THE SYSTEMATICS OF THE BURROWING WATER BEETLES (COLEOPTERA: ADEPHAGA: NOTERIDAE)

BY

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Abstract

The aquatic beetle family Noteridae (Coleoptera: Adephaga) comprises a group with poorly studied diversity that has received limited systematic study. Despite the corroboration of multiple phylogenic reconstructions, many relationships within Noteridae remain poorly supported or unresolved. Here I address the questions surrounding the systematics of Noteridae in three ways. First, a review of previously constructed noterid phylogenies is presented and methods, variation in recovered relationships and the current classification of Noteridae are explored. Second, a phylogeny of Noteridae is inferred based on the analysis of DNA sequence data of five gene fragments: *COI*, *H3*, *16S*, *18S*, and *28S.* Our taxon sampling of Noteridae is the most robust of any phylogenetic investigation of Noteridae to date and includes representatives for 16 of the 17 current noterid genera. Bayesian and Maximum likelihood analyses produce highly supported trees that strongly contradict previous studies. Our results recover the monophyly of the following higher level groups: (1). Meruidae + Noteridae, though the exact nature of this relationship is unresolved; (2) Phreatodytinae + Notomicrinae; and (3) Noterinae. All known genera are found to be monophyletic except *Hydrocanthus* Say, found paraphyletic with respect to *Mesonoterus* Sharp and *Prionohydrus* Gomez & Miller, and *Suphisellus* Crotch, found to be paraphyletic with respect to *Pronoterus*. Thus the following changes in classification and taxonomy are proposed: the subgenus *Sternocanthus* Guignot is resurrected from synonymy **stat. rev.** and elevated to the genus rank **stat. n**. to contain Old World members of the genus *Hydrocanthus sensu lato;* and *Pronoterus* Sharp **syn. n.** is placed in synonymy with *Suphisellus* Crotch. All tribes within the Noterinae are recovered as paraphyletic or invalid due to synonymy and the a revised classification is thus proposed: (1) Noterini Thomson **sensu n**. is redefined

contain the genera *Noterus* Clairville and *Neohydrocoptus* Satô, thus including *Neohydrocoptini* Zalat *et al*. **syn. n.** as a junior synonym ;(2) Tonerini Miller ***sensu n.*** is redefined to hold the genera *Synchortus* Sharp, *Tonerus* Miller, and *Liocanthydrus* Guignot; (4) Renotini **trib. n.** is erected to contain the genus *Renotus* Guignot; (5) Suphisini Sharp **rev. stat.** is resurrected from synonymy to hold the genera *Suphis* Aubé, *Canthysellus* Baca & Toledo **gen. n.**, *Suphisellus* Crotch incl. *Pronoterus* Sharp, and a tentative new noterid genus; and (6) Hydrocanthini Sharp **stat. rev.** is resurrected from synonymy to hold the genera *Canthydrus* Sharp, *Sternocanthus* Guignot, *Hydrocanthus* Say, *Mesonoterus* Sharp and *Prionohydrus* Gomez & Miller. A discussion of relationships, classification and morphology is presented. Finally, the poor documentation of noterid diversity is addressed with the description of the genus *Canthysellus* Baca & Toledo **gen. n.,** here erected to contain three species *Canthysellus buqueti* (Laporte, 1835), *C. sipaliwini* **sp. n**. and *C. peruanus* **sp. n**. Descriptions, diagnoses, illustrations of diagnostic characters and a key to species of *Canthysellus* are provided.

Acknowledgements

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I am also thankful for my family, especially my parents; their support of my education, tolerance of my many pet creatures and patience for my obscure hobbies allowed me to pursue my passion and made this all possible; for my friends here in Lawrence, specifically those of PSB who have kept me sane and supply an endless laughter and guidance; and for my friends back home in New Mexico (you know who you are) for giving me a home to go back to. And special thanks to Grey Gustafson, friend, mentor and fellow metal head, your wisdom has been a huge help.

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CHAPTER 1

OVERVIEW OF PHYLOGENETIC STUDIES OF NOTERIDAE

INTRODUCTION

Noteridae Thomson (Coleoptera: Adephaga), also known as the burrowing water beetles, is a small family with representatives that can be found in aquatic habitats throughout the world. Noterids are superficially similar to the adephagan family Dytiscidae, but are easily distinguished by the elevated expansions of their inner metacoxal lamellae, which form the "noterid platform". In the subfamily Noterinae, which contains the majority of noterid genera, this structure is contiguous with an elevated portion of the metaventrite, extending the platform anteriorly (Fig. 3.4, 3.5 in Chapter 3). Most members of Noteridae are small in size and very few species exceed 5 mm in length.

Particularly abundant in the tropics, noterids are most commonly found in the vegetative margins of shallow lentic habitats that are exposed to sunlight (Miller, 2009; Baca *et al*., 2014). Collecting data also shows that some species are found in small creeks, forest pools, rock seeps, and even terrestrial leaf litter (Miller, 2009; Baca *et al*., 2014; Baca & Toledo, in review, Ch. 3; unpublished data), with some species being very specific their respective habitats. (Miller, 2009; Baca *et al*., 2014; unpublished data).

Beyond habitat data indicating specific ecologies, the behavior and life histories of noterid species have been poorly documented. As Miller (2009) noted, the common name 'burrowing water beetles' is attributed partly to a burrowing behavior observed in larvae of the genus *Noterus*, otherwise it appears that burrowing is assumed based on adult morphology. The

adults of the tribe Noterini (as currently defined; Miller, 2009; Nilsson, 2011; Gomez & Miller, 2013) present modified protibia modified with an enlarged spur and setal fringe and it is suspected that these structures are used for burrowing. This behavior has not been observed in the larvae of any other genus except *Noterus*, nor has it been verified in the adults of any noterid species (Miller, 2009 and references therein).

In terms of diversity, Noteridae is relatively small compared to other beetle families, consisting of ca. 270 described species (Nilsson, 2011). The current classification of the family divides these among 17 genera, six tribes and three subfamilies (Nilsson, 2011; Gomez & Miller, 2013; Baca *et al.*, 2014; Baca & Toledo, in review). Despite its small size, the diversity of the family remains poorly documented. Miller (2009) ascribed the lack of attention paid to Noteridae to the family's separation from Dytiscidae; whereas noterids were historically investigated as a subgroup within Dytiscidae, the latter half of the last century saw most dytiscid workers exclude noterids from their studies (Miller, 2009; Nilsson 2011; but see F.N. Young 1978; 1979; 1985). In turn, many species are known only from their original and often dated descriptions and many genera are in need of revision.

An interest in the systematics of Adephaga has led to noterids being included in several phylogenetic studies and, following the treatment of the family by Miller (2009), several new contributions were made by various investigators, thus expanding our understanding of noterid diversity (Garcia *et al.* 2012; Miller 2013; Gomez & Miller 2013; Baca *et al*. 2014, Guimarães & Ferreira-Jr 2015; Baca & Toledo, in review).

Even with these recent works, many questions surrounding the systematics of Noteridae remain. The prior phylogenetic analyses, including Miller (2009), have left some relationships within Noteridae unresolved (Fig 1.2), and others with poor support. The relationships recovered

by these analyses also imply some interesting cases of homoplasious character evolution with respect to adult morphology (Miller, 2009). Here, previous phylogenetic reconstructions and current classifications are explored and summarized.

REVIEW OF PREVIOUS STUDIES, RELATIONSHIPS AND CLASSIFICATION

Previous Studies

To infer the phylogenetic placement of the noterid genus *Notomicrus* Sharp, Beutel & Roughley (1987) performed a phylogenetic analysis using a matrix of 13 morphological characters and a taxon sampling that included eight noterid genera. Their cladistic analyses recovered the genus *Notomicrus* Sharp as being sister to the rest of Noteridae. The genus *Phreatodytes* Uéno was not included in this analysis as no specimen was available for their study, however Beutel and Roughley (1987) discussed the systematic placement of *Phreatodytes* based on the description by Uéno (1957) and *Phreatodytes* was hypothesized to be sister to all noterids, including *Notomicrus*. Results of this study are depicted in Fig. 1.2 A.

Belkaceme (1991) conducted a thorough examination of the musculature and exoskeleton of the head and thorax of *Noterus leavis* Sturm, 1834. This study concluded with a discussion of noterid phylogeny including a detailed discussion of morphological characters. Belkaceme (1991) found morphological support for the monophyly of Noteridae and hypothesized an ingroup phylogeny of the family using 47 characters (Fig. 1.2B). These characters were not coded into a matrix and no strict cladistic analysis was performed. The primary impact of the study was that it established many character concepts used in later studies (e.g. Beutel *et al.*, 2006; Miller, 2009).

The investigation performed by Beutel *et al.* (2006) sought to resolve the phylogenetic placement of the newly discovered beetle family Meruidae and infer the phylogenies of some of the smaller adephagan families. Their study included 148 characters (90 adult and 58 larval) coded into a matrix and subjected to a parsimony analysis (Fig. 1.2C). However, the study focused on Adephaga as a whole, and many of the characters included were not informative for inferring relationships within Noteridae. It should also be noted, that the larvae for many noterid genera, and also for Meruidae, were unavailable or undescribed, leaving many noterid genera with missing data for the larval characters used in the analysis.

Balke *et al*. (2008; Fig. 1.2E) performed an investigation using molecular sequence data from 6 gene fragments. The primary focus of this study was to explore the phylogenetic placement of Meruidae and therefore very few noterid taxa were sampled. The study recovered Meruidae as sister to Noteridae (Fig. 1.2E). In a subsequent study, Kato *et al*. (2010; Fig 1.2F) used the data published by Balke, *et al*. (2008) to place the genus *Phreatodytes*. The resulting tree was identical to that of Balke, *et al.*, (2008), but found *Phreatodytes* sister to other noterids (Fig. 1.2F).

Alarie *et al.* (2011) conducted a phylogenetic analysis following the description of the larvae of *Meru phyllisae* Spangler & Steiner, 2005 (Meruidae). The analysis consisted of 28 larval characters and recovered Meruidae as sister to all Dytiscoidea (Fig. 1. 3E). In addition to the analysis, Alarie *et al*. (2011) also provided strong morphological evidence for the classification of Meruidae as an independent family.

Dressler *et al.* (2011; Fig.1.2 H) performed their analysis with a dataset that was nearly identical to that of Beutel *et al.* (2006), with the same objective of finding the phylogenetic placement of Meruidae, but modified the dataset to include the recently described larvae of

Meruidae (Alarie *et al.* 2011), with few other minor changes in characters and codings (145 total characters, 56 larval). No additional noterid larvae were added, and the resulting tree topology was almost identical to that of Beutel *et al.* (2006), with increased support for the monophyly of Noteridae + Meruidae (Fig. 1.2H).

Miller (2009; Fig. 1.3B) carried out the most robust investigation testing relationships and classification of Noteridae. The analysis consisted of 33 adult characters and taxon sampling that included representatives of nearly all noterid genera recognized at the time and also the there described *Tonerus wheeleri* Miller, 2009 (*Phreatodytes* was not included as no specimens were available). The resulting tree showed a topology very similar to previous studies (e.g. Beutel & Roughley 1987, Belkaceme 1991, Beutel *et al.*, 2006), with differences limited to relationships within the Noterini (Fig. 1.3 B). *Tonerus* Miller was shown not to fit within any then-known tribal concept, and Tonerini Miller was erected as sister to all other Noterinae. *Canthydrus* Sharp was shown to be paraphyletic with respect to the subgenus *Liocanthydrus* Guignot, and thus, *Liocanthydrus* was elevated to the genus rank. The study concluded with a treatment of all noterid genera, complete with diagnoses for each subfamily, tribe and genus, and a diagnostic key to noterid genera. Since the resulting phylogenies followed previous hypotheses, much of the classification used in Miller (2009) had been previously established (Nilsson, 2005; 2011; Fig. 1.3 A).

Gomez & Miller (2013) replicated the analysis performed in Miller (2009), but modified the character matrix to include the three members of the new genus *Prionohydrus* Gomez & Miller. The resulting tree showed the same topology as Miller (2009), but placed *Prionohydrus* as a sister to *Mesonoterus* Sharp, together comprising a monophyletic lineage (Fig. 1.3B).

As noted by Gomez & Miller (2013), and explained in detail by Baca *et al*. (2014) and Baca & Toledo (in press; CH. 3), the specimen of *Liocanthydrus* used in Miller (2009) was misidentified. It was discovered through observation of the type species of *Liocanthydrus*, that *Siolius* Balfour-Brown was a junior synonym of this genus, and the species used by Miller (2009) requires the erection of a new genus *Canthysellus* Baca & Toledo **gen. n.** (CH. 3). Names have been changed throughout this current work to reflect the taxonomic action taken by Baca *et al*. (2014) and Baca & Toledo (in press).

Taxonomic Status and Phylogenetic Placement of Noteridae

Historically, Noteridae, was treated as a subtribe, tribe, or subfamily within Dytiscidae (e.g. Thomson 1860; Sharp 1882; Zimmermann 1920). According to Nilsson (2011), Noteridae was first elevated to the status of family by Bertrand (1928), who noted the lack of resemblance of larval noterids to larval dytiscids. This classification was increasingly followed over the next several decades (Nilsson, 2005), eventually becoming the general consensus among workers on Hydradephaga (Nilsson, 2005; Miller, 2009). The classification of Noteridae as a separate family would later be supported by modern phylogenetic analyses of Adephaga (Ribera *et al.*, 2002 and citations therein; Balke *et al.*, 2005; Beutel *et al.*, 2006; 2008; Alarie *et al*., 2011; Fig. 1.1).

Recent phylogenetic reconstructions have recovered various relationships of the Hydradephaga depending on the taxon sampling, data type (i.e. molecular or morphological), and method of analysis. However, the results of these studies consistently recover Noteridae (+ Meruidae where included; but see Alarie *et al*. 2011; Fig. 1.1E) as monophyletic and nested within the Dytiscoidea, almost always sister to a clade comprised of the remaining Dytiscoid families (Fig 1.1). Beyond this there is some contention as far as whether or not the

Hydradephaga is monophyletic, with some studies finding Haliplidae and Gyrinidae as successive sisters to the Dytiscoidea and others finding Hydradephaga paraphyletic, with Carabidae sister to the Dytiscoidea or Haliplidae (Ribera *et al.*, 2002 and citations therein; Balke *et al.*, 2005; Beutel *et al.*, 2006; 2008; Maddison *et al*., 2009).

Relationships within Noteridae

Noteridae Thomson, 1860 and Meruidae Spangler & Steiner, 2005. Since the discovery of *Meru* Spangler & Steiner, a monotypic seep dwelling genus placed in its own family Meruidae, a handful of studies have attempted to resolve its placement among the Adephagan families. In their description, Spangler & Steiner (2005) noted the similarities between Meruidae and Noteridae and hypothesized a close relationship between these families. Subsequently most studies have recovered Meruidae as sister to Noteridae (Beutel *et al*., 2006; Balke *et al*., 2008; Kato *et al*., 2010; Dressler *et al*., 2011), with the exception of Alarie *et al*. (2011) which found Meruidae sister to all Dytiscoidea *sensu* Alarie *et al.* (2011). There has been some speculation concerning whether or not *Meru* should be subsumed within Noteridae (Dressler *et al*., 2011; but see Short *et al.*, 2012), a claim corroborated by the parsimony analysis of molecular data conducted by Balke *et al*. (2008; the Bayesian analysis in this study recovered *Meru* as sister to Noteridae). Balke *et al*. (2008) expressed skepticism for the results of his parsimony analysis and also for the position of Meruidae as sister to Noteridae. They believed that these placements could be caused by long branch attraction. This long branch seems to reflect the extreme morphological divergence of this family, which is one of the sources of the contention surrounding its classification. With the exception of Dressler *et al*. (2011), there is a

wide consensus recognizing the classification of Meruidae as a distinct family. This was supported by Short *et al*. (2012) who strongly refuted the arguments of Dressler *et al*. (2011).

Phreatodytinae Uéno, 1957 and Notomicrinae Zimmerman, 1919. Phreatodytinae Uéno, is a monotypic subfamily represented by six strictly stygobiontic species, all from Japan (Nilsson, 2011). Uéno (1957; 1996) made a case for his original treatment of Phreatodytinae at the status of family, citing its specialized features (e.g. eyes absent, reduction of swimming features) for support. However, this treatment was not widely accepted (Spangler, 1996 and citations therein) and Beutel & Roughley (1987) were able to find morphological evidence to support a sister relationship with the remaining Noteridae. The classification of *Phreatodytinae* as a noterid subfamily has since been widely recognized and supported (Belkaceme, 1991; Nilsson, 2005; 2011; Beutel *et al.*, 2006; 2008; Balke *et al*., 2008; Miller, 2009; Kato *et al*., 2010; Dressler *et al.*, 2011) Miller (2009) and Gomez & Miller (2013) did not include *Phreatodytes* in their analysis (Fig. 1.3 B), but evidence was provided for the inclusion and validity of the Phreatodytinae as a noterid subfamily, sister to the remaining Noteridae.

Notomicrinae Zimmerman, 1919 is a subfamily comprised of one tribe, Notomicrini Zimmerman, 1919 and two genera: *Speonoterus* Spangler and *Notomicrus* Sharp. While all studies considered here include the genus *Notomicrus* in their analyses, Miller (2009) and subsequently Gomez and Miller (2013) were the only studies to include the genus *Speonoterus* (Fig. 1.3 B). Similar to *Phreatodytes, Speonoterus* is subterranean, but morphological evidence suggests a close relationship with *Notomicrus* (Miller, 2009). All studies have found *Notomicrus* as sister to all remaining Noteridae.

Noterinae Thomson, 1860. Noterinae Thomson holds the majority of noterid diversity, and as currently defined, is comprised of 4 tribes and 14 genera. As seen in Figs.1.2 and 1.3,

previous studies recover the same general topologies within the Noterinae. The discovery of the monotypic Tonerini Miller (2009) produced no changes in tree structure, with the genus placing as sister to the rest of the Noterinae (Miller, 2009). The three basal taxa of the Noterinae form a phyletic grade of monotypic tribes in the sequence of Tonerini Miller, Neohydrocoptini Zalat *et al.* and Pronoterini Nilsson, progressively branching to the Noterini Thomson, the most diverse noterid tribe (Fig. 1.3B). This grade of tribes agrees with the morphology historically used to classify Noterinae

All studies have supported the monophyly of the Noterinae (Beutel & Roughley, 1987; Belkaceme, 1991; Beutel *et al*., 2006; 2008; Balke *et al*., 2008; Miller, 2009; Kato *et al*., 2010; Dressler *et al.*, 2011). Relationships found unresolved or contended by different studies are limited to those in the derived Noterini.

Noterini Thomson, 1860. There are 11 genera currently placed within the Noterini Thomson (Nilsson, 2011; Gomez & Miller, 2013; Baca & Toledo, in press, see CH. 3). In general most phylogenetic studies have found a similar topology (Figs. 1.2, 1.3B), with a progressive branching grade of the genera *Mesonoterus* Sharp, *Synchortus* Sharp and *Noterus* Clairville, as sisters to the derived genera of Noterini.

The more derived genera of the Noterini are distinguishable by various combinations of characters (Miller, 2009), but due to the homogeneous nature of these genera, it is difficult to recover phylogenetic signal in morphological based analyses from the limited availability of informative morphological characters (see Belkaceme, 1991; Beutel *et al.* 2006; Miller, 2009). This is reflected by the lack of resolution recovered by some studies (Figs. 1.2, 1.3B).

Discussion

Nearly all prior phylogenetic studies of the family were based on morphology. Most of the characters used in analyses rely heavily on previously held character concepts, e.g. those established by Belkaceme (1991), and in that aspect it is not surprising that most recovered the same tree topology. Many branches of the here examined phylogenies were found without strong support, especially in the derived Noterini. With the limited number of characters available for analysis, an incorrect homology statement, e.g. an error in character state coding, has higher potential to produce an erroneous tree topology. In this vein, some intriguing cases of homoplasy appear in the trees recovered. One interesting example is the case of *Pronoterus* Sharp and some of the derived genera of the Noterini. In *Pronoterus* the pygidium is modified with a retractable claw (Miller, 2009) and the prosternum presents with a prominent series of setae (Miller, 2009). These characters are shared with the monophyletic noterine genera *Suphis* Aube, *Suphisellus* Crotch, and *Canthysellus* Baca & Toledo, and are inferred to have evolved independently. *Pronoterus* also shares the character state of a serrate posterior metatibial spur with the noterines *Suphisellus, Canthysellus*, *Hydrocanthus* Say and *Prionohydrus* Gomez & Miller. The tree topology suggests this evolved independently at least 3 times (Miller, 2009; Gomez & Miller 2013).

CONCLUSION

This overview highlights the need for the discovery of new informative morphological characters that will hopefully better support or resolve relationships. The larvae of many important noterid taxa remain undescribed or unavailable for analysis or confirmation of character states, hence their omission in the analysis of Miller (2009; see also character state matrix in Beutel *et al.*, 2006 in which many genera are not coded for larval characters). Should the larvae of these genera be obtained and/or described, an entire new swath of potentially

informative characters would become available. Fortunately, with increased attention being paid to the diversity of Noteridae, it is likely that new characters will come to light.

Apart from morphology, this overview also shows the need for a phylogenetic investigation of Noteridae based on molecular sequence data. To date, no molecular based study has included a sufficiently robust taxon sampling of noterids to effectively test the relationships and classification recovered by morphology. Constructing a phylogeny that includes molecular sequence data from a robust noterid taxon sampling would be very valuable for elucidating relationships within the family. This could also shed light on character evolution and the cases of homoplasy within Noteridae. A robust phylogeny could also be used as a foundation for several avenues of study of the family, including ecology, biogeography and the documentation of diversity.

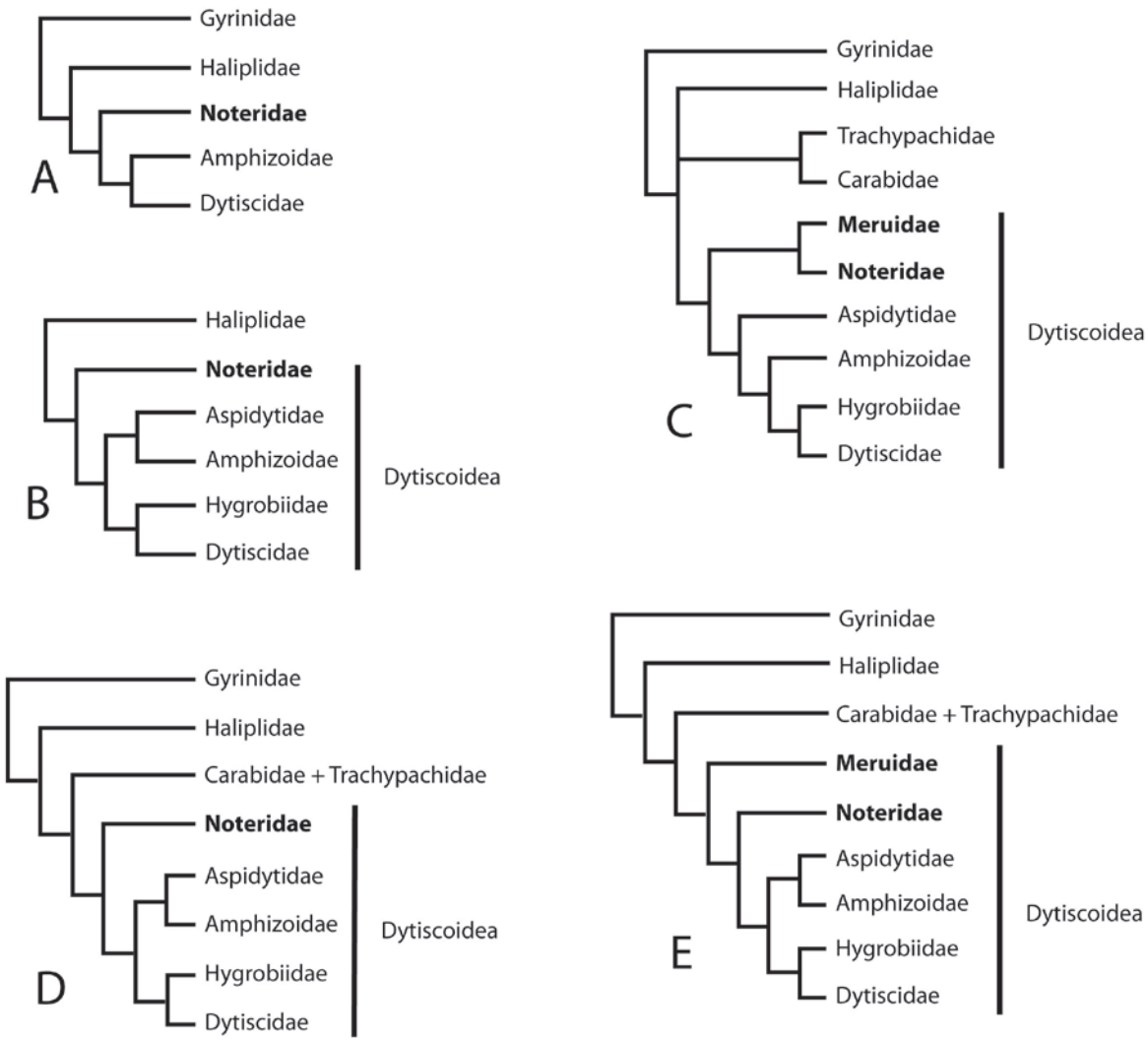


Figure.1.1. Phylogenetic hypotheses of Adephaga. A) Ribera *et al*. (2002); (B) Balke *et al*. (2005); (C) Beutel *et al*. (2006); (D) Beutel *et al*. (2008); (E) Alarie *et al*. (2011).

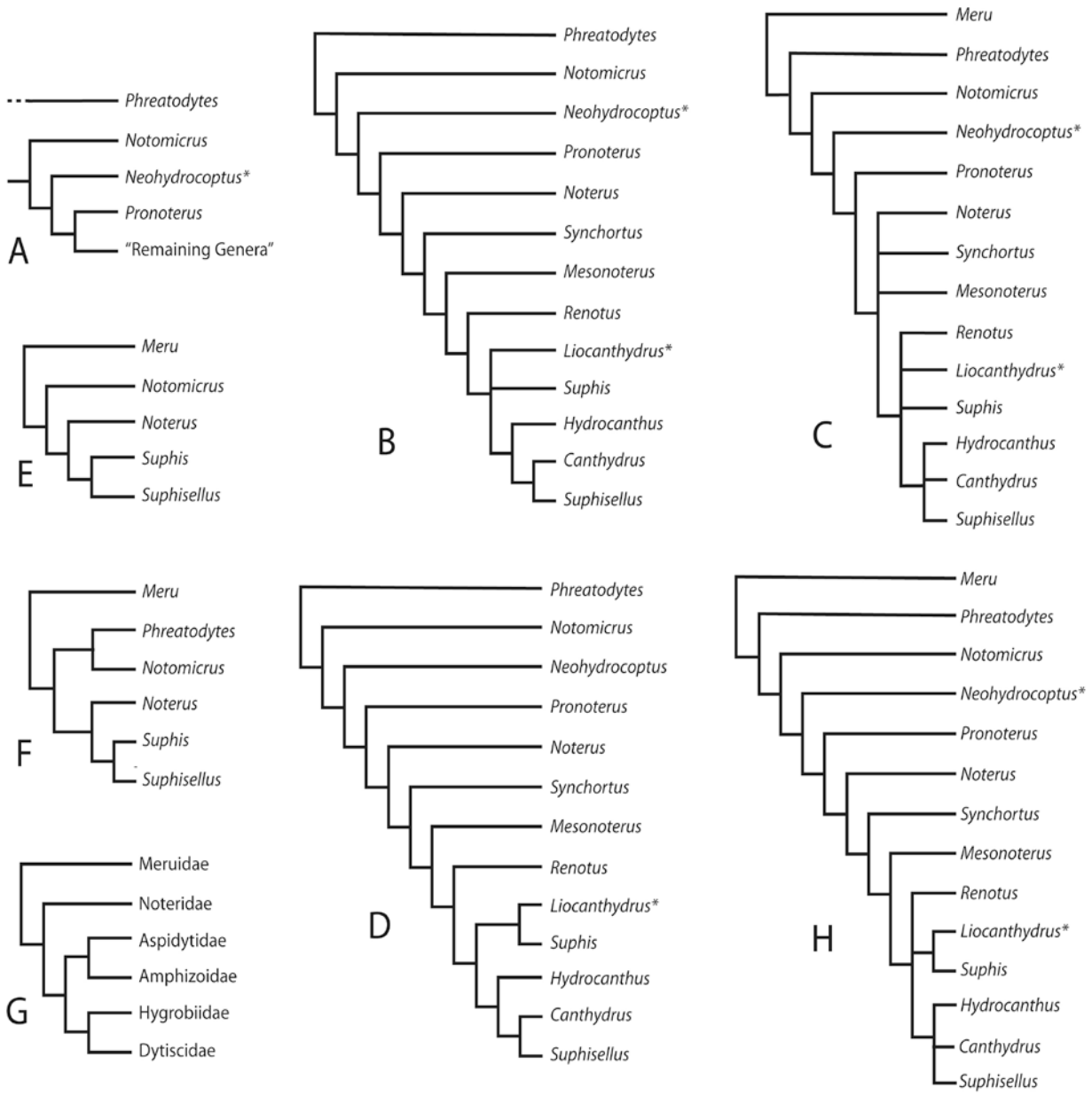


Figure. 1.2. Phylogenetic hypotheses of Noteridae + *Meru*. (A) Beutel & Roughley (1987); (B) Belkaceme (1991); (C) Beutel *et al*. (2006); (D) Beutel *et al*. (2008); (E) Balke *et al.*, (2008); (F). Kato *et al*. (2010); (G) Alarie *et al.*, (2011); Dressler *et al*. (2011). Note: Asterisks (*) indicates taxon name changed to follow recently published taxonomic actions..

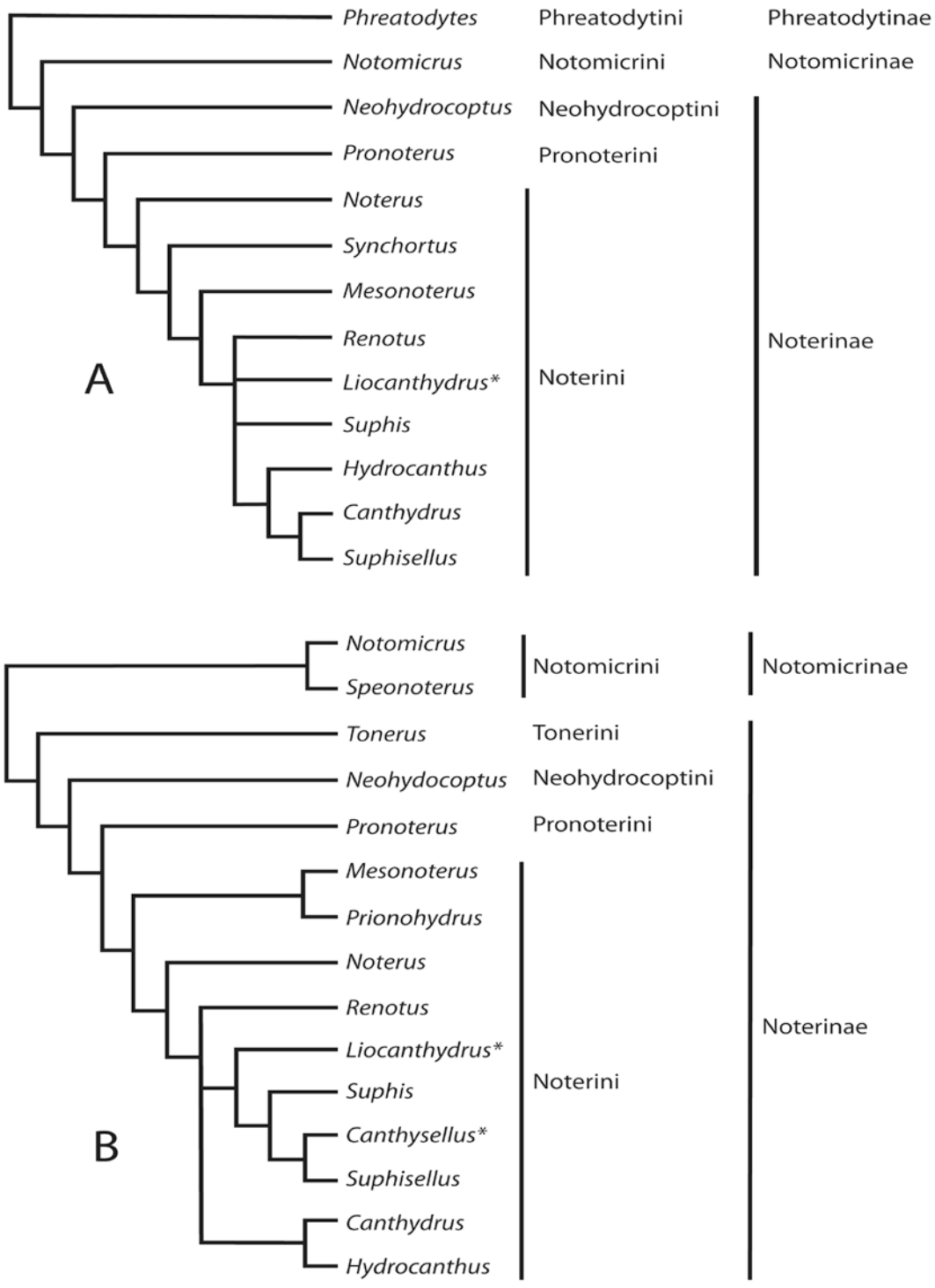


Fig. 1.3. Phylogenetic hypotheses and current classification of Noteridae. (A) synopsis of phylogenetic hypotheses by Nilsson (2005); (B) Gomez & Miller (2013), adapted from Miller (2009) to include *Prionohydrus*. Asterisks (*) indicates taxon name changed to follow current classification.

CHAPTER 2

PHYLOGENY OF NOTERIDAE (COLEOPTERA: ADEPHAGA) INFERRED FROM MOLECULAR SEQUENCE DATA

INTRODUCTION

Members of the family Noteridae have been included in many phylogenetic investigations, almost all of them based on morphology. While results of these studies have been relatively consistent and present similar tree topologies (Fig. 1.2), many have recovered noterid relationships lack strong support and others were sometimes unresolved (see Ch. 1). In an effort to address the lack of resolution and uncertainty surrounding phylogenetic hypotheses within the Noteridae, we conducted a phylogenetic investigation based on molecular sequence data from five gene fragments for 71 noterid exemplars, representing 16 of the 17 currently recognized genera and an additional eight Adephagan outgroup exemplars, including members of Meruidae, Amphizoidae, Haliplidae and Dytiscidae. The data is subjected to three types of analyses, Bayesian Inference, Maximum Likelihood, and Maximum Parsimony. With representatives of nearly all noterid genera included in our analysis, including dense sampling of diverse or problematic genera, this is the most robust phylogenetic investigation of Noteridae to date. The goal of this study is to construct a resolved phylogeny of the family Noteridae. The resulting relationships and trees recovered by our analyses are presented, and modified classifications of groups within Noteridae are proposed. Recovered relationships, implied morphological character evolution, biogeography, and ecology are discussed.

MATERIAL AND METHODS

Taxon sampling.

Ingroups. Following the generic concepts of Miller (2009); Gomez & Miller (2013) and Baca *et al.* (2014), representatives of all noterid subfamilies, tribes, and genera were sampled with the exception of *Speonoterus* Spangler (Notomicrinae), as no specimens were available for molecular study. Where possible, multiple species of each genus were selected. Larger genera such as *Suphisellus*, *Canthydrus*, and *Hydrocanthus* were sampled more densely to account for their respective diversity or geographic distribution. In some cases, multiple exemplars of a single species were sampled to affirm quality and identity of sequence data, especially in the cases of small or monotypic genera where additional species are unavailable or unknown.

Outgroups. Outgroup selection was guided by previous phylogenetic reconstructions of Adephaga (Balke *et al.*, 2005; *Beutel et al.*, 2006; 2008). Representatives of the families Meruidae, Haliplidae, Dytiscidae, and Amphizoidae were included for a total of eight exemplars. The representative taxa selected for each family was dependent on availability of data for overlapping gene regions and necessity for analysis. Two exemplars of *Meru phyllisae* were selected to assure sequence quality. See appendices 1.1 and 1.2 for complete list of all taxa used in analysis and source data.

Sequence Data Sources. Specimens and sequence data were obtained from several sources. Whole specimens were preserved in 95–100% ethanol and frozen at -20°C or below. Other sequence data were obtained via personal communication or GenBank. See appendix 1.1 for complete list of data source information.

Genes: Extraction, Amplification and Sequencing

DNA extraction. Whole genomic DNA was extracted using a Quiagen DNEasy kit following the provided protocol for animal tissues. Whole specimens were prepared by partially or completely separating the abdomen from the thorax before placing them in lysis buffer. After extractions were completed, specimens were mounted on points or cards and retained as vouchers. Extracted DNA was divided into multiple aliquots and frozen; stock aliquots were kept at -80°C and working aliquots at -20°C.

Targeted gene regions. Five gene fragments were targeted for PCR amplification and sequencing: Cytochrome Oxidase I mtDNA (COI; ca. 770 bp), Histone 3 nDNA (H3; ca. 280 bp), 16S rDNA (ca. 540 bp), 18S rDNA (ca. 2000 bp) and 28S rDNA (ca. 1000 bp). Fragments for COI, H3, 16S and 18S were targeted based on previous studies containing noterids and related taxa (e.g. Ribera *et al.* 2002; 2008; Balke *et al*. 2005; 2008). 28S is less commonly used in molecular studies of Hydradephaga, but has shown utility in beetle studies (e.g. Korte *et al*. 2004; Maddison *et al.*, 2009; Short & Fikáček 2013)

PCR reactions. Individual fragments of COI, H3, 16S and 28S were amplified in single PCR reactions. Two to four partially overlapping fragments of 18S were amplified and assembled to recover the complete targeted fragment of ca. 2000 bp. This required two separate PCR reactions for each sample, one targeting the 3' end of the fragment and the other, the 5' end.

Each PCR reaction used the following ingredients and concentrations: 1.0 µL template DNA, 2.0 µL 10x buffer, 1.0 µL 50mM Magnesium Chloride ($MgCl_2$) buffer, 1.5 µL deoxyribonucleotide triphosphate mixture (dNTP) with 2.5 mM component concentration, 0.3 µL of each forward and reverse primers diluted to 10 uM, 0.1 µL Platinum *Taq* Polymerase, and

13.8 μL sterile H_2O, for a total volume of 20 μL. For 28S, 0.5 μL of the promoter Dimethyl Sulfoxide (DMSO) was added to the mixture. Reactions were carried out in the University of Kansas Biodiversity Institute Molecular Laboratory. The general conditions used for each gene are as follows: initial denaturation of 4 min at 95°C (hot start); 30–38 cycles of denaturation at 95°C, followed by annealing for 30s at a temperature specific to the primers used and an extension of 1-1.5 min at 72°C; and a final extension for 5 min at 72. The hot start and denaturation temperatures were elevated to 98°C for 28S, and to 96°C for H3 and 18S. A hot start of 30s at 98°C and initial denaturation of 10s at 98° were used for some 18S samples. Annealing temperature ranges for each gene fragment were as follows: 47–49°C for COI, 50°C for H3, 50.5°C for 16S, 50–51°C for 18S, and 5154°C for 28S. At times the components of the PCR reaction mixtures or cycle protocols were altered slightly for troubleshooting purposes. Polymerase Chain Reaction products were viewed on stained agarose gels under UV light. Sanger sequencing of amplified products was conducted off-site using the sequencing services of either Macrogen (Macrogen inc., Seoul, Korea; http://macrogen.com) or Beckman Coulter Genomics (Beckman Coulter inc., Danvers, MA; http://beckmangenomics.com). Products were packaged and shipped per instructions from the respective service providers. In the case of Macrogen inc. PCR clean-up was performed with ExoSAP-*it*. (USB Corp, Cleveland OH.)

Sequence alignment and editing.

Sequence files were imported into Geneious version 5.1 (Kearse et al., 2012), for assembly and editing of contigs. Sequences of all gene regions were aligned using MUSCLE (Edgar 2004) as implemented in Geneious with default settings. Alignment of the protein-coding gene regions (COI, H3), which are of fixed length and free of indels, was trivial. The MUSCLE

alignments of the variable-length ribosomal gene regions (16S, 18S, 28S) were lightly edited by eye. Alignments for individual gene regions were imported into Mesquite 3.03 (http://mesquiteproject.org) reading frames of coding genes were checked and alignments of all genes were concatenated to be used for phylogenetic analysis. Edited sequence data for several gene regions of ingroup taxa were directly obtained from Kelly Miller at the University of New Mexico. Sequence data for nearly all outgroup taxa, and some ingroup taxa were obtained from GenBank. These taxa were selected depending on data availability for gene regions targeted and anticipated necessity taxa for analysis. See table 2 for complete list of gene regions sequenced and appendices 1.1 for sources of data.

Phylogenetic analysis

Iterative preliminary analyses were run in Garli 0.951 (Zwicki, 2006; www.bio.utexas.edu/faculty/antisense/garli/Garli.html) as sequence data for individual gene regions were obtained. This was done to check for incongruent gene regions and guide the choice of subsequent gene regions to be amplified and sequenced. No conflicts were found and a concatenated data set of 5072 bp was used for our final analyses. For Bayesian and Maximum Likelihood analyses, partitions and corresponding models of substitution were searched with PartitionFinder 1.1.1 (Lanfear et al., 2012) ran in python, using the *greedy* algorithm, and either the *mrbayes* or *raxml* model sets to produce two different model schemes, one for MrBayes 3.2.5 (Ronquist *et al.*, 2012) and one for RAxML (Stamatakis, 2006) since these use different sets of substitution models. Models were searched with non-protein coding gene regions (16S, 18S, 28S) divided into one partition per gene fragment and protein coding gene regions (COI, H3)

partitioned by coding position for a total of nine partitions. Models were compared for fit under the Akaike Information Criterion corrected (AICc).

Bayesian analysis. The Bayesian analysis was run using MrBayes 3.2.5 (Ronquist *et al*. 2012) on the online computing platform CIPRES 3.3 (Miller *et al.*, 2010; https://www.phylo.org/). Two independent and simultaneous analyses were run, each consisting of eight Markov chain Monte Carlo (MCMC, one cold, seven heated) running for 30 million generations, with trees sampled every 1000 generations to calculate posterior probabilities (PP). The root was set *a priori* as *Peltodytes rotundatus* (Coleoptera: Adephaga: Haliplidae). Models and partitions were set using the model scheme recovered by PartitionFinder. Convergence of the runs were observed visually via the reported standard deviation of split frequencies for the sampled trees. Trees converged quickly in the analyses (SD of split frequencies < 0.05 at ca. 45,000 generations) and it was determined that the default burn-in of 25% was sufficient to restrict samples to a log-likelihood plateau. The remaining samples were used to generate a 50% majority rule consensus tree. A calculated pp ≥0.95 is considered to indicate strong support for a given clade (Erixon *et al.*, 2003).

Maximum Likelihood analysis. The Maximum Likelihood (ML) analysis was ran in RAxMLGUI (Stamatakis, 2006), under the GTR + Gamma + Proportion Invariant (GTR+G+I) model following the model scheme recovered by PartitionFinder, and with root set *a priori* as *Peltodytes rotundatus*. 500 bootstrap (bs) replicates were performed under the rapid bootstrap option to investigate the level of support at each node. A calculated bs ≥ 70 is considered an indication of strong support for a given clade (Hillis & Bull, 1993).

Parsimony analysis. The maximum parsimony analysis was run in T.N.T 1.1.1 (Goloboff *et al.*, 2008). Trees were searched in four different ways, twice under a New

Technology Search (NTS) and twice under a Traditional Search. Both NTS searches were conducted using Sectorial Search, Ratchet, Drift, and Tree fusing algorithms, with one tree obtained from a driven search with 10 initially added sequences, and the other from a search with 10 random addition sequences. Traditional searches were conducted under the Wagner trees setting with one random seed and 10 additional sequences, one tree search using the subtree-pruning-regrafting (SPR) swapping algorithm, and the other using the tree bisection reconnection (TBR) swapping algorithm. All four searches yielded the same single best tree. Bootstrap support values (pbs) were calculated using a standard bootstrap with 500 replicates under default settings. A calculated pbs ≥ 70 is considered an indication of strong support for a node (Hillis & Bull, 1993).

RESULTS

The topologies of the trees obtained from both Bayesian (BI) and Maximum Likelihood (ML) analyses were very similar and recovered high support values for most nodes (Figs. 2.2; 2.3). However the results strongly contradict prior studies, with many groups found to be para- or polyphyletic with respect to historical classification. The BI analysis recovered a poorly supported paraphyletic Noteridae, with Meruidae sister to *Phreatodytes* + *Notomicrus*, all forming a monophyletic clade sister to the rest of Noteridae. The ML analysis recovered Noteridae to be monophyletic with Meruidae placed sister to it; again *Phreatodytes* + *Notomicrus* forming a monophyletic sister to the rest of Noteridae; this result agrees with most previous phylogenetic reconstructions (Miller, 2009 and citations therein; Balke *et al.*, 2008; Beutel *et al.*, 2008; but see Alarie *et al*. 2011). The subfamily Noterinae is found to be

monophyletic with variable support between analyses (pp = 1.0/bs = 54) and within this subfamily the tribes Tonerini, Neohydrocoptini, and Pronoterini are all nested within the tribe Noterini *sensu* Miller, 2009; Nilsson, 2011; Gomez & Miller, 2013 (Figs. 2.1–2.3). Here, Noterinae is resolved to consist of 5 successfully branching clades. First, *Neohydrocoptu*s and *Noterus* are resolved as monophyletic (>0.99/85) and sister to the remaining Noterinae (0.99/54). Second, a clade comprised of *Synchortus* and *Tonerus* + *Liocanthydrus* is recovered with high BI support at all nodes (0.99/49) and high support for *Tonerus* + *Liocanthydrus* from both BI and BL analyses (100/99); this is sister to the remaining clades (1.0/90). Third, *Renotus*, a monotypic African genus, is isolated as sister to the remaining clades, but with lower support (0.89/75). Finally, the remaining genera of the derived Noterini are resolved as two large, successively branching sister clades (0.98/81). The first of these two is comprised of *Canthysellus* + *Suphis* (1.0/93) sister to *Suphisellus* + *Pronoterus* (0.99/88). Here The Bayesian and ML trees differ somewhat here with respect to relationships between members of *Suphisellus* and the placement of *Pronoterus* (Figs. 2.2, 2.3), but in both analysis *Suphisellus* is found to be paraphyletic, with *Pronoterus* resolved as nested within this genus. A single species, identified as "*Suphisellus sp. 8*" is found sister to the *Suphisellus* + *Pronoterus* clade and likely represents a new genus. Within the final clade, *Canthydrus* is found to be sister to *Hydrocanthus* (0.99/53). *Hydrocanthus* is resolved as paraphyletic with *Mesonoterus* + *Prionohydrus* (1.0/100) sister to the New World members of *Hydrocanthus* with very high support (1.0/100) and with the Old World and Australian members of *Hydrocanthus* (formally subgenus *Sternocanthus* Guignot) sister to them, also with very high support (1.0/100). The New World members of *Hydrocanthus* were resolved as monophyletic (1.0/100), as too were the Old World species (1.0/100) and Australian species

(1.0/100) of this genus, with the latter two clades being sisters (1.0/100) The monophyly of all individual genera not found to be paraphyletic was strongly supported by our analyses (1.0/100).

The maximum parsimony (MP) analyses recovered a single most parsimonious tree with a length of 13,868 steps (Figs. 2.4, 2.5). This tree found several peculiar relationships, e.g. *Meru* and *Phreatodytes* as successive sisters to several members of *Hydrocanthus*. The bootstrapped replicates found no support for several deep nodes, resulting in a largely collapsed tree (Figs. 2.6, 2.7). However, bootstrap support (pbs = 98) was found for Meruidae + Noteridae as a monophyletic clade. Support was also found for the monophyly of several clades that were also recovered by the BI and ML analyses: *Neohydrocoptus* + *Noterus* (94); *Tonerus* + *Liocanthydrus* (93), *Suphis* + *Canthysellus* + *Suphisellus* + *Pronoterus* (99); *Suphis* and *Canthysellus* are resolved as monophyletic (85), and sister to *Suphisellus;* the genus *Pronoterus* is recovered as nested within *Suphisellus* with high support (99). Though sometimes placement was unresolved, the monophyletic status of all genera with multiple representatives sampled was supported (pbs > 70, usually recovered to be 100), with exception of those found paraphyletic, i.e. *Hydrocanthus* and *Suphisellus*.

DISCUSSION

Performance of Analyses.

The BI and ML analyses performed very well. Both found very similar tree topologies, and recovered very few poorly supported nodes (Figs 2.2, 2.3). The MP analysis resulted in a resampled tree with a collapsed backbone and almost no resolution with respect to generic relationships. Though it is difficult to assess at this time, it is suspected that this result was at least partially caused by missing gene fragments for some taxa in our data set. The following

discussion of noterid classification and relationships will be based on the results of the BI and ML analyses as summarized in Figure 2.1

Classification

The trees recovered by analyses show topologies that conflict strongly with those of previous studies. With the strong support recovered for our trees, it is necessary to make changes to our current classification.

The classification of Noteridae + Meruidae is difficult to assess here due to a conflict of resolution recovered by our trees. If Meruidae is in fact part of a monophyletic clade with Phreatodytinae Uéno and Notomicrinae Zimmerman, it is likely that a new family would have to be erected to contain these tribes as separate from the Noteridae. The alternative would be to include *Meru* as a member of Noteridae. This classification would not be incorrect, but given the lack of similarity between Meruidae and Notomicrinae, Phreatodytinae and Noteridae, it may be more informative to opt for a more divided classification. By either treatment, the validity of the subfamilies Notomicrinae and Phreatodytinae is upheld. Here no changes in classification are made with respect to the relationship of Noteridae and Meruidae, and all noterid subfamilies are treated as valid.

The relationships recovered within Noterinae Thomson strongly contradict previous phylogenetic hypotheses and necessitate several changes in classification (Fig 2.1). First with the generic concept of *Suphisellus* Crotch is expanded to include the junior synonym *Pronoterus* Sharp **syn. nov.** as *Suphisellus* is the older name and takes priority. Next, *Hydrocanthus* is also found paraphyletic and divided into distinct Old World and New World clades. The subgenus *Sternocanthus* Guignot **stat. rev.** is thus resurrected and elevated to the genus rank **stat. nov.** to

contain the Old World members of *Hydrocanthus sensu lato*. With all other tribes of the Noterinae found nested within Noterini *sensu lato*, Noterini Thomson ***sensu* nov.** is here restricted to contain its type genus *Noterus* Clairville and *Neohydrocoptus* Satô, thereby including the tribe *Neohydrocoptini* Zalat *et al.* **syn. nov.** The remaining genera of the Noterinae are then split into various other tribes. The following classification is thus proposed: Tonerini Miller ***sensu* nov**., containing the genera *Synchortus* Sharp, *Liocanthydrus* Guignot and *Tonerus* Miller; Renotini **trib. nov.**: containing the monotypic genus *Renotus;* Suphisini Sharp **stat. rev.**, a former tribe resurrected from synonymy (Nilsson, 2005) to contain *Suphis* Aube, *Canthysellus* Baca & Toledo, a tentative new genus of noterid ("sp. 8"), and *Suphisellus* Crotch, here expanded to include *Pronoterus* Sharp, thus sinking Pronoterini Nilsson **syn. nov**. within Suphisini; and finally Hydrocanthini Sharp **stat. rev.**, a tribe resurrected from synonymy (Nilsson, 2005) to contain *Canthydrus* Sharp, *Sternocanthus* Guignot, *Hydrocanthus* Say, *Mesonoterus* Sharp and *Prionohydrus* Gomez & Miller.

The splitting of *Hydrocanthus* is relatively straight forward. The genus was recovered as split into New World and Old World clades, and a name already exists for the Old World clade: *Sternocanthus* Guignot. The task is more difficult in the case of *Suphisellus*. With the diversity of *Suphisellus*, it seems most appropriate to split the clade into separate genera or subgenera rather than synonymize *Pronoterus*. However, this will require extensive investigation. *Suphisellus sensu lato* is in dire need of revision and given the relationships recovered here, it would be difficult to know where to split the genus and then properly place its members. Because of this, the best course of action is to synonymize *Pronoterus* with *Suphisellus* to avoid incorrect classification until further investigation can be conducted. The exception to this latter problem is the case of "*Suphisellus* sp. 8", which is morphologically and genetically distinct

from all members *Suphisellus*. This species will hereby be considered to represent a tentative new genus of noterid.

Relationships within Noteridae.

The tree recovered by our analysis presents is strongly incongruent from those of previous studies with several prior hypothesized relationships contradicted with strong support. Most genera were found to be reciprocally monophyletic following their previous concepts with two exceptions: *Hydrocanthus* Say and *Suphisellus* Crotch.

Meruidae Spangler & Steiner, 2005 and Noteridae Thomson, 1960. While all our analyses recover a strongly supported Meruidae + Noteridae, they conflict with regards to the relationship between these two families. The BI analysis finds Noteridae paraphyletic with respect to *Meru* (pp = 0.82) while the ML analysis recovers Meruidae as sister to all noterids (bs = 89). The ML tree recovers the better support out of these two analyses and Meruidae placing sister to Noteridae agrees with most previous reconstructions (Beutel *et al.,* 2006; Balke *et al.,* 2008; Kato *et al.* 2010; Dressler *et al.*, 2011, but see Alarie *et al.,* 2011 and the parsimony analysis of Balke *et al*., 2008), though the congruence of this relationship in other studies may be an artifact of incomplete sampling of basal taxa such as *Phreatodytes* or *Notomicrus*. Both analyses show *Meru* on a very long branch, suggesting that the meruid genome has diverged extensively. This is also supported by the very high morphological divergence of this family. The discrepancies between our analyses and those of previous studies make it difficult to confidently affirm the phylogenetic position of Meruidae here, but in general this study (in part) and those previous studies show more convergence on the placement of Meruidae as sister to all noterids. This

relationship will be further explored in the future, with the hope that increased resolution could be gained from more data and/or different approaches to analysis.

Subfamilies Phreatodytinae Uéno, 1957 , Notomicrinae Zimmerman, 1919 and Noterinae Thomson, 1960.

Both Bayesian and ML analyses confirmed Phreatodytinae + Notomicrinae, together forming a clade sister to the remaining Noteridae (subfamily Noterinae). Recovered as successively branching sisters to Noterinae by previous studies (Beutel & Roughley, 1987; Belkaceme, 1991; Beutel *et al.*, 2008; Miller, 2009 and citations therein; Kato *et al.*, 2010; Dressler et al., 2011; Gomez & Miller, 2013), ours is the first to find the subfamilies Phreatodytinae and Notomicrinae as monophyletic. Miller (2009) recovered *Speonoterus*, another subterranean noterid genus, as member of this lineage also, and included it as a member of the Notomicrinae. Despite both *Speonoterus* and *Phraetodytes* being subterranean, inhabiting limestone caves and aquifers respectively, morphology supports the monophyletic relationship of *Speonoterus* and *Notomicrus* (Spangler, 1996; Miller 2009), but specimens were unavailable for molecular study. Our analyses support the monophyly of *Notomicrus* with the Old World *Notomicrus tenellus* (Clark, 1863) sister to the monophyletic New World species. With data of only one species of *Phraetodytes* available, the monophyly of this genus was not tested here, but given the strong morphological evidence and all species being endemic to Japan, it is reasonable to assume the monophyly of this genus (Uéno, 1996). Even if *Meru* were to be resolved as part of this clade, it would not necessarily contradict the validity of the current classification of Notomicrinae and Phreatodytinae as distinct subfamilies and no changes in the classification of these groups are proposed here.

Noterinae Thomson, 1960.

The subfamily Noterinae was found to be monophyletic with variable support by both BI and ML analyses (1.0/54). However, the relationships within Noterinae recovered by our analyses heavily contradict all previous phylogenetic reconstructions (Figs. 1.2, 1.3), and the tribe Noterini as found to paraphyletic, with all other tribes of the Noterinae (Tonerini, Neohydrocoptini, Pronoterini) placing within it.

Noterini Thomson 1960 *sensu nov.*

Neohydrocoptus and Noterus. The genera *Neohydrocoptus* Satô and Noterus Clairville are resolved as monophyletic with strong support from all analyses (0.99/85/pbs = 94), thus sinking the tribe Neohydrocoptini **syn. nov.** Both genera are absent in the New World, with *Noterus* occurring only in the Palearctic and *Neohydrocoptus* occurring throughout the Old World including Australia (Nilsson, 2005). Unfortunately, little is known about the specific ecologies of these taxa and their members.

The relationship recovered here contradicts the hypotheses supported by previous studies (Fig.1.2, 1.3). This grouping was unexpected as both genera differ greatly in many of the morphological characters classically used for phylogenetic inference. For example, *Neohydrocoptus* lacks many modifications of the protibia seen in *Noterus* and other members of the Noterini, including the rounded anteroapical angle, robust spur, setal fringe, and lateral (vs. apical) attachment of the protarsus (see Miller, 2009 and citations therein). The morphological character states that are shared by these two genera were generally treated as plesiomorphic or homoplasious with respect to other genera, e.g. the narrow and rounded prosternal process, the

broad sensorial field of the labial palpi, presence of the posterior protibial spur and absence of setae on the apical lobes of the metacoxae (Miller, 2009). Our analyses find *Noterus* and *Neohydrocoptus* on long branches the end of long branches, suggesting a large amount of genetic evolution, which is supported by the cases of derived morphology exhibited by these genera. Even with the consideration of a false grouping due to long branch attraction, it is difficult to ignore the highly supported convergence of our analyses.

Tonerini Miller, 2009 *sensu nov.*

***Synchortus* Sharp, *Tonerus* Miller and *Liocanthydrus* Guignot.** Our analyses are the first to include all genera here found to comprise the expanded Tonerini (0.99/48). The relationships recovered are not well supported by our current knowledge of morphology, but there is some support to be gained from their biogeography, with both *Tonerus* Miller *and* *Liocanthydrus* Guignot being Neotropical taxa, while their sister, *Synchortus* Sharp, is Afrotropical.

Our results imply some interesting evolutionary trends in terms of ecology. *Liocanthydrus* tends to be specific to lotic habitats (Baca *et al.*, 2014), while *Tonerus* is found only in vegetative mats of shallow bedrock seeps (Miller, 2009). This suggests a potential evolved shift to a seep habitat from a stream or lotic habitat, which has been suggested to be the most logical mode of a taxon arriving to this specific niche. This pattern remains untested, but the stream to rock-seep habitat shift could explain why *Tonerus* lacks some uniting morphological characters with these genera, e.g. the spur and setal fringe of the protibia. It has been suggested that these structures are used for burrowing (Roughly & Larson 2001; Dettner, 2005), so it is possible that shifting to a habitat with different substrate could drive the rapid

evolution of these structures. Of course, these hypotheses warrant further investigation before any claims can be made. The specific ecologies of members of *Synchortus* are unknown, personal observation shows them to hold the more general noterid preference to weedy ponds and marshes.

Previous phylogenetic reconstructions recovered these genera to occupy very disparate positions within Noterinae (Belkaceme, 1991; Beutel *et al.,* 2006; 2008, Miller, 2009; Dressler 2011). The previous placements of these genera reflect their lack of morphological synapomorphies. *Synchortus* and *Liocanthydrus* do share in some features considered to be plesiomorphic for the Noterini, such as modifications of the protibia (Beutel & Roughly 1987; Belkaceme 1991; Beutel *et al.,* 2006; Miller, 2009), but still were found separated by several other genera (Figs. 1.2, 1.3). *Tonerus* lacks many of these and presents a protibia without a large spur, setal fringe or rounded dorsoapical angle. Morphological characters previously found to be homoplasious (Miller, 2009), but supporting the nesting of *Tonerus* with other members of Tonerini include the broad prosternal process (narrow in *Synchortus*) the elongate and narrow sensorial field of the labial palp (Miller, 2009). In the case of *Tonerus* and *Liocanthydrus* the female genitalia are observed to have short laterotergites that extend posteriorly beyond the gonacoxae (Miller, 2009). The female genitalia of *Synchortus* have yet to be observed.

Liocanthydrus exhibits some morphological differences that are not shared with the clade of more derived genera of Noterinae it was once placed with. The female genitalia of these generally all have relatively elongate laterotergites that do not extend beyond the base of the gonacoxae, while those of *Liocanthydrus* are short and do extend beyond the bases. Several genera have serrate posterior metatibial spurs (except in *Mesonoterus* and *Suphis*, likely due to secondary loss), whereas *Liocanthydrus* lacks this serration. Finally many of the derived noterine

genera have a series of stiff setae on the prosternum (excluding *Hydrocanthus*, *Mesonoterus*, *Prionohydrus*; Miller, 2009; Gomez and Miller, 2013), and in many cases also have setaceous prosternal processes and noterid platforms (Miller, 2009; personal observation). These structures are glabrous in all members of *Liocanthydrus* (Baca *et al*.2014)

Renotini trib. nov.

This tribe is monogeneric with *Renotus* being a monotypic genus found only in central Africa. Our analyses find the relative position of *Renotus* Guignot altered largely only due to changes in the positions of other taxa. As in prior reconstructions, *Renotus* is still found to be closely related to the genera here placed in the tribes Suphisini and Hydrocanthini. Though the relationship of *Renotus* to these genera was sometimes unresolved (Beutel *et al*., 2006), most studies found the same relationship recovered by our BI and ML analyses (Belkaceme, 1991; Beutel *et al.*, 2008; Miller, 2009), with *Renotus* sister to the derived genera of the Noterini.

Suphisini Sharp, 1882+ Hydrocanthini Sharp, 1882

Our results recovered two derived and diverse clades here classified as two separate tribes. Miller (2009) recovered a relationship similar to that found here, with *Suphis* Aubé, *Suphisellus* Crotch and *Canthysellus* Baca & Toledo forming a monophyletic group sister to a clade comprised of *Canthydrus* Sharp and *Hydrocanthus* Say. Our results also recover *Pronoterus* Sharp, *Mesonoterus* Sharp, and *Prionohydrus* Gomez & Miller as part of this clade, nested within other genera. Phylogenetic reconstructions prior to Miller (2009) and Gomez and Miller (2013) varied in topology in this region of the tree and usually found only limited resolution (Fig 1.1). Most recovered *Hydrocanthus*, *Suphisellus* and *Canthydrus* as

monophyletic, some with *Hydrocanthus* sister to *Suphisellus* + *Canthydrus* (Belkaceme, 1991; Beutel *et al.*, 2008), others found no resolution for this clade (Beutel *et al.,* 2006; Dressler *et al.,* 2011). *Suphis* and *Liocanthydrus* were recovered as sister to these genera, usually as part of an unresolved polytomy that sometimes included *Renotus* (Belkaceme, 1991; Beutel *et al.*, 2006; 2008; Dressler *et al.*, 2011; Fig 1.2). Some studies recovered *Suphis* and *Liocanthydrus* as monophyletic (Beutel *et al*., 2008; Dressler *et al.,* 2011; Fig. 1.2).

Suphisini Sharp, 1882 stat. rev.

The tribe Suphisini was erected by Sharp (1882) to house the genus *Suphis* Aubé and was formally synonymized as a member of the Noterini *sensu lato* by Nilsson, 2005. Here the tribe is resurrected from synonymy to accommodate the New World genera *Suphis* Aubé, *Canthysellus* Baca & Toledo, *Suphisellus* Crotch including *Pronoterus* Sharp **syn. nov.** and an additional undescribed noterid genus.

***Suphis* Aubé and *Canthysellus* Baca & Toledo.** Here we find the genera *Suphis* and *Canthysellus,* a new genus here described (CH. 3) to be monophyletic (Figs 2.1 2.3). What little is known of their ecology presents a less distinct evolutionary pattern. Dettner (2005) suggested that *Suphis* prefers ponds and marshes. This is supported by personal observations. *Canthysellus* on the other hand can be found in a variety of aquatic habitats, but seems to prefer forested areas. It is difficult to draw implications of the evolution of these ecologies. As for biogeography, the clade is almost entirely Neotropical, with only a single species of *Suphis* occurring in the southeastern United States.

It was speculated that *Canthysellus* was closely related to the genera *Canthydrus*, *Suphis* and *Suphisellus.* This followed the results of Miller (2009), who recovered the same

monophyletic relationship of these three genera (not including *Pronoterus*), but with a different combination of relationships: *Canthysellus* and *Suphisellus* were recovered as monophyletic, with *Suphis* as their sister. This is not surprising considering *Canthysellus* and *Suphisellus* share several characters such as serrate posterior metatibial spurs, series of stiff setae on the prosternum, and setal fringe of the protibia. Several of these characters are lost in *Suphis.* Our analysis finds *Canthysellus* and *Suphis* monophyletic (pp = 1.0; bs = 93; pbs = 85). Morphological support for this relationship is found in the similarity of the female genitalia, both presenting with very long and narrow laterotergites, and gonocoxae with only a single anterior apodeme, rather than two as seen in many other genera of the Suphisini. Both genera are also rather convex, especially *Suphis*. Many other characters that these genera share are either plesiomorphic or homoplasious. The morphology of *Suphis* is a very highly derived and this genus has secondarily lost many characters shared by the Suphisini, making it difficult to assess morphologically.

A new genus of Noteridae. In the course of selecting taxa for our sampling, we noticed a peculiar species that initially identified as an aberrant member of *Suphisellus*, and given the morphospecies label “sp. 8”. This species is very small, ca. 1.5 – 2.0 mm and convex, superficially appearing very similar to members of the genus *Canthysellus* (Figs. 3.1–3.3), but has an almost indistinct crease on the pronotum and very narrow pronotal bead, as in *Suphisellus*. Given the morphological disparity from other known members of *Suphisellus* and the great amount of genetic distance recovered in our results, this species is here considered to belong to another genus of suphisine noterid, and will be described separately, pending further examination of morphology.

***Suphisellus* Crotch.** Our results recovered the monogeneric Pronoterini Nilsson, 2005 nested within *Suphisellus* Crotch (1.0/100/99). Even prior to this discovery, *Suphisellus* was known to be very diverse and in need of revision (Miller, 2009). Currently, very little is known of the specific life histories or ecology of this genus, but most species seem to share the general noterid preference for vegetative ponds and marshes (personal observation). Its members can be especially abundant in the Neotropics, but several species have ranges extending into the Nearctic.

The placement of *Pronoterus* Sharp within *Suphisellus* is a significant change from the current classification. All prior phylogenetic studies found *Pronoterus* to occupy a much farther removed position, with Pronoterini sister to Noterini (Figs 1.2, 1.3). *Suphisellus* is a particularly large and diverse genus that was united by a synapomorphic crease at the posterior lateral angle of the pronotum (see Fig. 7 in Miller, 2009). Pronoterus lacks this crease, and many other synapomorphies of the Suphisini, specifically those of the protibia and prosternal process (Miller, 2009). Generally less robust and parallel sided, *Pronoterus* would appear to be more closely related to *Mesonoterus* and *Prionohydrus* as previously thought (e.g. Miller 2009). However there are several characters that unite *Pronoterus* with *Suphisellus* and other derived genera of the Noterini that were thought to be homoplasious (Miller, 2009; Gomez & Miller, 2013). The most distinct of these is the pygidium modified with a distinct retractable claw (Fig. 8 in Miller, 2009). This is a feature shared by all other members of the Suphisini with varying degrees of development. Some members of *Suphisellus*, such as *S. nigrinus* (Aube, 1838) and similar species, found here to form a monophyletic group of species with variable support (99/36/-), lack this feature entirely, apparently due to secondary loss. The *Suphisellus subsignatus* (Sharp, 1882) species group (1.0/97/92) retains a reduced form of this claw, and as

our ML results show, *Pronoterus* is found sister to this species group, but with weak support (-/24/-). An additional feature that supports this relationship is the bifurcate apex of the ventral sclerite of the genital capsule, found in both *Pronoterus* and the *S. subsignatus* group, but not in other members of *Suphisellus* or *Canthysellus* (that of *Suphis* is notched, but not nearly bifurcate as in *Pronoterus* and members of *Suphisellus*). It appears that characters of the genital capsule, and the male genitalia in general, have been overlooked or omitted in past analyses, but further examination is needed to evaluate their usefulness for phylogenetic inference, especially at deeper nodes. Other characters that unite *Pronoterus* with this larger clade of *Suphis*, *Canthysellus*, and *Suphisellus* include the series of stiff setae on the prosternum, serrate metatibial spur, and very long laterotergites of the female genitalia. In *Pronoterus* and *Suphisellus* the bases of the laterotergites are also very broadly expanded.

Hydrocanthini Sharp 1882

Hydrocanthini was erected by Sharp (1882), to hold the genera *Hydrocanthus* Say and *Canthydrus* Sharp. Here the tribe is resurrected to again contain *Hydrocanthus* and *Canthydrus*, but also *Sternocanthus* Guignot **stat. rev.**, *Mesonoterus* Sharp and *Prionohydrus* Miller and Gomez.

***Canthydrus* Sharp.** This genus is diverse and needs systematic attention, but is still better documented than some other genera such as *Suphisellus*. The specific ecologies of this genus are poorly documented, but collecting data and personal observation indicates a general preference for vegetative ponds. The placement of *Canthydrus* Sharp as sister to *Hydrocanthus* Say (0.97/ 53) is similar to Miller (2009). Some prior analyses found it sister to *Suphisellus* or unresolved (Belkaceme, 1991; Beutel *et al.*, 2006; 2008; Dressler *et al.*, 2011; Fig. 1.2). Other

than the characters that unite broadly the genera of the Suphisini and Hydrocanthini, this grouping of *Canthydrus* sister to *Hydrocanthus* finds weak morphological support, united only by the synapomorphy of a distinctly serrate lateral pronotal margin (Miller, 2009). Personal observation has shown that this serrate appearance is caused by the margins being lined with several very small, but stout setae. Similar setae have been observed in other genera, e.g. *Liocanthydrus* and *Canthysellus,* but they are nearly indistinct and much sparser than in *Canthydrus* or *Hydrocanthus*. These setae are particularly minute, and further investigation, possibly incorporating Scanning Electron Microscopy, would be needed to assess their structure and reliability of as phylogenetically informative.

***Sternocanthus* Guignot, *Hydrocanthus* Say, *Mesonoterus* Sharp *and Prionohydrus* Gomez & Miller.** Of all relationships recovered by our analyses, perhaps the most surprising was the recovery of *Hydrocanthus sensu lato* as paraphyletic. The Old World *Sternocanthus* Guignot and New World *Hydrocanthus* Say are here decisively resolved as distinct monophyletic clades (1.0/100/-), with *Mesonoterus* and *Prionohydrus* recovered as monophyletic sister to *Hydrocanthus* (1.0/100/-). Our current understanding of morphology poorly supports these relationships. Biogeography is one of the few correlates that do support our results as the genera *Prionohydrus*, *Mesonoterus* and *Hydrocanthus* all have their geographic ranges restricted to the New World, while their sister *Sternocanthus* is widespread throughout Africa and also occurs in parts of Australia and the Oriental geographic region.

Despite the lack of morphological differences within the genus (Miller, 2009), the splitting of *Hydrocanthus sensu lato* into Old World and New World clades follows some previous work such as that by Guignot (1948) who erected the subgenus *Sternocanthus* to contain all Old World species (Miller, 2009; Nilsson 2011). The nesting of *Mesonoterus* and

Prionohydrus was unforeseen as there are no obvious morphological characters that unite these genera with *Hydrocanthus* other than those that placed them within the Noterini (e.g. protibial modifications). One potential character that does draw some attention is the serrate posterior metatibial spur shared by *Sternocanthus, Hydrocanthus* and *Prionohydrus,* but not *Mesonoterus,* which have the spurs smooth (also in *Canthydrus*). *Mesonoterus* and *Prionohydrus* also lack any serration or setae on the lateral margins of the pronotum.

Morphology and Phylogenetic Signal.

The lack of corroboration between morphological and molecular data is likely a multifactorial issue. Noteridae is a very homogeneous family, and it is difficult to find distinct morphological characters that provide reliable phylogenetic signal. As a result, previous analyses were left with a limited amount of characters to work with and even then, it seems that the informative quality attributed to these characters was possibly misplaced. As we discussed, there are characters that provide signal that corroborates our results, and it is possible that some of these have been overlooked in previous studies. However, it is intriguing that some of the specialized structures classically used to classify Noterinae do not appear to be as informative as once thought. This could be because these characters have close ties to the ecology of the group and are thereby subject to selective pressures. A case of this could be the specialized structures of the protibia. If these structures are in fact important for an interaction with the substrate (Roughly & Larson 2001; Dettner, 2005), then one might expect that evolving into different ecological roles might drive the evolution of this structure to homoplasious forms via secondary loss. This is a naïve suggestion of course, but it does offer a potential explanation.

Another reason for the lack of corroboration could be due to errors in coding. For example, it is possible that some of these characters are linked and should not be coded as independent in a morphological matrix. Some characters of the proleg, such as the protarsal furrow and pit were excluded by Miller (2009) because of the strong correlation to the presence of the robust protibial spur. Another example could be the location of the attachment of the protarsus. The lateral attached state of this character seems to occur only in taxa with a robust protibial spur. It is possible that the lateral attachment occurs as a result of the expanded size of this spur, which leaves little room for an apical attachment. In this vein, previous analyses based on morphology, relied on character concepts from previous work (e.g. Belkaceme, 1991; see Miller, 2009). A reassessment of the structural homology of these characters with respect to modifications and transformation series (e.g. in the setae and spurs of the protibia), could result in codings that provide better phylogenetic signal.

Both morphological and molecular data present some interesting cases of homoplasy. While some speculation can be offered here, it is difficult to know the processes of evolution that produced these structures, especially when so little is yet known of correlated ecological data and what function these structures serve. If any conclusion could be drawn here, it is that homoplasies will be present by any phylogenetic reconstruction. This suggests that there is a strong need for the discovery of new informative morphological characters and also for the reassessment of the morphology historically used to classify Noteridae.

Biogeography

The trees recovered by the analyses reveal an interesting pattern with respect to biogeography. As can be seen in several of the recovered clades, there is a repeating pattern of a

derived New World clade from an Old World ancestor. This is true for *Notomicrus*, a primarily New World genus with the Old World *Phreatodytes* and *Notomicrus tenellus* (Clark, 1863) recovered as its sisters; for *Liocanthydrus* + *Tonerus*, both New World genera with the Old World genus *Synchortus* as their sister; Suphisini + Hydrocanthini, a largely New World clade with the Old World Renotini as its sister; and within the Hydrocanthini, with , *Hydrocanthus*, *Mesonoterus* + *Prionohydrus* a New World clade with the Old World genera *Sternocanthus* and *Canthydrus* as its sisters. Though the implications of this will not be explored in detail here, the pattern obtained by our analyses suggests that Noteridae would be an excellent candidate for a biogeographical analysis. It would be interesting to see what patterns would emerge beyond showing that several of these monophyletic clades exist in the same biogeographical regions.

Conclusions

Our analyses successfully recovered a resolved and highly supported phylogenetic estimate for the family Noteridae. There is still much left to investigate however. Even with our analyses finding strong resolution for relationships within Noteridae, there is an immediate necessity to conduct an investigation of morphology. First, illuminating the cause for the lack of consensus between the phylogenetic signals of morphological and molecular data is needed for a more complete understanding the evolution of the family; not to mention the great need for finding synapomorphies that allow for the diagnoses of the clades recovered by our analyses. Care must be taken to avoid too strong of a biased approach to the future investigation of morphology, but with the strong support here recovered from DNA sequence data, and uncertainty in the analyses based on morphology, our results may shine new light on prior concepts and help us discover new informative characters.

Our recovered phylogeny thus provides the basis for future work. Besides further systematic studies, perhaps taking the form of total evidence analyses incorporating both morphological and molecular data, our results indicate intriguing biogeographical and ecological patterns. Indeed, our phylogeny and supporting data grant us new tools to evaluate past work, and also take the study of Noteridae into new realms of investigation.

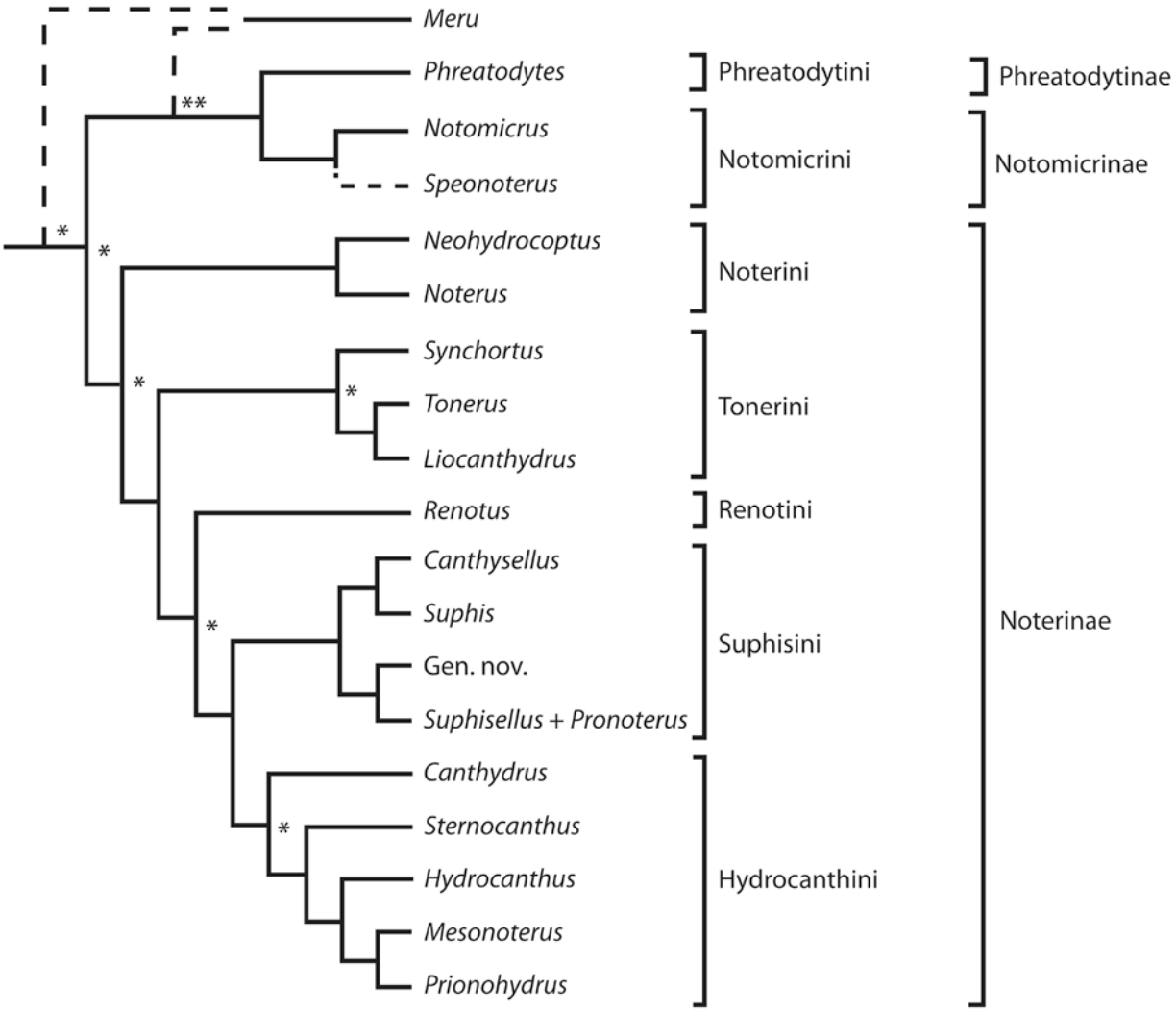


Figure 2.1. Summarized phylogeny of Noteridae combining BI and ML analysis of five genes with resulting relationships and classification depicted. Dashed lines indicate incongruent results or missing taxa. Asterisks indicate nodes for which one (*) or both (**) BI and ML analyses recovered insignificant support (pp < 0.95/ bs < 70)

Figure 2.2. Tree resulting from Bayesian analysis with 30 million generations and 25% burn-in. Values indicate Bayesian posterior probabilities.

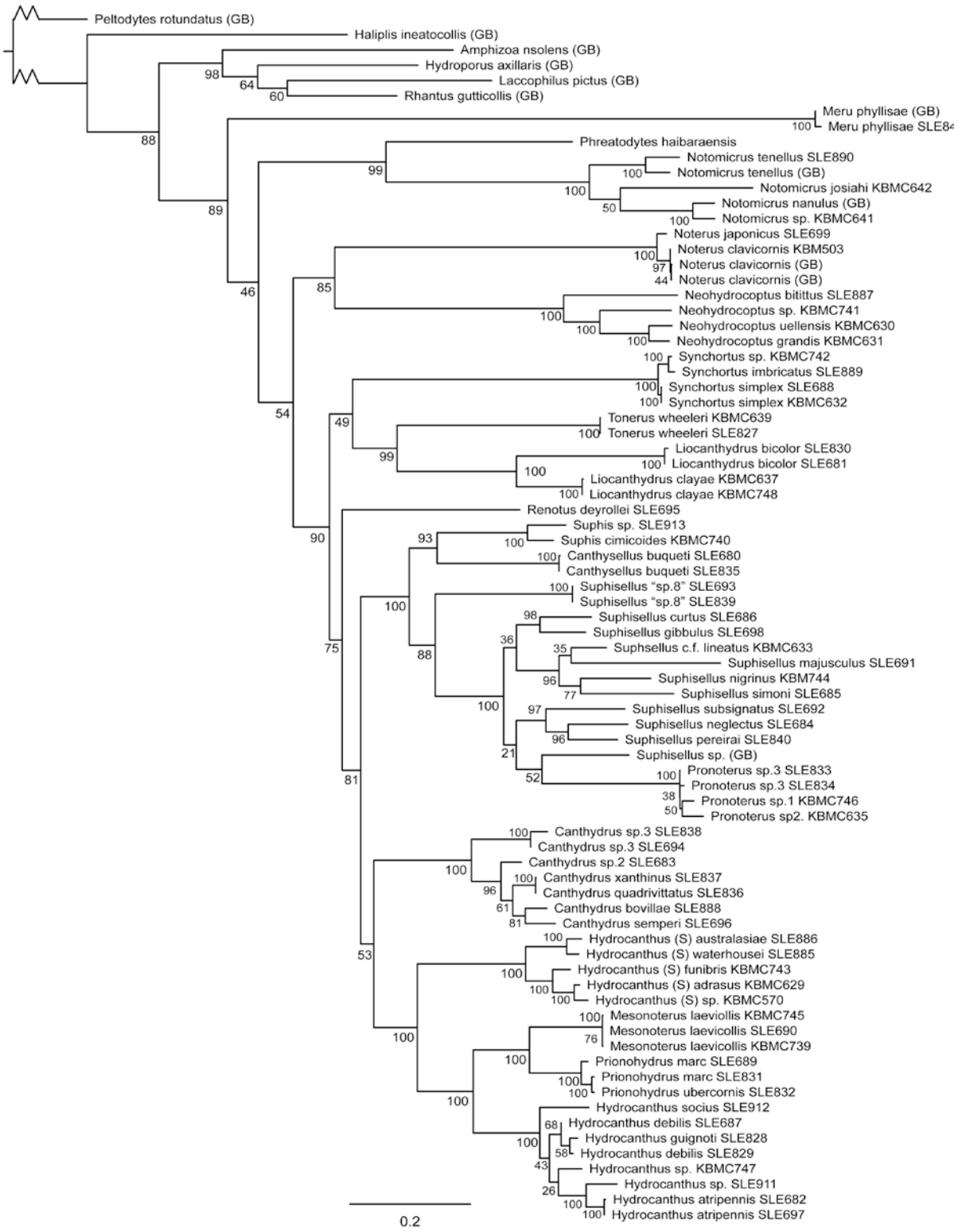


Figure 2.3. Tree resulting from Maximum Likelihood analysis with 500 bootstrap replicates. Values indicate recovered bootstrap support.

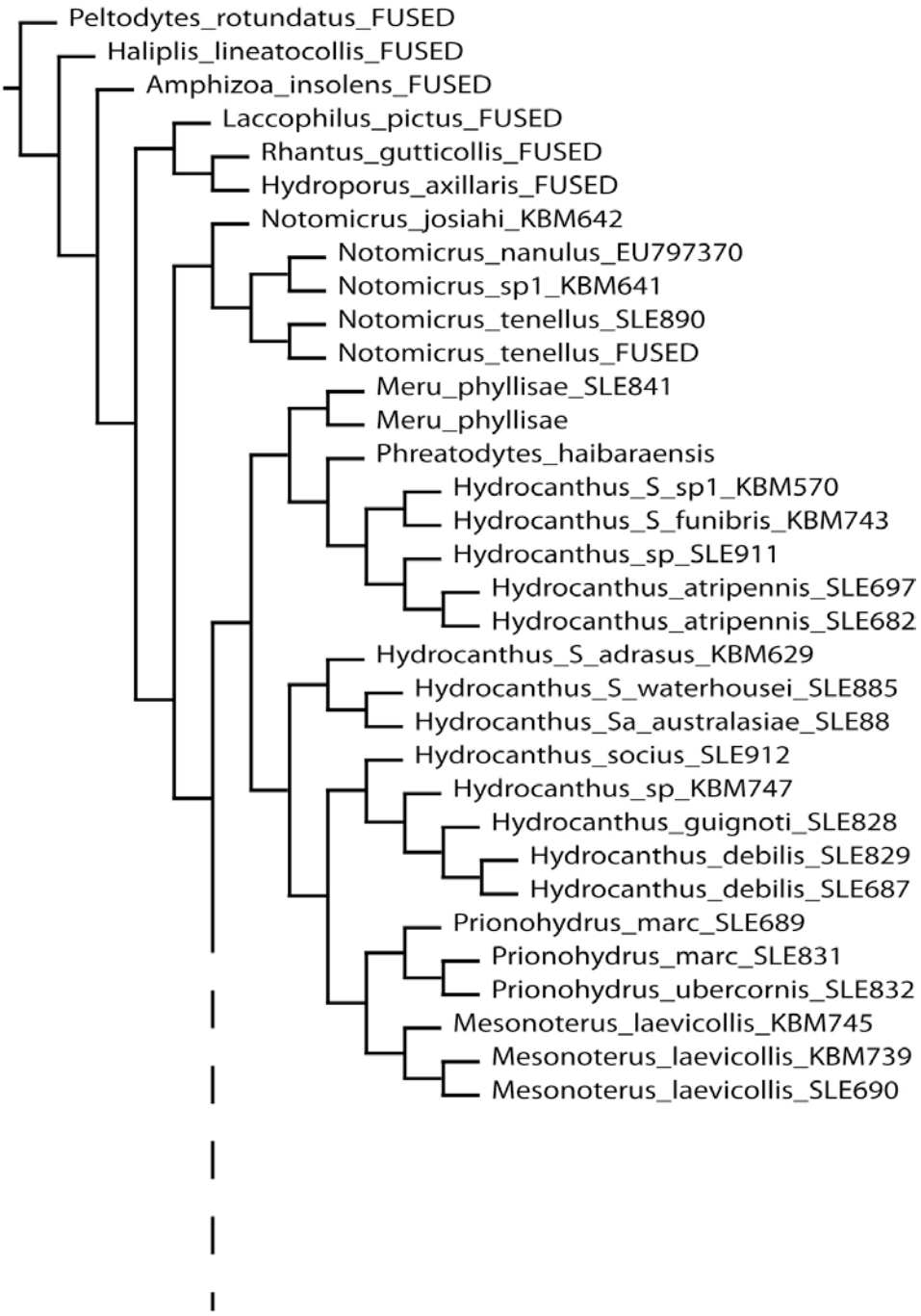


Figure 2.4. Part 1 of most parsimonious tree recovered by NTS driven search with 10 initially added sequences in TNT. Length = 13868.

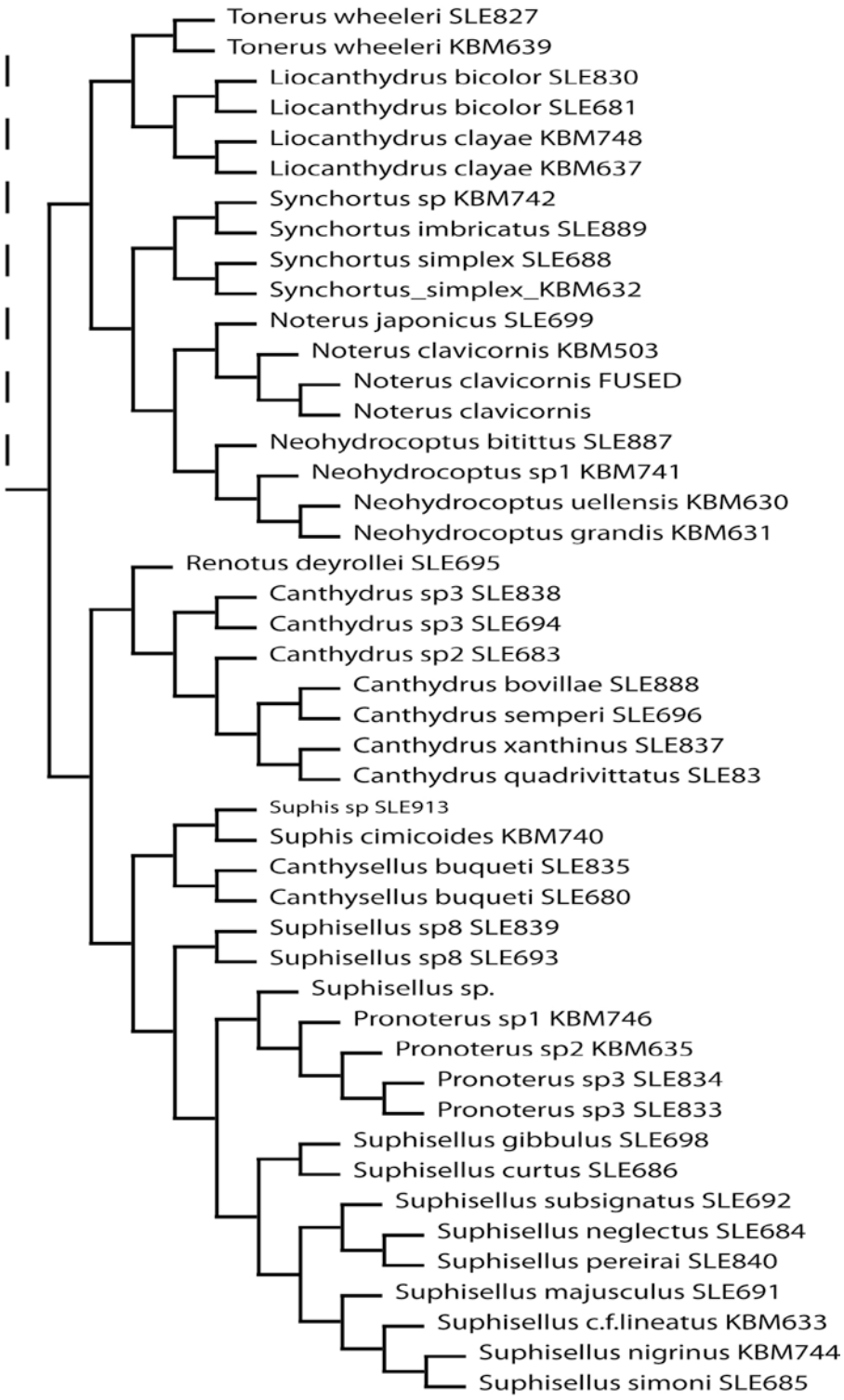


Figure 2.5. Part 2 of most parsimonious tree recovered by NTS driven search with 10 initially added sequences in TNT. Length = 13868

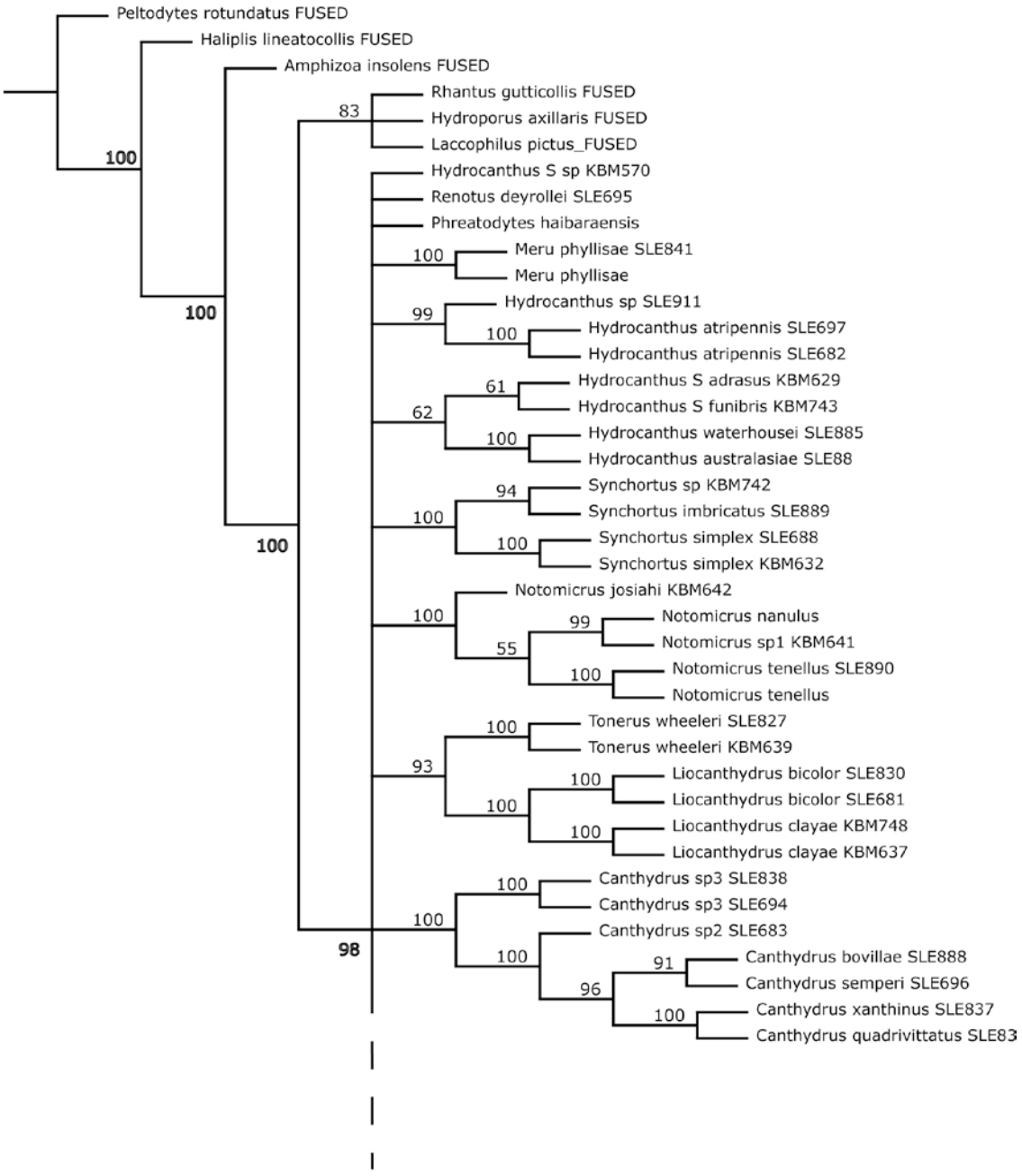


Figure 2.6. Part 1 of most parsimonious tree resampled for 500 bootstrap replicates. Values indicate recovered bootstrap support (pbs). Nodes with pbs < 50 are collapsed.

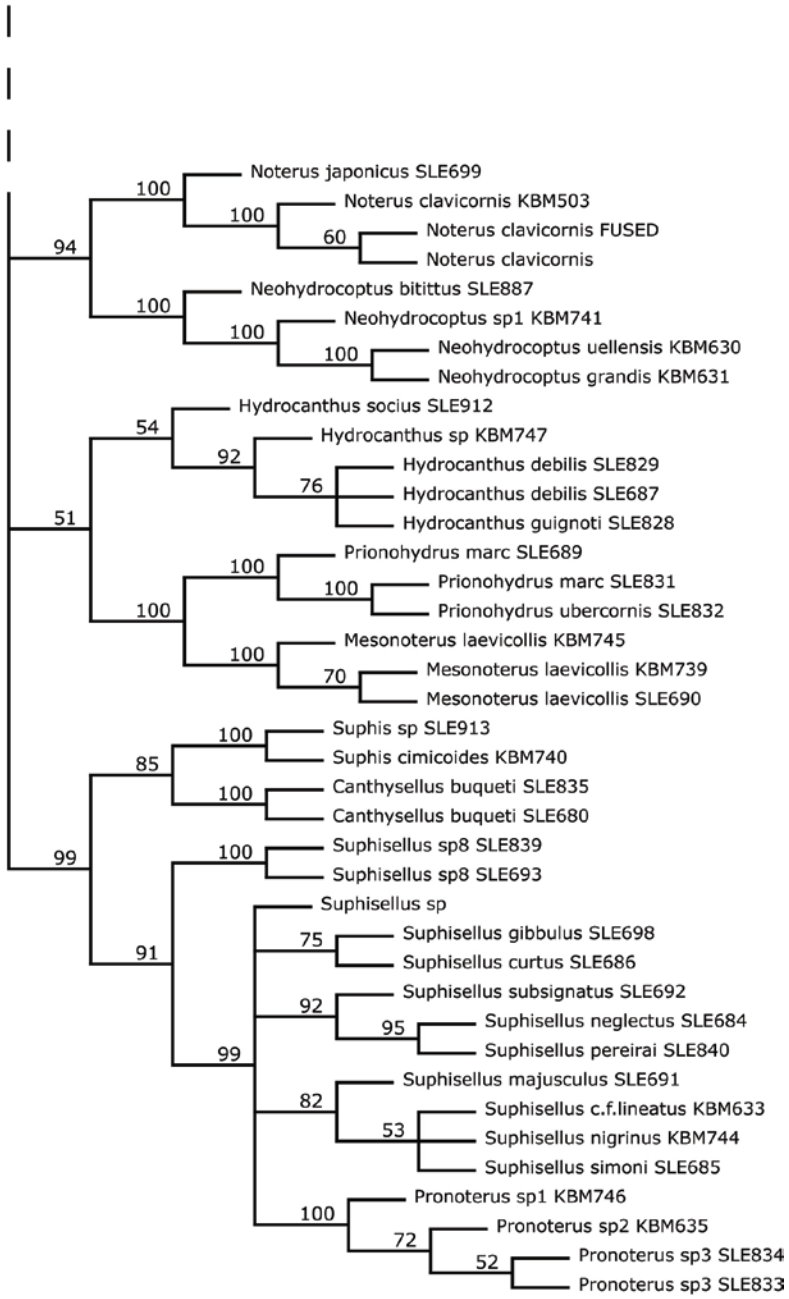


Figure 2.7. Part 2 of most parsimonious tree resampled for 500 bootstrap replicates. Values indicate recovered bootstrap support (pbs). Nodes with pbs < 50 are collapsed.

Table 2.1. List of primers used in PCR reactions

Gene	Forward Primer	Reverse Primer
COI	Jerry, CAACAYTTATTTTGATTTTTTGG	Pat ATCCATTACATATAATCTGCCATA
H3	H3aF ATGGCTCGTACCAAGCAGACAGCGC	H3aR ATATCCTTAGGGCATAGAT(AG)GTGAC
16S	LR-N-13398 CGCCTGTTTAACAAAAACA	LR-J-12887, CCGGTCTGAACTCAGATCACGT
18S 5' end	18S5'I, GACAACCTGGTTGATCCTGCCAGT	18Sb0.5, TAACCGCAACAACTTTAAT
18S 3' end	18S3'I, CACCTACGGAAACCTTGTTACGAC	18Sa1.0, GGTGAAATTCTTGGACCGTC
28S	NLF184-21, ACCCGCTGAAYTTAAGCATAT	LS1041R, TACGGACRTCCATCAGGGTTTCCCCTGACTTC

CHAPTER 3

CANTHYSELLUS, A NEW GENUS OF BURROWING WATER BEETLE FROM SOUTH AMERICA (COLEOPTERA: NOTERIDAE: SUPHISINI)

INTRODUCTION

With the redefinition and redescription of *Liocanthydrus* Guignot (Baca *et al*., 2014), it became clear that *Noterus buqueti* Laporte, 1835, a species formally inserted in *Liocanthydrus* does not fit any generic definitions within Noteridae, necessitating the erection of a new genus to retain the monophyletic integrity of existing genera. This is supported by the phylogenetic analysis of Miller (2009), in which a congener of *N. buqueti* was treated at the genus rank, though under the mistaken identity of *Liocanthydrus* (see Baca *et al.,* 2014; and 'Taxonomic History' below).

Here, the genus *Canthysellus*, **new genus**, (Coleoptera: Noteridae: Noterinae) is erected and described to accommodate *Canthysellus buqueti* (Laporte, 1835), **new combination**, here redescribed, plus two new species recently found in the course of the revision of *Liocanthydrus* Guignot (Baca *et al*., 2014) and this current study: *Canthysellus sipaliwini*, **new species**, (Suriname) and *Canthysellus peruanus*, **new species**, (Peru) here described.

Taxonomic History. *Noterus buqueti* Laporte, 1835 was among the earliest described New World species of Noteridae. As the understanding of noterid diversity grew, successive authors transferred *Noterus buqueti* into more suitable genera. Aubé (1838) moved *N. buqueti* to *Hydrocanthus* Say based on the broad and truncate prosternal process and broad labial palps (these are not characteristic of the genus *Noterus* Clairville, which has a narrow and non-truncate

prosternal process and narrower and distinctly bifid labial palps). Later, Sharp (1882) erected the genus *Canthydrus,* characterized by a less broad prosternal process and more slender hind legs than *Hydrocanthus* and transferred *N. buqueti* to it. Guignot (1957) subsequently erected the subgenus *Canthydrus* (*Liocanthydrus*) to which he transferred *N. buqueti*. He characterized *Liocanthydrus* as having an elongate body form, smooth and impunctate dorsal surface and a broad and glabrous prosternal process and noterid platform. Strangely, with a convex and non-elongate body form, and distinctly non-glabrous noterid platform and prosternal process, *N. buqueti* does not actually share many of these character states. Miller (2009) elevated *Liocanthydrus* from subgenus to genus status based on the morphological analysis in his systematic treatment of Noteridae. Finally, Baca *et al.* (2014) placed *N. buqueti incertae sedis* after it was discovered that *N. buqueti* and the species used by Miller (2009; this species is described here as *Canthysellus peruanus*) as a basis to elevate *Liocanthydrus* to genus were not actually congeners of the type species of *Liocanthydrus*, to which the genus *Siolius* Balfoure-Browne was a junior synonym. (Gomez & Miller, 2013; Baca *et al*., 2014).

MATERIAL AND METHODS

Material Examined. 267 specimens of *Canthysellus* were examined for this study, including the only known syntype of *Noterus buqueti* Laporte, 1935. Specifics of the material examined can be found with the species descriptions below. This material is deposited at the following institutions:

CBDC Center for Biological Diversity, University of Guyana, Georgetown, Guyana

MIZA	Museo del Instituto de Zoologia Agricola, Maracay, Venezuela (L.J. Joly)
MNHN	Museum National d'Histoire Naturelle, Paris, France (T. Deuve)
MSBA	Museum of Southwestern Biology Division of Arthropods, University of New Mexico (K.B. Miller)
NHMW	Naturhistorisches Museum Wien, Austria (H.V. Shaverdo)
NZCS	National Zoological Collection of Suriname (P. Ouboter)
SEMC	The Snow Entomological Collection, University of Kansas (A.E.Z. Short)

Specimen Preparation. Specimens of *Canthysellus buqueti* and *C. peruanus* were cleared for examination and illustration. No specimens of *C. sipaliwini* were cleared. Specimens were relaxed in hot water for ca. 10 minutes, cleared in unheated KOH solution for 24–36 hours, thoroughly rinsed with deionized water and placed in glycerin for examination. The aedeagi for all species and the female genitalia of *C. buqueti* were prepared following Miller (2001), except female genitalia were allowed to clear in unheated KOH overnight (ca. 14 hours) to prevent accidental damage from the hot KOH method. Male and female genitalia were also thoroughly rinsed in deionized water to neutralize the reaction rather than acetic acid.

Images and Illustrations. Digital photographs were taken using a Visionary Digital micro-photographic system equipped with an Infinity K2 microscope, CF4 and 5 × objectives, and Helicon Focus imaging software. Raw photos were aligned and stacked using CombineZP (www.hadleyweb.pwp.blueyonder.co.uk) and prepared using Adobe Photoshop. Illustrations were made by tracing digital photographs of cleared structures in Adobe Illustrator.

Type labels. The labels of type material are transcribed verbatim in the following manner: the transcription of each individual label is denoted by quotations (“ ”); individual lines

of each label are separated by a backslash (/); and finally, each label is followed by a respective physical description (e.g. color, handwritten or printed, etc.) which is denoted by brackets ([ ]).

Measurements. Measurements were made with a calibrated ocular micrometer on an Olympus SZX7 Zoom stereomicroscope. Measurements were taken for all specimens of *C. peruanus* and *C. sipaliwini*. For *C. buqueti*, the largest and smallest representatives from both sexes were measured along with 10 males and 10 females chosen at random. Measurements include: length (L), measured from anterior margin of pronotum to elytral apices as head orientation can affect the total length measurement, making it less useful for comparisons between species; total length (TL), measured from head to elytral apices; greatest width (GW); width of head (HW), measured at the posterior margin of the eyes; shortest distance between the eyes (EW), greatest width of lateral pronotal bead, (PntB); and width of Antennomere VII (AntVII). Measurements are also presented as ratios (L/GW, HW/EW, PntB/AntVII) to provide relative sizes.

Terminology. The use of terms pertaining to morphology follows previous authors (Young 1979; 1985; Beutel and Roughley 1987; Belkaceme 1991; Miller 2001; 2009; Miller and Nilsson 2003). **Noterid platform:** The ‘noterid platform’ is a synapomorphy of Noteridae, referring to the raised projection of the thorax comprised of the inner lamellae of the metacoxae and anteromedial portion of the metaventrite (Figs3.4,3.5). **Genitalia:** The genitalia of Noteridae are rotated from their homologous positions as in Dytiscidae. They have been described here following Miller and Nilsson (2003) with respect to their fundamental positions rather than their rotated state. Female genitalia is described following Miller (2001; 2009**). Abdominal ventrites:** Abdominal ventrites are described following Belkaceme (1991) which recognizes that abdominal

ventrite I is hidden from view by the metathorax. Here the first visible abdominal ventrite is would be described as ventrite II.

Structures of Taxonomic Importance. Prosternal setae: Members of *Canthysellus* have a small transverse line or tuft of setae medially on the prosternal disc (Figs.3.4a, b, 3.5a). The number and spacing of setae vary between species and are valuable for distinguishing species. The lateral length of the line of setae is described relative to the lateral margins of the narrowest portion of the prosternal process, where it meets the prosternal disc basally. For example, the line of setae of *C. peruanus* does not extend laterally beyond the lateral margins of the prosternal process at this point, whereas that of *Canthysellus buqueti* does. **Inner margin of metatibia and metatarsomere I:** The setae of the inner margin of the metatibia and first metatarsomere differ greatly between some species of *Canthysellus*. The setae occur as either an evenly spaced row of ca. 10 stiff setae (Fig. 3.6a), as in *C. buqueti*, or as a dense line or strip of slender, hair-like setae (Fig. 3.7a), as in *C. peruanus*. This can be a very useful external character for distinguishing species of *Canthysellus*. **Size:** Though there is some intraspecific variation, species of *Canthysellus* show distinct interspecific differences in the ranges of size. This is an especially valuable external character for distinguishing between *C. buqueti* and *C. sipaliwini*, which are otherwise very similar. Measurements for length (L) and greatest width (GW) are provided. Length is measured from anterior margin of the pronotum to the apices of the elytra to prevent measurements from being distorted by the orientation of the head. **Pronotal bead:** The relative width of the lateral pronotal bead was observed to vary between species. The relative width is presented as a ratio of the greatest width of the pronotal bead and the greatest width of antennomere VII (PntB/AntVII), the first of the expanded antennomeres. The width of antennomere VII was chosen for comparisons because it is appropriately sized, easily accessible,

and the width was very consistent throughout the genus. **Aedeagus:** Observed interspecific differences in the aedeagus include the shape and size the median and lateral lobes, in various aspects, and the orientation and length of the setae of the left lateral lobe. Aedeagi are described according to their fundamental positions following Miller and Nilsson (2003). Illustrations depict various aspects of the median lobe and the inner (medial) surfaces of the lateral lobes. This is done to better communicate diagnostic shapes and structures. The aedeagus provides the most definitive characters for diagnosing species of *Canthysellus*.

DISCUSSION

The erection of *Canthsellus* is here justified by distinguishing morphological features, and phylogenetic analysis. The treatment of *Canthysellus* as a distinct genus of the subfamily Noterinae is supported by the phylogenetic analysis of Miller (2009) and the subsequent analysis of Gomez & Miller (2013) We also find support for this grouping through our analysis of DNA sequence data, further more we find *Canthysellus* to be a member of the tribe Suphisini and also molecular data.

The relationship recovered by the molecular analysis is supported by the morphological features that unite the genera *Canthydrus, Canthysellus, Suphis,* and *Suphisellus,* with *Pronoterus* being a bit odd in that respect. *Canthysellus* being sister to *Suphis* is somewhat surprising as the former shares more diagnostic characters with *Suphisellus* such as the fringe of setae of the protibia, series of stiff prosternal setae, and serrate posterior spur of the metatibia (some of these plesiomorphic for the clade). However, *Suphis* appears to have many characters highly modified, and does not share in many diagnostic characters of any related genera. There is

some superficial resemblance between *Canthysellus* and *Suphis* as members of both genera are very convex (more so in *Suphis*), and the female genitalia are also similar, with the gonocoxosternites bearing only a single apodeme and the laterotergites lacking the broad anterior expansion found in other related genera.

The species here described are also supported by morphological evidence. The species *Canthysellus peruanus* is clearly distinct from other species as evidenced by the setae of the metatibia and metarsus I and also the aedeagus. *Canthysellus buqueti* and *c. sipaliwini* are more similar. At first, the variation presented by these two species was assumed to be intraspecific, with some specimens larger and presenting differences in aedeagus morphology. However, as more specimens were examined it became apparent the variation was bimodal and lacking intermediates. Differences of the aedeagus were specific to the smaller and larger sized groups of specimens respectively. With this finding contesting the assumption of intraspecific variation, it was decided that these two variations should be described as distinct species.

TAXONOMY

Canthysellus Baca and Toledo, new genus

Type Species. *Noterus buqueti* Laporte, 1834, here designated.

Diagnosis. *Canthysellus* is distinguished from other genera of Noterinae by the following combination of characters: (1) prosternal process broad (Figs.3.4, 3.5); (2) prosternal disc with a

short, closely-spaced, linear series of stout setae anterior to procoxal cavities (Figs. 3.4a, b, 3.5a); (3) lateral bead of pronotum distinct, broad; (4) posterior metatibial spur serrate (Fig. 3.6b).

Comparative Diagnosis. In certain ways *Canthysellus* is very similar to the genera *Canthydrus* Sharp and *Suphisellus* Crotch. *Canthysellus* superficially resembles many members of *Canthydrus* in body shape, however the serrate posterior metatibial spur and isolated tuft of setae on the prosternum distinguishes *Canthysellus* from *Canthydrus*. *Canthysellus* shares more diagnostic characters with *Suphisellus*, including the distinct linear series of stiff setae on the prosternum and a serrate posterior metatibial spur. However, *Canthysellus* lacks the key synapomorphy of *Suphisellus*: the lateral crease, or interrupted bead, subtending the lateral margins of the pronotum. Following Miller's (2009) survey of female genitalia, the female genitalia of *Canthysellus*, with long laterotergites, non-dentate gonacoxae and pointed gonacoxasternites, are similar to that of both *Suphisellus* and *Canthydrus*. However, the laterotergites of *Canthysellus* are much more slender and each gonacoxasternite is with only one elongate apodeme rather than two, similar to the genitalia of the genus *Suphis* Aubé and *Pronoterus* Sharp. *Canthysellus* does not otherwise share in many diagnostic characters with *Suphis* or *Pronoterus* and in comparison these are clearly distinct genera (see Miller 2009). **Note:** Miller (2009: 208) mistakenly diagnoses *Canthysellus* (though as *Liocanthydrus*) as having a non-serrate [posterior] metatibial spur, though an examination of his character matrix shows that this spur was correctly coded as serrate in the phylogenetic analysis.

Description. Medium sized beetles, TL= 2.65–3.50 mm; body form convex, robust, broadly attenuate posteriorly. **Color and Appearance**: Shiny, elytra superficially iridescent. Color of head and pronotum ranging from yellow to reddish brown; color of elytra dark reddish brown to nearly black, with elytral maculae appearing as interrupted transverse bands or spots,

color similar to head and pronotum, but often slightly lighter. Color of venter yellowish brown to reddish brown with noterid platform and sutures darkened. **Head:** Eyes well developed. Antennae with 11 antennomeres, length ca. ¾ × head width, antennomeres XII–X expanded, subserrate, each with sensory field extending ca. half-length of antennomere to anterodistal angle; antennomere XI length ca. 1.5 × length of antennomere X, attenuate, with sensory field extending ca. half-length to apex. Apical maxillary palpomeres nearly fusiform, with apices slightly bifid and with small sensory field. Microsculpture fine, consisting of small isodiametric cells and evenly spaced micropunctures. **Thorax:** Pronotum glabrous, anterior margin subtended by series of punctures producing sparse, slender setae; lateral margins and pronotal bead with sparse setose punctation. Lateral pronotal bead broad, ceasing at anterolateral angles, attenuate posteriorly. Elytra glabrous, with series of fine punctures extending laterally at elytral base and three longitudinal series of fine sporadic punctures, one medial, one discal and one lateral, submarginal; medial series more distinct than others; punctures more sporadic in distal half of elytra, many punctures bearing very fine setae of varying length, especially along lateral margins and in distal half of elytra; elytra and pronotum with fine reticulate microsculpture. Prosternum narrow, glabrous, with tuft of short, longitudinal series of stiff setae on prosternal disc, anterior to procoxae and prosternal process (Figs. 3.4, 3.5). Prosternal process broad, triangular, narrow between procoxae, broad posteriorly, with lateral margins bordered by bead; posterior margin subtruncate, sinuate. Posterior lobes of noterid platform extending posteriorly just beyond first visible abdominal ventrite (ventrite II); lobes rounded at apex, bearing small transverse line of stout setae; surface of noterid platform, and prosternal process setose, setae produced from punctures (Figs. 3.4, 3.5). Protibia with very large spur, strongly curved posteriorly; with fringe of stout setae arising along lateral margin, reduced and discontinuous at apex. Metafemur with

series of closely spaced setae on distal 1/3 of anteroventral margin, ceasing at anteroapical angle (Figs. 3.6, 3.7). Posterior metatibial spur serrate. **Abdomen:** Ventral surface glabrous, with nearly indistinct microsculpture consisting of slender, laterally elongate cells; ventrites III and IV fused, suture indistinct; ventrites IV–VI with sparse, slender setae on lateral margins; ventrites V and VI with sparse line of setae extending medially from lateral margin, line discontinuous, not reaching median. Ventrite VII with several long, slender setae near apex. Pygidium modified with very small spur at apex; spur fused, not articulate. **Males:** Protarsomeres I–III weakly dilated, with three to four distinct adhesive discs, protarsomeres IV and V slender. Mesotarsomeres I and II weakly dilated with three adhesive discs, mesotarsomeres III–V slender. Ventral sclerite of genital capsule bifurcate, lacking setae or setae indistinct at apices. Aedeagus asymmetrical; median lobe dorsally curved, divided ventrally by large groove, left side broad in lateral aspect, composing the greater part of the aedeagus, groove ceasing and sides meeting at or before apex; left lateral lobe broad, attenuate to rounded or weakly lobed apex, with dense tuft of setae produced subapically on inner surface; right lateral lobe broad, subtriangular, but with ventral margin broadly rounded. **Females:** Pro– and mesotarsi not dilated, slender and without adhesive discs. Female genitalia as in Fig. 3.11; laterotergites very long, slender; gonacoxae short, not dentate; gonocoxosternites broad, apically pointed, with a single anterior apodeme.

Biology. Members of *Canthysellus* can be found in a variety of aquatic habitats, including the vegetated margins of forested ponds, detrital pools, streams and morichales. In Fig. 3.13 are depicted two sites in which members of *Canthysellus* were collected.

Distribution. *Canthysellus* is restricted to the Neotropics and is known to occur in Brazil (Amazonas), French Guiana, Guyana, Peru, Suriname, and Venezuela (Fig. 12).

Classification. Following Miller (2009), though under the mistaken identity of *Liocanthydrus* (see Gomez & Miller, 2013, Baca *et al.,* 2014) *Canthysellus* is treated as member of Noterinae ThomsonAs is mentioned above, this genus is morphologically very similar to the genera *Canthydrus* and *Suphisellus*. The morphological analysis conducted by Miller (2009) placed *Canthysellus* (again as *Liocanthydrus*) as sister to *Suphisellus* in a monophyletic group comprised of *Suphis, Canthysellus,* and *Suphisellus,* though with relatively low support. The results of our Molecular analysis find Canthysellus as monophyletic, and sister to the genus Suphis Aubé, together forming a monophyletic clade sister to *Suphisellus* incl. *Pronoterus.* This clade is here found to comprise the resurrected tribe Suphisini Sharp.

Canthysellus buqueti (Laporte, 1835), new combination

(Figs. 3.1, 3.4, 3.6, 3.8, 3.11, 3.12)

Noterus buqueti Laporte, 1835: 105 (orig. descr.); Baca, *et al.,* 2014: 232.

Noterus buquetii Dejean, 1836:63 (nomen nudum, Cayenne).

Hydrocanthus buqueti (Laporte); Aubé 1838: 407.

Canthydrus buqueti (Laporte); Sharp 1882: 272; Branden 1885: 16; Zimmermann 1920: 1920: 10; 1921: 187.

Canthydrus (*Liocanthydrus*) *buqueti* (Laporte); Guignot 1957: 43; Nilsson 2005: 109.

Liocanthydrus buqueti (Laporte); Nilsson 2011: 28; Baca, *et al.,* 2014: 231.

Type Locality. French Guiana (Cayenne).

Type Material. Lectotype (1 female, MHNP), here designated: specimen previously pinned on the right side, then subsequently glued on white card with a female symbol handwritten [with any probability by David Sharp], on which is also glued the right half of lateral metasternal expansion and metacoxal plate with the right metasternal leg articulated ”Noterus buquetii [*sic*!] de Laporte/ h. Cayenne, D. Buquet” [large rectangular green label folded into two parts, handwritten by Laporte] “Noterus buqueti/ de Laporte, h. Cay-/enne, D. Bouquet/ ex mus. Dejean./ Type mihi D.S.” [white rectangular label handwritten by David Sharp] “Ex Musaeo Dejean” [white rectangular label, printed with a thin black frame] “D. Sharp monogr.” [white rectangular label, printed with a thin black frame] “LECTOTYPE/ *Noterus buqueti* Laporte, 1835/ Toledo & Baca des. 2015” [red rectangular label].

Additional Material Examined (243 exs.). VENEZUELA: Bolívar State: Guayaraca, Auyán-Tepui, 1100m, 17.iv.1956, leg. F. Fernandez & C.J. Rosales (1 ex. MIZA); 40°28.233’N, 61°35.559’W, 867 m, Gran Sabana, Paulji: Esmeraldes, 16.vii.2010 , leg. Short, Tellez & Arias, detrital pools by forested stream, VZ10-0716-02A (1 ex. SEMC). **GUYANA: Region IX:** 2°05.095’N, 59°14.174’W, 250 m, Parabara, trail to mines, detrital pools in forest, leg. Short, Isaacs & Salisbury, 2.ix.2013, GY13-1102-01A (1 ex. SEMC); 2°06.311’N, 59°14.072’W, 267 m, Parabara, N side of river, small detrital pool in forest, leg. Short, 3.xi.2013, GY13-1103-01A (1 ex. SEMC); 2°06.492’N, 59°13.653’W, 274 m, small flowing forested creek, detritus margins and leaf packs, leg. Short, Isaacs & Salisbury, 3.xi.2013, GY13-1103-02A (4 exs. CDBC, SEMC). **SURINAME: Sipaliwini District:** 2°10.524’N, 56°47.244’W, 228 m, Camp 1, on Kutari River, leg. Short & Kadosoe, forest stream, 20.viii.2010, SR10-0820-01A, 2010 CI-RAP Survey (85 exs. SEMC); 2°10.521’N, 56°47.244’W, 228 m, on Kutari River, Short & Kadosoe, forested swamp, 19.viii.2010, SR10-0819-01A, Camp 1, 2010 CI-RAP Survey (4 exs. SEMC);

2°10.521’N, 56°47.244’W, 228 m, on Kutari River, Short & Kadosoe, forest stream, SR10-0819-02A (5 exs. SEMC); 2°10.521’N, 56°47.244’W, 228 m, on Kutari River, Short & Kadosoe, forest swamp, 22.viii.2010, SR10-0822-02A (17 exs. SEMC); 2°10.973’N, 56°47.235’W, 210 m, Camp 2, on the Sipaliwini River, leg. Short & Kadosoe, small detrital stream, 28.viii.2010, SR10-0828-03A, 2010 CI-RAP Survey (5 exs. SEMC) 2°10.973’N, 56°47.235’W, 210 m, Camp 2, on the Sipaliwini River, leg. Short & Kadosoe, Inselberg, 29–30.viii.2010, SR10-0829-01A, 2010 CI-RAP Survey (1 male ex. SEMC); 2°10.973’N, 56°47.235’W, 210 m, Camp 2, on the Sipaliwini River, leg. Short & Kadosoe, forest creek, 31.viii.2010, SR10-0831-01A, 2010 CI-RAP Survey (4 exs. SEMC); 02°21.776’N, 56°41.861’W, 237 m, Camp 3, Wehepai, leg. Short & Kadosoe, pooled up detrital creek, 3.ix.2010, SR10-0903-01A, 2010 CI-RAP Survey (3 exs. SEMC); 02°22.259’N, 56°41.277’W, 229 m, Camp 3, Werehpai, SE Kwamala, detrital pools in dense forest, 3-5.ix.2010, leg Short & Kadosoe, SR10-0903-02A, 2010 CI-RAP Survey (16 exs. SEMC), 02°21.776’N, 56°41.861’W, 237 m, Camp 3, Wehepai, leg. Short & Kadosoe, sandy forest creek, 4-6.ix.2010, SR10-0904-01A, 2010 CI-RAP Survey (7 exs. SEMC); 02°21.776’N, 56°41.861’W, 237 m, Camp 3, Wehepai, leg. Short & Kadosoe, small stream, 5.ix.2010, SR10-0905-01A, 2010 CI-RAP Survey (1 ex. SEMC); 2.47700°N, 55.62941°, 275 m, Camp 1, Upper Palumeu, leg. Short, small forest pool, 10.iii.2012, SR12-0310-02A, 2012 CI-RAP Survey (1 ex. SEMC); 2.97731°N, 55.38500°W, 200 m Camp 4 (low), Kasikasima, Sandy stream on trail to METS camp, 20.iii.2012, leg. Short, SR12-0320-02A, 2012 CI-RAP Survey (11 exs. SEMC); 04°42.480’N, 56°13.159’W, 24 m Raleighvallen Nature Reserve, trail to Raleighvallen, creek margins, leg. Short, Mcintosh, & Kadosoe, 27.vii.2012, SR12-0727-03A (1 ex. SEMC); 04°40.910’N, 56°11.138’W, 78 m, Raleighvallen Nature Reserve, Voltzberg trail, margin of stream, leg. C Maier, V. Kadosoe, 30.vii.2012, (5 exs. SEMC); 3°53.600’N, 56°11.300’W, 600

m, CSNR: Tafelberg Summit, nr. Augustus Creek Camp, pond on trail into Arrowhead basin leg. Short & Bloom, 16.viii.2013, SR13-0816-02A (47 exs. SEMC); 04°40.910’N, 56°11.138’W, 78 m, Raleighvallen Nature Reserve, Voltzberg trail, margin of stream, leg. C Maier & V. Kadosoe, 30.vii.2012, SR12-0730-01A (5 exs. SEMC); 3°53.600’N, 56°11.300’W, 600 m, CSNR: Tafelberg Summit, nr. Augustus Creek Camp, pools and creeks on trail into Arrowhead basin, leg. Short & Bloom, 17.viii.2013, SR13-0817-01A (3 exs. SEMC); 3°53.942’ N, 56°10.849, 733 m, CSNR: Tafelberg Summit, nr. Caiman Creek Camp, stream margins, leg. Short & Bloom, 18.viii.2013, SR13-0818-02A (2 exs. SEMC); 3°53.600’N, 56°11.300’W, 600 m, CSNR: Tafelberg Summit, nr. Augustus Creek Camp, detrital pond, train to Arrowhead basin, leg. Short & Bloom, 22.viii.2013 SR13-0822-02A (5 exs. SEMC); **Commewijne District:** 5°45.359’N, 54°44.401’W, 13 m, East-West Hwy, ca. 19 km W. of Moengo, creek crossing rd. leg. Short, Bloom, & Kadosoe, 9.viii.2013, SR13-0809-03A (1 ex. SEMC); **Brokopondo District:** Brokopondo, 05°13’N, 55°30’W, Coesewijne Project, 16.iv.1970, leg. N. Nieser (SN 419) (6 exs. NHMW). **BRAZIL: Amazonas State:** Tucano, 200 m, 1.v.1964, leg. J. & B. Bechyne (1 ex. MIZA).

Diagnosis. *Canthysellus buqueti* is distinguishable from its congeners by the following combination of characters: (a) metatibia as in Fig. 3.6a, with distinctly spaced line of moderately stout setae on inner margin, metatarsomere I with similar row of setae (Fig. 3.6); (b) line of setae on prosternum as in Fig. 3.4a, b, with 5–9 setae, extending laterally to or past anterolateral margins of prosternal process, usually discontinuous, reduced or more widely spaced medially; (c) head only weakly infuscate at base and between eyes; (d) size smaller, 2.40–2.95mm; (f) Aedeagus as in Fig. 3.8a–e; median lobe expanded ventrally and attenuated to acute apex in

lateral aspect (Fig. 3.8a, c); left lateral lobe with dense tuft of setae produced subapically from shallow impression on inner surface; setae distinctly extending beyond dorsal margin (Fig. 3.8d).

Comparative Diagnosis. *Canthysellus buqueti* is very similar to *C sipaliwini* sp. n. Externally it is most easily distinguished by its smaller size, and head being only weakly infuscate or darkened at base and between the eyes (Fig. 3.1). *Canthysellus sipaliwini* is larger, with the area between the eyes and base of the head capsule distinctly darkened, nearly black (Fig. 3.2). The aedeagi of these two species are also similar (Figs. 3.8a–c, 3.9a–c), but the median lobe of *C. buqueti* is apically less slender and not elongated at apex. The left lateral lobe of *C. buqueti* (Fig. 3.8d) is also not as broad as that of *C. sipaliwini* (Fig. 3.9d), and has setae that extend well beyond the dorsal margin. The left lateral lobes of these two species are the most easily distinguishable characters of the aedeagi.

Redescription. Male. **Color and Appearance:** Shiny, elytra superficially iridescent. Maculate, bicolorous; color of head and pronotum yellow to brownish yellow; color of elytra dark brown to black; color of maculae yellow to brownish yellow, similar to color of head and pronotum. Color of venter brownish yellow to dark brownish yellow, with noterid platform brown to reddish brown; color of legs slightly lighter than color of venter. Maculae as in Fig. 1, each elytron with 3 spots: 1 slightly elongate, as a short transverse band, in distal third of elytron and 2 laterally oriented just anterior to half-length of elytron, with medial spot near elytral suture, anterolaterally oblique and sometimes broken into 2 smaller spots, and lateral spot submarginal, oval. **Thorax:** Pronotum with lateral bead very broad, width 1.2–1.5 × width of antennomere VII, width of bead broader in larger specimens. Prosternum medially with transverse line of 5–9 stiff setae, anterior to procoxae, often discontinuous or more wildly spaced medially. Prosternal process and noterid platform setose; setae short, stiff, evenly distributed and

produced from distinct punctures. Metatibia as in Fig. 3.6, with row of ca. 8–10 evenly spaced setae on inner margin, few additional setae produced near inner distal angle; metatarsomere I with similar row of 3–5 setae on inner margin. **Abdomen:** Aedeagus as in Figs. 3.8a–e; median lobe strongly curved, ventrally divided by large ventral groove running from base to apex, twisting at apex, left lateral side expanded ventrally and attenuate to acute apex; left lateral lobe broad, slightly curved inward towards median lobe, ventral margin broadly curved, dorsal margin straight, with dense tuft of setae subapically produced from shallow impression extending from apex to ca. lobe half-length; setae long, extending well past lobe margin (Fig. 3.8d). Right lateral lobe broad, subtriangular, ventrally rounded. **Measurements:** L = 2.40–2.95 mm, males = 2.40–2.75 mm, females = 2.60–2.95 mm; TL = 2.65–3.25 mm; GW = 1.50 –1.85 mm; HW = 0.80–0.95 mm; EW = 0.50–0.60 mm, PntB = 0.08–0.10, AntVII = 0.06–0.07; L/GW = 1.59-1.71; HW/EW = 1.6–1.75, PntBW/AntVII = 1.20–1.50. (Lectotype: female L = 2.50 mm; GW = 1.60 mm).

Variation. Specimens of *C. buqueti* vary most notably in the prominence of the elytral maculae. Most specimens appear as in Fig. 3.1; while patterning remains consistent, many were observed to have the maculae reduced to smaller bands or spots. Some variation was also observed in color, with the elytra ranging from dark brown to black, the head, pronotum and maculae ranging from yellow to brownish yellow, the venter ranging from brownish yellow to dark brownish yellow, and the noterid platform ranging from brown to reddish brown. The variation observed in the spacing of the setae of the prosternum is depicted in Figs.3. 4a, b, with the line widely spaced to completely discontinuous at median. The number of these setae also vary from 5–10. The number of setae of the inner margins of the metatibia and metatarsomere I varied slightly with those of the metatibia ranging from ca. 8–11 and those of metatarsomere I

ranging from ca. 3–5 in number. Some variation was also observed in size (see '*Measurements*' above). Females were generally slightly larger and more robust than males; female genitalia as in Fig. 3. 11.

Biology. *Canthysellus buqueti* is found in both lotic and lentic habitats in forested areas, with specimens collected from small streams and creeks to forested ponds, swamps and forest pools. Collecting data indicate that this species may have a preference for lotic-associated habitats. Specimens were often found in detritus, such as leaf packs, detrital margins of streams and creeks or detrital pools (e.g. Fig. 3.13b). A few specimens were also collected at lights.

Distribution. *Canthysellus buqueti* is currently known from Venezuela, Guyana, Suriname, and French Guiana (Fig. 3.12). A single female specimen from Amazonas, Brazil was examined and determined to be a conspecific.

Canthysellus sipaliwini Baca and Toledo, new species

(Figs. 3.2, 3.9)

Type locality. Suriname, Sipaliwini District, Kutari River

Type material. Holotype (male): "SURINAME: Sipaliwini District/ 2°10.521'N, 56°41.861'W, 228 m/ Camp 1, on Kutari River; leg. Short/ & Kadosoe; forest stream/ 20.viii.2010, SR10-0820-01A/ 2010 CI-RAP Survey" [printed], "SEMC0913912/ KUNHM-ENT" [barcoded label], "Photo Voucher/ PV__/ Short Lab – KU NHM" [green label, printed], "HOLOTYPE/ *Canthysellus/ sipaliwini*/ Baca & Toledo, 2015" [red label, printed] (NZCS). **Paratypes (11 exs.):** "SURINAME: Sipaliwini District/ 2°21.776'N, 56°41.861'W, 237 m/, Camp 3, Wehepai, leg. Short &/ Kadosoe, sandy forest creek/ 4–6.ix.2010, SR10-0904-01A/ 2010 CI-RAP Survey"

[printed] “SEMC0930390/ KUNHM-ENT” [barcoded label] (1 ex. SEMC); “SURINAME: Sipaliwini District/ 2°10.521’N, 228 m/ Camp 1, on Kutari River, leg. Short/ & Kadosoe, forest stream/ 20.viii.2010, SR10-0820-01A/ 2010 CI-RAP Survey” [printed] “SEMC0913977/ KUNHM-ENT”, “SEMC0913853/ KUNHM-ENT” and “SEMC0914003/ KUNHM-ENT” [all barcoded labels] (1 male; 3 females exs. SEMC); “SURINAME: Sipaliwini District/ 2°10.521’N, 56°47.244’W, 228 m/ Camp 1, on Kutari River/ Short & Kadosoe, forest swamp/ 22.viii.2010, SR10-0822-02A/ 2010 CI-RAP Survey” [printed] “SEMC0912971/ KUNHM-ENT” [barcoded label] (1 male ex. SEMC); “SURINAME: Sipaliwini District/ 2°10.973’N, 56°47.235’W, 210 m/ Camp 2, on Sipaliwini River/ Short & Kadosoe, forest creek/ 31.viii.2010, SR10-0831-01A/ 2010 CI-RAP Survey” [Printed] “SEMC0914696/ KUNHM-ENT” [Barcoded label] (1 female ex. SEMC); “SURINAME: Sipaliwini District/ 02°22.259’N, 56°41.227’W, 229 m/ Camp 3: Werehpai, SE Kamala/ detrital pools in dense forest/ 3–5.ix.2010, leg. Short & Kadosoe/ CI-RAP Survey, SR10-0903-02A” [Printed] “SEMC0912303/ KUNHM-ENT”, “SEMC0912212/ KUNHM-ENT” and “SEMC0912064/ KUNHM-ENT” [all barcoded labels] (3 females exs. SEMC); ‘SURINAME: Sipaliwini District/ N 2.47700°, W 55.62941, 275 m/ Camp 1, Upper Palumeu/ leg. A. Short, Flight Intercept Trap/ 10–16.iii.2012, SR12-0310-TN1/ 2012 CI-RAP Survey” [Printed] “ SEMC1089356/ KUNHM-ENT” [Barcoded label] (1 male ex. SEMC). All paratypes with “PARATYPE/ *Canthysellus/ sipaliwini*/ Baca & Toledo, 2015” [blue label, printed].

Diagnosis. *Canthysellus sipaliwini* sp. n. is distinguishable from other members of the genus by the following combination of characters: (a) metatibia as in Fig. 3.6, with distinctly spaced line of moderately stout setae on inner margin, metatarsomere I with similar row of setae; (b) line of setae on prosternum as in Figs.3.4a, b, with 5–9 setae, extending laterally to or past

anterolateral margins of prosternal process, usually discontinuous, reduced or more widely spaced at medially; (c) head very dark at base and between eyes (Fig. 3.2); (d) size larger, 3.00–3.30 mm; (e) aedeagus as in Figs. 3.9a–f; median lobe expanded ventrally and attenuated to a point apically in lateral aspect; left lateral lobe very broad with dense tuft of setae produced subapically on inner surface; setae extending to or only just beyond lobe margin (Fig. 3.9d).

Comparative Diagnosis. *Canthysellus sipaliwini* sp. n. is very similar to *C. buqueti.* Externally it is most easily distinguished by its larger size and the darkened, nearly back head between the eyes and at its base (Fig. 3.2). *Canthysellus buqueti* is smaller, with the head only weakly infuscate at the base and between the eyes. The aedeagi of these species are also similar, but the median lobe of *C. sipaliwini* is apically more elongate and attenuate than that of *C. buqueti* (Figs. 3.9a–c) and the left lateral lobe is broader, with a tuft of setae that extend only to, or slightly beyond, the dorsal margin (Fig. 3.9d). That of *C. buqueti* is not as broad and has setae that extend well beyond the dorsal margin (Fig. 3.8d). The left lateral lobes are the most distinguishable characters of the aedeagi of these two species.

Description. Holotype. Male. **Color and Appearance:** Shiny, elytra superficially iridescent. Maculate, bicolorous; color of head brownish yellow with base and area between eyes strongly infuscate, nearly black; color of pronotum brownish yellow; color of elytra very dark brown, nearly black; color of maculae brownish yellow, similar to color of pronotum. Color of venter dark brownish yellow, with noterid platform and sutures darker, brown; color of legs slightly lighter than venter. Maculae as in Fig. 3.3, each elytron with 3 spots: 1 slightly elongate, as a short transverse band, in distal third of elytron, and 2 laterally oriented just anterior to the half-length of elytron, with medial spot near elytral suture, anterolaterally oblique and sometimes broken into 2 smaller spots, and lateral spot submarginal, oval. **Thorax:** Pronotum with lateral

bead very broad, 1.73 × width of Antennomere VII. Prosternal disc similar to Fig. 4b; with transverse line of 8 stiff setae, widely separated at median, appearing as 2 smaller lines or tufts anterior to lateral margins of prosternal process. Prosternal process and noterid platform setose; setae short, stiff, evenly distributed and produced from distinct punctures (as in Fig. 4). Metatibia as in Fig. 3.6, with row of ca. 9 evenly spaced setae on inner margin (Fig. 6a), additional few setae produced submarginally on posterior surface near mediodistal angle; metatarsomere I with similar row of 4–5 setae on inner margin (Fig. 3.6a). **Abdomen:** Aedeagus as in Figs. 3.9a–e; median lobe strongly curved, ventrally divided by large ventral groove running from base to apex, twisting at apex, left lateral side expanded ventrally and attenuate to acute apex (Figs. 3.9a, c); left lateral lobe very broad, curved slightly inward towards median lobe, ventral margin broadly curved, dorsal margin straight, with dense tuft of setae subapically produced, setae short, only barely extending past lobe margin (Fig. 3.9d). Right lateral lobe broad, subtriangular, ventrally rounded (Fig. 3.9e). **Measurements:** Holotype: L = 3.00 mm; TL = 3.35 mm; GW = 1.80 mm; HW = 0.95 mm; EW = 0.55 mm; PntB= 0.12 mm; AntVII = 0.07 mm; L/GW = 1.65, HW/EW = 1.68, PntB/AntVII = 1.73. Paratypes: L = 3.00–3.30 mm, males = 3.00–3.10 mm, females = 3.10–3.30 mm; TL = 3.35–3.50 mm; GW = 1.80–1.95 mm; HW = 0.95–1.05 mm; EW = 0.55–0.60 mm; PntB = 0.11–0.13 mm; AntVII = 0.06–0.07 mm; L/GW = 1.62–1.72; HW/EW = 1.63–1.74; PntB/AntVII = 1.63–1.88.

Variation. Members of *C. sipaliwini* vary most noticeably in the prominence of the maculae of the elytra. Though most specimens appear as in Fig. 3.2, the maculae of some specimens are reduced to more slender bands or spots, though orientation remains consistent. Very little variation was observed in color, though some were very slightly darker or lighter than holotype. The setae of the prosternum (Fig. 3.4) varied slightly in number and spacing. The

number of setae ranges from ca. 6–9 in total and though the spacing of these setae most commonly appear as in Fig. 3.4b, with the series widely discontinuous at median, a few specimens were observed to have these setae less widely spaced. Additionally, a few specimens were observed to have this spacing in setae filled by a very small, lone seta. Inconsequential variation in the number and placement setae were also observed elsewhere, e.g. the metatibia. Finally, members of this species display variation in size (see '*Measurements*' above). Females are notably more robust than males.

Biology. *Canthysellus sipaliwini* sp. n. was collected in small numbers from a variety of aquatic habitats in forested areas, including creeks, streams, detrital pools and swamps (Fig. 3.13a). One specimen was collected in a flight intercept trap.

Distribution. *Canthysellus sipaliwini* sp. n. is known only from southwestern Suriname, near the Guyanese boarder (Fig. 3.12)

Etymology. The specific epithet is the name of the type locality. It is treated as a noun in apposition.

Canthysellus peruanus Baca and Toledo new species

(Figs. 3.3, 3.5, 3.7, 3.10, 3.12)

Type Locality. Peru, Madre de Dios Region, Rio Tambopata.

Type Material. Holotype (male): "PERU: Rio Tambopata/ Explorer's Inn/ 12°50.208' S 069°17.605' W/ 10 December 2003/ coll. K.B. Miller" [Printed], "Photo Voucher/ PV__/ Short Lab – KU NHM" [green label, printed], "HOLOTYPE/ *Canthysellus/ peruanus*/ Baca & Toledo, 2015" [red label, printed] (MSBA). **Paratypes (11 exs.):** Same data as holotype. (3 males; 6

females exs. MSBA, 1 male; 1 female exs. SEMC). All paratypes with “PARATYPE/ *Canthysellus/ sipaliwini*/ Baca & Toledo, 2014” [blue label, printed].

Diagnosis. *Canthysellus peruanus* sp. n. is distinguished by the following combination of characters: (a) metatibia as in Fig. 3.7, with inner margin densely setose, setae slender, hair-like, metatarsomere I with similarly setose; (b) line of setae on prosternum as in Fig. 3.5a, not extending laterally past lateral margins of narrowest portion of prosternal process; (c) aedeagus as in Fig. 3.10a–e; median lobe only weakly expanded ventrally, distally parallel sided and weakly attenuate to subtruncate apex in lateral aspect (Fig. 3.10a, c), left lateral lobe with dense tuft of setae produced from weakly lobed apex (Fig. 3.10d).

Comparative Diagnosis. *Canthysellus peruanus* is easily distinguishable from other species by any of the characters above. The setae of the metatibia and the median lobe of aedeagus are especially diagnostic.

Description. Holotype. Male. **Color and Appearance:** Shiny, elytra superficially iridescent; maculate, weakly bicolorous with elytra only slightly darker than head and pronotum. Color of head, pronotum and maculae reddish brown; color of elytra very dark reddish brown; maculae as in Fig. 3.3, each elytron with 1 spot distally near apex and with an irregular band near elytral midlength extending from lateral margin to suture, often broken into a series of 2 or 3 spots with margins blurred and meeting. Color of venter dark reddish brown, with color of noterid platform and sutures only slightly darker than rest of ventral surface; color of legs slightly lighter than venter, margins dark. **Head:** Dorsal surface with microsculpture consisting of small, round isodiametric cells**. Thorax:** Pronotum with lateral bead broad, 1.13 × width of antennomere VII. Prosternum medially with close transverse line or tuft of 5 stiff setae, line of setae continuous medially, not extending past lateral margins of prosternal process. Prosternal

process, and noterid platform setose, setae very short, stout, produced from punctures, distinctly spaced and evenly distributed (Fig. 3.5). Metatibia densely setose on inner margin (Fig. 3.7a); setae slender, hair-like, expanding from single line at base to dense field distally; field restricted to inner margin. Metatarsomere I with inner margin similarly setose to metatibia. **Abdomen:** Aedeagus as in Fig. 3.10a–e; median lobe curved dorsally, divided ventrally by deep groove, groove ceasing and sides meeting at ca. midlength of lobe, left side expanded ventrally at midlength, distal 1/3 of lobe subparallel and distally attenuate to truncate apex in lateral aspect, distal portion distinctly curved in dorsal aspect; left lateral lobe broad, weakly curved toward median lobe, with dense setal tuft produced apically from inner surface of weakly lobed apex (Fig. 3.10d); right lateral lobe broad, ventral margin broadly rounded (Fig. 3.10e).

Measurements: Holotype: L = 3.10 mm; TL= 3.40 mm; GW = 1.90; HW = 1.05; EW = 0.65; PntB = 0.09 mm; AntVII = 0.08; HW/EW = 1.62; PntB/AntVII = 1.13. Paratypes: L = 3.05–3.35 mm, males = 3.10–3.35 mm, females = 3.05–3.30 mm; TL = 3.25–3.40 mm GW = 1.9–2.1 mm, HW = 1.00–1.10 mm; EW = 0.55–0.65 PntB = 0.7–0.9, AntVII = 0.07–0.08; L/GW = 1.55–1.65, HW/EW = 1.59–1.75, PntB/AntVII = 1.00–1.25.

Variation. Variation in *C. peruanus* is difficult to accurately assess as all examined specimens were part of a limited series from a single collecting event. The variation that was observed was primarily limited to slight differences in size (see '*Measurements*' above).

Biology. Though specific habitat data for *C. peruanus* were not recorded on specimen labels, the series of specimens is believed to have been collected out of a marshy inlet or pond just south of the Explorer's Inn (K. B. Miller, personal communication), a lodge on the Rio Tambopata in the Madre de Dios region of Peru.

Distribution. *Canthysellus peruanus* is known only from a single series of specimens collected from the Madre de Dios region in Peru (Fig. 3.12).

Remarks. The setae of the inner margins of the metatibia and first metatarsomere are excellent for distinguishing *C. peruanus* from other members of *Canthysellus*. However, it should be noted that these setae are often clumped on dried specimens and to the observer may at first appear as stout setae.

Etymology. The specific epithet is referred to the country where this species was collected, meaning 'inhabiting Peru'. It is treated as an adjective in the nominative singular.

KEY TO SPECIES OF *CANTHYSELLUS*

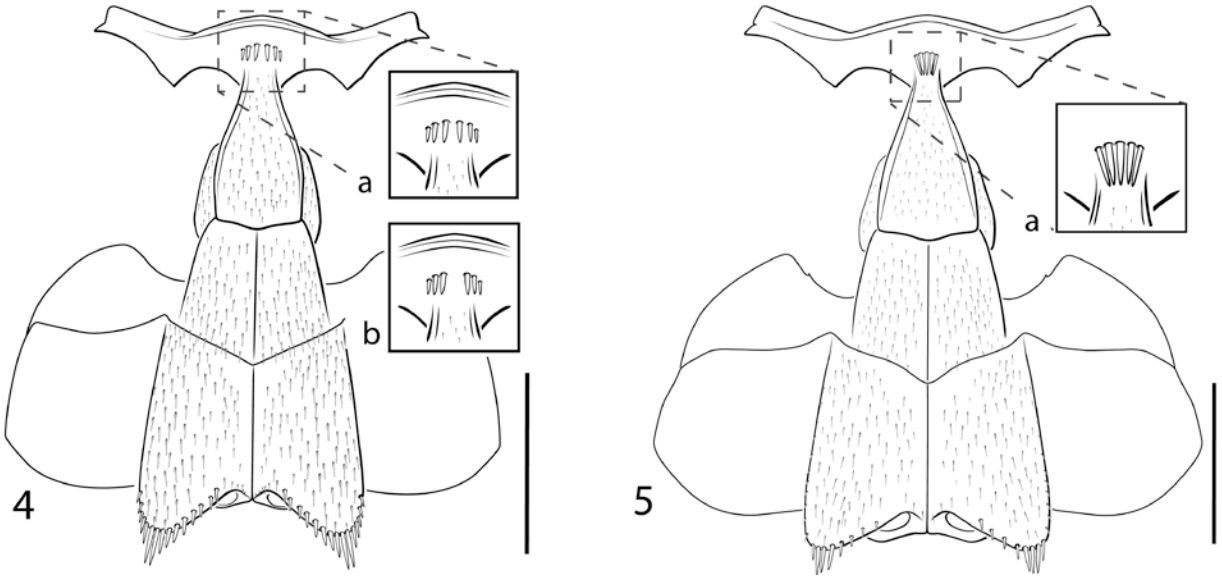
1. Metatibia and metatarsomere I with inner margin as in Fig. 3.7, densely setose; setae slender, hair-like; aedeagus as in Figs.3.11a–e. … ***C. peruanus*, new species.**

1′. Metatibia and metatarsomere I with inner margin as in Fig. 6, with single line of ca. 8–10 evenly spaced, stiff setae. … 2

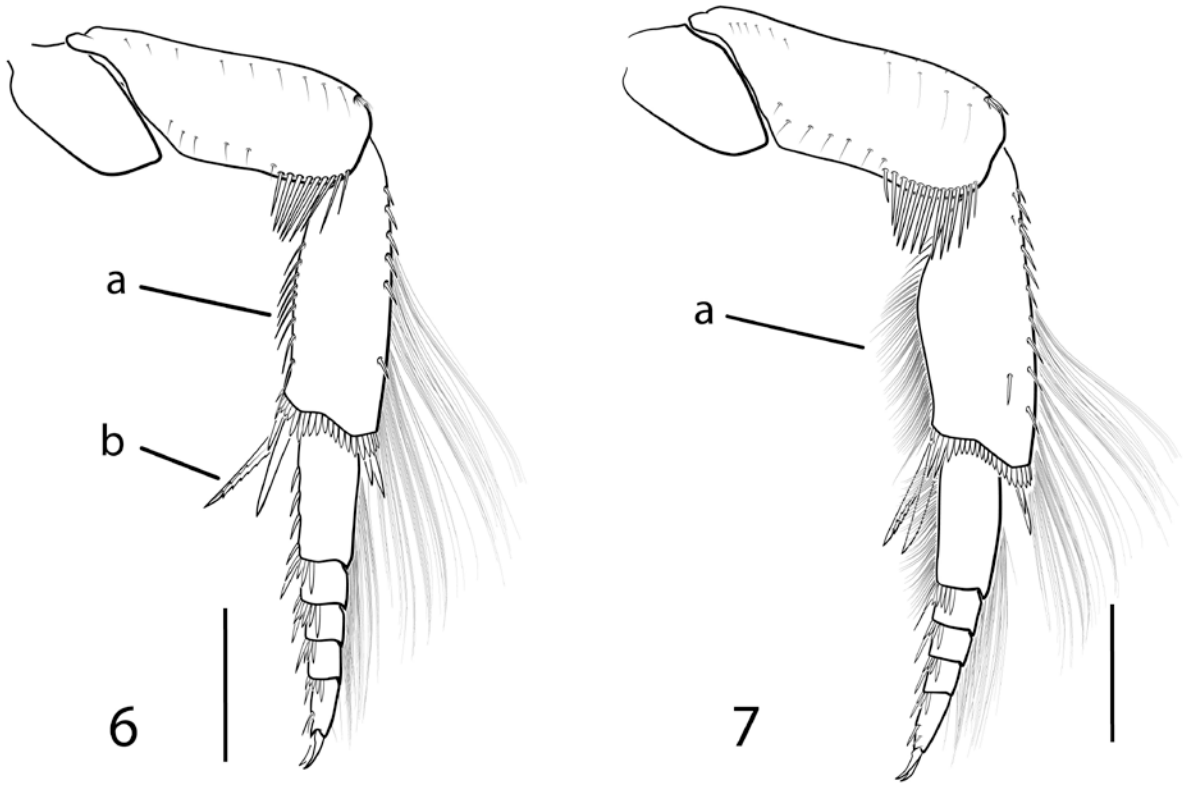
2. Size smaller, 2.40–2.95 mm from elytral apices to anterior margin of pronotum; base of head usually only weakly infuscate (Fig. 3.1); Aedeagus as in Figs. 3.8a–e, left lateral lobe broad with setae extending well beyond lobe margin (Fig. 3.8d); median lobe with apex pointed, but not elongate in lateral aspect (Figs. 3.8a, c). … ***C. buqueti* (Laporte, 1835)**

2′. Size larger, 2.95 mm–3.30 mm from elytral apices to anterior margin of the pronotum; base of head usually strongly infuscate, nearly black (Fig. 3.2); Aedeagus as in Figs. 3.9a–e, left lateral lobe very broad with setae extending just to or only slightly past lobe margin (Fig. 3.9d); median lobe with apex elongate in lateral aspect (Figs. 3.9a, c). … ***C. sipaliwini*, new species**

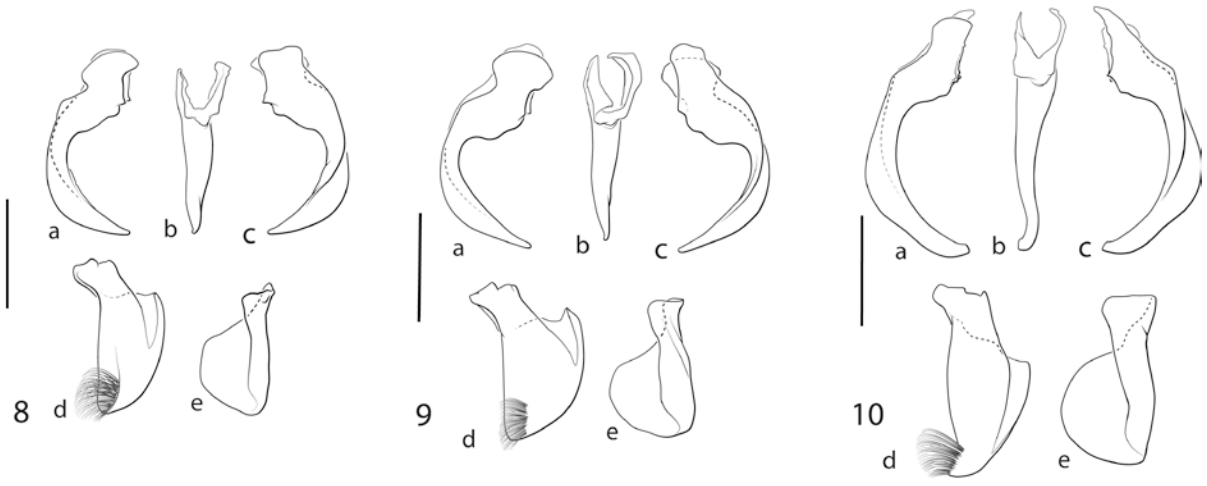
Figures 3.1–3.3. Dorsal and lateral habitus of *Canthysellus* species. (1) *Canthysellus buqueti*, male; (2) *Canthysellus sipaliwini*, Holotype, male; (3) *Canthysellus peruanus*, Holotype, male (imaged before dissection). Scale bar = 1 mm.



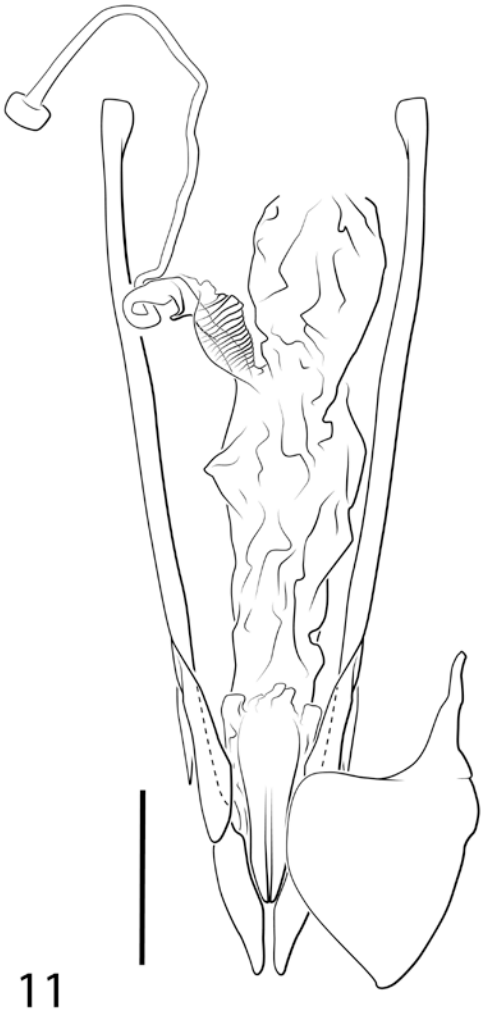
Figures3.4,3. 5. Prosterna, metasterna, and metacoxae (noterid platform) of *Canthysellus species* with studies of prosternal setae. (4) *C. buqueti*, male, (4a, b) variation of prosternal setae; (5) *C. peruanus*, Paratype, male. Scale bar = 0.5 mm.



Figures 3.6, 3.7. Metalegs of *Canthysellus* species. (6) *C. buqueti*, male, a) setae of inner margin of metatibia, (b) posterior metatibial spur, serration is diagnostic of the genus; (7) *C. peruanus*, Paratype, male, a) setae of inner margin of metatibia. Scale bars = 0.25 mm



Figures. 3.8–3.10. Aedeagi of *Canthysellus* species. (8) *C. buqueti*, Suriname; (9) *C. sipaliwini*, Holotype, Suriname; (10) *C. peruanus*, Paratype, Peru. (a) median lobe, left lateral



aspect, (b) median lobe, dorsal aspect, (c) median lobe, right lateral aspect, (d) left lateral lobe, (e) right lateral lobe. Scale bars = 0.25 mm.

Figure 3.11. Female genitalia of *C. buqueti*. Scale bar = 0.25 mm.

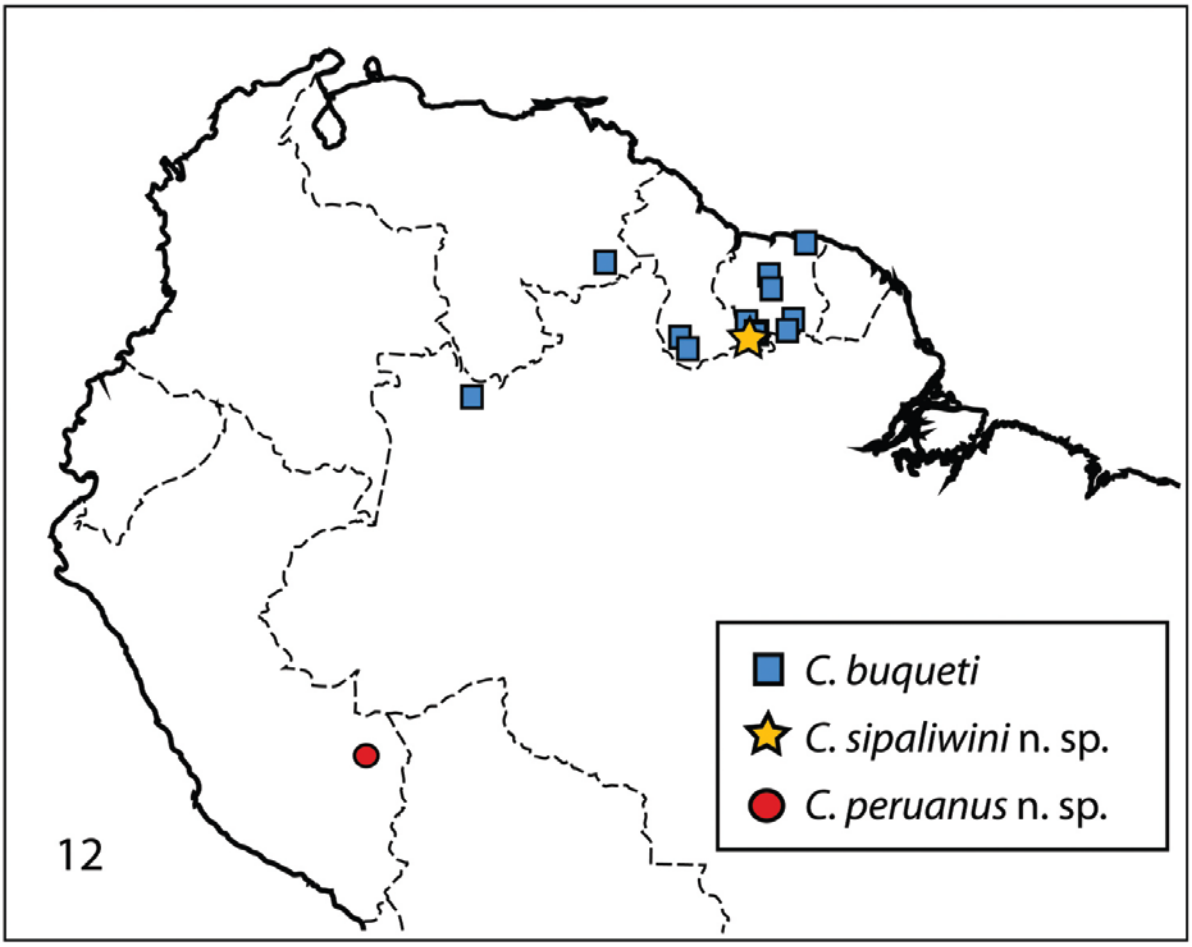


Figure 3.12. Distribution map of *Canthysellus* species.

Figure 3.13. Habitats of *Canthysellus* species. (a) Type locality of *C. sipaliwini*; Suriname: Sipaliwini District, stream near the Kutari River, collecting event SR13-0816-02A. (b) Example habitat of *C. buqueti*; Suriname: Sipaliwini District, summit of Tafelberg Tepui, collecting event SR13-0816-02A.

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Appendix 1.1. Taxon sampling for phylogenetic analysis: supporting data.

Genus (Subgenus)	Species	Authority	Voucher	Locality	Source	Collection Code
Amphizoa	*insolens*	LeConte, 1853	GenBank	N/A	N/A	N/A
Hydroporus	*axillaris*	LeConte, 1853	GenBank	N/A	N/A	N/A
Laccophilus	*pictus*	Laporte, 1835	GenBank	N/A	N/A	N/A
Rhantus	*gutticollis*	(Say, 1830)	GenBank	N/A	N/A	N/A
Haliplus	*lineatocollis*	(Marsham, 1802)	GenBank	N/A	N/A	N/A
Peltodytes	*rotundatus*	(Aubé, 1836)	GenBank	N/A	N/A	N/A
Meru	*phyllisae*	Spangler & Steiner, 2005	SLE841	Venezuela, Bolivar	A. E. Z. Short	VZ09-0113-01C
Meru	*phyllisae*	Spangler & Steiner, 2005	SLE901	Venezuela, Bolivar	A. E. Z. Short	VZ09-0113-01C
Canthydrus	*bovillae*	Blackburn, 1890	SLE888	Austrailia, Queensland	K. B. Miller	KBM16031101
Canthydrus	*quadrivittatus*	(Boheman, 1848)	SLE836	Congo (DRC), Bas Congo Prov.	R. Sites	L-1444
Canthydrus	*semperi*	(Whencke, 1876)	SLE696	Phillippines, Boracay	I. Ribera	IR606
Canthydrus	sp. 2		SLE683	Kenya, Taita Tavita Co.	S. M. Baca	SMB230613-A
Canthydrus	sp. 3		SLE694	Kenya, Narok Co., N. Mara	S. M. Baca	SMB140613-A
Canthydrus	sp. 3		SLE838	Kenya, Makueni Co.	S. M. Baca	SMB210613-A

Canthydrus	*xanthinus*	Régimbart, 1895	SLE837	Tanzania, Morogoro Reg.	R. Sites	L-1630
Canthysellus	*buqueti*	(Laporte, 1835)	SLE680	Suriname, Sipaliwini	A. E. Z. Short	SR10-0820-01A
Canthysellus	*buqueti*	(Laporte, 1835)	SLE835	Guyana, Region 9	A. E. Z. Short	GY13-1103-02A
H. (Sternocanthus)	*adrasus*	Guignot, 1950	KBMC629	Zambia, Copperbelt Prov.	K. B. Miller	KBM01110701
H. (Sternocanthus)	*australasiae*	Wehncke, 1876	SLE886	Austrailia, Queensland	K. B. Miller	KBM19031102
H. (Sternocanthus)	*funibris*	Fairmaire, 1869	KBMC743	Madagascar, Fianarantsoa	K. B. Miller	KBM09110801
H. (Sternocanthus)	sp.		KBMC570	Zambia, Northwestern Prov.	K. B. Miller	KBM07110702
H. (Sternocanthus)	*waterhousei*	Blackburn, 1888	SLE885	Austrailia, Queensland	K. B. Miller	KBM14031104
Hydrocanthus	*atripennis*	Say, 1830	SLE697	USA, Georgia	I. Ribera	IR425
Hydrocanthus	*atripennis*	Say, 1830	SLE682	USA, Mississippi	G. T. Gustafson	GTG062313LT
Hydrocanthus	*debilis*	Sharp, 1882	SLE687	Venezuela, Zulia	A. E. Z. Short	VZ12-0127-02A
Hydrocanthus	*debilis*	Sharp, 1882	SLE829	Suriname, Commewijne	A. E. Z. Short	SR13-0808-01A
Hydrocanthus	*guignoti*	Young, 1985	SLE828	Venezuela, Barinas	A. E. Z. Short	VZ12-0125-02A

Hydrocanthus	*socius*	R.F. Sahlberg, 1844	SLE912	Suriname, Marowijne	A. E. Z. Short	SR13-0809-03A
Hydrocanthus	sp.		SLE911	Peru, Madre de Dios	K. B. Miller	N/A
Liocanthydrus	*bicolor*	(Balfour-Browne, 1969)	SLE681	Suriname, Sipaliwini	A. E. Z. Short	SR10-0820-01A
Liocanthydrus	*bicolor*	(Balfour-Browne, 1969)	SLE830	Guyana Region 9	A. E. Z. Short	GY13-1103-02A
Liocanthydrus	*clayae*	(Balfour-Browne, 1969)	KBMC637	Venezuela, Bolivar	A. E. Z. Short	VZ09-0113-01X
Liocanthydrus	*clayae*	(Balfour-Browne, 1969)	KBMC748	Venezuela, Guarico	A. E. Z. Short	VZ09-0110-01A
Mesonoterus	*laevicollis*	Sharp, 1882	KBMC739	Venezuela, Apure	A. E. Z. Short	VZ09-0118-03X
Mesonoterus	*laevicollis*	Sharp, 1882	KBMC745	Panama, Veraguas Prov.	K. B. Miller	KBM07060902
Mesonoterus	*laevicollis*	Sharp, 1882	SLE690	Venezuela, Barinas	A. E. Z. Short	VZ12-0125-01A
Neohydrocoptus	*bivittus*	(Motschulsky, 1859)	SLE887	India, Kametaka	K. B. Miller	N/A
Neohydrocoptus	*grandis*	(Balfour-Browne, 1961)	KBMC631	Zambia, Northwestern Prov.	K. B. Miller	KBM07110702
Neohydrocoptus	*seriatus*	(Sharp, 1882)	GenBank	N/A	N/A	N/A
Neohydrocoptus	sp.		KBMC741	Thailand, Phang Nga Prov.	R. Sites	L-946 (Robert Sites)

Neohydrocoptus	*uellensis*	(Guignot, 1953)	KBMC630	Zambia, Copperbelt Prov.	K. B. Miller	KBM01110701
Noterid Gen. nov	sp.		SLE693	Venezuela, Amazonas	A. E. Z. Short	VZ09-0116-01X
Noterid Gen. nov	sp.		SLE839	Venezuela, Amazonas	A. E. Z. Short	VZ09-0116-01X
Noterus	*clavicornis*	(De Geer, 1774)	KBMC503	Italy, Sardinia, Nuoru Prov.	K. B. Miller	KBM1604064
Noterus	*clavicornis*	(De Geer, 1774)	GenBank	N/A	N/A	N/A
Noterus	*clavicornis*	(De Geer, 1774)	GenBank	N/A	N/A	N/A
Noterus	*japonicus*	Sharp, 1873	SLE699	Mongolia, Tov Aimag	I. Ribera	IRS-220
Notomicrus	*josiahi*	Miller, 2013	KBMC642	Venezuela, Amazonas State	A. E. Z. Short	VZ09-0113-01
Notomicrus	sp.		KBMC641	Bolivia, Santa Cruz	N/A	N/A
Notomicrus	*tenellus*	(Clark, 1863)	NHM-IR92*	Australia, Northern Territory	I. Ribera	IR-92
Notomicrus	*tenellus*	(Clark, 1863)	SLE890	Australia, Queensland	K. B. Miller	KBM13031101
Notomicrus	*nanulus*	(LeConte, 1863)	GenBank	N/A	N/A	N/A
Phraetodytes	*haibaraenis*	Uéno	GenBank	Japan	N/A	N/A

Prionohydrus	*marc*	Gomez & Miller, 2013	SLE689	Venezuela, Bolivar State	A. E. Z. Short	VZ10-0717-03A
Prionohydrus	*marc*	Gomez & Miller, 2013	SLE831	Guyana, Region 9	A. E. Z. Short	GY13-1024-02B
Prionohydrus	*ubercornis*	Gomez & Miller, 2013	SLE832	Venezuela, Zulia	A. E. Z. Short	VZ09-0129-03X
Pronoterus	sp. 1		KBMC746	Panama, Veraguas Prov.	A. E. Z. Short	KBM07060902
Pronoterus	sp. 2		KBMC635	Bolivia, Santa Cruz	K. B. Miller	N/A
Pronoterus	sp. 3		SLE833	Venezuela, Monagas	A. E. Z. Short	VZ10-0202-01B
Pronoterus	sp. 3		SLE834	Venezuela, Tachira	A. E. Z. Short	VZ12-0126-02A
Renotus	*deyrollei*	(Sharp, 1882)	SLE695	Congo, Bas Congo Prov.	R. Sites	L-1434
Suphis	*cimicoides*	Aubé, 1837	KBMC740	Venezuela, Apure	A. E. Z. Short	VZ09-0118-02X
Suphis	sp.		SLE913	Suriname, Marowijne	A. E. Z. Short	SR12-0304-06A
Suphisellus	c.f. *lineatus*	(Horn, 1871)	KBMC633	Venezuela, Amazonas	A. E. Z. Short	VZ09-0114-03A
Suphisellus	*curtus*	(Sharp, 1882)	SLE686	Venezuela, Trujillo	A. E. Z. Short	VZ12-0128-06A

Suphisellus	*gibbulus*	(Aubé, 1838)	SLE698	USA, Georgia	I. Ribera	IRS-424
Suphisellus	*majusculus*	(Sharp, 1882)	SLE691	Venezuela, Bolivar	A. E. Z. Short	VZ09-0112-01A
Suphisellus	*neglectus*	Young, 1979	SLE684	Venezuela, Tachira	A. E. Z. Short	VZ12-0126-02A
Suphisellus	*nigrinus*	(Aubé, 1838)	KBMC744	Panama, Veraguas Prov.	K. B. Miller	KBM07060902
Suphisellus	*pereirai*	Guignot, 1958	SLE840	Guyana, Region 9	A. E. Z. Short	GY13-1025-01A
Suphisellus	*simoni*	(Régimbart, 1889)	SLE685	Venezuela, Delta Amacuro	A. E. Z. Short	VZ09-0813-07A
Suphisellus	*subsignatus*	(Sharp, 1882)	SLE692	Venezuela, Zulia	A. E. Z. Short	VZ09-0129-03X
Suphisellus	*sp.*		NHM-IR110*	Venezuela	GenBank	IR-110
Sychortus	*imbricatus*	(Klug, 1853)	SLE889	Tanzania, Mbeya Reg.	R. Sites	L-1208
Sychortus	*simplex*	Sharp, 1882	KBMC632	Zambia, Northwestern Prov.	K. B. Miller	KBM01110701
Sychortus	*simplex*	Sharp, 1882	SLE688	Kenya, Narok Co.	S. M. Baca	SMB150613A
Sychortus	sp.		KBMC742	Ghana, Western Region	K. B. Miller	KBM0706051
Tonerus	*wheeleri*	Miller, 2009	KBMC639	Venezuela, Amazonas	A.E.Z. Short	VZ09-0114-01F

Tonerus	*wheeleri*	Miller, 2009	SLE827	Venezuela, Amazonas	A.E.Z. Short	VZ09-0114-01F

Appendix 1.2. Gene sampling. KUBI indicates sequences obtained using the KU Biodiversity Institute Molecular Genenics Lab; KBM-PC indicates sequences provided by Kelly B. Miller; accession numbers are provided for sequences downloaded from GenBank; dash (-) indicates missing data. FUSE modifier indicates taxa represented by sequence data from multiple specimens.

Family	Genus (subgenus)	Species	Voucher	COI	H3	16S	18S	28S
Amphizoidae	*Amphizoa*	*insolens* FUSE	GenBank	AY071796	AY745672	AY071770	EU797401	EU797339
Dytiscidae	*Hydroporus*	*axillaris* FUSE	GenBank	AY365301	JX434724	AY365267	JX434782	EU797358
Dytiscidae	*Laccophilus*	*pictus* FUSE	GenBank	AJ850657	EF670218	AJ850409	HM156707	EU797363
Dytiscidae	*Rhantus*	*gutticollis* FUSE	GenBank	KJ637973	KJ637998	KJ637884	KJ637901	EU797382
Haliplidae	*Haliplus*	*lineatocollis* FUSE	GenBank	AY071803	AY745682	AY071777	AJ318666	-
Haliplidae	*Peltodytes*	*rotundatus* FUSE	GenBank	AY071806	AY745684	AY071790	AJ318668	-
Meruidae	*Meru*	*phyllisae* FUSE	GenBank	JQ684026	-	FM163591	FM163592	-
Meruidae	*Meru*	*phyllisae*	SLE841	-	-	KUBI	-	-
Noteridae	*Canthydrus*	*bovillae*	SLE888	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthydrus*	*quadrivittatus*	SLE836	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthydrus*	*semperi*	SLE696	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthydrus*	sp. 2	SLE683	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthydrus*	sp. 3	SLE838	KUBI	KUBI	-	KUBI	KUBI
Noteridae	*Canthydrus*	sp. 3	SLE694	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthydrus*	*xanthinus*	SLE837	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthysellus*	*buqueti*	SLE680	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Canthysellus*	*buqueti*	SLE835	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	Gen. Nov.	sp	SLE693	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	Gen. Nov.	sp	SLE839	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Hydrocanthus*	*atripennis*	SLE682	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Hydrocanthus*	*atripennis*	SLE697	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Hydrocanthus*	*guignoti*	SLE828	-	KUBI	KUBI	KUBI	KUBI
Noteridae	*Hydrocanthus*	*debilis*	SLE829	-	KUBI	KUBI	KUBI	KUBI

Noteridae	*Hydrocanthus*	*debilis*	SLE687	-	KUBI	KUBI	-	-
Noteridae	*Hydrocanthus*	*socius*	SLE912	KUBI	KUBI	KUBI	-	KUBI
Noteridae	*Hydrocanthus*	sp.	KBM747	-	KBM-PC	KBM-PC	-	KUBI
Noteridae	*Hydrocanthus*	sp.	SLE911	KUBI	KUBI	KUBI	-	KUBI
Noteridae	*H. (Sternocanthus)*	*adrasus*	KBMC629	KUBI	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*H. (Sternocanthus)*	*australasiae*	SLE886	KUBI	KUBI	KUBI	-	KUBI
Noteridae	*H. (Sternocanthus)*	*funibris*	KBMC743	-	KBM-PC	KUBI	KUBI	KUBI
Noteridae	*H. (Sternocanthus)*	sp.	KBMC570	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*H. (Sternocanthus)*	*waterhousei*	SLE885	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Liocanthydrus*	*bicolor*	SLE681	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Liocanthydrus*	*bicolor*	SLE830	KUBI	-	KUBI	KUBI	KUBI
Noteridae	*Liocanthydrus*	*clayae*	KBMC637	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Liocanthydrus*	*clayae*	KBMC748	KUBI	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Mesonoterus*	*laevicollis*	KBMC739	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Mesonoterus*	*laevicollis*	KBMC745	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Mesonoterus*	*laevicollis*	SLE690	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Neohydrocoptus*	*bivittus*	SLE887	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Neohydrocoptus*	*grandis*	KBMC631	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Neohydrocoptus*	sp.	KBMC741	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Neohydrocoptus*	*uellensis*	KBMC630	KBM-PC	KBM-PC	KUBI	KUBI	KUBI
Noteridae	*Noterus*	*clavicornis*	KBMC503	KBM-PC	KBM-PC	KJ458358	KUBI	KUBI
Noteridae	*Noterus*	*clavicornis*	GenBank	AY071814	-	-	-	-
Noteridae	*Noterus*	*clavicornis* (fuse)	GenBank	DQ155741	AY745689	-	-	-
Noteridae	*Noterus*	*japonicus*	SLE699	KUBI	-	KUBI	KUBI	KUBI
Noteridae	*Notomicrus*	*josiahi*	KBMC642	KUBI	KBM-PC	KJ548385	KUBI	KUBI
Noteridae	*Notomicrus*	sp.	KBMC641	KUBI	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Notomicrus*	*tenellus*	IR91	AY071813	AY7456888	AY071787	AJ318671	-
Noteridae	*Notomicrus*	*tenellus*	SLE890	KUBI	KUBI	KUBI	KUBI	KUBI

Noteridae	*Notomicrus*	*nanulus*	GenBank	-	-	-	-	EU797370
Noteridae	*Phraetodytes*	*haibaraenis*	GenBank	GU999994	GU999996	GU999997	GU999993	-
Noteridae	*Prionohydrus*	*marc*	SLE689	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Prionohydrus*	*marc*	SLE831	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Prionohydrus*	*ubercornis*	SLE832	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Pronoterus*	sp. 1	KBMC746	KUBI	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Pronoterus*	sp. 2	KBMC635	-	KBM-PC	KBM-PC	-	-
Noteridae	*Pronoterus*	sp. 3	SLE833	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Pronoterus*	sp. 3	SLE834	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Renotus*	*deyrollei*	SLE695	KUBI	-	KUBI	KUBI	KUBI
Noteridae	*Suphis*	*cimicoides*	KBMC740	KUBI	KUBI	KBM-PC	KUBI	KUBI
Noteridae	*Suphis*	sp.	SLE913	-	KUBI	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	c.f. *lineatus*	KBMC633	KBM-PC	KUBI	KBM-PC	KUBI	KUBI
Noteridae	*Suphisellus*	*curtus*	SLE686	KUBI	-	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	*gibbulus*	SLE698	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	*majusculus*	SLE691	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	*neglectus*	SLE684	KUBI	-	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	*nigrinus*	KBMC744	KBM-PC	KBM-PC	KBM-PC	KUBI	KUBI
Noteridae	*Suphisellus*	*pereirai*	SLE840	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	*simoni*	SLE685	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Suphisellus*	sp.	IR110	AY071818	AY745691	AY071792	AJ318669	-
Noteridae	*Suphisellus*	*subsignatus*	SLE692	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Sychortus*	*imbricatus*	SLE889	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Sychortus*	*simplex*	KBMC632	KBM-PC	KBM-PC	KUBI	KUBI	KUBI
Noteridae	*Sychortus*	*simplex*	SLE688	KUBI	KUBI	KUBI	KUBI	KUBI
Noteridae	*Sychortus*	sp.	KBMC742	KBM-PC	KBM-PC	KUBI	KUBI	KUBI
Noteridae	*Tonerus*	*wheeleri*	KBMC639	KJ548556	KBM-PC	KJ548384	KUBI	KBM-PC
Noteridae	*Tonerus*	*wheeleri*	SLE827	KUBI	KUBI	KUBI	KUBI	KUBI