACTGTGGGAATAGATGTTGATACTCGAGCCTATTTCACTTCAGCAACTATAATCATTG
CTGTACCTACAGGAATTAAAATCTTCAGATGATTAGCAACATTACATGGAAGAACCA
TGACATTTTCCCCAAGAATATTATGAGCATTAGGATTTGTATTCCTATTCACAATTGG
AGGTTTAACAGGAGTAATACTAGCCAACTCAAGAATTGATATTGTTCTTCACGATAC
ATACTATGTAGTAGCACATTTTCAC???
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???GTTCGCCGCCTGTCGGTGTTACTGGCAT
GTCGCGGCATGTCCTGTCGGTGGTGAATGAAATCC--------------------------------------
CTGGTGC---TTACGTAGGCT-TTTAATAGCTGAAG-T-TTGTG-CCG----------TG-G-
TGAATTC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
TTATTGGTTTTAGGAATATGAGGTAATGATCAATGTGGACTGGCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACC??
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??GTAGGTGGTAAACTTCA
TCTAAGGCTAAATACAACCACGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGT
TGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAAC
GGAGAAGATCTGAA--TATCCGAAAGGGGAGATTCACGTCTTACCAT---
TTGAATGGCTTTAAAATGC----TTTTGAGATGGGAA-TTC-GCCCTATCTAG----TGAAT--
ACTGTG--ATAG-AGGGTTTTACCGCTCGCATTTT-ATT----
AGTAAGGTTCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGCCTGTTT-A-AAGATT--ATAAAAT---------------TTATTTTA------------------
TAACCATTTTACAGC-TTTAA--TTA--AT----TTT---ACTGGGTATTTA---------
TTTTCTGACAGTAACGAATGATGG-TGTAGAGCCACTTAAAAATT------------ATTTATA-
----ATT----TTATAAGTGTCCA---ATTTTTTTTGATTGCC-GTTTACAA-GTGGGTTTTT-----
AGGTATTAGTT-A-ATGTCAAACTT-TT--------GTTCGTCTAA-CTA-AGCCGCCTA-
CTGTTTGTA----AAC-TG--TG-CCTTG--GACAG--TGCTTA--
CAACACCGGTCAGCAGCGATCCAGGTTCAGGCTCTTATCCG?????????????????????????
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?????????????????????????????????TATTTAG---------------------------------------TAT---TT-
ATATTAAG-TA---------------TA-TTTAAAATTTAGA-TTCCCGCATTCCCAGGGCGCTTG-
TATCTCGCTT--TG-
CGAGATTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT-----------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAC-
CTCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGGATTTGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAAC
TGGC-----
GA????????????????????????????CCAGAAGTTTACATTTTAATTTTACCAGGATTTGGAA

TTATTTCGCACATTATTGCAATAGAAACCGGTAAAAATGAAGCATTCGGCTCATTGG
GGATAATCTATGCAATAATCACTATTGGATTATTGGGGTTCATTGTCTGAGCTCATCA
CATATTTACTGTAGGGATAGATGTAGATACTCGAGCCTACTTCACTTCGGCAACTATA
ATTATCGCTGTACCAACAGGAATCAAAATCTTTAGATGATTAGCAACATTACAAGGC
AGTATCATATTATTTTCTCCTAGAATGATATGAGCCCTTGGCTTCGTATTTTTATTCAC
AATTGGAGGATTAACAGGTGTCATACTCGCTAATTCAAGAATTGATATTATCCTCCAT
GATACTTATTACGTAGTAGCACATTTCCA??
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????????????????CGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAAC
TTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGATC
TGAA--TATCCGAAAGGGGAGATTCACGTCTTACCAC---TTGCTCGACTTTGAAGTGC--
--TCTTGAGATGGTAA-TTC-GCCCTATCCAG----TGCAT--ACTGTG--ATAG-
AGGGTTTTACCGCTCGCATTTT-ATA----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGGA--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGCCTGTTT-A-AATGTT--ATAAAATTT-------------ATATTTTA---------------
TAACTTTATTTTTACAGC-TTTAA--TTA--AT----TTT---ACTGGGTATTTT-----
TTTTTGTTCTGACAGTAACGACTGATGG-TGTAGAGCCACTTAAACATT---------
ATTTTTTATA-----ATG-----TAAAAGTGTCGCCT-TATTCTTTTTTTTGCT-GTTTACAA-
GTGGGTTTAA------GGTATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-
AGCCGCCTA-CTGTTTGTA----AAC-TG--TGCCCTTG--GACAG--
TGC???
??????????????????????ACGCAAGTCATTGGGTGAT-
AGAAAACCCAAAGGCGTAATGAAAGTAAAGAGTATAAAGATAGAAG-------------------
AAGAAAAT--------TCATTTTCATCTTTGAT---------------TCT-

TTCTCTCAAGGGAAGATGG--ATAT-----------CTTATTTTAAATAA-TATTTAG--------------
------------TAT---TT-TTATTAAG-TA---------------TT-TTTAAAATTTAGA-
TTCCCGCATTCCCAGGGCGCTTG-TATCTCGCTC--TG-
CGAGTCTACGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCAAT------------T---
GTGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGATTCGGAT???
????????????????????????????????TATATATTCTCATTTTACCAGGATTTGGCTTAATTTCACAT
ATTATCGCAACAGAGACTGGTAAAAGTGAAGCTTTTGGATCATTAGGAATAATTTAT
GCAATATTAACAATTGGATTATTAGGATTTATTGTTTGAGCACACCATATATTTACTG
TAGGTATAGATGTAGACACCCGAGCATATTTTACCTCTGCAACCATAATTATTGCAGT
ACCTACAGGAATTAAAATTTTTAGATGACTAGCCACTCTTCATGGAAGATCTACAAA
ATTCTCACCAAGAATACTATGAGCATTAGGATTCGTATTCCTTTTCACTATTGGTGGA
TTAACGGGAGTAGTACTTGCAAACTCAAGAATTGATATTATTTTACATGACACTTATT
ATGTAGTAGCCCACTTCCA???
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Toxopus_fisheri

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?????????????CTGTGCTAAGGTAGCATAATCAATTGTCTTTTAATTGTGGCTAGTATG
AAAGGTTGCACGAAACATCTACTTTCTTT-TAATTAT--
TTAATGAATTTAATTTTTAAGTTAAAAAGCTTA-
AATATTTTTGAGGGACGAGAAGACCCTATAGATCTTTATATATAA-TAAG--
ATTGATTTTTTTT---GTTTATAA-----
TTGTATTATCAATTTTATAATTATTTCATTGGGGTGATAGGAGAATTA-
TAATAACTTCTCT--TTA-ATTGTTTCATATATG---TATGT--TTTTTTGATCCATT---
GTGAATGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTAATTTTTTTGGAGAGTTCTTATTGATAAAGAAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAGTT-ATAAGTGCAGGAGCTT-ATTTA-
CTGGGTCTGTTCGACCTTTAAATT-
TTTACATGATCT???
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???AAGGCTAAATACAACCACGAGTCCG
ATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAA
GAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGATCTGAA--
TATCCGAAAGGGGAGATTCACGTCTTACCAC---TTGCTCGACTTTGAAGTGC----
TCTTGAGATGGTAA-TTC-GCCCTATCCAG----TGCAT--ACTGTG--GTAG-
AGGGTTTTACCGCTCGCATTTT-ATT----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAAAT--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGTCTGTCT-A-AAGGTT--ATAAAAT---------------TTATTTTA---------------
TAACATTTATTAAACAGC-TTTAATTTTA--AT----TTT---ACTGGGTATTTA------
TTTTTTTTTGACAGTAACAAATGATGG-TGTAGAGCCACTTAAACATT------------
ATTTATA-----ATG-----TAAAAGTGTCCA-----------TTTTTGCC-GTTTACAA-
GTTGGTTTAAGGT-ATTTTTTTAGTT-ATTAGTCGAACTT-TT--------GTTCGTCTAA-
CTA-AGCCGCCTA-CTGTTTGTA----AAC-TG--TG-CCTTG--GACAG--TGCTTA--
CAACACCGTTCGGCAGCGATCCAGG???
???????????AGGAGTTTATTGTGTACGCAAGTCATTGGGTGAT-
AGAAAACCCAAAGGCGTAATGAAAGTAAAGAGTAGAAAGATAGAAG-------------------
AAGAAAAT--------TAATTTTCATCTTTGAT---------------TCT-
TTCTCTCAAGGGAAGATGG--ATAT-----------CTTATTTTAAATAA-TATTTAG---------------
------------TAT---TT-ATATTGAG-TA---------------TA-TTTAAAATTTAGA-
TTCCCGCATTCCCAGGGCGCTTG-TATCTCGCTC--TG-
CGAGTCTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCTTAAAA-------------------
TGAAGCCGT??
?????????????????????TACATTTAATTCTACCCGGATTCGGATTAATTTCCCATATTATC
GCAATAGAAACAGGAAAAAATGAAGCATTTGGATCTCTAGGGATAATTTATGCAAT
ACTTACTATTGGACTATTAGGATTTATTGTTTGGGCCCATCATATATTTACAGTTGGA
ATAGATGTAGATACCCGAGCTTATTTCACTTCAGCAACAATAATTATTGCCGTACCTA
CCGGTATTAGGATTTTTAGTTGACTAGCTACAATACATGGAAGTATTATAACTTTCTC
ACCCAGAATATTATGAGCATTAGGATTCGTATTTTTATTCACAATTGGAGGATTAACA
GGAGTTATTTTGGCAAACTCTAGAATTGATATTATTTTACATGATACTTATTATGTAG
TTGCACACTTCCAT???
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??TTCCAGCTCCAATAGCGTAT
ATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTT
CGCCGCCTGTCGGTGTTACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAATGAAA
TCC------------------------------------CCGGTGC----TACGTAGGCT-TTTATTAGCTGAAG-T-
TTGTG-CCG----------TG-G-TGACTTC--ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
TTATTGGTTTTAGGAATATGAGGTAATGATCAATGTGGACTGGCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCT-
A??
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???AAGGCT
AAATACAACCACGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAA
CTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGAT
CTGAA--TATCCGAAAGAGGAGATTCACGTCTTACCAC---
TTGCTCGACTTTGAAGTGC----TCTTGAGATGGTAA-TTC-GTCCTATCCAG----TGAAT--
ACTGTG--GTAG-AGGGTTTTACCGCTCGCATTTT-TTT----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGAGTCTGTTT-A-AAGGTT--ATAAAAT--------------TTATTTTG--------------
TAACTTTTTTTTTACAGC-TTTGA--TTA--AT----TTT---ACTGGGTATTTT--------
TTATTCTGACAGTATCGACTGATGG-TGTAGAGCCACTTAAACATT-----------
ATTTATA-----ATG----TTTAAAGCGTCCA-----------TTGTTGCC-GTTTACAA-
GTGGGTTAAG-GT--ATTAATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-
AGCCCCCTA-CTGTTTGTA----AAC-TG--TG-CCTTG--GACAG--TTCTTA--
CAACACCGGTCAGCAGCGATCCAGGT??
???GGCGTAATGAAAGTAAAGA
GTAGAAAGATAGAAG------------------AAGAAAT---------TTATTTTCATCTTTGAT---------
-----TCT-TTCTCTCAAGGGAAGATGG--ATAT-----------C-TAATTTAAATTA------------------
----------------TAT---TTATTATTAAGTTA---------------TA-TTTAAAATTTAGA-
TTCCCGCATTCCCAGGGCGCTTG-TATTTCGCTT--TG-
CGAGTCTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCACTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCTTAAAA------------------
TTGAAGCCGTGGGATTCGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAAC
TGGC------
G???????????????????????????????????????TTCTTATTTTACCGGGATTTGGATTAATTT
CACATATTATTTCAATAGAAACTGGGAAAAACGAAGCGTTTGGATCACTTGGAATAA

TCTACGCCATAATTACAATTGGATTATTAGGATTCATTGTATGAGCGCATCATATATT
TACAGTAGGAATAGATGTAGATACCCGAGCTTATTTACATCAGCAACTATAATCAT
TGCAGTACCAACAGGTATTAAAATCTTTAGATGATTAGCAACCATACACGGTAGTGT
TACTATATCTTCACCTAGAATACTTTGAGCATTAGGATTTGTATTCCTATTTACCATTG
GGGGATTAACAGGAGTTGTATTAGCCAACTCAAGAATTGATATTATTTACACGATA
CATATTATGTAGTAGCCCACT??
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?????????????CCACGAGTCCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAA
CTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAGAAGAT
CTGAA--TATCCGAAAGGGGAGATTCACGTCTTACCAC---
TTGCTCGACTTTGAAGTGC----TTTTGAGATGGTAA-TTC-GCCCTATCCAG----TGCAT--
ACTGTG--GTAG-AGGGTTTTACCGCTCGCATTTT-ATT----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGTCTGTCTTA-AAGGTT--ATAAAAT--------------TTATTTA-----------------
TAATCTTTTTTACAGC-TTTAA--TTA--AT----TTT---ACTGGGTATTT----------
TTTGCTGACAGTAACGACTGATGG-TGTAGAGCCACTTTTACACA-----------
CATTCATGTGTGTGTG-----TTAAAGTGTCCT-----AAATAATTTTTGCC-GTTTACAA-
GTGGGTTTAAGGT--ATTAATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-
AGCCGCCTA-CTGTTTGTA----AAC-TG--TG-CCTTG--GACAG--TGCTTA--
CAACACCGGTCGGCA???
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??TCTTTGAT--------------TCT-
TTCTCTCAAGGGAAGATGG--ATAY-----------CTTGTTTTAAATTTTTATTTAG-------------
-------------TATTTATT-ATATTAAG-TA---------------TA-TTTAAAATTTAGA-

TTCCCGCATTCCCAGGGCGCTTG-TATCTCGCTC--TG-
CGAGTCTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTC??
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????????AGTTTATATTTTAATTTTACCAGGATTTGGTTTAATTTCCCACATTATCGCAA
CAGAAACCGGAAAAAAACGAAGCATTCGGATCACTAGGTATAATTTATGCTATACTTA
CCATTGGATTATTAGGGTTCATCGTCTGAGCCCATCACATATTTACAGTGGGAATAG
ATGTAGACACTCGAGCCTATTTCACATCAGCAACCATGATTATTGCAGTACCTACAG
GAATTAAAATTTTTAGATGATTAGCAACAATACACGGTAGAATTATAACCTTTTCAC
CCAGAATACTATGAGCCTTGGGATTCGTTTTCCTATTTACTATTGGGGGACTTACAGG
AGTTATCCTAGCAAATTCAAGAATCGATATTATTCTCCATGATACTTATTATGTAGTT
GCCCACTTCCATT??
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Toxopus_vazimba ?????????????AAAACATGGTTTTAGT---------
TAATTATTTA-AGATTGGGCCTGCCCAATGA---
TGTTTATTTAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCATTTGTCTTT
TAATTAAGGGCTTGTATGAATGGTCGGACGAGGTATTATCTTTCTTT-TAATTAT--
CTTGTGAATTTAATTTTTGAGTTAAAAAGCTTA-
AATTTTTTTGAGGGACGAGAAGACCCTATAGATCTTAATATTTAT-AGAT--
TTTTGATTTGTTT---GTTTTAT------
TGAAGAATTTAATGTTTTAGGTATTTTGTTGGGGTGACAGGAGAATTTATAATAACTT
CTTT--TTAGTTTTTATCATTTATT---TATGT--
TTTTTTGATCCATTTATTTAAATGATTATAAGTTTAAGTTACCTTAGGGATAACA-
GCGTAATTTTCTTGGAAAGTTCTTATTGATGGGGAAGTTTGCGACCTCGATGTTGGAT
TATAA-TAAGTTGTAAGGTGTAGTAGCTT-ACTTA-
CTGGGTCTGTTCGACCTTTAAATT-
TTTACATGATCTGAGTT??
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???TAAAAAGCTCGTAGTTGGT
TCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTTACTGGCATGTCGCGGCATG
TCCTGTCGGTGGTGAATGAAATCC-----------------------------------CCGGTGC----
TACGTAGGCT-TTTATTAGCTGAAG-T-ATGTG-CCG----------TG-G-TGACTTC--
ATTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATATCTGCCTGAATAGTGGTGCATGGAATAATAAAATAGGACCTCGGTTCTATT
TTATTGGTTTTAGGAATATGAGGTAATGATCAATGTGGACTGGCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCG??

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???????????????????????????????????CCACGAGTCCGATAGCGAACAAGTACCGTGAGGG
AAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGG
TAAACGGAGAAGATCTGAA--TATCCGAAAGGGGAGATTCACGTCTTACCAC---
TTGCTCGACTTTGAAGTGC----TCTTGAGATGGTAA-TTC-GCCCTATCCAG----TGCAT--
ACTGTG--ATAG-AGGGTTTTACCGCTCGCATTTT-ATA----
AGTAAGGTGCAGTGGTGGATCGCACTTCTCCTTTAGT-
AGGACGTTGCGACCTGTCAGGA--AAT-----ACTCTAAGT--AT-A-----GTTAA---
AGTGCCTGTTT-A-AATGTT--ATAAAATTT------------ATATTTTA--------------
TAACTTTATTTTTACAGC-TTTAA--TTA--AT----TTT---ACTGGGTATTTTTTT--
TTTTTTTTTTGACAGTAACAACTGAGGG-GGGAGAGCCCCTTAAAAATT----------
TTTTTTTTA-----AAG----TAAAAAGGGTCGCTTATTTTTTTTTTTTTGCC-GTTTACAA-
GTGGGTTTTA-----AGGTATTAGTT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-CTA-
AGCCGCCTA-CTGTTTGTA----AAC-TG--TGCCCTTG--GACAG--TGCTTA--
CTACACCGGTCGGCAGCGAT???
?????????????????????GTACGCAAGTCATTGGGTGAT-
AGAAAACCCAAAGGCGTAATGAAAGTAAAGAGTATAAAGATAGAAG------------------
AAGAAAAT--------TCATTTTCATCTTTGAT--------------TCT-
TTCTCTCAAGGGAAGATGG--ATAT-----------CTTATTTTAAATAA-TATTTAG--------------
------------TAT---TT-TTATTAAG-TA--------------TG-TTTAAAATTTAGA-
TTCCCGCATTCCCAGGGCGCTTG-TATCTCGCTC--TG-
CGAGTCTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCAAT-----------T---
GTGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
CCCCGGCTTTCTTAAAA-----------------
TTGAAGCCGTGGATTCGGATCAGAGTGCCAAG?????????????????????????????????????
????????????????????????????AGAAGTATATATTCTAATTTTACCAGGATTCGGATTAAT
TTCACATATTATCGCAACAGAGACTGGTAAAAATGAAGCTTTCGGATCCCTGGGAAT
AATCTATGCAATATTAACAATTGGATTGTTAGGATTTATTGTATGAGCACACCACATA
TTCACTGTAGGAATAGACGTGGATACACGAGCATATTTCACCTCTGCAACAATAATT
ATTGCAGTACCCACAGGAATTAAAATTTTCAGATGACTAGCCACTCTCCATGGAAGA
ACTACAACATTCTCCCCAAGAATGTTGTGAGCACTAGGATTCGTATTTCTATTTACTA
TTGGAGGATTAACAGGAGTGGTTCTCGCAAACTCAAGAATTGATATCATTTTACATG
ATACTTATTATGTTGTAGCCCATTTC???
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Tribelocephala_peyrierasi CGCCTGTTTATCAAAAACATGTCCTTTTGT---------
TATTTATATA-AGGTCTAACCTGCCCAATGA-----
ATATTTGAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCAATTGTCTCTT
AATTGGGGGCTGGAATGAATGGTTGTACGAAATATTTACTTTCTTT-AATTTAT--
ATGTTTAATTTAACTTTTTAGTTAAAAGGCTTA-
AATTTTTTTAAGGGACGAGAAGACCCTATAGATCTTTATATTTAACTGGT-

TATGGATTAAATTG---GTGTTAAT-----
AATTATTTTATTTAGTTGAATATTTTGTTGGGGTGATGTTGAAATTT-
TAATAACTTTCAT--AT---ATTTTTCATTAATT---AGTGTA-TTTAATGATCTTTT---
ATTATTGATTATAAGATTAAGTTACCTTAGGGATAACA-
GCGTTATTTTTACGGAGAGTTCTTATCGATGTATGAGTTTGCGACCTCGATGTTGGAT
TAAAA-TAAATG-ATAGGTGTAGTAGTTT-ATTAA-
TTAGGTCTGTTCGACCTTTAAATT-
TTTACATGATCTGAGTTCAAACCGGAGGCAGCAGGCACGCAAATTACCCACTCCCGG
CACGGGGAGGTAGTGACAAAAAATAACGATCGGGGACTCTATTGAGGCCCCGTAAT
CGGAATGAGTACACTTTAAAT-CCTTTAACAAGGATCCA-TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCAATAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTTGCCGCCTGTCGGTGTA
ACTGGCATGTCTCGGCATGTCCTGTCGGTGGTGAATGTAATCTGGCCAATAGGTTTA
AGGGTTAGTAGTTCGATGTGCGCTAATGCGC----TACACGGGCT-
TTTCCCCTTCTAACTTGTTGGT-TTT----------TT-T-TGATTAT--
GTTTACCGATTTTTTTTCCTACTCCGGTGCTCTTAAACGAGTGTCGAAGTAGGCCGAC
ACGTTCACTTTGAACAAATTAGAGTGCTTAAAGCAGGCTGGAAATATCTGCCTGAAT
AGTGGTGCATGGAATGATAAAATAGGACCTCGGTTCTATTTTATTGGTTTTAGGAATA
TGAGGTAATGATCAATATGGACTGGCGGGGGCATTCGTATTGCGACGTTAGAGGTGA
AATTCTTGGATCGTCGCAAGACGCACTAGAGCGAAAGCATTTGCCAAGTATGTCTTA
ATTGATCAAAAACGAAAGTTAGAGGTTCCAA-
GCGATCAGATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGA
TGTTCCTTTAATGACTCGGCGGGGAGCTTTT-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACT
CAACACGGGAAACCTCA???
????????????????CGTGTTGCTTGATAGTGCAGCCCTAAGTAGGTGGTAAACTCCATCTA
AGGCTAAATAGTACCACGAGACCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAA
AAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAA
AAGACCTGAA--TATTCGAAAGGGGAGATTCACGTCTTACCGC---
ATGTTTAACTTTTTATCTT----TTATGAGATGATTT-TTC-GCCCTGTCCAGTTTTTTTAT--
ACTGTG--ATGGTTGGGTTAAATCGCTCGTATATA-ATT-----
AGTAAAAACAGCGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGACTCGTGGGAC--AATATATTATTCTAAGC-TAT-------ATTAA---
AGTGTCTTTAT-A-TATTGT--ATGTAGCAT----------------TGTTA----------------
TTTATAATATATATAGC-TATAA--TAA--ATAA------ATGCTGAATA-------------
ATTTCCGACAGTAACGAATGATAG-TGTTGAGCCGCTAATTTTTT----------------------------
---TCTTTAGCGTT--------------TTGACCA-ATTTACAA-GTGGGGTAKG------
AATAATTATT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-TAT-GTTCTCCTA-
CTGTTGGTA----AAT-TGTTTG-TTTCA--AACAA--GGCTTA--
TAACACTGATCAGCAGCGATCCAGTTTCAGGCTCTTATCCGGTCCGT?????????????????
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???????????????TGCAGCCCAAAGTAGGTGGTAAACTCCATCTAAGGCTAAATAGTACCACGAGACCGATAGCGAACAAGTACCGTGAGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAAGAGTACGTGAAACCGCTCAGGGGTAAACGGAAAAGACCTGAA--TATTCGAAAGGGGAGATTCACGTCTTACCGC---ATGTTTAACTTTTTATCTT----TTATGAGATGATTT-TTC-GCCCTGTCCAGTTTTTTTAT--ACTGTG--ATGGTTGGGTTAAATCGCTCGTATATA-ATT-----AGTAAAAACAGCGGTGGACCGCACTTCTCCCTTAGT-AGGACGTTGCGATTTGTTGGAC--AATATATTATTCTAAGC-TAT-------ATTAA---AGTGTCTTTAT-A-TATTGT--ATGTAGCAT---------------TGTTA---------------TTTATAATATATATAGC-TATAA--TAA--ATAA------ATGCTGAATA-------------ATTTCCGACAGTAACGAATGATAG-TGTTGAGCCGCTAATTTTTT---------------------------

---TCTTTAGCGTT--------------TTGACCA-ATTTACAA-GTGGGGTATG------
AATAATTATT-A-ATGTCGAACTT-TT--------GTTCGTCTAA-TAT-GTTCTCCTA-
CTGTTGGTA----AAT-TGTTTG-TTTCA--AACAA--GGCTTA--
TAACACTGATCAGCAGCGATCCAGTTTCAGGTACTTATCCGACCCGTCTTGAAA?????
??????????????????????????????????????TGTACGCAAGTCATTGGGTAAATATTAAACCC
AAAGGCATAATAAAAGTAAATATAATGTAAAAAAAAA-------------------GGAAAAAT----
----ACTTTTTTAATTTTTTT---------------TTTACATTACAAAGAGAAGATGG--TATA---------
--TTGTTTTTTGTACT--CTT-
TGGTATAAAAGAT-TGCCCGCATTCTCAGGGCGCTATTACTCTCGCTT--TG-
CGAGTGTATGCGCACCCAGAGCGTACACGATAATACCCGAAAGATGGTGAACTATG
CCTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACG
TGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAG
TAGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGTG-----------AT---
GTGATTAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAA-
GGCCGGCTTTCTTAAAA------------------TTGAAGCCG------------------
GTCAGATATATTTGTTTTGTTTTGGATAA???
AGTATATATTCTTATTCTACCGGGATTCGGACTCATTTCACATATTATTTCTATAGAA
ACAGGAAAAAATGAAGCTTTTGGAGTACTAGGAATAATTTATGCCATATTAGCTATT
GGACTTCTGGGATTTATTGTTTGAGCACATCATATGTTCACAATCGGAATGGACGTA
GATACACGGGCCTATTTTACATCAGCTACAATAATTATTGCTGTGCCAACAGGTATTA
AAATCTTCAGATGATTAGCCACATTGCATGGAAGAGTAATTATATATAATCCAAGAA
TTTTATGAGCCTTAGGATTTGTATTCCTATTCACAATCGGGGGATTAACAGGAGTTAT
TCTCGCTAATTCAAGAATTGACATTGTACTACACGACACCTATTATGTAGTAGCCCAC
TTCCA???
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TACCCACTCCCGGCACGGGGAGGTAGTGACAAAAAATAACGATACGGGACTCTATT
GAGGCCCCGTAATCGGAATGAGTACACTTTAAAT-CCTTTAACAAGGATCTA-
TTGGAGGGCAAGTCT--
GGTGCCAGCAGCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGT
TAAAAAGCTCGTAGTTGGTTCTGCGTGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTA
ACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAACGAGAATC-----------------------------
---------CTGGTAC----TGCTTAGGCC---TAACGGCCAAAG-T-TTGTA-CCG----------TG-G-
TGTTTTC--GTTTGCCGA---
TTTCTCCTACTCCGGTGCTCTTAAACGAGTGTCGAGGTAGGCCGACACGTTCACTTTG
AACAAATTAGAGTGCTTAAAGCAGGCT-
AAAATCTCTGCCTGAATAGTGGTGCATGGAATGATAAAATAGGACCTCGGTTCTATT

TTATTGGTTTTAGGAATATGAGGTAATGATCAATATGGACAGTCGGGGGCATTCGTA
TTGCGACGTTAGAGGTGAAATTCTTGGATCGTCGCAAGACGCACTAAAGCGAAAGCA
TTTGCCAAGTATGTCTTAATTGATCAAGAACGAAAGTTAGAGGTTCGAAGGCGATCA
GATACCGCCCTAGTTCTAACCATAAACGATGCCAGCCAGCGATCCGCCGATGTTCCT
TTAATGACTCGGCGGGGAGCTTCC-
ACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTGCAAAGCTGAAACT
TAAAGGAATTGACGGAAGGGCACCACCAGGAGTGGAGCCTGCGGCTTAATTTGACT
CAACACGGGAAACCTCACCAGGCCAGGACATTGTAATGATTGACAGATTGATAGCTC
TTTCTT??TA
AGGCTAAATACAACCACGAGACCGATAGTAAACAAGTACCGTGAGGGAAAGTTGAA
AAGAACTTTGAAGAGAGAGTTCAATAGTACGTGAAACCGCTCAGGGGTAAACGGAG
AAGACCTGAA--TATCCGAAAGGGGAGATTCACGTCTTACCAT---
ATGTTCAACTATAAAATGT------TTGAGATGGCCA-TTC-GCCCTATCCAA----TGCAA--
ATTGTG--ATAG-AGGGTTTGTTTACTCGCATTTTTTTT----
TAGTAAGAACAGTGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGACCTGTCAAAT--AAT-----ACTCTAAGT--AA-A----TGTTAA---
AGTGACTGTAT-T-TATAGG------------------------
TTTTTTTAAATTGTAAAAGATTTAAATGCCATTTTACAGC-TTTAA--CAATAAA----
ATT---ACTGGATATT-----------TGTATTGACAGTATAGACTGATGT-
TGTTGAGCCACTTATTATAA--------------------------ACATTTAATAAGTGTC--------------
TTTGGCC-GTTTGCAA-GTAGGTAGGT------ATTTTTAGTT-A-ATGTTGGGCTT-TT--------
GTCCGTCTAA-CTA-ATCCTCTTA-CTGTTGGTA----AAC-TG--TG-TCTCT--GACAG--
TGCTTA??
???GACCAAGGAGTTTATTGTGTACGCAAGTCATTGGATAAT--
TAAAATCCAAAGGCGAAATGAAAGTAAAGAGTTTTTTTAAGTTTTTAATA---------------
---------------ATTTTATTAATCTC----------------TTGGA-AAAACTCAAGGGAAGATGG--
AACA-----------CTAATTTTAATAAT---------------------------------TGATAATA-
TTTCTTTTAATATTATTTG---------GTT-ATTTTAATATAGG-
TTCCCGCATTCCCAGGGCGCTTG-TTTCTCGTTT--TA-
CGAGTCTATGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATGC
CTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACGT
GCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCGAACCATCTAGT
AGCTGGTTCCCTCTGAAGTTTCCCTCAGGATAGCTTGCACTCAAT------------T---
GAGACGAGTCTCATCAGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAT-
CCCCGGCTTTCTTAAAA----------------
TTGAAGCCGTGGGATTCGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAA--

ACTGGCG??
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Xenocaucus_n_sp ???????????CAAAAACATGTCCTTTTGT---------
TATTTATATA-AGGTCTAACCTGCTCTATGA-----
TTTATTAAATGGTCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCAATTGTCTTTT
AATTGGAGAATGGGATGAAGGGTTGAACGAAGTATTGACTTTTTTT-ATTTCTG--
TGGATGAATTTAATTTTTTAGTTAAAAAGCTAG-
AATAGTTTTAAGGGACGAGAAGACCCTATAGATCTTTGTGTAGAT-ATAG--
ATAAAGTGTATTTTG-GTTTTTTA--
TTTGATATTTTTATTTGATATTTTTATTTGGCTGGGGTGGCTGTGGAAATT--
TTTAACTTCTAT--TGG-GTTAGTTCATGGATT---AGTGTTTATATATGATCTTGT---
ATTAATGATTTTAAGATTAAGATACCTTAGGGATAACA-
GCGTTATCTTTTCGGAGAGTTCTTATTGATGAGGGGGATTGCGACCTCGATGTTGAAT
TAAAG-TGAATA-TTAAGTGTAGAAGTTT-
ATATAATTAGGTCTG??
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????????????????????????????????????TCGGGTTGCTTGAGAGTGCAGCCCTAAGTAGGTG
GTAAACTTCATCTAAGGCTAAATACAACCATGAGACCGATAGCGAACAAGTACCGTG
AGGGAAAGTTGAAAAGAACTTTGAAGAGAGAGTTCAATAGTACGTGAAACCGCTCA
GGAGTAAACGGAAAAGACCTGAA--TATTCGAAAGGGGAGATTCACGTCTTACATT---
TGGCTAAACTATTAAATAC----TTTTGAGATGGTCA-GTC-GCCCTATCTAG----TGCAA--
ACTGTG--ATGG-AGGGATTGGCCGCTCGTATTTA-ATT----
AAGTGAGAGCCGTGGTGGACCGCACTTCTCCCTTAGT-
AGGACGTTGCGACCTGTCAGAT--AAT-----ACTCTAAGT--AT-A-----
GTTAATAGCGCGACTGTAT-T-AAAATT--TAAAAAGTT---------TTATACTTTTA---------
--------TTTTCTTTTTGCAGCTTTTAA--CAA--AT----TGT---ACAGAGTATA-----------
ATTTTTGACAGTATCGAATGATGG-TGTCGAGTCACTTTTCAATT------------ATTTATA--
---A------TTGAAAGAGTT--------------TATAGCC-GTTTGCAA-GTGGGTTTAG-----
GTAATTAAGCT-A-ATGTCTGACAA-TT--------GTCCGTCTAG-CTA-AACCTCCTA-
CTGCTGGCA----GAC-TG--AG-TTTAT--AACGG---GCTTA--
CAACACCAGTCGGCAGCGATCCAGGTTCAGCCTCTTTTCCGACCCGTCTTGAAACAC
GGACCAAGGA-
GTTTGAAACACGGACCAAGGAGTTTATTGTGTACGCAAGTCATTGAGTGAT--
TAAAACTTAAAGGCTAAATGAAAGTAAAGAGTTGATTGATTGTAAGAAGAAGA-------
----AAGGAATTTATTCTTTTTTTTCTTTTTATTTAT---------------CCA-
ATCTCTCAAGGGAAGATGG--AAGT-----------TTTATTATTTTGAG----------------------------
-----ATAATT-TTTTATTAAAAGTT---------------AT-TAATAATAAAGTT-
TTCTCGCATTCCTGGGGCGCTTG-TCTCTCGCAT--TG-
CGAGTACGTGCGCACCTAGAGCGTACACGATGATACCCGAAAGATGGTGAACTATG
CCTGGCCAGGACGAAGCCAGGGGAAACCCTGGTGGAGGTCCGCAGCGATTCTGACG

```
TGCAAATCGATCGTCAGAGCTGGGTATAGGGGCGAAAGACCAATCAAACCGTCTAG
TAGCTGGTTCCTTCTGAAGTTTCCCTCAGGATAGCTTGCGCTCGGT------------T---
GAGAAGAGTCTCATCCGGTAGAGCGAATGATTAGAGGCATTGGGGTCG-
AAACGACCTCAACCTATTCTCAAACTCCAAATAGATGAGAG-
CCCCGGCTTTCTTAAAA-----------------
TTGAAGCCGTGGGAATAGGATCAGAGTGCCAAGTGGGCCAATTTTGGTAAGCAGAA
CTGGC------
G?????????????????????????????????????????????????????????????????????????????????????????????????
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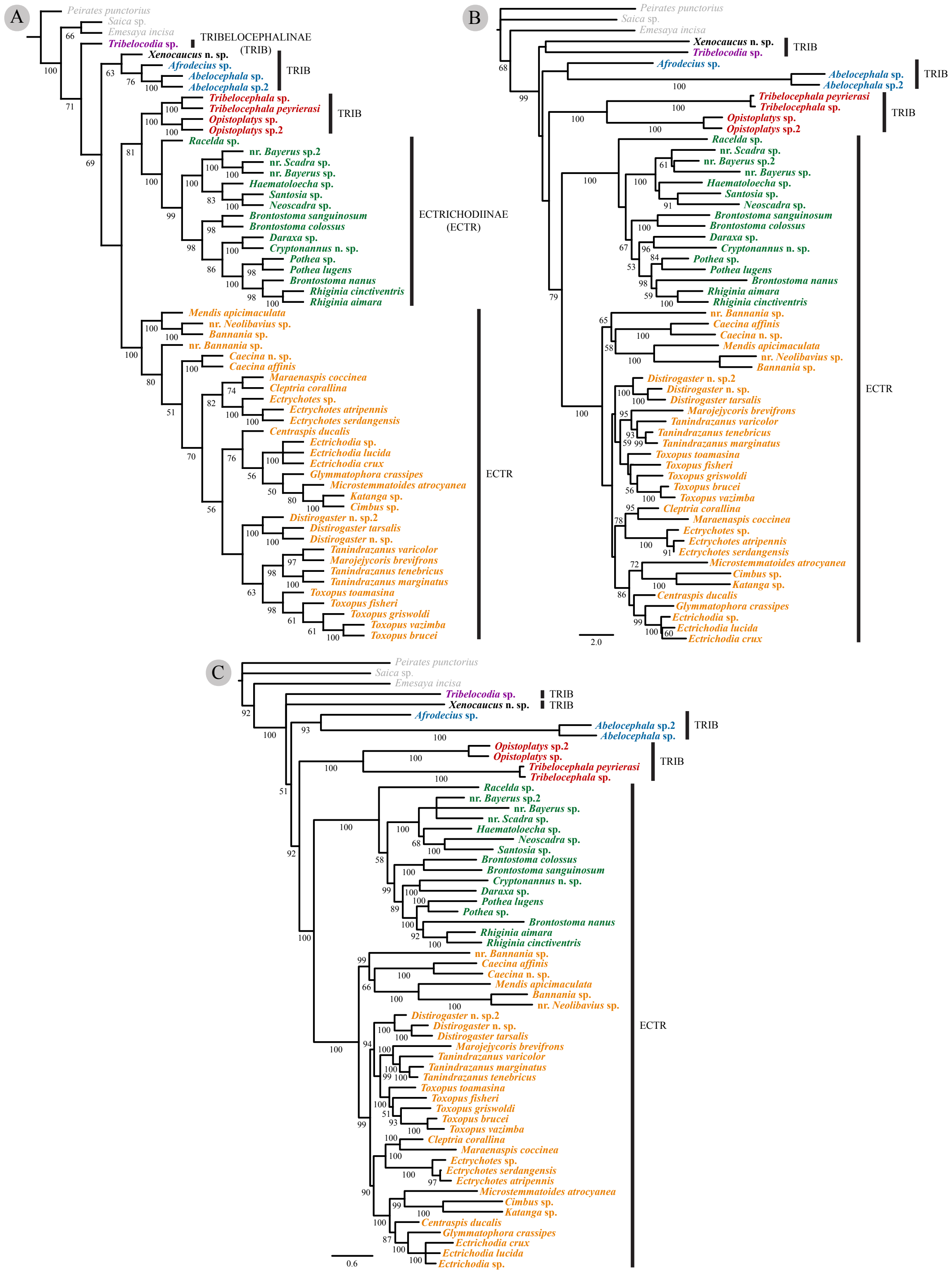
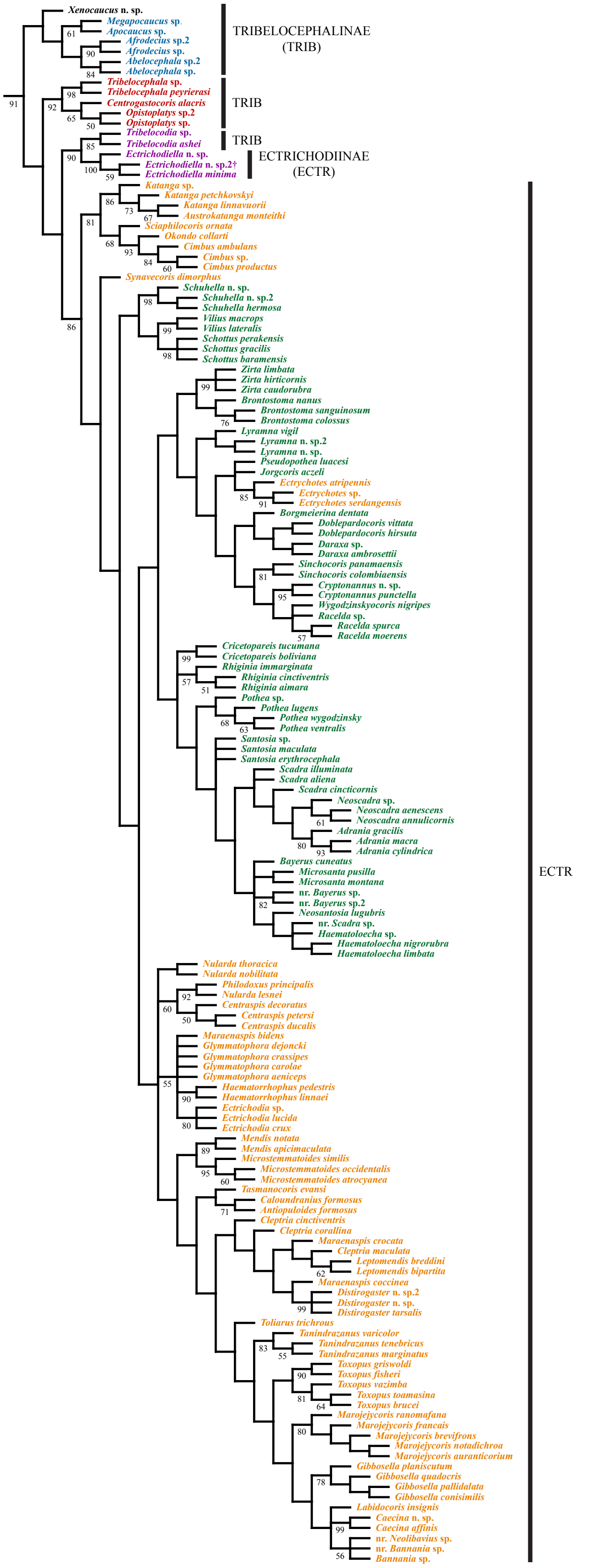
;
END;
BEGIN SETS;
	CHARSET 16S = 1-599;
	CHARSET 18S = 600-1624;
	CHARSET 28S_D2 = 1625-2475;
	CHARSET 28S_D3_D5 = 2476-3243;
	CHARSET COI = 3244-3714;
	CHARSET Wg = 3715-4055;
END;
```

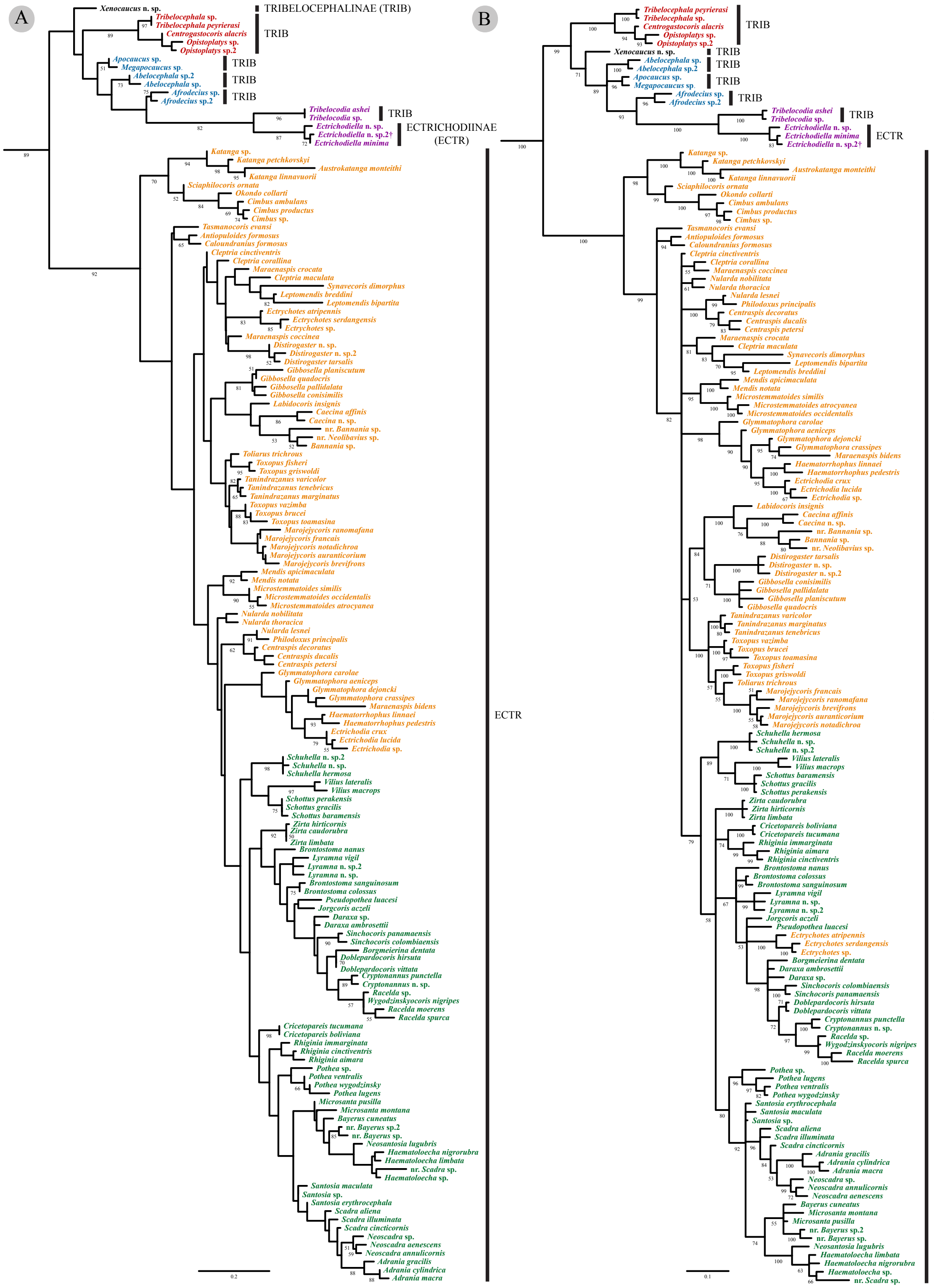
Supplementary material 4.5. Molecular phylogenetic analyses of 59 taxa. Terminal taxon names are colored by clades recovered in the combined morphological and molecular ML best tree in Fig. 4.2 for comparison. A. Strict consensus tree from two parsimonious trees (length = 9,181 steps; RI = 0.484; CI = 0.306). B. ML best tree (final Ln = –38,481.3284) based on three partitions and models of sequence evolution: 16S, 28S D2, 28S, D3–D5 (GTR+Γ+I); 18S, COI codon positions 1 and 2, Wg (GTR+Γ+I); COI codon position 3 (HKY+Γ+I). C. Bayesian MCMC majority-rule consensus tree based on the same three partitions and models of sequence evolution. Bootstrap values ≥50 are reported in A. and B. Posterior probabilities ≥50 are reported in C.


A
Peirates punctorius
Saica sp.
Emesaya incisa
Tribelocodia sp.
TRIBELOCEPHALINAE (TRIB)
Xenocaucus n. sp.
Afrodecius sp.
Abelocephala sp.
Abelocephala sp.2
TRIB
Tribelocephala sp.
Tribelocephala peyrierasi
Opistoplatys sp.
Opistoplatys sp.2
TRIB
Racelda sp.
nr. Bayerus sp.2
nr. Scadra sp.
nr. Bayerus sp.
Haematoloecha sp.
Santosia sp.
Neoscadra sp.
Brontostoma sanguinosum
Brontostoma colossus
Daraxa sp.
Cryptonannus n. sp.
Pothea sp.
Pothea lugens
Brontostoma nanus
Rhiginia cinctiventris
Rhiginia aimara
ECTRICHODIINAE (ECTR)
Mendis apicimaculata
nr. Neolibavius sp.
Bannania sp.
nr. Bannania sp.
Caecina n. sp.
Caecina affinis
Maraenaspis coccinea
Cleptria corallina
Ectrychotes sp.
Ectrychotes atripennis
Ectrychotes serdangensis
Centraspis ducalis
Ectrichodia sp.
Ectrichodia lucida
Ectrichodia crux
Glymmatophora crassipes
Microstemmatoides atrocyanea
Katanga sp.
Cimbus sp.
Distirogaster n. sp.2
Distirogaster tarsalis
Distirogaster n. sp.
Tanindrazanus varicolor
Marojejycoris brevifrons
Tanindrazanus tenebricus
Tanindrazanus marginatus
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Toxopus vazimba
Toxopus brucei
ECTR
B
Peirates punctorius
Saica sp.
Emesaya incisa
Xenocaucus n. sp.
Tribelocodia sp.
TRIB
Afrodecius sp.
Abelocephala sp.
Abelocephala sp.2
TRIB
Tribelocephala peyrierasi
Tribelocephala sp.
Opistoplatys sp.
Opistoplatys sp.2
TRIB
Racelda sp.
nr. Scadra sp.
nr. Bayerus sp.2
nr. Bayerus sp.
Haematoloecha sp.
Santosia sp.
Neoscadra sp.
Brontostoma sanguinosum
Brontostoma colossus
Daraxa sp.
Cryptonannus n. sp.
Pothea sp.
Pothea lugens
Brontostoma nanus
Rhiginia aimara
Rhiginia cinctiventris
nr. Bannania sp.
Caecina affinis
Caecina n. sp.
Mendis apicimaculata
nr. Neolibavius sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus tenebricus
Tanindrazanus marginatus
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Toxopus brucei
Toxopus vazimba
Cleptria corallina
Maraenaspis coccinea
Ectrychotes sp.
Ectrychotes atripennis
Ectrychotes serdangensis
Microstemmatoides atrocyanea
Cimbus sp.
Katanga sp.
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia sp.
Ectrichodia lucida
Ectrichodia crux
ECTR
2.0
C
Peirates punctorius
Saica sp.
Emesaya incisa
Tribelocodia sp.
TRIB
Xenocaucus n. sp.
TRIB
Afrodecius sp.
Abelocephala sp.2
Abelocephala sp.
TRIB
Opistoplatys sp.2
Opistoplatys sp.
Tribelocephala peyrierasi
Tribelocephala sp.
TRIB
Racelda sp.
nr. Bayerus sp.2
nr. Bayerus sp.
nr. Scadra sp.
Haematoloecha sp.
Neoscadra sp.
Santosia sp.
Brontostoma colossus
Brontostoma sanguinosum
Cryptonannus n. sp.
Daraxa sp.
Pothea lugens
Pothea sp.
Brontostoma nanus
Rhiginia aimara
Rhiginia cinctiventris
nr. Bannania sp.
Caecina affinis
Caecina n. sp.
Mendis apicimaculata
Bannania sp.
nr. Neolibavius sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Marojejycoris brevifrons
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Toxopus brucei
Toxopus vazimba
Cleptria corallina
Maraenaspis coccinea
Ectrychotes sp.
Ectrychotes serdangensis
Ectrychotes atripennis
Microstemmatoides atrocyanea
Cimbus sp.
Katanga sp.
Centraspis ducalis
Glymmatophora crassipes
Ectrichodia crux
Ectrichodia lucida
Ectrichodia sp.
ECTR
0.6

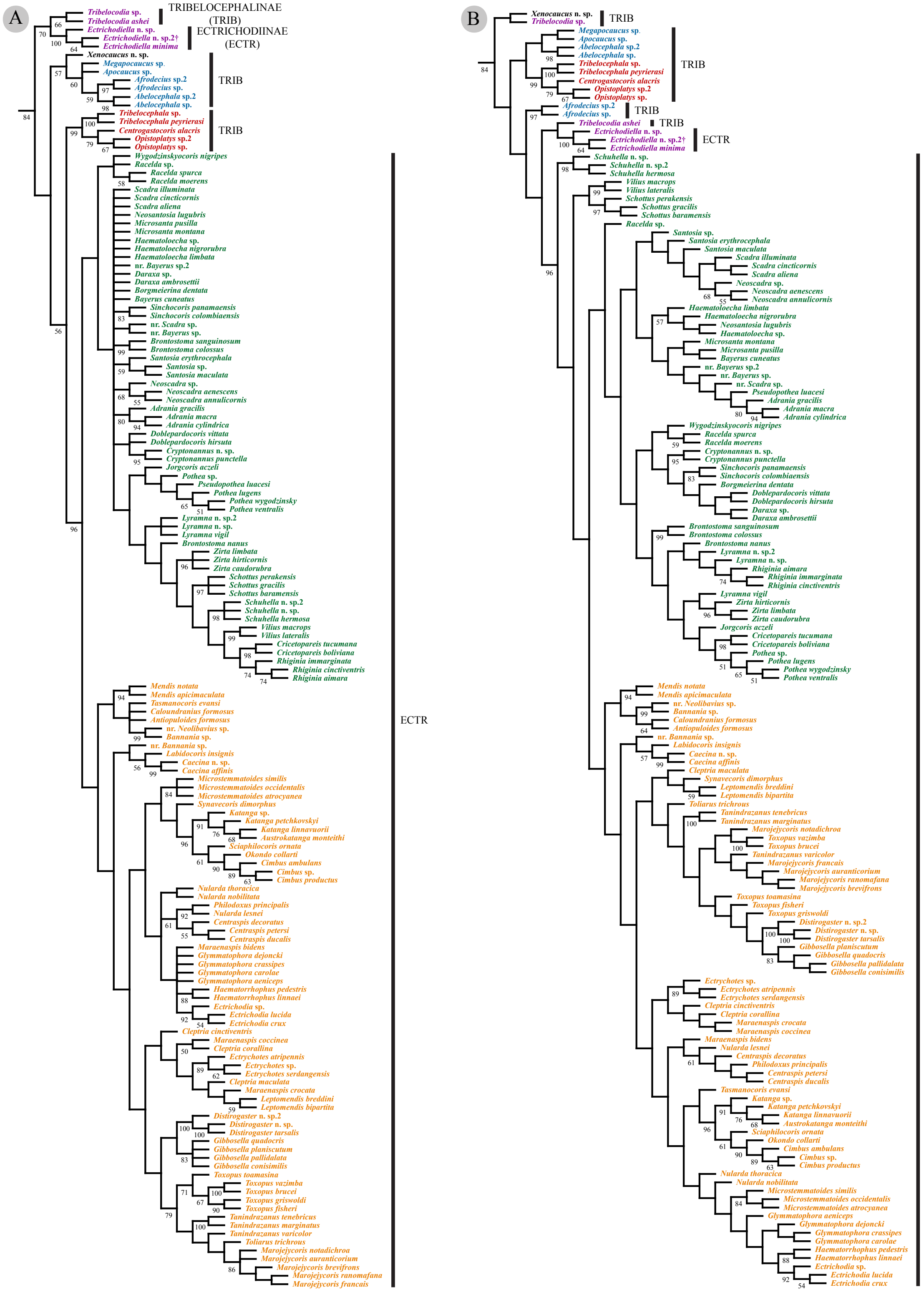
Supplementary material 4.6. Strict consensus tree from 269 parsimonious trees (length = 1,203 steps; RI = 0.705; CI = 0.174) based on TNT analysis of 156 taxa (outgroups removed from figure) and morphological data. Terminal taxon names are colored by clades recovered in the combined morphological and molecular ML best tree in Fig. 4.2 for comparison. Bootstrap values ≥50 are reported.


Xenocaucus n. sp.
Megapocaucus sp.
61
Apocaucus sp.
Afrodecius sp.2
90
Afrodecius sp.
Abelocephala sp.2
84
Abelocephala sp.
TRIBELOCEPHALINAE
(TRIB)
Tribelocephala sp.
98
Tribelocephala peyrierasi
91
92
Centrogastocoris alacris
Opistoplatys sp.2
65
50
Opistoplatys sp.
TRIB
Tribelocodia sp.
85
Tribelocodia ashei
TRIB
90
Ectrichodiella n. sp.
100
Ectrichodiella n. sp.2†
59
Ectrichodiella minima
ECTRICHODIINAE
(ECTR)
Katanga sp.
86
Katanga petchkovskyi
73
Katanga linnavuorii
67
Austrokatanga monteithi
81
Sciaphilocoris ornata
68
Okondo collarti
93
Cimbus ambulans
84
Cimbus sp.
60
Cimbus productus
Synavecoris dimorphus
86
Schuhella n. sp.
98
Schuhella n. sp.2
Schuhella hermosa
Vilius macrops
99
Vilius lateralis
Schottus perakensis
Schottus gracilis
98
Schottus baramensis
Zirta limbata
Zirta hirticornis
99
Zirta caudorubra
Brontostoma nanus
Brontostoma sanguinosum
76
Brontostoma colossus
Lyramna vigil
Lyramna n. sp.2
Lyramna n. sp.
Pseudopothea luacesi
Jorgcoris aczeli
Ectrychotes atripennis
85
Ectrychotes sp.
91
Ectrychotes serdangensis
Borgmeierina dentata
Doblepardocoris vittata
Doblepardocoris hirsuta
Daraxa sp.
Daraxa ambrosettii
Sinchocoris panamaensis
81
Sinchocoris colombiaensis
Cryptonannus n. sp.
95
Cryptonannus punctella
Wygodzinskyocoris nigripes
Racelda sp.
Racelda spurca
57
Racelda moerens
Cricetopareis tucumana
99
Cricetopareis boliviana
Rhiginia immarginata
57
Rhiginia cinctiventris
51
Rhiginia aimara
Pothea sp.
Pothea lugens
68
Pothea wygodzinsky
63
Pothea ventralis
Santosia sp.
Santosia maculata
Santosia erythrocephala
Scadra illuminata
Scadra aliena
Scadra cincticornis
Neoscadra sp.
Neoscadra aenescens
61
Neoscadra annulicornis
Adrania gracilis
80
Adrania macra
93
Adrania cylindrica
Bayerus cuneatus
Microsanta pusilla
Microsanta montana
nr. Bayerus sp.
82
nr. Bayerus sp.2
Neosantosia lugubris
nr. Scadra sp.
Haematoloecha sp.
Haematoloecha nigrorubra
Haematoloecha limbata
ECTR
Nularda thoracica
Nularda nobilitata
Philodoxus principalis
92
Nularda lesnei
60
Centraspis decoratus
50
Centraspis petersi
Centraspis ducalis
Maraenaspis bidens
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
55
Haematorrhophus pedestris
90
Haematorrhophus linnaei
Ectrichodia sp.
80
Ectrichodia lucida
Ectrichodia crux
Mendis notata
89
Mendis apicimaculata
Microstemmatoides similis
95
Microstemmatoides occidentalis
60
Microstemmatoides atrocyanea
Tasmanocoris evansi
Caloundranius formosus
71
Antiopuloides formosus
Cleptria cinctiventris
Cleptria corallina
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
62
Leptomendis bipartita
Maraenaspis coccinea
Distirogaster n. sp.2
99
Distirogaster n. sp.
Distirogaster tarsalis
Toliarus trichrous
Tanindrazanus varicolor
83
Tanindrazanus tenebricus
55
Tanindrazanus marginatus
Toxopus griswoldi
90
Toxopus fisheri
Toxopus vazimba
81
Toxopus toamasina
64
Toxopus brucei
Marojejycoris ranomafana
80
Marojejycoris francais
Marojejycoris brevifrons
Marojejycoris notadichroa
Marojejycoris auranticorium
Gibbosella planiscutum
78
Gibbosella quadocris
Gibbosella pallidalata
Gibbosella conisimilis
Labidocoris insignis
Caecina n. sp.
99
Caecina affinis
nr. Neolibavius sp.
nr. Bannania sp.
56
Bannania sp.

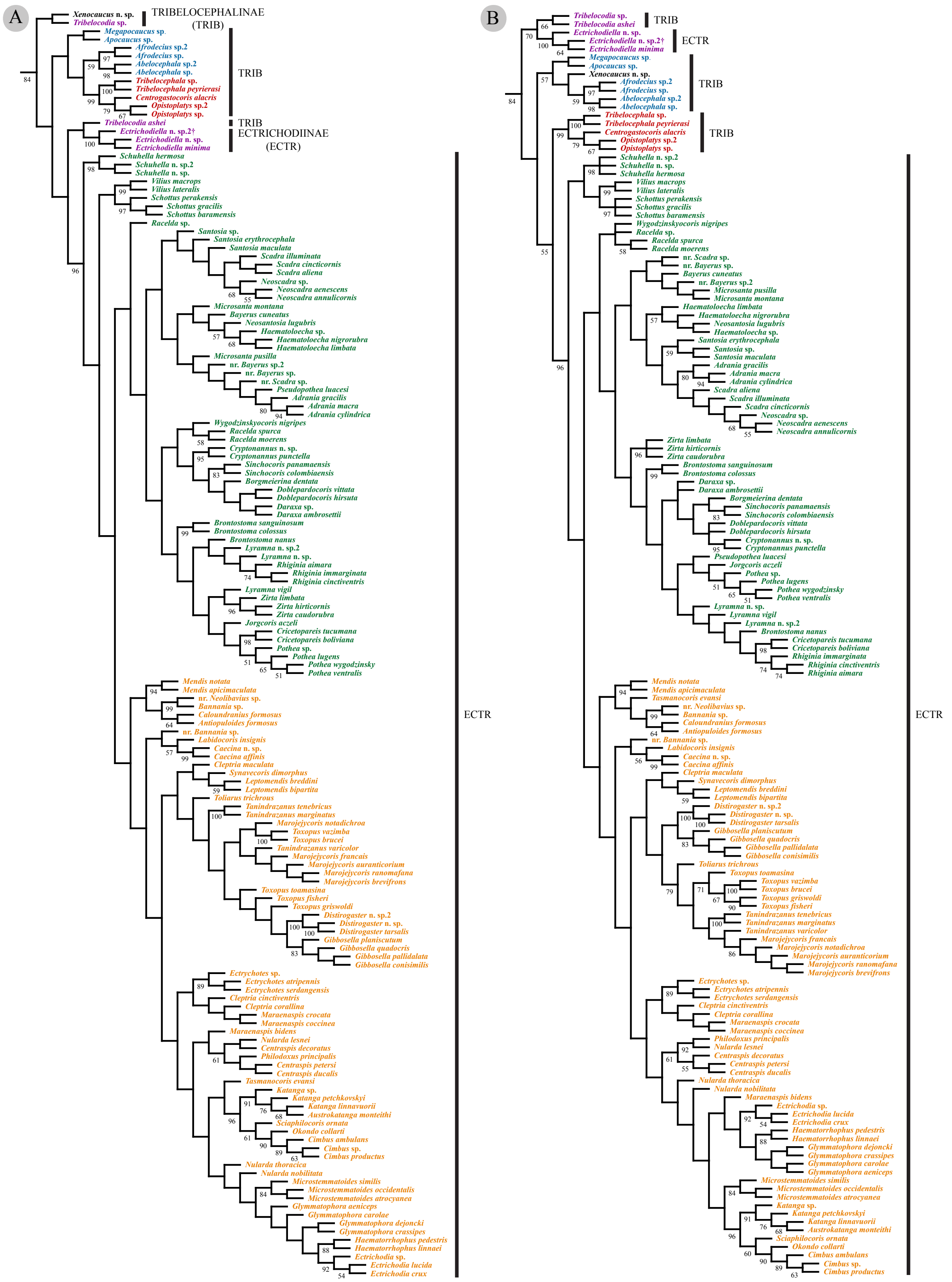
Supplementary Material 4.7. Morphological phylogenetic analyses of 156 taxa (outgroups removed from figure). Terminal taxon names are colored by clades recovered in the combined morphological and molecular ML best tree in Fig. 4.2 for comparison. A. ML best tree (final Ln = –5,215.5335) based on Lewis' (2001) Mkv model of morphological evolution. B. Bayesian MCMC majority-rule consensus tree based on the same models of morphological evolution. Bootstrap values ≥50 are reported in A. Posterior probabilities ≥50 are reported in B.


A
B
Xenocaucus n. sp.
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.
Opistoplatys sp.2
TRIBELOCEPHALINAE (TRIB)
TRIB
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.2
Abelocephala sp.
Afrodecius sp.
Afrodecius sp.2
Tribelocodia ashei
Tribelocodia sp.
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
ECTRICHODIINAE (ECTR)
ECTR
Katanga sp.
Katanga petchkovskyi
Austrokatanga monteithi
Katanga linnavuorii
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Tasmanocoris evansi
Antiopuloides formosus
Caloundranius formosus
Cleptria cinctiventris
Cleptria corallina
Maraenaspis crocata
Cleptria maculata
Synavecoris dimorphus
Leptomendis breddini
Leptomendis bipartita
Ectrychotes atripennis
Ectrychotes serdangensis
Ectrychotes sp.
Maraenaspis coccinea
Distirogaster n. sp.
Distirogaster n. sp.2
Distirogaster tarsalis
Gibbosella planiscutum
Gibbosella quadocris
Gibbosella pallidalata
Gibbosella conisimilis
Labidocoris insignis
Caecina affinis
Caecina n. sp.
nr. Bannania sp.
nr. Neolibavius sp.
Bannania sp.
Toliarus trichrous
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus tenebricus
Tanindrazanus marginatus
Toxopus vazimba
Toxopus brucei
Toxopus toamasina
Marojejycoris ranomafana
Marojejycoris francais
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Mendis apicimaculata
Mendis notata
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Nularda nobilitata
Nularda thoracica
Nularda lesnei
Philodoxus principalis
Centraspis decoratus
Centraspis ducalis
Centraspis petersi
Glymmatophora carolae
Glymmatophora aeniceps
Glymmatophora dejoncki
Glymmatophora crassipes
Maraenaspis bidens
Haematorrhophus linnaei
Haematorrhophus pedestris
Ectrichodia crux
Ectrichodia lucida
Ectrichodia sp.
Schuhella n. sp.2
Schuhella n. sp.
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus gracilis
Schottus baramensis
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Brontostoma nanus
Lyramna vigil
Lyramna n. sp.2
Lyramna n. sp.
Brontostoma sanguinosum
Brontostoma colossus
Pseudopothea luacesi
Jorgcoris aczeli
Daraxa sp.
Daraxa ambrosettii
Sinchocoris panamaensis
Sinchocoris colombiaensis
Borgmeierina dentata
Dobleparдocoris hirsuta
Doblepardocoris vittata
Cryptonannus punctella
Cryptonannus n. sp.
Racelda sp.
Wygodzinskyocoris nigripes
Racelda moerens
Racelda spurca
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia cinctiventris
Rhiginia aimara
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Microsanta pusilla
Microsanta montana
Bayerus cuneatus
nr. Bayerus sp.2
nr. Bayerus sp.
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha limbata
nr. Scadra sp.
Haematoloecha sp.
Santosia maculata
Santosia sp.
Santosia erythrocephala
Scadra aliena
Scadra illuminata
Scadra cincticornis
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Adrania gracilis
Adrania cylindrica
Adrania macra
0.2
0.1

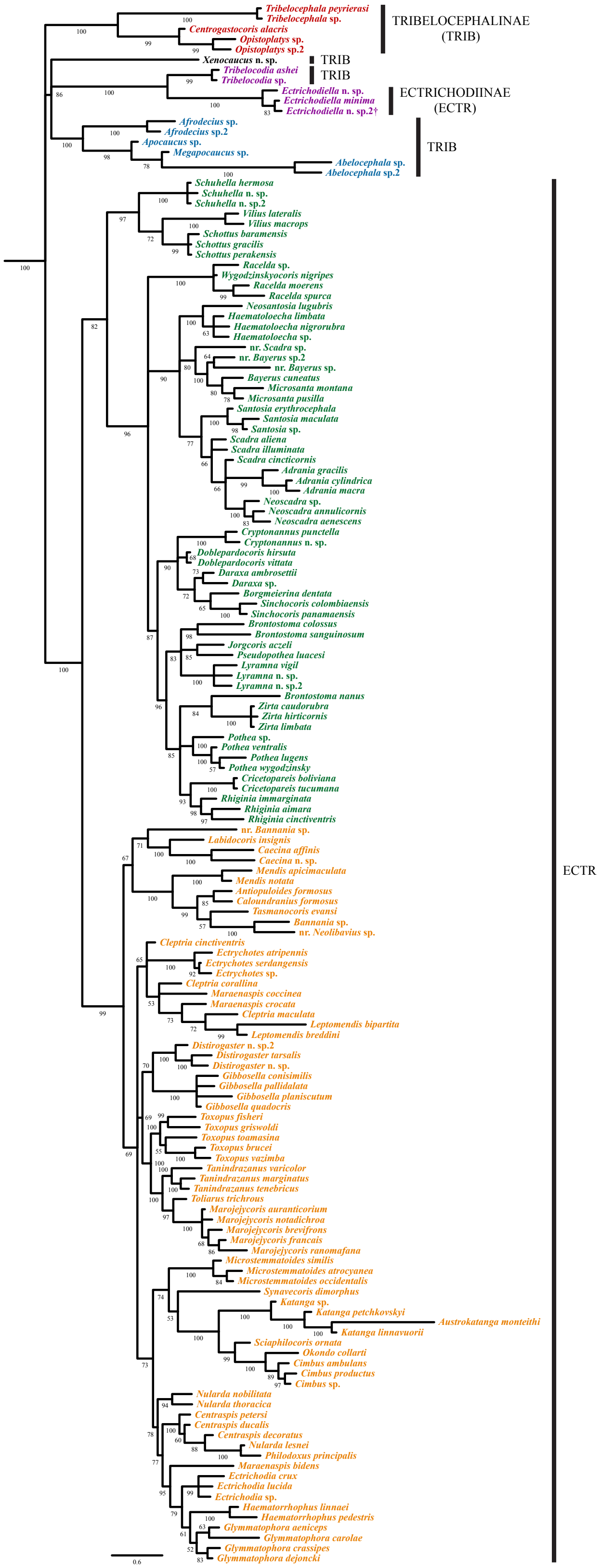
Supplementary material 4.8. Combined morphological parsimony phylogenetic analyses of 156 taxa (outgroups removed from figure). Terminal taxon names are colored by clades recovered in the combined morphological and molecular ML best tree in Fig. 4.2 for comparison. Bootstrap values ≥50 are reported. A. Strict consensus tree from 664 parsimonious trees (length = 10,458 steps; RI = 0.527; CI = 0.288) based on an equal weights TNT analysis. B. Single most parsimonious tree (length = 753.08685 steps; RI = 0.519; CI = 0.285) based on an implied weights (k = 3.000000) TNT analysis.


A
Tribelocodia sp.
Tribelocodia ashei
TRIBELOCEPHALINAE (TRIB)
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
ECTRICHODIINAE (ECTR)
Xenocaucus n. sp.
Megapocaucus sp.
Apocaucus sp.
Afrodecius sp.2
Afrodecius sp.
Abelocephala sp.2
Abelocephala sp.
TRIB
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
TRIB
Wygodzinskyocoris nigripes
Racelda sp.
Racelda spurca
Racelda moerens
Scadra illuminata
Scadra cincticornis
Scadra aliena
Neosantosia lugubris
Microsanta pusilla
Microsanta montana
Haematoloecha sp.
Haematoloecha nigrorubra
Haematoloecha limbata
nr. Bayerus sp.2
Daraxa sp.
Daraxa ambrosettii
Borgmeierina dentata
Bayerus cuneatus
Sinchocoris panamaensis
Sinchocoris colombiaensis
nr. Scadra sp.
nr. Bayerus sp.
Brontostoma sanguinosum
Brontostoma colossus
Santosia erythrocephala
Santosia sp.
Santosia maculata
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Doblepardocoris vittata
Doblepardocoris hirsuta
Cryptonannus n. sp.
Cryptonannus punctella
Jorgcoris aczeli
Pothea sp.
Pseudopothea luacesi
Pothea lugens
Pothea wygodzinsky
Pothea ventralis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Brontostoma nanus
Zirta limbata
Zirta hirticornis
Zirta caudorubra
Schottus perakensis
Schottus gracilis
Schottus baramensis
Schuhella n. sp.2
Schuhella n. sp.
Schuhella hermosa
Vilius macrops
Vilius lateralis
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia cinctiventris
Rhiginia aimara
Mendis notata
Mendis apicimaculata
Tasmanocoris evansi
Caloundranius formosus
Antiopuloides formosus
nr. Neolibavius sp.
Bannania sp.
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus sp.
Cimbus productus
Nularda thoracica
Nularda nobilitata
Philodoxus principalis
Nularda lesnei
Centraspis decoratus
Centraspis petersi
Centraspis ducalis
Maraenaspis bidens
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Haematorrhophus pedestris
Haematorrhophus linnaei
Ectrichodia sp.
Ectrichodia lucida
Ectrichodia crux
Cleptria cinctiventris
Maraenaspis coccinea
Cleptria corallina
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria maculata
Maraenaspis crocata
Leptomendis breddini
Leptomendis bipartita
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella pallidalata
Gibbosella conisimilis
Toxopus toamasina
Toxopus vazimba
Toxopus brucei
Toxopus griswoldi
Toxopus fisheri
Tanindrazanus tenebricus
Tanindrazanus marginatus
Tanindrazanus varicolor
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris ranomafana
Marojejycoris francais
ECTR
B
Xenocaucus n. sp.
Tribelocodia sp.
TRIB
Megapocaucus sp.
Apocaucus sp.
Abelocephala sp.2
Abelocephala sp.
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
TRIB
Afrodecius sp.2
Afrodecius sp.
TRIB
Tribelocodia ashei
TRIB
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
ECTR
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius macrops
Vilius lateralis
Schottus perakensis
Schottus gracilis
Schottus baramensis
Racelda sp.
Santosia sp.
Santosia erythrocephala
Santosia maculata
Scadra illuminata
Scadra cincticornis
Scadra aliena
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Haematoloecha limbata
Haematoloecha nigrorubra
Neosantosia lugubris
Haematoloecha sp.
Microsanta montana
Microsanta pusilla
Bayerus cuneatus
nr. Bayerus sp.2
nr. Bayerus sp.
nr. Scadra sp.
Pseudopothea luacesi
Adrania gracilis
Adrania macra
Adrania cylindrica
Wygodzinskyocoris nigripes
Racelda spurca
Racelda moerens
Cryptonannus n. sp.
Cryptonannus punctella
Sinchocoris panamaensis
Sinchocoris colombiaensis
Borgmeierina dentata
Doblepardocoris vittata
Doblepardocoris hirsuta
Daraxa sp.
Daraxa ambrosettii
Brontostoma sanguinosum
Brontostoma colossus
Brontostoma nanus
Lyramna n. sp.2
Lyramna n. sp.
Rhiginia aimara
Rhiginia immarginata
Rhiginia cinctiventris
Lyramna vigil
Zirta hirticornis
Zirta limbata
Zirta caudorubra
Jorgcoris aczeli
Cricetopareis tucumana
Cricetopareis boliviana
Pothea sp.
Pothea lugens
Pothea wygodzinsky
Pothea ventralis
Mendis notata
Mendis apicimaculata
nr. Neolibavius sp.
Bannania sp.
Caloundranius formosus
Antiopuloides formosus
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Cleptria maculata
Synavecoris dimorphus
Leptomendis breddini
Leptomendis bipartita
Toliarus trichrous
Tanindrazanus tenebricus
Tanindrazanus marginatus
Marojejycoris notadichroa
Toxopus vazimba
Toxopus brucei
Tanindrazanus varicolor
Marojejycoris francais
Marojejycoris auranticorium
Marojejycoris ranomafana
Marojejycoris brevifrons
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella planiscutum
Gibbosella quadocris
Gibbosella pallidalata
Gibbosella conisimilis
Ectrychotes sp.
Ectrychotes atripennis
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis crocata
Maraenaspis coccinea
Maraenaspis bidens
Nularda lesnei
Centraspis decoratus
Philodoxus principalis
Centraspis petersi
Centraspis ducalis
Tasmanocoris evansi
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus sp.
Cimbus productus
Nularda thoracica
Nularda nobilitata
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Glymmatophora aeniceps
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Haematorrhophus pedestris
Haematorrhophus linnaei
Ectrichodia sp.
Ectrichodia lucida
Ectrichodia crux
ECTR

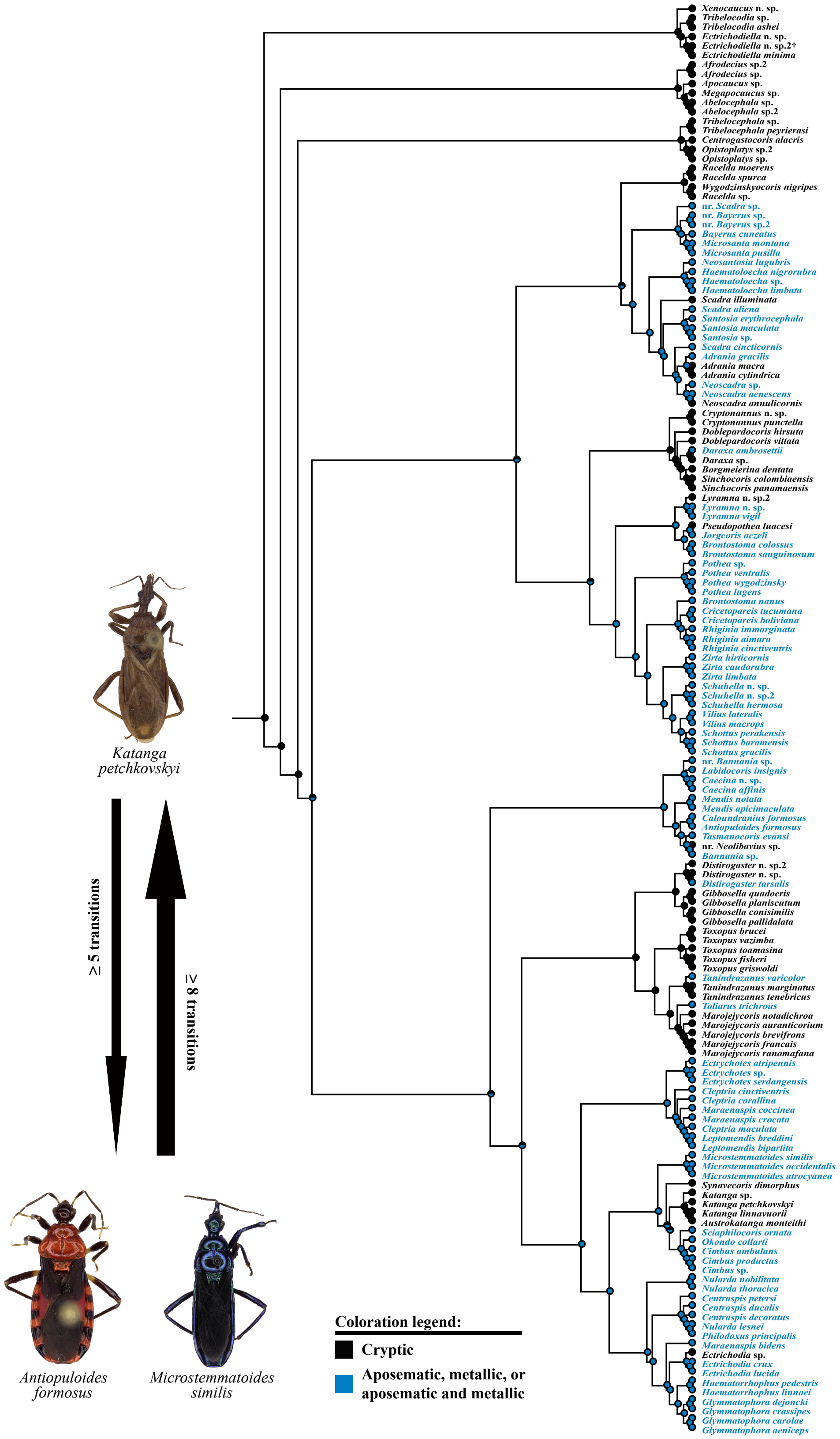
Supplementary material 4.9. Combined morphological parsimony phylogenetic analyses of 156 taxa (outgroups removed from figure). Terminal taxon names are colored by clades recovered in the combined morphological and molecular ML best tree in Fig. 4.2 for comparison. Bootstrap values ≥50 are reported. A. Single most parsimonious tree (length = 652.35368 steps; RI = 0.520; CI = 0.285) based on an implied weights (k = 4.266835) TNT analysis. B. Strict consensus tree from three parsimonious trees (length = 274.39610 steps; RI = 0.526; CI = 0.288) based on an implied weights (k = 18.980060) TNT analysis.


A
Xenocaucus n. sp.
Tribelocodia sp.
TRIBELOCEPHALINAE (TRIB)
Megapocaucus sp.
Apocaucus sp.
Afrodecius sp.2
Afrodecius sp.
Abelocephala sp.2
Abelocephala sp.
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
TRIB
Tribelocodia ashei
TRIB
Ectrichodiella n. sp.2†
Ectrichodiella n. sp.
Ectrichodiella minima
ECTRICHODIINAE (ECTR)
Schuhella hermosa
Schuhella n. sp.2
Schuhella n. sp.
Vilius macrops
Vilius lateralis
Schottus perakensis
Schottus gracilis
Schottus baramensis
Racelda sp.
Santosia sp.
Santosia erythrocephala
Santosia maculata
Scadra illuminata
Scadra cincticornis
Scadra aliena
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Microsanta montana
Bayerus cuneatus
Neosantosia lugubris
Haematoloecha sp.
Haematoloecha nigrorubra
Haematoloecha limbata
Microsanta pusilla
nr. Bayerus sp.2
nr. Bayerus sp.
nr. Scadra sp.
Pseudopothea luacesi
Adrania gracilis
Adrania macra
Adrania cylindrica
Wygodzinskyocoris nigripes
Racelda spurca
Racelda moerens
Cryptonannus n. sp.
Cryptonannus punctella
Sinchocoris panamaensis
Sinchocoris colombiaensis
Borgmeierina dentata
Doblepardocoris vittata
Doblepardocoris hirsuta
Daraxa sp.
Daraxa ambrosettii
Brontostoma sanguinosum
Brontostoma colossus
Brontostoma nanus
Lyramna n. sp.2
Lyramna n. sp.
Rhiginia aimara
Rhiginia immarginata
Rhiginia cinctiventris
Lyramna vigil
Zirta limbata
Zirta hirticornis
Zirta caudorubra
Jorgcoris aczeli
Cricetopareis tucumana
Cricetopareis boliviana
Pothea sp.
Pothea lugens
Pothea wygodzinsky
Pothea ventralis
Mendis notata
Mendis apicimaculata
nr. Neolibavius sp.
Bannania sp.
Caloundranius formosus
Antiopuloides formosus
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Cleptria maculata
Synavecoris dimorphus
Leptomendis breddini
Leptomendis bipartita
Toliarus trichrous
Tanindrazanus tenebricus
Tanindrazanus marginatus
Marojejycoris notadichroa
Toxopus vazimba
Toxopus brucei
Tanindrazanus varicolor
Marojejycoris francais
Marojejycoris auranticorium
Marojejycoris ranomafana
Marojejycoris brevifrons
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella planiscutum
Gibbosella quadocris
Gibbosella pallidalata
Gibbosella conisimilis
Ectrychotes sp.
Ectrychotes atripennis
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis crocata
Maraenaspis coccinea
Maraenaspis bidens
Nularda lesnei
Centraspis decoratus
Philodoxus principalis
Centraspis petersi
Centraspis ducalis
Tasmanocoris evansi
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus sp.
Cimbus productus
Nularda thoracica
Nularda nobilitata
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Glymmatophora aeniceps
Glymmatophora carolae
Glymmatophora dejoncki
Glymmatophora crassipes
Haematorrhophus pedestris
Haematorrhophus linnaei
Ectrichodia sp.
Ectrichodia lucida
Ectrichodia crux
ECTR
B
Tribelocodia sp.
Tribelocodia ashei
TRIB
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
ECTR
Megapocaucus sp.
Apocaucus sp.
Xenocaucus n. sp.
Afrodecius sp.2
Afrodecius sp.
Abelocephala sp.2
Abelocephala sp.
TRIB
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
TRIB
Schuhella n. sp.2
Schuhella n. sp.
Schuhella hermosa
Vilius macrops
Vilius lateralis
Schottus perakensis
Schottus gracilis
Schottus baramensis
Wygodzinskyocoris nigripes
Racelda sp.
Racelda spurca
Racelda moerens
nr. Scadra sp.
nr. Bayerus sp.
Bayerus cuneatus
nr. Bayerus sp.2
Microsanta pusilla
Microsanta montana
Haematoloecha limbata
Haematoloecha nigrorubra
Neosantosia lugubris
Haematoloecha sp.
Santosia erythrocephala
Santosia sp.
Santosia maculata
Adrania gracilis
Adrania macra
Adrania cylindrica
Scadra aliena
Scadra illuminata
Scadra cincticornis
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Zirta limbata
Zirta hirticornis
Zirta caudorubra
Brontostoma sanguinosum
Brontostoma colossus
Daraxa sp.
Daraxa ambrosettii
Borgmeierina dentata
Sinchocoris panamaensis
Sinchocoris colombiaensis
Doblepardocoris vittata
Doblepardocoris hirsuta
Cryptonannus n. sp.
Cryptonannus punctella
Pseudopothea luacesi
Jorgcoris aczeli
Pothea sp.
Pothea lugens
Pothea wygodzinsky
Pothea ventralis
Lyramna n. sp.
Lyramna vigil
Lyramna n. sp.2
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia cinctiventris
Rhiginia aimara
Mendis notata
Mendis apicimaculata
Tasmanocoris evansi
nr. Neolibavius sp.
Bannania sp.
Caloundranius formosus
Antiopuloides formosus
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Cleptria maculata
Synavecoris dimorphus
Leptomendis breddini
Leptomendis bipartita
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella planiscutum
Gibbosella quadocris
Gibbosella pallidalata
Gibbosella conisimilis
Toliarus trichrous
Toxopus toamasina
Toxopus vazimba
Toxopus brucei
Toxopus griswoldi
Toxopus fisheri
Tanindrazanus tenebricus
Tanindrazanus marginatus
Tanindrazanus varicolor
Marojejycoris francais
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris ranomafana
Marojejycoris brevifrons
Ectrychotes sp.
Ectrychotes atripennis
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis crocata
Maraenaspis coccinea
Philodoxus principalis
Nularda lesnei
Centraspis decoratus
Centraspis petersi
Centraspis ducalis
Nularda thoracica
Nularda nobilitata
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia lucida
Ectrichodia crux
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus sp.
Cimbus productus
ECTR

Supplementary Material 4.10. Bayesian MCMC majority-rule consensus tree based on of 156 taxa (outgroups removed from figure) and a combined morphological and molecular dataset. Molecular data were divided into three partitions and models of sequence evolution: 16S, 28S D2, 28S, D3–D5 (GTR+Γ+I); 18S, COI codon positions 1 and 2, Wg (GTR+Γ+I); COI codon position 3 (HKY+Γ+I). Morphological data were analyzed under Lewis' (2001) Mkv model of morphological evolution. Terminal taxon names are colored by clades recovered in the combined morphological and molecular ML best tree in Fig. 4.2 for comparison. Posterior probabilities ≥50 are reported.


Tribelocephala peyrierasi
Tribelocephala sp.
Centrogastocoris alacris
Opistoplatys sp.
Opistoplatys sp.2
TRIBELOCEPHALINAE
(TRIB)
Xenocaucus n. sp.
TRIB
Tribelocodia ashei
Tribelocodia sp.
TRIB
Ectrichodiella n. sp.
Ectrichodiella minima
Ectrichodiella n. sp.2†
ECTRICHODIINAE
(ECTR)
Afrodecius sp.
Afrodecius sp.2
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
TRIB
Schuhella hermosa
Schuhella n. sp.
Schuhella n. sp.2
Vilius lateralis
Vilius macrops
Schottus baramensis
Schottus gracilis
Schottus perakensis
Racelda sp.
Wygodzinskyocoris nigripes
Racelda moerens
Racelda spurca
Neosantosia lugubris
Haematoloecha limbata
Haematoloecha nigrorubra
Haematoloecha sp.
nr. Scadra sp.
nr. Bayerus sp.2
nr. Bayerus sp.
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra aliena
Scadra illuminata
Scadra cincticornis
Adrania gracilis
Adrania cylindrica
Adrania macra
Neoscadra sp.
Neoscadra annulicornis
Neoscadra aenescens
Cryptonannus punctella
Cryptonannus n. sp.
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Brontostoma colossus
Brontostoma sanguinosum
Jorgcoris aczeli
Pseudopothea luacesi
Lyramna vigil
Lyramna n. sp.
Lyramna n. sp.2
Brontostoma nanus
Zirta caudorubra
Zirta hirticornis
Zirta limbata
Pothea sp.
Pothea ventralis
Pothea lugens
Pothea wygodzinsky
Cricetopareis boliviana
Cricetopareis tucumana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
nr. Bannania sp.
Labidocoris insignis
Caecina affinis
Caecina n. sp.
Mendis apicimaculata
Mendis notata
Antiopuloides formosus
Caloundranius formosus
Tasmanocoris evansi
Bannania sp.
nr. Neolibavius sp.
Cleptria cinctiventris
Ectrychotes atripennis
Ectrychotes serdangensis
Ectrychotes sp.
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis bipartita
Leptomendis breddini
Distirogaster n. sp.2
Distirogaster tarsalis
Distirogaster n. sp.
Gibbosella conisimilis
Gibbosella pallidalata
Gibbosella planiscutum
Gibbosella quadocris
Toxopus fisheri
Toxopus griswoldi
Toxopus toamasina
Toxopus brucei
Toxopus vazimba
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris auranticorium
Marojejycoris notadichroa
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Microstemmatoides similis
Microstemmatoides atrocyanea
Microstemmatoides occidentalis
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Austrokatanga monteithi
Katanga linnavuorii
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia crux
Ectrichodia lucida
Ectrichodia sp.
Haematorrhophus linnaei
Haematorrhophus pedestris
Glymmatophora aeniceps
Glymmatophora carolae
Glymmatophora crassipes
Glymmatophora dejoncki
ECTR
0.6

Supplementary material 4.11. Parsimony ancestral state reconstruction on the ML phylogram (Fig. 4.2) for Tribelocephalinae and Ectrichodiinae taxa (tree converted to cladogram for visual) and color character 198. Terminal taxa coded as cryptic (black) or either aposematic, metallic, or aposematic and metallic (blue).

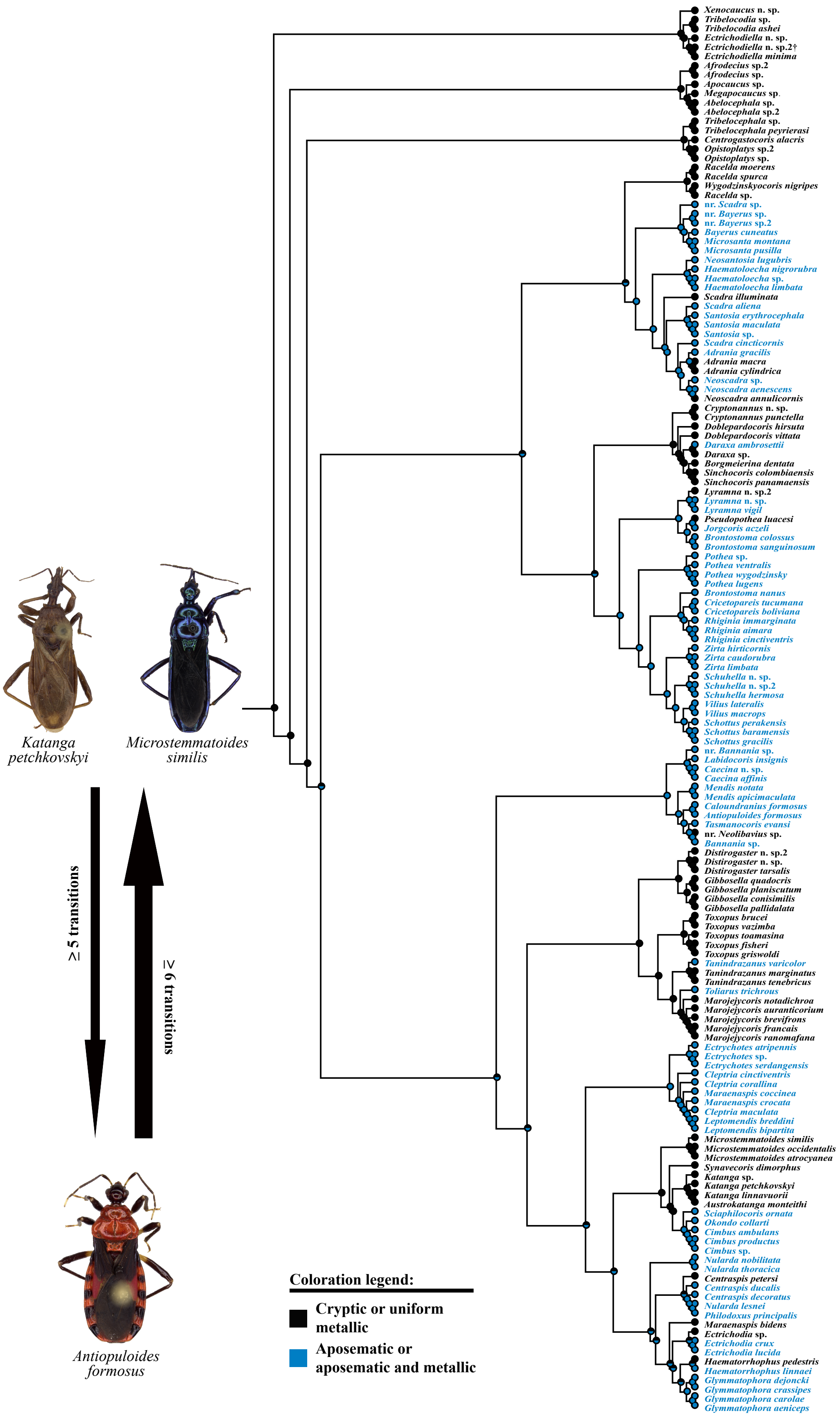

Xenocaucus n. sp.
Tribelocodia sp.
Tribelocodia ashei
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
Afrodecius sp.2
Afrodecius sp.
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
Racelda moerens
Racelda spurca
Wygodzinskyocoris nigripes
Racelda sp.
nr. Scadra sp.
nr. Bayerus sp.
nr. Bayerus sp.2
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Cryptonannus n. sp.
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
Brontostoma sanguinosum
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Mendis notata
Mendis apicimaculata
Caloundranius formosus
Antiopuloides formosus
Tasmanocoris evansi
nr. Neolibavius sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
Leptomendis bipartita
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia crux
Ectrichodia lucida
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Katanga petchkovskyi
≥ 5 transitions
≥ 8 transitions
Antiopuloides formosus
Microstemmatoides similis
Coloration legend:
Cryptic
Aposematic, metallic, or aposematic and metallic

Supplementary material 4.12. Figshare data repository link to BayesTraits MultiState ML and MCMC ancestral state reconstruction output for color character 198 on ML phylogram and ultrametric trees. The gray panel lists internal node IDs and subtending terminal taxa. The blue panel are results from ML ancestral state reconstruction. The yellow panel are results from MCMC ancestral state reconstruction. Abbreviations: Ultra 0, ultrametric tree generated with penalty set to 0; Ultra 10, ultrametric tree generated with penalty set to 10; Ultra 10000, ultrametric tree generated with penalty set to 10000.

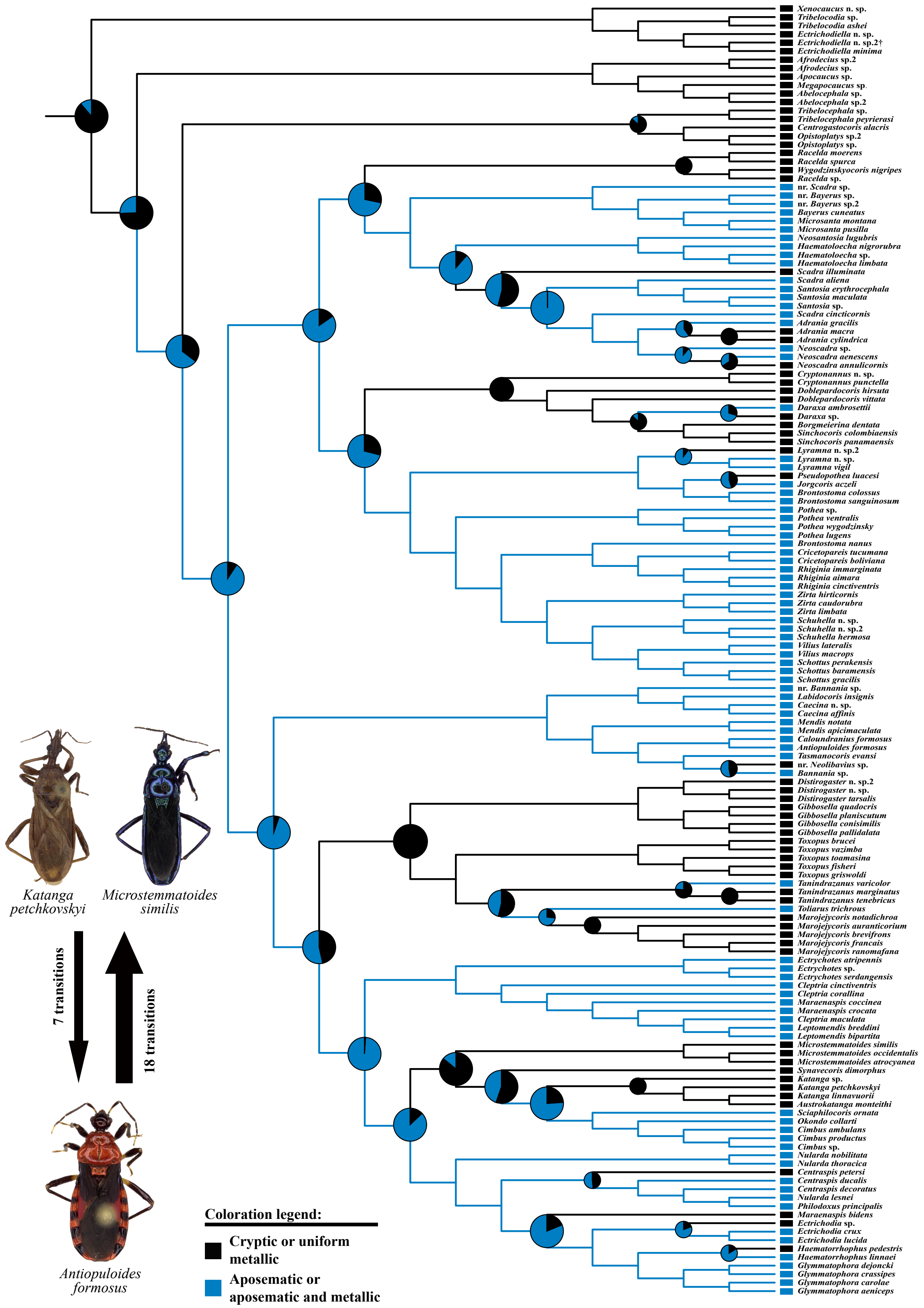
Figshare data repository link: https://figshare.com/s/f0d20be1ac405a64a727

Figshare doi: 10.6084/m9.figshare.2908249

Supplementary material 4.13. Parsimony ancestral state reconstruction on the ML phylogram (Fig. 4.2) for Tribelocephalinae and Ectrichodiinae taxa (tree converted to cladogram for visual) and color character 199. Terminal taxa coded as cryptic (black) or either aposematic, metallic, or aposematic and metallic (blue).


Xenocaucus n. sp.
Tribelocodia sp.
Tribelocodia ashei
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
Afrodecius sp.2
Afrodecius sp.
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
Racelda moerens
Racelda spurca
Wygodzinskyocoris nigripes
Racelda sp.
nr. Scadra sp.
nr. Bayerus sp.
nr. Bayerus sp.2
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Cryptonannus n. sp.
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
Brontostoma sanguinosum
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Mendis notata
Mendis apicimaculata
Caloundranius formosus
Antiopuloides formosus
Tasmanocoris evansi
nr. Neolibavius sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
Leptomendis bipartita
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia crux
Ectrichodia lucida
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Katanga petchkovskyi
Microstemmatoides similis
≥ 5 transitions
≥ 6 transitions
Antiopuloides formosus
Coloration legend:
■ Cryptic or uniform metallic
🟦 Aposematic or aposematic and metallic

Supplementary material 4.14. BayesTraits MultiState ML ancestral state reconstruction of color character 199 on the ML phylogram (Fig. 4.2) for Tribelocephalinae and Ectrichodiinae taxa (tree converted to cladogram for visual). Terminal taxa coded as cryptic or uniform metallic (black) or aposematic or aposematic and metallic (blue). Pie charts at select nodes show probability values from the ML reconstructions; branches are colored to reflect the highest probability of a color state at that branch.


Xenocaucus n. sp.
Tribelocodia sp.
Tribelocodia ashei
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
Afrodecius sp.2
Afrodecius sp.
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
Racelda moerens
Racelda spurca
Wygodzinskyocoris nigripes
Racelda sp.
nr. Scadra sp.
nr. Bayerus sp.
nr. Bayerus sp.2
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Cryptonannus n. sp.
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
Brontostoma sanguinosum
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Mendis notata
Mendis apicimaculata
Caloundranius formosus
Antiopuloides formosus
Tasmanocoris evansi
nr. Neolibavius sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
Leptomendis bipartita
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia crux
Ectrichodia lucida
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps
Katanga petchkovskyi
Microstemmatoides similis
7 transitions
18 transitions
Antiopuloides formosus
Coloration legend:
■ Cryptic or uniform metallic
🟦 Aposematic or aposematic and metallic

Supplementary material 4.15. Figshare data repository link to BayesTraits MultiState ML and MCMC ancestral state reconstruction output for color character 199 on ML phylogram and ultrametric trees. The gray panel lists internal node IDs and subtending terminal taxa. The blue panel are results from ML ancestral state reconstruction. The yellow panel are results from MCMC ancestral state reconstruction. Abbreviations: Ultra 0, ultrametric tree generated with penalty set to 0; Ultra 10, ultrametric tree generated with penalty set to 10; Ultra 10000, ultrametric tree generated with penalty set to 10000.

Figshare data repository link: https://figshare.com/s/f81b72ae4f384d8daace

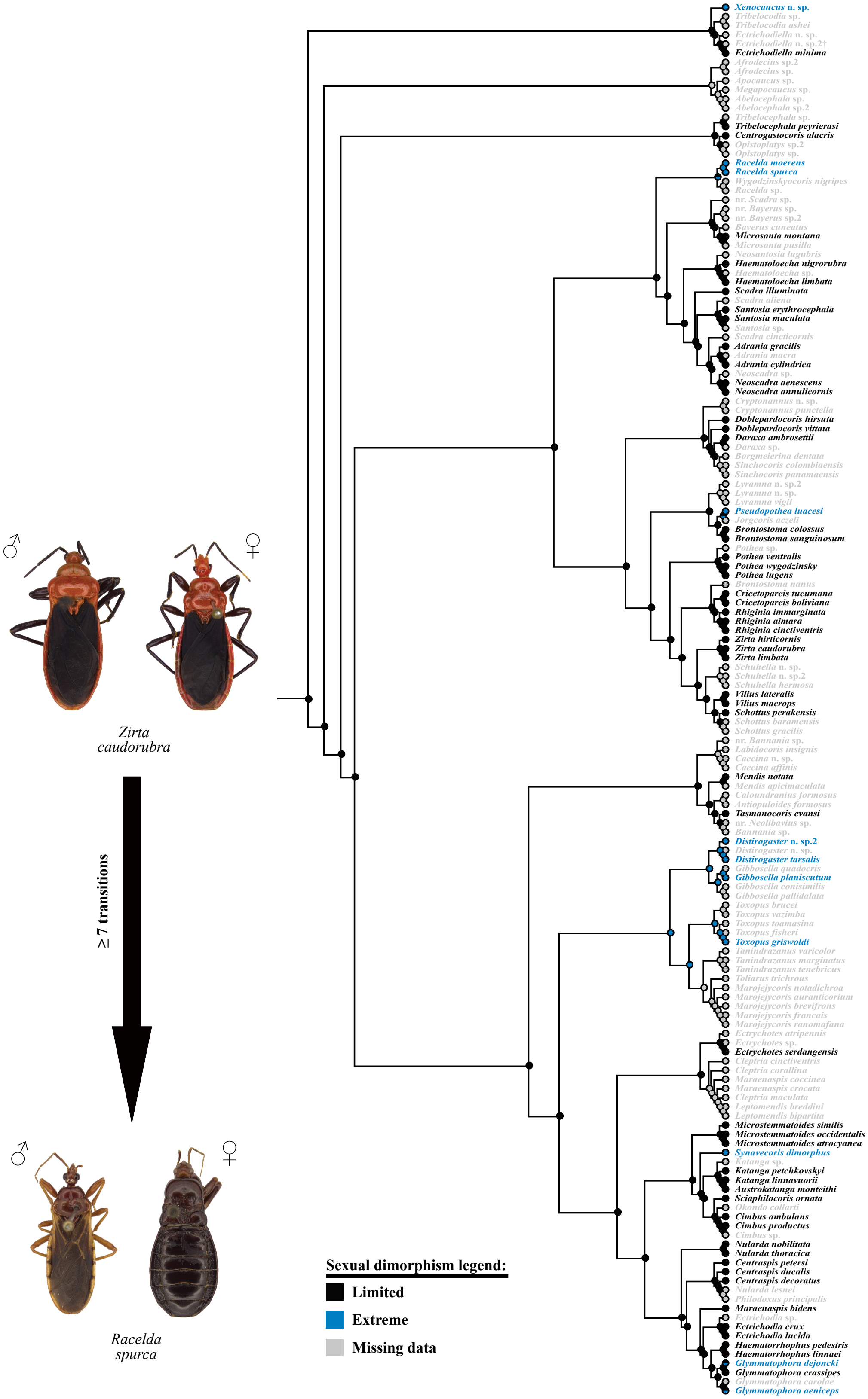
Figshare doi: 10.6084/m9.figshare.2909611

Supplementary material 4.16. Phylogenetic logistic regression parameter estimates for the effects of log-transformed male body length on coloration in 133 Ectrichodiinae and Tribelocephalinae species. Cryptic and uniform metallic coloration is treated as one state with aposematic and aposematic and metallic color patterns as a separate state. Parameters are phylogenetic signal (*a*), intercept (b_0), and the regression coefficient (b_1), and p-values ≤0.05 are indicated in bold. Abbreviations: Phylo, phylogram; Ultra0, ultrametric tree generated with penalty set to 0; Ultra10, ultrametric tree generated with penalty set to 10; Ultra10000, ultrametric tree generated with penalty set to 10000; Par, parameter; SE, standard error; BS, bootstrap; C, converged; NC, non-converged.

Tree/dataset	**Par**	**Estimate**	**SE**	***p*-value**	**BS mean (C and NC)**[a]	**BS confidence interval (C and NC)**[a]	**BS *p*-value (C and NC)**[a]	**BS mean (C only)**	**BS confidence interval (C only)**
Phylo C+UM									
	a	–1.0391			–1.4282	(–2.6531, –0.4579)	**0.0052**	–1.3942	(–2.6406, –0.4433)
	*b*0	–0.0466	0.4660	0.9205	–0.0419	(–2.4529, 2.6352)	0.8712	–0.0340	(–2.2389, 2.5531)
	*b*1	0.6073	0.2262	**0.0082**	0.3744	(–2.5873, 2.8295)	0.4488	0.3830	(–2.4233, 2.5408)
Ultra0 C+UM									
	a	–0.6724			–0.9606	(–3.3316, 0.4277)	**0.0184**	—	—
	*b*0	–0.3662	0.5515	0.5078	–0.3904	(–1.6487, 0.9075)	0.5128	—	—
	*b*1	0.6804	0.2264	**0.0032**	0.7669	(0.2764, 1.4656)	**0.0016**	—	—
Ultra10 C+UM									
	a	–0.0837			–0.0510	(–3.0062, 0.9890)	**0.0192**	–0.5191	(–2.9789, 0.9509)
	*b*0	–0.2572	0.6808	0.7063	–0.2964	(–1.6978, 1.2196)	0.7000	–0.2884	(–1.6878, 1.2196)
	*b*1	0.6209	0.2245	**0.0065**	0.7305	(0.2352, 1.3738)	**0.0064**	0.7300	(0.2355, 1.3701)
Ultra10000 C+UM									
	a	–0.0832			–0.4968	(–2.8611, 0.9529)	**0.0164**	–0.4983	(–2.8414, 0.9391)
	*b*0	–0.2572	0.6908	0.7063	–0.2817	(–1.6744, 1.2164)	0.6944	–0.2815	(–1.6710, 1.2164)
	*b*1	0.6208	0.2245	**0.0065**	0.7266	(0.2371, 1.3525)	**0.0048**	0.7268	(0.2380, 1.3525)

[a] Parametric bootstrapping was performed to obtain means and confidence intervals, as well as test the null hypotheses that there is no phylogenetic signal in the residuals, (H_0: $a = -4$, 1-tailed test) and that the regression coefficient equals 0 (H_0: $b_1 = 0$, 2-tailed test).

Supplementary material 4.17. Parsimony ancestral sexual dimorphism reconstruction on the ML phylogram (Fig. 4.2) for Tribelocephalinae and Ectrichodiinae taxa (tree converted to cladogram for visual). Sexual dimorphism for terminal taxa coded as limited (black) or extreme (blue). Missing data (gray) for terminals is indicated.


♂
♀
Zirta caudorubra
≥ 7 transitions
♂
♀
Racelda spurca
Sexual dimorphism legend:
Limited
Extreme
Missing data
Xenocaucus n. sp.
Tribelocodia sp.
Tribelocodia ashei
Ectrichodiella n. sp.
Ectrichodiella n. sp.2†
Ectrichodiella minima
Afrodecius sp.2
Afrodecius sp.
Apocaucus sp.
Megapocaucus sp.
Abelocephala sp.
Abelocephala sp.2
Tribelocephala sp.
Tribelocephala peyrierasi
Centrogastocoris alacris
Opistoplatys sp.2
Opistoplatys sp.
Racelda moerens
Racelda spurca
Wygodzinskyocoris nigripes
Racelda sp.
nr. Scadra sp.
nr. Bayerus sp.
nr. Bayerus sp.2
Bayerus cuneatus
Microsanta montana
Microsanta pusilla
Neosantosia lugubris
Haematoloecha nigrorubra
Haematoloecha sp.
Haematoloecha limbata
Scadra illuminata
Scadra aliena
Santosia erythrocephala
Santosia maculata
Santosia sp.
Scadra cincticornis
Adrania gracilis
Adrania macra
Adrania cylindrica
Neoscadra sp.
Neoscadra aenescens
Neoscadra annulicornis
Cryptonannus n. sp.
Cryptonannus punctella
Doblepardocoris hirsuta
Doblepardocoris vittata
Daraxa ambrosettii
Daraxa sp.
Borgmeierina dentata
Sinchocoris colombiaensis
Sinchocoris panamaensis
Lyramna n. sp.2
Lyramna n. sp.
Lyramna vigil
Pseudopothea luacesi
Jorgcoris aczeli
Brontostoma colossus
Brontostoma sanguinosum
Pothea sp.
Pothea ventralis
Pothea wygodzinsky
Pothea lugens
Brontostoma nanus
Cricetopareis tucumana
Cricetopareis boliviana
Rhiginia immarginata
Rhiginia aimara
Rhiginia cinctiventris
Zirta hirticornis
Zirta caudorubra
Zirta limbata
Schuhella n. sp.
Schuhella n. sp.2
Schuhella hermosa
Vilius lateralis
Vilius macrops
Schottus perakensis
Schottus baramensis
Schottus gracilis
nr. Bannania sp.
Labidocoris insignis
Caecina n. sp.
Caecina affinis
Mendis notata
Mendis apicimaculata
Caloundranius formosus
Antiopuloides formosus
Tasmanocoris evansi
nr. Neolibavius sp.
Bannania sp.
Distirogaster n. sp.2
Distirogaster n. sp.
Distirogaster tarsalis
Gibbosella quadocris
Gibbosella planiscutum
Gibbosella conisimilis
Gibbosella pallidalata
Toxopus brucei
Toxopus vazimba
Toxopus toamasina
Toxopus fisheri
Toxopus griswoldi
Tanindrazanus varicolor
Tanindrazanus marginatus
Tanindrazanus tenebricus
Toliarus trichrous
Marojejycoris notadichroa
Marojejycoris auranticorium
Marojejycoris brevifrons
Marojejycoris francais
Marojejycoris ranomafana
Ectrychotes atripennis
Ectrychotes sp.
Ectrychotes serdangensis
Cleptria cinctiventris
Cleptria corallina
Maraenaspis coccinea
Maraenaspis crocata
Cleptria maculata
Leptomendis breddini
Leptomendis bipartita
Microstemmatoides similis
Microstemmatoides occidentalis
Microstemmatoides atrocyanea
Synavecoris dimorphus
Katanga sp.
Katanga petchkovskyi
Katanga linnavuorii
Austrokatanga monteithi
Sciaphilocoris ornata
Okondo collarti
Cimbus ambulans
Cimbus productus
Cimbus sp.
Nularda nobilitata
Nularda thoracica
Centraspis petersi
Centraspis ducalis
Centraspis decoratus
Nularda lesnei
Philodoxus principalis
Maraenaspis bidens
Ectrichodia sp.
Ectrichodia crux
Ectrichodia lucida
Haematorrhophus pedestris
Haematorrhophus linnaei
Glymmatophora dejoncki
Glymmatophora crassipes
Glymmatophora carolae
Glymmatophora aeniceps

Supplementary material 4.18. Figshare data repository link to BayesTraits MultiState ML and MCMC ancestral state reconstruction output for sexual dimorphism character 200 on ML phylogram and ultrametric trees. The gray panel lists internal node IDs and subtending terminal taxa. The blue panel are results from ML ancestral state reconstruction. The yellow panel are results from MCMC ancestral state reconstruction. Abbreviations: Ultra 0, ultrametric tree generated with penalty set to 0; Ultra 10, ultrametric tree generated with penalty set to 10; Ultra 10000, ultrametric tree generated with penalty set to 10000.

Figshare data repository link: https://figshare.com/s/433681e7784d456e9a8d

Figshare doi: 10.6084/m9.figshare.2912692

Conclusion

The research conducted in this dissertation has significantly advanced our understanding of Ectrichodiinae biodiversity, natural history, and evolution, as well as Reduviidae phylogeny and classification. Prior to this work, there was a lack of thorough taxonomic treatments and phylogenetic hypotheses for the subfamily. No tribal-level classification existed, and relationships between genera had not been cladistically investigated, with the exception of one genus-level phylogeny of the New World fauna. Faunistic checklists and descriptions of single taxa based on few specimens of a single sex have dominated the Ectrichodiine literature.

In Chapter 1, Ectrichodiinae predatory behaviors were reviewed and supplemented with observations on *Rhiginia cinctiventris* (Stål), 1872, in Costa Rica. The predator-prey association between Ectrichodiinae and millipedes was first documented almost a century ago. However, feeding behaviors have since received little attention, rendering this intriguing phenomenon largely inaccessible. About 2% of Ectrichodiinae species have been documented to prey on millipedes, leaving ample room to further test the claim that Ectrichodiinae, as a group, specialize on millipedes. Ectrichodiinae appear to have a preference for benzoquinone-producing juliform millipedes (Spirostreptida and Spirobolida), wtih Polydesmida rarely attacked. Furthermore, Ectrichodiinae insert maxillary and mandibular stylets at the millipede's intersegmental membranes on the ventral and ventrolateral trunk area or between the head and collum. Whether these areas are attacked in relation to the location of the millipede nervous system or defense glands remains to be investigated. Lastly, immature and adult Ectrichodiinae exhibit both solitary and communal predation. The majority of observations suggest that immatures typically exhibit communal predation, while adults usually engage in solitary predation.

The second chapter highlights our incomplete knowledge of the Madagascan invertebrate fauna, especially for the Ectrichodiinae. However, this situation is improving as a result of large taxonomic surveys, such as the one that enabled this taxonomic project. Prior to the dissertation, only 10 described Madagascan Ectrichodiinae species were known. Here, 63 new species and three new genera of Ectrichodiinae that are endemic to the island are described. *Toxopus* Bergroth, 1905, *Gibbosella* Chłond, 2010, *Gibbosella elongata* Chłond, 2010, *Glymmatophora crassipes* Horváth, 1914, and *Maraenaspis bidens* (Reuter), 1887, are redescribed, with the first description of males for each taxon. *Cleptria signoretii* Reuter, 1887, is transferred to *Toxopus*.

Undoubtedly, the ~80 my isolation of Madagascar from other landmasses, along with geologic and climatic factors within Madagascar and throughout the Indian Ocean, has influenced the evolution of the island's biota. However, few systematic analyses incorporating modern divergence dating and biogeographic analyses have focused on Madagascan insects. The drastic increase of the described diversity in Chapter 2 presented an opportunity to investigate the timing and origin of Madagascan Ectrichodiinae using phylogenetic, divergence dating, and biogeographic analyses in Chapter 3. Based on the phylogenetic results, Madagascan Ectrichodiinae do not form a monophyletic group, with different clades closely related to Afrotropical and Oriental lineages. Ectrichodiinae are shown to have colonized the island within the last ~68 my via transoceanic dispersal at least twice from the Oriental region and once from the Afrotropical region. Some biogeographic models also infer a single out-of-Madagascar dispersal event to the Afrotropical region. Dispersal from the Oriental region to Madagascar may have been facilitated by the Seychelles-Mascarene Plateau and volcanic islands in the Indian Ocean. Factors facilitating dispersal from the Afrotropical region to Madagascar are more difficult to determine, but aerial dispersal via stepping-stone islands in the Mozambique Channel is the most probable hypothesis when accounting for ancient oceanographic reconstructions.

In the final chapter, the the evolution of sexual dimorphism, aposematic coloration, and the relationship between coloration and body size in Ectrichodiinae is investigated. Investigating

aposematic coloration in a phylogenetic context has been limited compared to the numerous published microevolutionary studies in animals. Few phylogenetic comparative studies in vertebrates and Lepidoptera have shown a positive correlation of body size and aposematic coloration. However, one lepidopteran study found no correlation between these two traits, a result that may be confounded by larval gregariousness. Adult Ectrichodiinae are typically solitary and afford an opportunity to test for a coloration-body size relationship. The evolution of extreme sexual dimorphism is also explored in a phylogenetic context. Aposematic coloration is shown to have evolved from a cryptic ancestor early in the evolutionary history of Ectrichodiinae+ Tribelocephalinae, with subsequent reversals and regains. A positive association between aposematic coloration and body length is recovered when phylogenetic logistic regressions are conducted on ultrametric trees but not on phylograms, which may be an artifact of the method. Extreme sexual dimorphism is shown to evolve multiple times from a more limited condition. Thus, careful consideration must be given to the use of female morphology in phylogenetic investigations and taxonomic decisions. Lastly, a new classification based on phylogenetic results is proposed for Ectrichodiinae.