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On the systematics of Noteridae (Coleoptera: Adephaga: Hydradephaga): Phylogeny, description of a new tribe, genus and species, and survey of female genital morphology

Abstract A phylogenetic analysis of Noteridae Thomson, 1860 is presented based on 33 adult morphological characters with focus on placement of a new genus and species from Venezuela, *Tonerus wheeleri*, gen. nov, sp. nov. Characters are derived from many used previously in Noteridae systematics with many new characters, especially from a survey of the female genitalia. Exemplars from all noterid genera were included except *Phreatodytes* Uéno, 1957 and *Synchortus* Sharp, 1882 with outgroups from Paelobiidae, Amphizoidae and Dytiscidae. Relationships among the genera were found to be (*Notomicrus* Sharp + *Speonoterus* Spangler) + (*Tonerus* + (*Neohydrocoptus* Sâto + (*Pronoterus* Sharp + (*Mesonoterus* Sharp + (*Noterus* Clairville + (*Renotus* Guignot + (*Siolius* Balfour-Browne + (*Suphis* Aubé + (*Canthydrus* [*Liocanthydrus*] Guignot + *Suphisellus* Crotch)) + (*Canthydrus* Sharp *sensu stricto* + *Hydrocanthus* Say)))))))). *Tonerus* occupies a phylogenetic position that requires a new tribe, **Tonerini** tr. nov. characterised by the following character states: (1) the metacoxa and metafurca are fused laterally forming a complete ring, (2) the noterid platform extends anteriorly onto the metaventricle, (3) the female laterotergites are short and anteriorly not broadly expanded and posteriorly extending well beyond the gonocoxae bases, (4) the gonocoxae are apically rounded, (5) the protarsus is attached at the apex of the protibia, (6) there is a distinct dorsoapical protibial angle, and (7) there are several stout, straight spines at the apex of the protarsus. Three subfamilies of Noteridae are recognised: (1) Phreatodytinae Uéno, including only *Phreatodytes*; (2) Notomicrinae Zimmermann, including *Notomicrus* and *Speonoterus*, and (3) Noterinae, including all other genera. Phreatodytinae and Notomicrinae each include a single tribe. Noterinae includes the tribes Tonerini (*Tonerus*), Neohydrocoptini Zalat, Saleh, Angus and Kaschef (*Neohydrocoptus*), Pronoterini Nilsson (*Pronoterus*) and Noterini (all other genera of Noterinae). *Canthydrus* is polyphyletic with the subgenus *Liocanthydrus* sister to *Suphisellus* and *Canthydrus s. str.* sister to *Hydrocanthus*, so *Liocanthydrus* is elevated from subgenus to genus rank (**new status**). Characters historically used to define *Hydrocanthus* (*Sternocanthus*) Guignot were determined to be unreliable, and *Sternocanthus* is placed in synonymy with *Hydrocanthus* (**new synonym**). The resulting phylogeny is compared with published hypotheses, and the evolution of characters is discussed.

Key words Burrowing water beetles, Neotropical, taxonomy, systematics, morphology

Introduction

Members of the small family Noteridae Thomson (Coleoptera: Adephaga) are commonly encountered beetles in aquatic habitats throughout most of the world, especially in tropical areas. Since they were historically classified together as a subfamily of diving beetles (Dytiscidae), workers on that larger family also investigated noterids. Although a few fairly modern researchers still regard the group as a subfamily of Dytiscidae (e.g. Pederzani, 1995), and despite the general overall similarity of members of the group to dytiscids, there has been a general consensus that noterids are not as closely related to Dytiscidae as are other families of Adephaga (specifically Paelobiidae and Amphizoidae) based on both morphological (e.g. Beutel *et al.*, 2006) and molecular (e.g. Ribera *et al.*, 2002) data. Removal of noterids from the Dytiscidae resulted in the ‘orphaning’ of the family so that fewer workers now include them in their studies.

These beetles are frequently called ‘burrowing water beetles’ based (in part) on observations of the larvae of some *Noterus* which burrow in soft substrate around plant roots (Roughley, 2001; Dettner, 2005). However, it is not known whether other larvae also burrow, and it is not clear whether adults of any species do any true ‘burrowing’, or whether this has been simply assumed based on their enlarged front legs. In several genera, a large, curved protibial spur that fits into a groove and/or pit on the basal protarsomere has been implicated as a burrowing device, though this behaviour has not been comprehensively observed. Noterids are usually found in sunny, shallow lentic habitats, often in extremely large numbers, and not generally in situations that imply burrowing.

Noteridae, as currently defined, are distributed among three subfamilies, 14 genera and approximately 250 species (Nilsson & van Vondel, 2005). The species are primarily tropical with relatively few species extending into the Holarctic and southern temperate regions. However, in tropical areas noterids can be extremely abundant and relatively speciose.

This project has three primary goals. The first is to present a phylogenetic analysis of the genera in the family and use this to improve the higher classification as needed. There are a relatively few significant modern analyses of the group with comprehensive sampling including those by Beutel and Roughley (1987), Belkaceme (1991) and Beutel *et al.* (2006). Beutel and Roughley (1987) developed some evidence for relationships within Noteridae, but their primary goal was to examine the placement of *Notomicrus* Sharp within the Hydradephaga, and they found convincing evidence for its placement as sister to all other Noteridae except, perhaps, *Phreatodytes* Uéno (Fig. 1A). Belkaceme (1991) presented a very detailed morphology of *Noterus laevis* Sturm, but also compared this taxon with other genera in the group and hypothesised a phylogeny for Noteridae based on numerous morphological features from adults (Fig. 1B). Finally, Beutel *et al.* (2006) were primarily concerned with the phylogenetic placement of Meruidae within the Hydradephaga, but also developed a robust analysis of the ‘smaller’ families of Hydradephaga (including Noteridae) using a broad range of characters from adults and larvae (Fig. 1C). A summary of information from several of these analyses was

presented by Nilsson (2005, Fig. 1D). Despite the meticulous approach of these analyses, it appears that several characters used historically have been interpreted differently by different authors suggesting that a more thoroughgoing comprehensive examination of specimens is required.

Therefore, the second goal is to survey the morphology of the group with particular regard to discovery of new characters that may contribute to a better understanding of the phylogeny of Noteridae. The female genitalia, in particular, are surveyed across the group. In the related Dytiscidae, female genitalia has become an extremely rich source of character information at several taxonomic levels (Miller, 2001), suggesting that, perhaps, the same may be true in Noteridae. Other than relatively cursory examination by certain authors (e.g. Burmeister, 1976; Franciscolo, 1979; Miller, 2001), little has been reported about noterid female genital morphology. In this paper the female genitalia of species from all major groups is described and illustrated, and character information included in the phylogenetic analysis. A search for additional new characters was also conducted and these are included in the analysis as well.

Finally, the primary impetus for this project was the discovery of a new species from Venezuela that not only does not fit any current generic concepts, but also does not seem to fit any concepts for tribes within the family. The third major goal of this project is to describe this new taxon and classify it based on the phylogeny of the family.

Materials and methods

Measurements. For the species description, measurements were taken with an ocular scale on a Wild M3C dissecting microscope. Intact specimens were measured, and an attempt was made to measure the largest and smallest specimens available. Measurements include: (1) total length (TL), (2) greatest width (GW), (3) greatest length of the pronotum (PL), (4) greatest width of the pronotum (PW), (5) greatest width of the head (HW), (6) distance between the eyes (EW), (7) greatest width of the metafemur (FW), (8) greatest length of the metafemur (FL), and (9) greatest width of the prosternal process (SW). Various ratios of these are provided to give an indication of shape.

Taxon sampling. Exemplar taxa included in the phylogenetic analysis are shown in Table 1. Specimens were examined from the author’s research collection housed in the Museum of Southwestern Biology Division of Arthropods (MSBA), the United States National Museum of Natural History, Smithsonian (USNM, W. Steiner) and Universidad Central de Venezuela, Maracay, Venezuela (MIZA). The holotype and 10 paratypes of the new species are deposited in MIZA. The other paratypes are distributed among the MSBA, the USNM, the MIZA, the University of Kansas Snow Entomological Collection (SEMC, M. Engel) and the collection of Mauricio García (Universidad del Zulia). Members of each currently recognised genus-group in Noteridae were included except the unusual *Phreatodytes* Uéno (Pheratodytinae) and the African *Synchortus* Sharp, each of which were not available.

	0000000001	1111111112	2222222223	333
	1234567890	1234567890	1234567890	123
<i>Amphizoa lecontei</i>	10000-0000	0000000110	0000000000	001
<i>Hygrobia hermanni</i>	00000-0000	0000000110	0000000000	001
<i>Matus bicarinatus</i>	0000010000	0000000110	0000001000	001
<i>Agabus seriatus</i>	0000010000	0000000110	0000001000	001
<i>Laccornis oblongus</i>	0000010000	0000000110	0000001000	001
<i>Notomicrus</i> sp.	0100010000	1101000110	0010000000	001
<i>Speonoterus bedosae</i>	0100010000	1??1000110	0010000???	???
<i>Tonerus wheeleri</i>	1110000100	1111100110	0100000000	001
<i>Neohydrocoptus bivittis</i>	1100000000	1111100110	0100000111	100
<i>Neohydrocoptus subvittulus</i>	1100000000	1111100110	0100000111	100
<i>Neohydrocoptus</i> sp. (Zambia)	1100000000	1111100110	0100000111	100
<i>Pronoterus</i> sp.	1110000010	1111100110	1101010201	010
<i>Mesonoterus crassicornis</i>	1110000000	1111101001	1100010301	110
<i>Mesonoterus grandicornis</i>	1110000000	1111101001	1100010301	110
<i>Noterus clavicornis</i>	1100000001	1111112101	1100000001	010
<i>Noterus laevis</i>	1100000001	1111112101	1100000001	010
<i>Renotus deyrolle</i>	1110000100	1??1112001	11000100??	???
<i>Canthydrus morsbachi</i>	1110100120	1111112001	1100110001	010
<i>Canthydrus luctuosus</i>	1110100120	1111112001	1100110001	010
<i>Liocanthydrus</i> sp.	1110000110	1111112001	1101110201	010
<i>Suphisellus puncticollis</i>	1111010110	1111112001	1101110201	010
<i>Suphisellus</i> sp.	1111010110	1111112001	1101110201	010
<i>Hydrocanthus sharpi</i>	1110100101	1111112001	1101110001	010
<i>Hydrocanthus iricolor</i>	1110100101	1111112001	1101110001	010
<i>Hydrocanthus debilis</i>	1110100101	1111112001	1101110001	010
<i>Hydrocanthus</i> sp. (Zambia)	1110100101	1111112001	1101110001	010
<i>Suphis cimicoides</i>	1110011100	1111012000	1100100201	110
<i>Suphis fluviatilis</i>	1110011100	1111012000	1100100201	110
<i>Siolius</i> sp. 1	1110000100	1111112001	1100110000	011
<i>Siolius</i> sp. 2	1110000100	1111112001	1100110000	011

Table 1 Taxa, characters and character states analysed in phylogenetic analysis of Noteridae. Character 17 is treated as additive.

Multiple representatives of most genera were examined to assess variation within genera and to test monophyly of genera to the extent possible. A single specimen of *Speonoterus* Spangler was examined (apparently female paratype, USNM), but it was not dissected, and so internal features were not coded for this taxon. Only male specimens of *Renotus* Guignot were available for examination. Because several noterid genera (e.g. *Pronoterus* Sharp, *Siolius* Balfour-Browne, *Nehydrocoptus* Sâto) have not been adequately revised, and there appear to be numerous new species in some of these groups, specimens examined were not always identifiable to species. Nomenclature for Noteridae follows Nilsson (2005), and that work should be examined for more extensive treatment of noterid names. Several representatives from Dytiscidae, Amphizoidae and Paelobiidae (other groups in the Dytiscoidea) were included as outgroup taxa (see Table 1), and the resulting trees were rooted between these other Dytiscoidea and Noteridae based on evidence from several studies (most recently Beutel *et al.* (2006)) that Noteridae is sister to a clade containing these other dytiscoids.

Morphology. Methods of morphological examination (including dissection and preparation of female genitalia) followed closely the methods of Miller (2001). Entire specimens of all examined taxa except *Speonoterus* and *Renotus* were cleared to more extensively examine morphological features.

Parsimony analysis. The data matrix was created and edited using WinClada (Nixon, 2002), and data were analysed using NONA (Goloboff, 1995) as implemented in WinClada. The commands 'hold 10000', 'hold/50', 'mult*100' and 'max*' were used to find the most parsimonious trees. Character state optimisations were examined using WinClada. Trees were viewed and summarised in WinClada. Bremer support values (Bremer, 1994) were calculated in NONA using the commands 'hold 10000', 'suboptimal = 10' and 'bsupport = 10'. Bootstrap support values were calculated in NONA with 1000 replications and saving the consensus of each replication.

Characters. The 33 characters coded for the analysis are described below, and coded states are presented in Table 1.

Several of these characters have been used extensively in historical classifications of the family. Others have been used in previous phylogenetic analyses (specifically Beutel & Roughley, 1987; Belkaceme, 1991; Beutel *et al.*, 2006) and these papers are recommended for additional description and illustration of many of these characters. Several additional characters, however, are new, particularly those from the female genitalia. All new characters are illustrated and described in greater detail than other characters. Character 17 was treated as additive with all others treated as non-additive.

A number of characters included in other analysis focused on or including a number of Noteridae (specifically Beutel & Roughley, 1987 and Beutel *et al.*, 2006) were not included here. In Beutel *et al.* (2006), characters 10 and 12 (*Expansion of antennomeres 5 and 9*) were not included since these features appear to be gradational or indistinct across the species included in this analysis. Characters 72 and 84 were not included since they are of limited value in resolving groups within Noteridae. Other characters in Beutel *et al.* (2006) useful within Noteridae are mainly larval characters which were not surveyed for this study, and could not be confirmed. The larva of *Tonerus* is not known. Certain characters included by Beutel and Roughley (1987) also were not included in this study. This includes their character 4 (*Profemoral excavation*) which they regard as a synapomorphy of Noteridae, but which appears to be more variable within Adephaga than they indicate, and, in any case, does not appear to provide grouping information within the Noteridae. Their character 13 (*Swimming hind legs*) is interpreted differently here. *Phreatodytes* was not examined, but *Notomicrus*, which they regard as lacking swimming modifications to the hind legs, appears to have natatory setae and other swimming adaptations.

Head

1. *Midgular apodeme* (char. 2 Beutel & Roughley, 1987): (0) absent, (1) present (Fig. 2). A midgular pit corresponding to an internal apodeme is present in Amphizoidae and all Noteridae except *Notomicrus* and *Speonoterus*.
2. *Scape* (char. 1 Beutel & Roughley, 1987): (0) simple, (1) pseudosegmented. State 1 is characteristic of Noteridae as described and illustrated by Beutel and Roughley (1987).
3. *Sensorial field at apex of labial palp* (char. 20, Belkaceme, 1991; char. 18 Beutel *et al.*, 2006): (0) rounded, (1) elongate and narrow. The noterids *Notomicrus*, *Speonoterus*, *Neohydrocoptus* and *Noterus* have the sensorial field rounded (0), all others (including *Tonerus*) have this field elongate and very slender (1).

Prothorax

4. *Crease at posterolateral angles of pronotum*: (0) absent (Fig. 3A), (1) present (Fig. 3B). State 1 has long historically defined *Suphisellus* and was only found in that taxon in this study.
5. *Lateral pronotal margins*: (0) not serrate, (1) serrate (Fig. 3A). Small serrations on the lateral pronotal margins (Fig. 3A) are present in Old World *Canthydrus* (though

not in the New World subgenus *Liocanthydrus*) and *Hydrocanthus*.

6. *Pronotum lateral bead*: (0) narrow (Fig. 3B), (1) broad (Fig. 3A). A relatively narrow lateral bead is present in *Suphis* and *Suphisellus* (Fig. 3B). A broader lateral bead is present in other Noteridae (Fig. 3A).
7. *Prosternum*: (0) longitudinally broad (Figs 2, 4A–F), (1) longitudinally extremely short, abruptly curved (Fig. 4G). State 1 is characteristic of *Suphis* (Fig. 4G).
8. *Prosternal process*: (0) narrow, apically pointed or rounded, widest near middle (Fig. 4A–D), (1) broad, apically broadly truncate, widest at or very near apex (Figs 2, 4E–G). This character roughly corresponds to char. 3 of Beutel and Roughley (1987), char. 35 of Belkaceme (1991) and char. 20 of Beutel *et al.* (2006) with some reassessment of homology. There are several different prosternal process shapes exhibited within Noteridae which are, in my estimation, difficult to homologise and difficult to quantify. The assessment included here reflects a general feature of the shape of the prosternal process and reflects most closely the assessment by Belkaceme (1991).
9. *Prosternal setae*: (0) absent or inconspicuous (Figs 3, 4A, B, D, F, G), (1) prominent series of stiff setae medially (Fig. 4C,E), (2) extensive field of stiff setae over most of prosternum and prosternal process. The prosternum has a distinct series of posteriorly directed stiff setae medially in species of *Pronoterus* (Fig. 4C), *Suphisellus* (Fig. 4E), and *Liocanthydrus*. *Canthydrus* (not *Liocanthydrus*) has an extensive field of stiff setae over much of the prosternal surface, but without a consolidation of these setae into a distinct series. Nevertheless, this is characteristic of those *Canthydrus* examined and appears to be a distinct state.
10. *Anteromedial apex of prosternum*: (0) not produced into hook, (1) produced as prominent hook (Fig. 3A). When viewed in lateral aspect the anteromedial margin of the prosternum is produced into a distinctive posteriorly directed hook in species of *Hydrocanthus* (Fig. 3A) and *Noterus*.

Metathorax

11. *Paramedian angle on anterior metacoxal phragma* (char. 8, Beutel & Roughley 1987): (0) absent, (1) present (Figs 2, 3). The anterior margin of the metacoxa has a distinct angle which corresponds to a prominent internal apodeme in all Noteridae (Figs 2, 3).
12. *Anterior portion of medial metacoxal phragma* (char. 9, Beutel & Roughley, 1987): (0) not extending anteriorly beyond origin of metacoxal furca, (1) extending anteriorly beyond origin of furca (Fig. 5A). The fused medial phragma form a process that extends anteriorly in all Noteridae (Fig. 5A).
13. *Metafurca fusion with metacoxa*: (0) not fused, (1) fused laterally with metacoxa forming complete ring (Fig. 5). The lateral arms of the metafurca are fused with the metacoxa laterally in an elongate strap making a continuous ring (Fig. 5) in all examined Noteridae except *Notomicrus* (*Speonoterus* was not examined for this character).

According to Balfour-Browne (1961) (and cited by Beutel & Roughley (1987), character 12) this fusion is not present in *Siolius*, but in the species of *Siolius* examined for this study it clearly is.

14. *Noterid platform*: (0) absent, (1) present (Figs 2, 4). The 'noterid platform' describes a characteristic shape of the medial portion of the metacoxae. The medial portions of the metacoxae together occur ventrad of the lateral portions with the lateral margins nearly straight to triangular or rounded apical lobes. This feature is difficult to describe or quantify in any meaningful way, but it is a characteristic common throughout Noteridae and not found in similar form in other Hydradephaga (Beutel & Roughley, 1987; Belkaceme, 1991; Beutel *et al.*, 2006).
15. *Extension of noterid platform onto metaventrte*: (0) not extended onto metaventrte, (1) extended onto metaventrte (Figs 4B–F). Noterids except *Notomicrus*, *Speonoterus* and *Suphis* have a distinct lateral margin of the metaventrte that is (or is nearly) continuous with the noterid platform described in Char. 14. Although regarded by Belkaceme (1991) and others as extending onto the metaventrte in *Suphis*, this does not really seem to be the case (Fig. 4G).

Legs

16. *Attachment of protarsus to protibia*: (0) apically (Fig. 6A–E), (1) laterally (Fig. 6F–K). In several noterid genera the protibia extends well beyond the base of the protarsus (Fig. 6F–K) whereas in the others the protarsus arises near the apex of the protibia (Fig. 6A–E).
17. *Apical protibial spurs*: (0) Multiple elongate spines (Fig. 6A–D), (1) a single, moderately large curved spine (Fig. 6E), (2), a single, extremely robust, curved spine (Fig. 6F–K). This character has a long history of use in classifying noterid genera and use in studying their phylogenetics (Belkaceme, 1991; Beutel *et al.*, 2006). Several genera have several apical spines on the protibia (Fig. 6A–D). Although some of these spines are more curved or more robust than others they are not, however, similar to the other two states. State 1 is characteristic of *Mesonoterus* which have a single, prominent spine that is apically slightly curved (Fig. 6E). The genera with state 2 have a single, robust, curved spine (Fig. 6F–K) that has been implicated in burrowing in some taxa (Dettner, 2005; Roughley & Larson, 2001). Whether they actually burrow extensively is not, however, well established. The spine is correlated with a characteristic furrow and/or pit on protarsomere I to receive the spine and its curved apex. This was also used as a phylogenetic character by Beutel *et al.* (char. 36, 2006). The spine and the furrow/pit appear to be closely correlated with *Mesonoterus* bearing a stout spine and a furrow and other taxa with a large, curved spine and a furrow and deep pit for the apex of the spine. Only a single character was included for this analysis with the assumption that the features are not independent.
18. *Posterior protibial spur* (char. 28, Belkaceme, 1991; char. 33, Beutel *et al.*, 2006): (0) absent, (1) present. The posterior protibial spine is absent in noterid genera except *Notomicrus*, *Speonoterus*, *Tonerus*, *Neohydrocoptus*, *Pronoterus* and *Noterus*.
19. *Protibia dorso-apical angle* (char. 35, Beutel *et al.*, 2006): (0) not distinct, rounded (Fig. 6E–J), (1) distinct, angulate (Fig. 6A–D). In some taxa the dorso-apical angle of the protibia is distinct and angulate (Fig. 6A–D), whereas in others this area of the protibia is rounded without an obvious angle (Figs 6E–J). This character has been used extensively in classifying Noteridae.
20. *Fringe of short setae along dorsal and anterior apical margins of protibia*: (0) absent (Fig. 6A–D, J), (1) present (Fig. 6E–I, K). This character was included by Beutel *et al.* (2006) but further refined. Their character (char. 34, 'Extended towards proximal part of tibia') was not coded similarly here since this state was not clearly evident in the taxa examined as they described it.
21. *First tarsomere on male pro- and mesotarsi* (char. 6, Beutel & Roughley, 1987; char. 50, Beutel *et al.*, 2006): (0) not elongate or apically expanded, (1) elongate and apically expanded (incrassate). Character state 1 (especially in the mesotarsi) occurs in all noterids examined except *Notomicrus*, *Tonerus* and *Neohydrocoptus*.
22. *Short, curved setae along posterior margins of protarsomeres I–III* (char. 16, Belkaceme, 1991; char. 37, Beutel *et al.*, 2006): (0) absent, (1) present. Members of Noteridae except *Notomicrus* and *Speonoterus* have these spines present (Spangler, 1996).
23. *Metacoxal fusion with metaventrte* (char. 7, Beutel & Roughley, 1987): (0) not fused with metaventrte laterally (Figs 2, 4B–G), (1) fused with metaventrte laterally, suture obscured (Fig. 4A). Members of *Notomicrus* and *Speonoterus* have the metacoxa fused with the metaventrte laterally (Spangler, 1996). The suture is evident medially. Other taxa have the suture complete between these two sclerites.
24. *Anterior metatibial spur*: (0) not serrate, (1) serrate (Fig. 7). Members of *Pronoterus*, *C. (Liocanthyrus)*, *Suphisellus* and *Hydrocanthus* have the anterior, larger metatibial spur minutely but distinctly serrate (Fig. 7). This character was specifically excluded by Beutel *et al.* (2006) but it does seem to be informative among Noteridae.
25. *Series of elongate, closely placed setae at antero-ventral angle of metafemur*: (0) absent, (1) present (Fig. 7). This character has been used historically in classifying Noteridae genera. Although most noterids have a series of stiff setae along the anteroventral margin of the metafemur, in several taxa they are developed apically into a series of more elongate, closely placed setae at the anteroventral angle (Fig. 7).
26. *Cluster of setae at apex of medial metacoxal lobe* (char. 69, Beutel *et al.*, 2006): (0) absent (Fig. 2, 4A, B, G), (1) present (Fig. 4C–F). The apical angle of the medial portion of the metacoxae in some taxa has a cluster of setae (Fig. 4C–F). Other taxa have this area without setae (Fig. 2, 4A, B, G).

27. *Metacoxa*: (0) not expanded anteriorly in broad lobe, (1) expanded anteriorly in broad lobe. Members of Dytiscidae have the lateral portions of the metacoxae extended in a broad lobe anteriorly, presumably providing for greater surface area for the origin of the large metacoxal swimming muscles. This feature is a synapomorphy of Dytiscidae (Miller, 2001). Members of Noteridae have this margin also curved anterad, but not as dramatically so and this modification looks different from that in Dytiscidae (Figs 2, 4).

Abdomen

28. *Apex of pygidium*: (0) unmodified, (1) with narrowed, up-curved apex (Fig. 8A, B), (2) with deep longitudinal depression and retractable hook (Fig. 8C, D), (3) apically narrowed, with medial spine (Fig. 8E). *Neohydrocoptus* has character state 1, state 2 appears to be characteristic of several taxa including *Pronoterus*, *Suphis*, *C. (Liocanthydus)* and *Suphisellus*, and state 3 is characteristic of *Mesonoterus*. See discussion below for more detailed explanation of this character.

Female genitalia

29. *Apex of gonocoxa*: (0) simple, (1) bilobed (Fig. 9). Members of *Neohydrocoptus* have the gonocoxa distinctly bilobed apically (Fig. 9).
30. *Laterotergites*: (0) not extremely long (Figs 9–12), (1) extremely long, anterior portion expanded (Figs 13–19). In some Noteridae the laterotergite is exceptionally long and slender with the anterior apex broadly expanded (Figs 13–19) presumably for attachment of muscles. Other Noteridae, including *Notomicrus*, *Tonerus* and *Siolius* have the laterotergite considerably shorter (Figs 9–12).
31. *Lateral margin of gonocoxae*: (0) not dentate (Figs 10–13, 15, 17–19), (1) dentate (Figs 9, 14, 16). Several noterid taxa including *Neohydrocoptus*, *Mesonoterus* and *Suphis* have the ventrolateral margin of the gonocoxa distinctly dentate (Fig. 9, 14, 16). Noterids apparently oviposit endophytically, and these denticles may be related to this syndrome.
32. *Gonocoxae*: (0) apically rounded (Figs 9–11), (1) together elongate, sharply pointed (Figs 12–19). *Neohydrocoptus*, which have the apex of the gonocoxa bilobed (Char. 26), are also coded as having character state 0 (Fig. 9).
33. *Laterotergites*: (0) not extending posteriorly beyond bases of gonocoxae (Figs 9, 13–19), (1) extending posteriorly beyond bases of gonocoxae (Figs 10–12). In most Noteridae the laterotergites articulate and originate at the base of the gonocoxae and extend only anteriorly when at rest (Figs 9, 13–19). In other taxa, the laterotergites articulate at the base of the gonocoxae and extend anteriorly but also extend posteriorly along the gonocoxae (Figs 10–12). This approaches the condition found in other Dytiscoidea (Amphizoidae, Hygrobiidae and Dytiscidae) wherein the laterotergites extend primarily posteriorly from the base of the gonocoxae, in some cases apparently forming a hinged apparatus for oviposition (Miller, 2001).

Results

The analysis resulted in a single parsimonious tree (Fig. 20, Length = 57, CI = 64, RI = 92). Noteridae is resolved as monophyletic with high support. Historical groups tested and found to be monophyletic in this analysis include Noteridae, Neohydrocoptini and each genus tested except *Canthydrus*. Noterini is monophyletic with the exception of *Speonoterus*, placed in Noterini by Nilsson (2005), but near *Notomicrus* by Spangler (1996) and Beutel *et al.* (2006). It is resolved as sister to *Notomicrus* in this analysis. The clade *Notomicrus* + *Speonoterus* is sister to the rest of Noteridae. The new taxon, *Tonerus* (see below) is resolved as sister to Noteridae except *Notomicrus* + *Speonoterus*. *Neohydrocoptus* and *Pronoterus* are each resolved in isolated positions in the phylogeny. *Canthydrus* was found to be polyphyletic with the Old World *Canthydrus sensu stricto* sister to *Hydrocanthus* and New World *Canthydrus (Liocanthydus)* sister to *Suphisellus*.

Support values are relatively high for relationships within Noteridae including the clades corresponding to the family, subfamily and tribes, including relationships of *Tonerus* with other taxa. Values for clades corresponding to genera within Noterini are relatively high, but relationships among those clades are not well supported, similar to findings by Beutel *et al.* (2006).

Discussion

Noteridae character evolution

Many of the characters important for the relationships and classification of the Noteridae are found in the front legs. These include the large, curved protibial spur that fits into a furrow and pit in protarsomere I (Figs 6E–K). This is derived from a condition of multiple spines along the entire anterior margin of the protibia (Figs 6A–D). The single spur in *Mesonoterus* is not as greatly enlarged nor as strongly curved and represents an intermediate condition (Fig. 6E). *Mesonoterus* also retains the plesiomorphic state of having the protarsus originating near the apex of the protibia (Fig. 6E) instead of on its side (as in Fig. 6F–K). A fringe of short setae along the margin of the protibia is also a derived condition (Fig. 6E–I, K). The greatest modification to the protibia is in the unusual genus *Suphis* in which the spur is exceptionally large and curved and there is secondary reduction in the setal fringe among other shape variation (Fig. 6J).

Among the most intriguing of characters examined here is in the apical abdominal tergum (tergum VIII). In *Neohydrocoptus*, there is a distinct, upturned process apically on this sclerite (Fig. 8A, B). In *Mesonoterus*, there is a longitudinal reinforced spine that terminates the tergum in an acuminate apex (Fig. 8E). This structure appears to be correlated with an elongate spinous process at the apex of abdominal sternum VI. This was not coded separately for the analysis since the two may be correlated. The most dramatic modification, however, occurs in several taxa with greatest development in *Pronoterus*. In these taxa there is a longitudinal groove in the dorsal surface of the tergum with an apical, retractable ‘claw’ with strong extensor

muscles attached at its base (Fig. 8C, D). This feature occurs in both sexes of taxa in which it is expressed, although in some taxa (e.g. *Suphis*) it is greatly reduced (but still evident). This character has never been previously described, and its function is not clear. Some noterids are thought to acquire oxygen from submerged plant vacuoles, at least as larvae (Roughley, 2001; Dettner, 2005), and it is possible that it functions in some way correlated with that behaviour, but this remains to be seen.

The female genitalia in Noteridae, in general, is not as variable as it is across Dytiscidae (Miller, 2001). There are, however, several informative features associated with its morphology. Plesiomorphic conditions include having apically rounded gonocoxae (Figs 9–11), short laterotergites (Figs 10, 11), and the laterotergites extending posteriorly beyond the bases of the gonocoxae (Figs 10, 11). Derived states include apically sharply pointed gonocoxae (Figs 12–19), exceedingly long laterotergites that are generally strongly expanded anteriorly (presumably forming the surface for attachment of large muscles; Figs 9, 13–19, reversed in *Siolius*, Fig. 12), and laterotergites extending only anteriorly from their attachments with the gonocoxae (Figs 9, 13–19, reversed in *Siolius*, Fig. 12). There are several independent derivations of serrations on the ventro-lateral margins of the gonocoxae (Figs 9, 14, 16). These modifications suggest increasing development of features related to endophytic oviposition.

Noteridae relationships and classification

With the addition and reinterpretation of morphological features, the resulting relationships from this analysis are similar to results from previous analyses. Congruent with Beutel and Roughley (1987) *Notomicrus* (along with *Speonoterus*) was found to be sister to the remaining Noteridae (excluding *Phreatodytes*) with *Neohydrocoptus* sister to noterids except *Notomicrus*, and *Pronoterus* sister to the remaining taxa (Fig. 20). With the addition of *Tonerus* as sister to Noteridae except *Notomicrus* + *Speonoterus* (excluding *Phreatodytes*) the main differences between this analysis and those by Belkaceme (1991) and Beutel *et al.* (2006) and the summary by Nilsson (2005) is in the Noterini (Figs 20, 21). In this analysis, *Canthydrus* is polyphyletic with *Liocanthydrus* sister to *Suphisellus* and *Canthydrus* sister to *Hydrocanthus*. Also, *Suphis* is resolved as sister to the clade *Liocanthydrus* + *Suphisellus*. In both Belkaceme (1991) and Beutel *et al.* (2006) these groups were not well resolved in general (Figs 2, 3).

Based on the results indicated above, Noteridae comprises three subfamilies, Phreatodytinae, Notomicrinae and Noterinae, the first two each with a single tribe and the last with four tribes (one new), supported by relatively high Bremer and bootstrap values. The main changes from the most recent classification (Nilsson, 2005) are placement of *Speonoterus* in the Notomicrinae (probably simply a mistake since this genus was clearly placed near *Notomicrus* by Spangler (1996) and Beutel *et al.* (2006)) and recognition of the new tribe Tonerini to include the new genus and new species described herein. In addition, numerous new apomorphies were discovered for many groups strengthening taxonomic concepts within the family.

The classification, of the family- and genus-groups of Noteridae, and character combinations are reviewed below.

Family Noteridae Thomson, 1860

Noterides Thomson, 1860

Type genus. *Noterus* Clairville, 1806.

Diagnosis. Noteridae are defined by the following synapomorphies: (1) the anterior margin of the metacoxal phragma extends anteriorly beyond the origin of the metacoxal furca (Fig. 5A, not confirmed in Phreatodytinae, see Beutel and Roughley (1987)), (2) the noterid platform is present (Figs 2, 3A–F), and (3) the scape is pseudosegmented. This last character was established by Beutel and Roughley (1987) as a synapomorphy of the family.

Comments. Members of the family Noteridae are, in most cases, phenetically similar to each other. They are dorsally relatively convex and ventrally flattened. They also tend to be broadest near the base of the pronotum, relatively broad anteriorly toward the head and tapered posteriorly toward the elytral apices, though, of course, this does not hold true in all cases. Discrete characters defining the group are more difficult to find and are less convincing, particularly with the inclusion of *Notomicrini* (*Notomicrus* and *Speonoterus*, see below), though Beutel and Roughley (1987) persuasively established this relationship.

Subfamily Phreatodytinae Uéno, 1957

Phreatodytidae Uéno, 1957

Type genus. *Phreatodytes* Uéno, 1957.

Diagnosis. Members of this subfamily are characterised by the following character combination: (1) metaventrite small, (2) eyes absent, (3) long sensory hairs present on the pronotum and elytra, (4) without curved apical protibial spur, (5) apico-dorsal angle of protibia angulate and prominent, (6) fringe of setae absent on antero-dorsal margin of protibia, (7) protarsomere I short and (8) paramedian angle of anterior metacoxal wall absent.

Relationships. According to Beutel and Roughley (1987), Belkaceme (1991) and Beutel *et al.* (2006), this subfamily is sister to all other Noteridae.

Comments. Members of this group are subterranean and appear to be modified in ways typical of subterranean aquatic Adephegagan beetles (e.g. eyes absent, sensory hairs long, reduced swimming features, (Uéno, 1996)). They are known from several species in Japan. After reviewing their distinct combination of character states, many of which appear to be plesiomorphic, Beutel and Roughley (1987) placed the group as sister to the rest of Noteridae, and recent work by Beutel *et al.* (2006) has confirmed this.

Phreatodytes Uéno, 1957

Phreatodytes Uéno, 1957

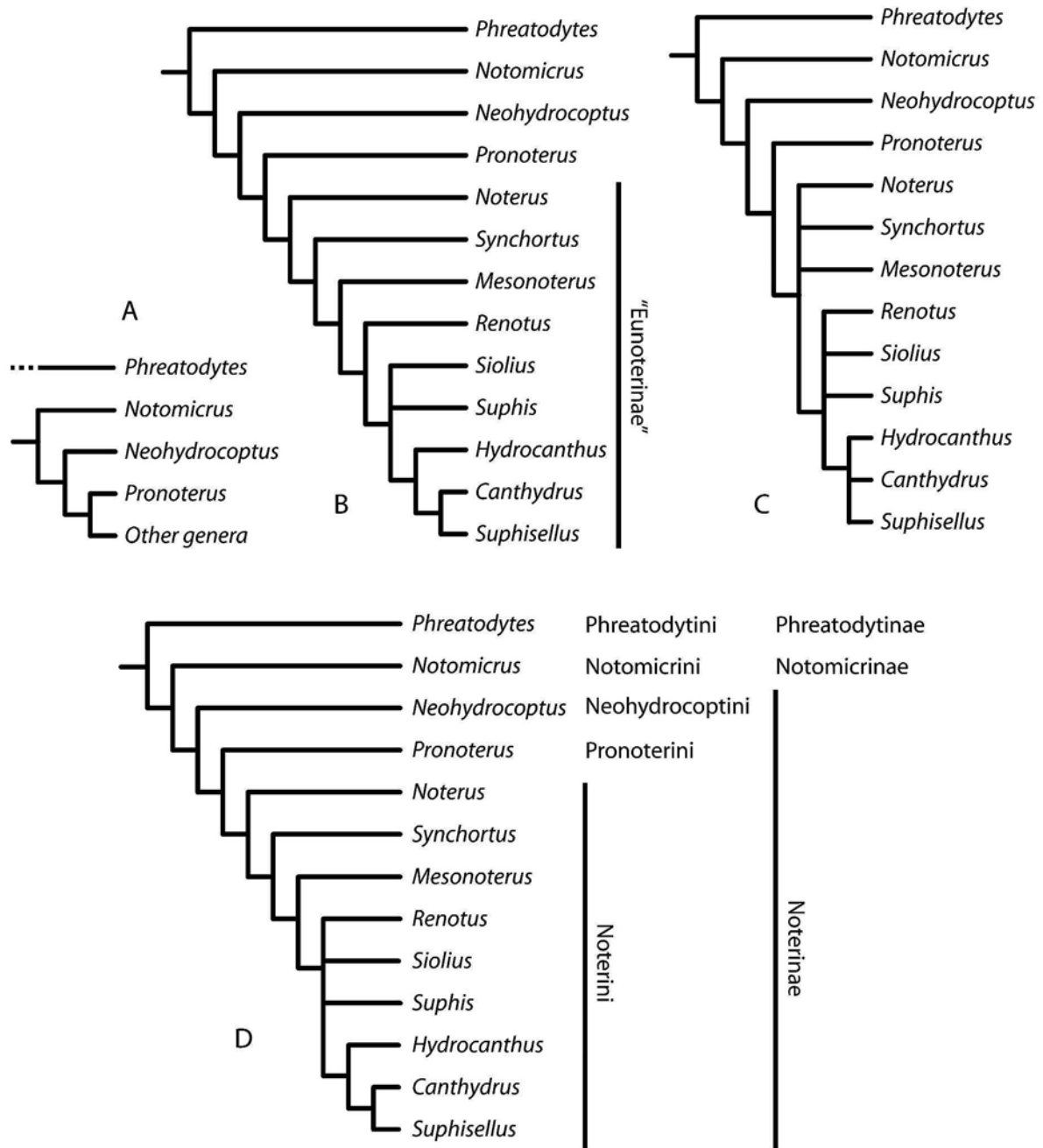


Figure 1 Summary trees depicting published phylogenetic hypotheses for Noteridae. A – Beutel and Roughley (1987). B – Belkaceme (1991). C – Beutel *et al.* (2006). D – Nilsson (2005).

Type species. *Phreatodytes relictus* Uéno, 1957 by original designation.

Diagnosis. This is the only genus in this subfamily and is characterised by its diagnostic combination (see above).

Distribution. Six species of this distinctive group occur in Japan in subterranean habitats.

Subfamily Notomicrinae Zimmermann, 1919

Notomicrini Zimmermann, 1919

Type genus. *Notomicrus* Sharp, 1882

Diagnosis. The primary synapomorphy uniting the two genera in this tribe is the partial fusion of the metacoxa and metaventrite (Fig. 4A). Other than this, the group is mainly characterised by plesiomorphies such as: (1) the metafurca and metacoxa are not fused laterally and do not form a complete ring, (2) the noterid platform does not extend anteriorly onto the metaventrite (Fig. 4A) and (3) the female laterotergite is short and extends posteriorly well beyond the base of the gonocoxa (Fig. 10). These noterids are extremely small (TL = 1.0–1.7 mm).

Relationships. This subfamily is sister to all other Noteridae (Noterinae, Figs 20, 21) except Phreatodytinae

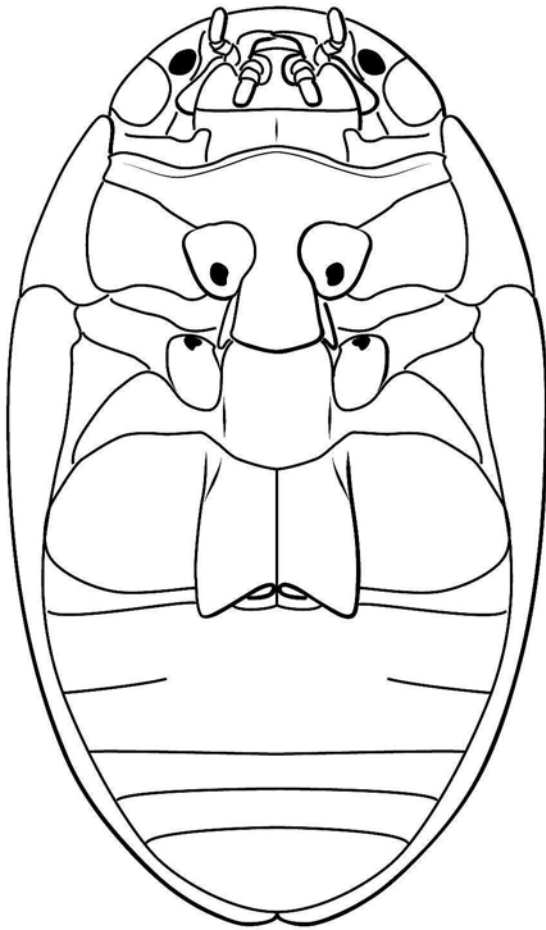


Figure 2 *Tonerus wheeleri*, ventral habitus. Scale bar = 1 mm.

(Beutel & Roughley, 1987; Belkaceme, 1991; Beutel *et al.*, 2006).

Comments. Beutel and Roughley (1987) defined the concept of this group based on *Notomicrus* as a plesiomorphic member of the Noteridae. The inclusion of *Speonoterus* (not examined by Beutel and Roughley (1987) since it was not yet described) is a revision of its placement based on Nilsson (2005) who put it in Noterinae, perhaps simply mistakenly since Spangler (1996) placed it clearly near *Notomicrus*. Although not specifically included in the analysis by Beutel *et al.* (2006), they did discuss many of the character states exhibited by *Speonoterus* and placed it as sister to *Notomicrus*. These are among the smallest of all water beetles with some *Notomicrus* about 1.0 mm in total length and none over 2.0 mm (Young, 1978). They are primarily tropical with representatives in southeastern North America, much of South America, Australia and Southeast Asia.

Speonoterus Spangler, 1996

Speonoterus Spangler, 1996

Type species. *Speonoterus bedosae* Spangler, 1996 by original designation.

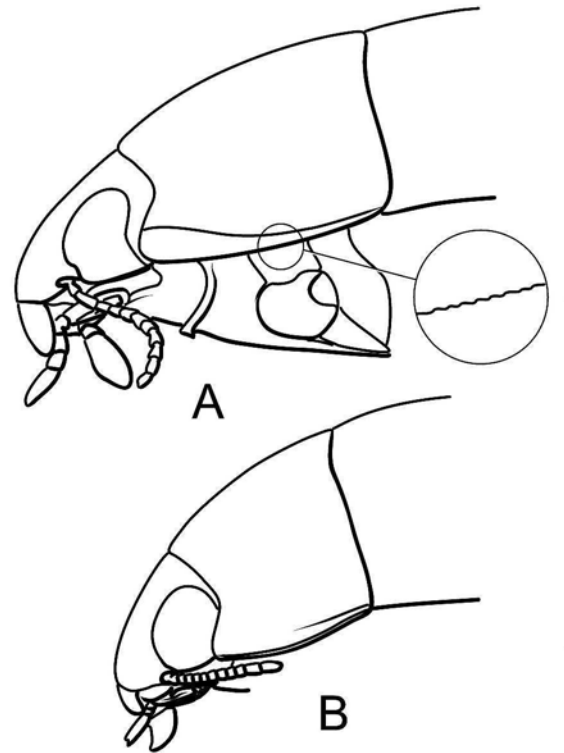


Figure 3 Noteridae species, head, pronotum and base of elytron, left lateral aspect. A – *Hydrocanthus iricolor*; B – *Suphisellus* sp. Scale bar = 1 mm.

Diagnosis. Within Notomicrini this genus is similar to *Notomicrus*, but has the eyes absent and has other characters associated with a subterranean habitat such as light sclerotisation, depigmentation, aptery, etc.

Relationships. This genus is sister to *Notomicrus* (Figs 20, 21).

Distribution. *Speonoterus* is known from a single Indonesian species.

Comments. This genus was originally described in Notomicrinae (Spangler, 1996) but placed in Noterinae by Nilsson (2005) (perhaps mistakenly). The small size of its members, the fusion of the metacoxa and metaventrite, and presence of numerous plesiomorphies clearly associate it with *Notomicrus*. Only a single specimen (apparently female paratype) was available for study (USNM), so internal characters and those of the female genitalia were not examined.

Notomicrus Sharp, 1882

(Figs 5, 14, 34)

Notomicrus Sharp, 1882

Type species. *Notomicrus brevicornis* Sharp, 1882 by subsequent designation of Guignot (1946).

Diagnosis. Within Notomicrini this genus differs from *Speonoterus* in having fully developed eyes and other characters

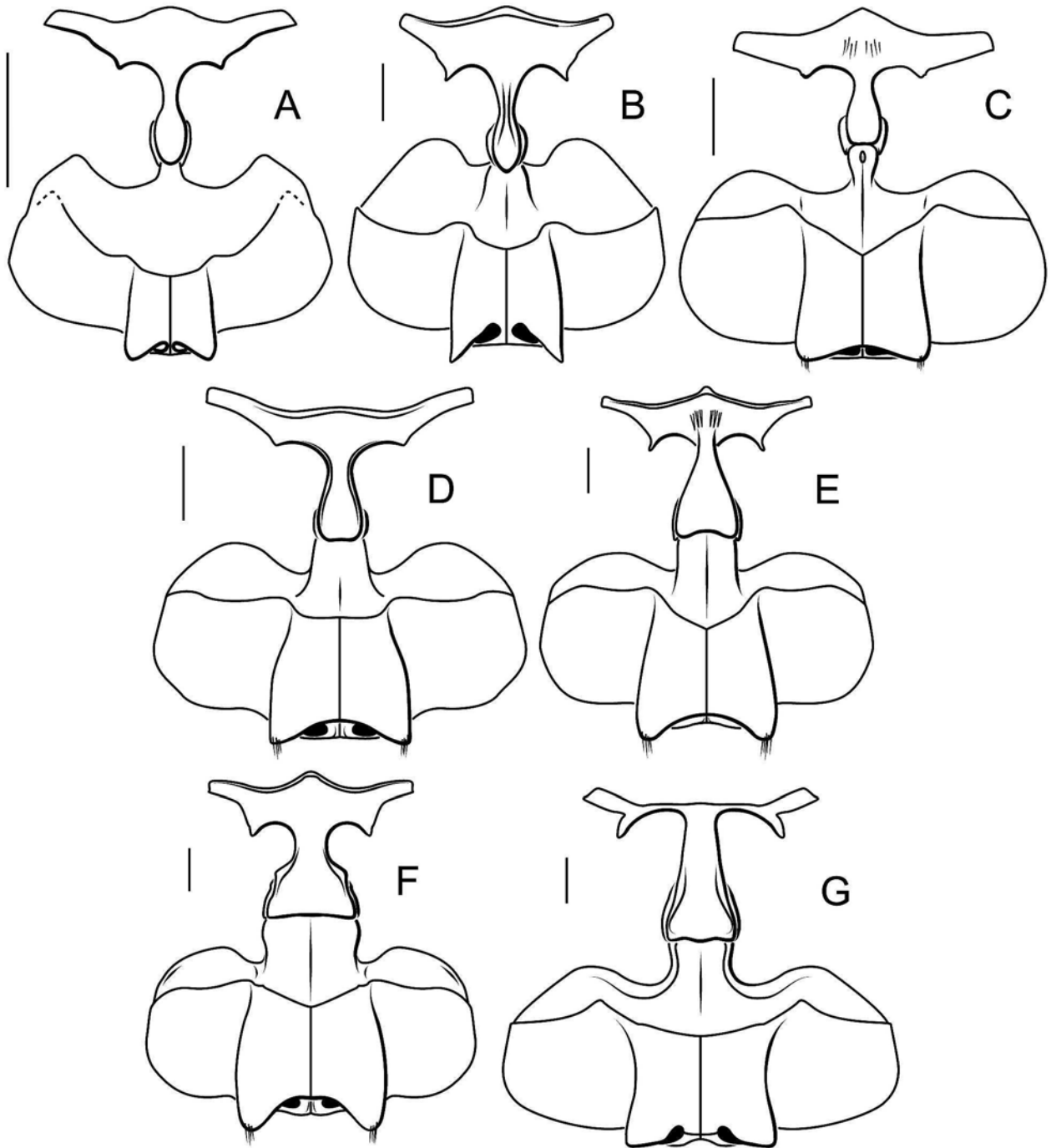


Figure 4 Noteridae species, Prosternum, mesoventrite and metacoxae. A – *Suphis cimicoides*. B – *Notomicrus* sp. C – *Neohydrocoptus bivittus*. D – *Pronoterus* sp. E – *Mesonoterus crassicornis*. F – *Suphisellus* sp. G – *Hydrocanthus iricolor*. Scale bars = 0.25 mm.

associated with a typical freshwater aquatic habitat rather than subterranean habitat.

Relationships. This genus is sister to *Speonoterus* (Figs 20, 21).

Distribution. Species assigned to this genus are found in North and South America, Australia and Southeast Asia.

Comments. This genus, because of its numerous plesiomorphies, was long uncertainly placed within Adephaga until Beutel and Roughley (1987) reviewed the problem and persuasively placed it within Noteridae.

Subfamily Noterinae Thomson, 1860

Noterides Thomson, 1860

Type genus. *Noterus* Clairville, 1806.

Diagnosis. This subfamily is characterised by the following character combination: (1) the metafurca and the metacoxa are fused laterally in a narrow band forming a complete ring (Fig. 5) and (2) the noterid platform extends anteriorly on the metaventre (Figs 2, 4A–F; secondarily lost in the genus *Suphis*, Fig. 4G).

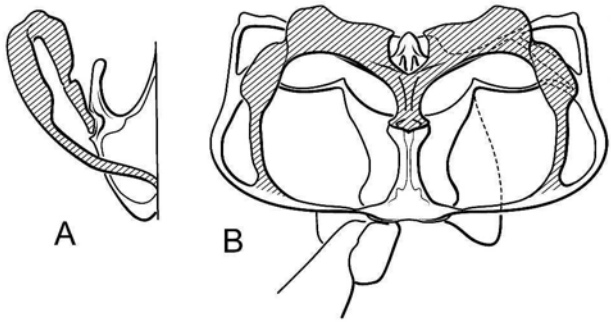


Figure 5 *Hydrocanthus iricolor*. A – metafurca, right lateral aspect. B – metafurca, dorsal aspect. Scale bar = 0.25 mm.

Relationships. This subfamily is sister to Notomicrinae (Figs 20, 21).

Comments. This is the largest subfamily in the family, and it includes the most commonly encountered Noteridae. Its members range in size from very small to relatively large (~7 mm), and although many in the group are often superficially very similar in appearance, there is a relatively high degree of morphological variability. The subfamily is divided into four tribes, one of them new.

Tonerini Miller, tr. nov.

Type genus. *Tonerus* Miller, gen. nov. by present designation.

Diagnosis. This new tribe has the following diagnostic combination of characters: (1) the metacoxa and metafurca are fused laterally forming a complete ring (as in Fig. 5), (2) the noterid platform extends anteriorly onto the metaventrite (Fig. 2), (3) the female laterotergites are short with the anterior apex not broadly expanded and the posterior apex extending posteriorly well beyond the bases of the gonocoxae (Fig. 11), and (4) the gonocoxae are apically rounded, not pointed (Fig. 11).

Relationships. This tribe is sister to the remaining Noterinae (Figs 20, 21).

Comments. Members of this group are similar in general appearance to members of Noterini in having a broad prosternal process and a similar habitus (Figs 2, 22). However, the female genitalia (specifically the ovipositor, Fig. 11) are plesiomorphic and much more similar to other members of Dytiscoidea than Noterini. Also, the protarsus is attached at the apex of the protibia (Fig. 6C), there is a distinct dorso-apical protibial angle (Fig. 6C); there are several moderately stout spines at the apex of the protarsus rather than a single prominent curved spur (Fig. 6C).

Tonerus Miller, gen. nov.

(Figs 2, 6C, 11, 22, 23)

Type species. *Tonerus wheeleri* Miller, new species by present designation.

Diagnosis and description. This is the only genus in the tribe and is characterised by its diagnostic combination (see above).

Etymology. '*Tonerus*' is an arbitrary rearrangement of the letters included in the name of the type genus of the Noteridae, *Noterus*.

Tonerus wheeleri Miller, sp. nov.

(Figs 2, 6C, 11, 22, 23)

Type locality. Venezuela, T. F. Amazonas [=Estado Amazonas], 40 km S Puerto Ayacucho, El Tobogán, Caño Coromoto.

Diagnosis. This species is the only one in the genus. In addition to the features characterising the genus and tribe (see above), members of the species have the following characteristics which may represent species-level states: (1) the body is broadly ovate and robust with continuous lateral margins and broadly rounded anterior and posterior apices (Fig. 22), (2) the elytron is dark to light red or reddish-yellow, usually with characteristic diffuse black areas laterally, medially, and broadly along the suture to the apex (Fig. 22), (3) the male median lobe has a deep, twisted ventral groove, is broadly curved in lateral aspect to the abruptly narrowed and narrowly rounded apex, and is moderately slender in ventral aspect to the narrowly rounded apex (Fig. 23).

Description. *Measurements* (in mm). TL = 2.12–2.46; GW = 1.23–1.31; PL = 0.54–0.64; PW = 1.16–1.25; HW = 0.78–0.82; EW = 0.49–0.54; FW = 0.21–0.25; FL = 0.37–0.44; SW = 0.23–0.32; TL/GW = 1.70–1.89; PL/PW = 0.46–0.51; HW/EW = 1.52–1.59; FW/FL = 0.55–0.59; GW/SW = 4.26–5.13.

Habitus (Fig. 22). Broadly ovate, broadest near anterior margin of elytra; lateral outline continuous between pronotum and elytron; anteriorly and posteriorly rounded.

Colouration. Pronotum and head red to reddish-yellow (Fig. 22); elytron red to reddish-yellow with vaguely defined, broad testaceous areas laterally, medially, and broadly along suture to apex (Fig. 22). Ventral surfaces dark red-brown except metaventrite, metacoxae, prosternal process and mesosternal wings broadly testaceous; antennae and palpi yellow; legs yellow to yellow-red.

Structure and sculpture. Head, pronotum and elytron shiny, but evenly covered with very fine, isodiametric cells; pronotum with lateral bead narrow posteriorly, evenly expanded anteriorly to broad anterior apex. Prosternum anteriorly broad, medially broadly convex, covered with very fine cells; prosternal process extremely broad and flat, widest at apex, apex broadly truncate. Metaventrite medially broad, evenly rounded, covered with fine, isodiametric cells. Front leg with protibia short, broad, apical angles each distinct, with numerous long, stout spines along dorsal, apical and ventral margins; middle leg similar to front leg in size and shape; hind leg with femur short, broad (FW/FL = 0.5–0.6) without prominent setae, metatibia short and broad, heavily spinous, spines not serrate.

Male genitalia. Median lobe with deep ventral groove curved along ventral surface, in lateral aspect broad near base, with deep ventral groove, evenly and abruptly curved, apex abruptly narrowed, apex narrowly rounded (Figs 23A,B);

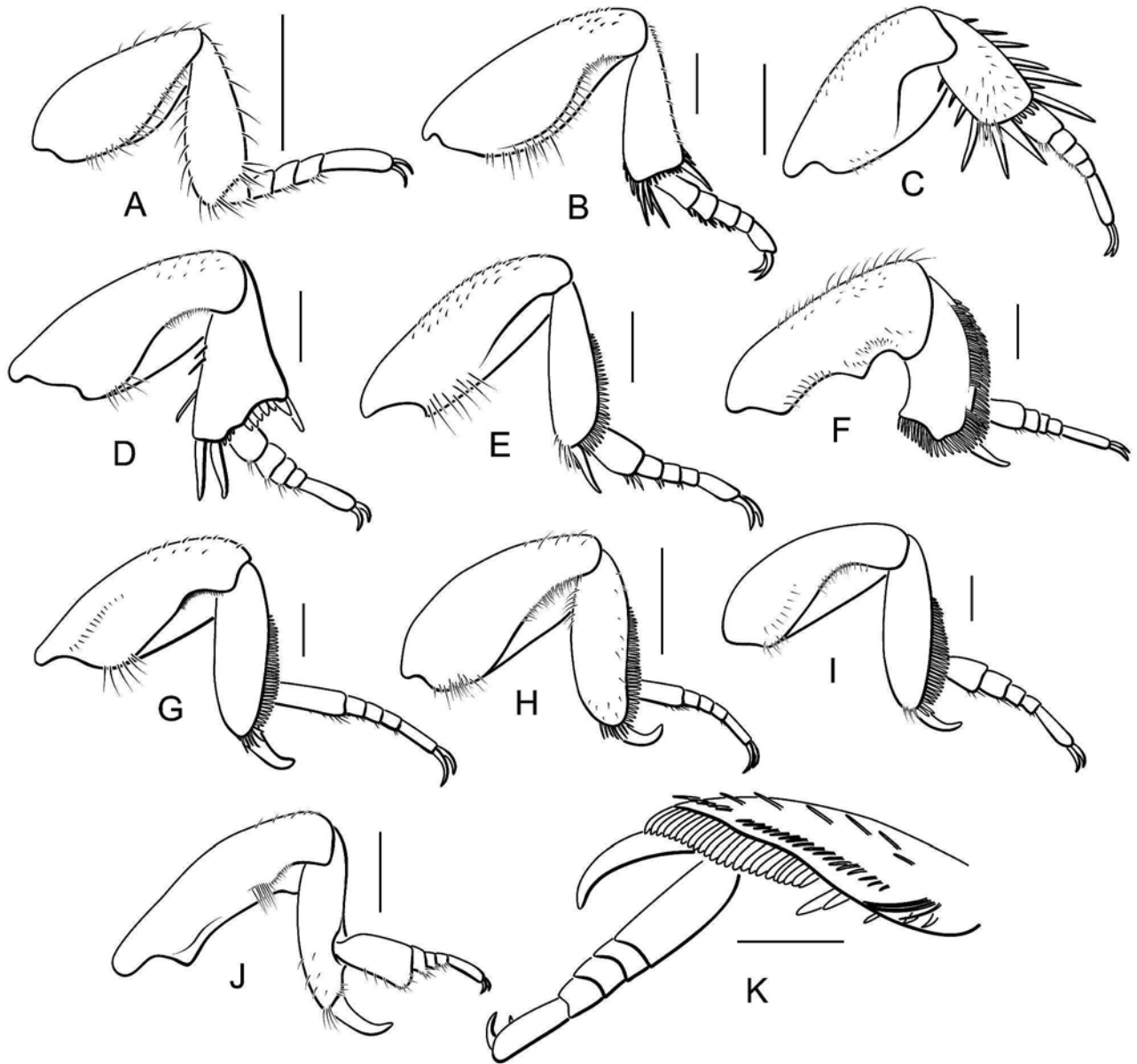


Figure 6 Noteridae species, left front leg, anterior aspect. A – *Notomicrus* sp. B – *Neohydrocoptus bivittus*. C – *Tonerus wheeleri*. D – *Pronoterus* sp. E – *Mesonoterus crassicornis*. F – *Noterus clavicornis*. G – *Hydrocanthus iricolor*. H – *Canthydrus luctuosus*. I – *Suphisellus* sp. J – *Suphis cimicoides*. K – *Noterus clavicornis*. Scale bars = 0.10 mm.

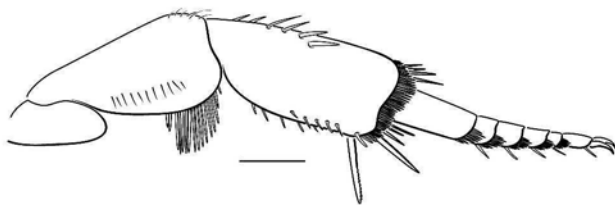


Figure 7 *Hydrocanthus iricolor*, right metaleg, anterior aspect. Scale bar = 0.25 mm.

in ventral aspect moderately narrow, apically evenly narrowed to narrowly curved apex (Fig. 23C). Right lateral lobe broad, distinctly curved, apically broadly truncate

(Fig. 23A); left lateral lobe about half width of right and longer (Fig. 23B).

Female genitalia. Gonocoxosternite broad, medial margin broadly rounded; gonocoxa short, moderately broad, apex broadly rounded, bearing numerous short setae; laterotergites short, slender, extending posteriorly along dorsal margin of gonocoxae (Fig. 11). Bursa relatively broad and short; spermathecal duct broad, elongate; spermatheca globular, with two larger differentiated regions; spermathecal gland duct elongate, spermathecal gland moderately broad and elongate; fertilisation duct slender (Fig. 11).

Variation. Males with pro- and mesotarsi expanded slightly, pro- and mesotarsomeres I and II each with a single,

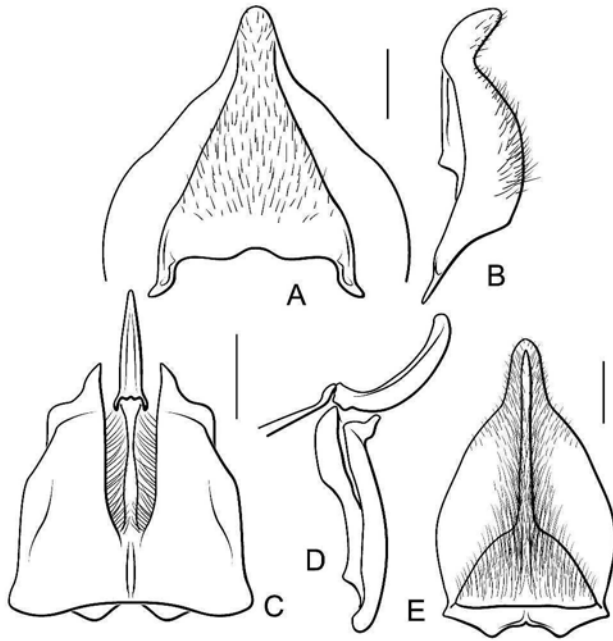


Figure 8 Noteridae species, abdominal tergum VIII. A – *Neohydrocoptus bivittatus*, dorsal aspect. B – *N. bivittatus*, right lateral aspect. C – *Pronoterus* sp., dorsal aspect. D – *Pronoterus* sp., right lateral aspect. E – *Mesonoterus crassicornis*, dorsal aspect. Scale bars = 0.25 mm.

moderately large, slightly ovoid adhesive seta and with series of short, curved setae along posterior margin; females without tarsomeres expanded and without adhesive and curved setae. Elytral colouration extremely variable from pale reddish-yellow to dark red and without dark markings to extensively marked with black.

Etymology. This species is named *wheeleri* in honour of Quentin D. Wheeler (Arizona State University), valued friend and colleague.

Distribution and habitat. This species is known only from Venezuela. According to the notes of collector, P.J. Spangler found in the United States National Museum, specimens of the new species described here were collected on an exposed bedrock seep at the edge of the vegetation. The water was flowing over the bedrock at a depth of 5 mm. The individuals were found in small depressions in the substrate that were covered by mats of vegetation. Label data also indicate that a couple of specimens were collected by stream shoreline washing.

Material examined. HOLOTYPE: ♂ in MIZA labelled ‘VENEZUELA, T.F.Amazonas Puerto Ayacucho (40 kmS) El Tobogán, Caño Coromoto 26 January 1989 seep, at upper shelter/ Collected PJSPangler RAFaitoute&CBBARR/ HOLOTYPE : *Tonerus wheeleri* Miller, 2008 [red label with double black line border].’ PARATYPES, 70 labelled same

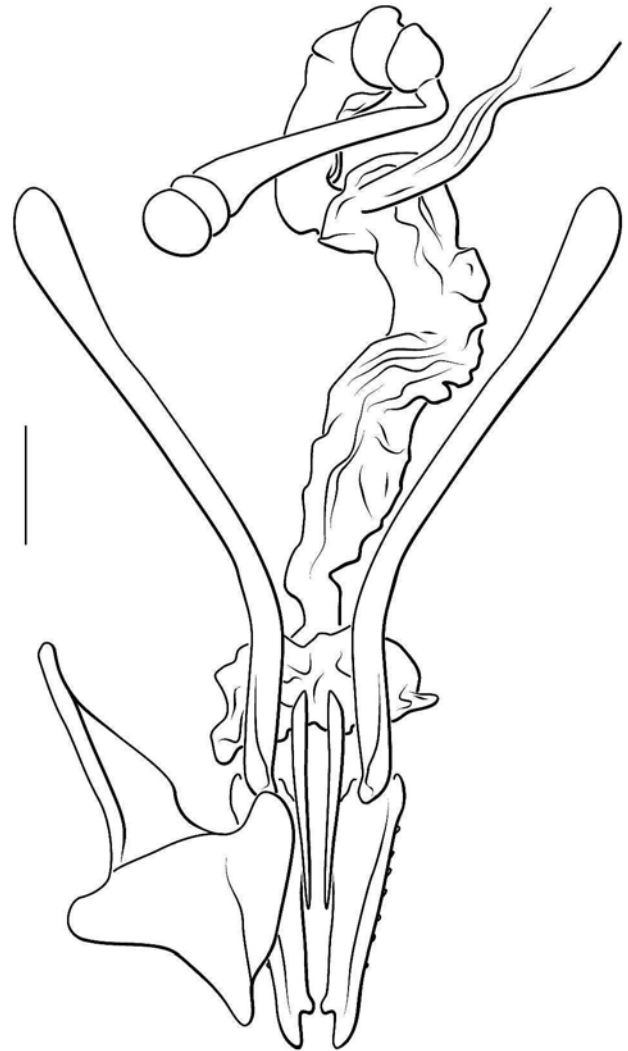


Figure 9 Female genitalia, ventral aspect, *Neohydrocoptus bivittatus*. Scale bar = 0.25 mm.

as holotype; 11, same but date 18 January 1989; 9 same but 26 January 1989, ‘stream edge at upper shelter’; 21 labelled ‘VENEZUELA: Amazonas State 5°23.207’N. 67°36.922’W; 125 m Tobogan de la Selva 5.i.2006; leg. M. Garcia’; 2 labelled ‘VENEZUELA, T.F.Amaz. Puerto Ayacucho (40 kmS) at Tobogán, 25 Feb 1986 P.J. Spangler, colln. #15’. 3 labelled ‘VENEZUELA, T.F. Amazonas Puerto Ayacucho (40 kmS) at Tobogán 18 Nov 1987, coll’n#13 PJSPangler&RAFaitoute/ Collected by pouring water over stream bank & washing insects into seine’.

Tribe Neohydrocoptini Zalát, Saleh, Angus and Kaschef, 2000

Neohydrocoptini Zalát, Saleh, Angus and Kaschef, 2000. *Hydrocoptini auctorum, nec* Branden, 1885.

Type genus. *Neohydrocoptus* Sâto, 1972.

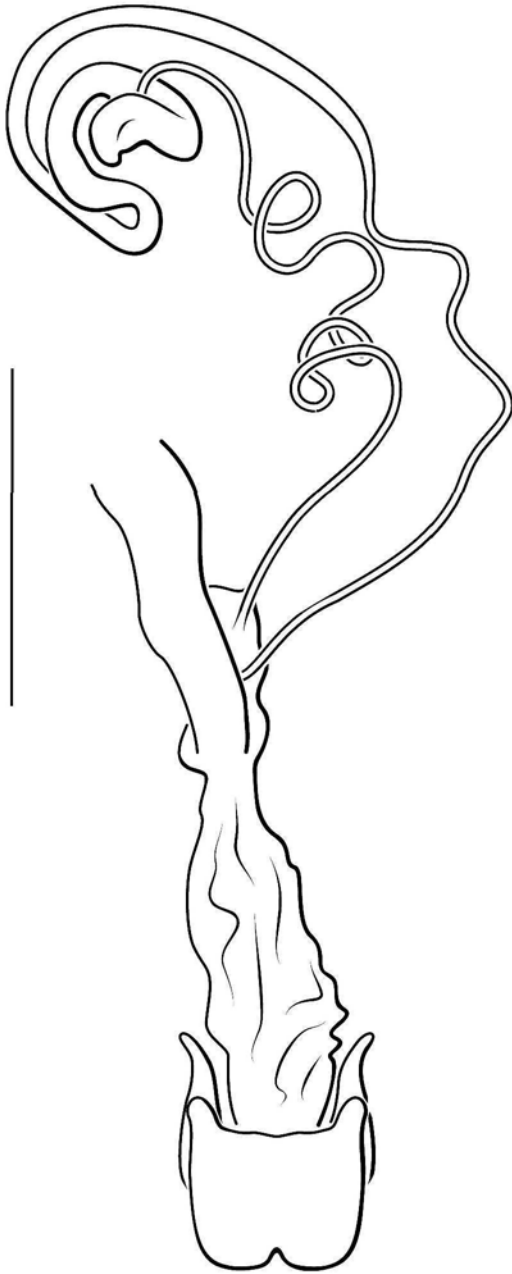


Figure 10 Female genitalia, ventral aspect, *Notomicrus* sp. Scale bar = 0.25 mm.

Diagnosis. This tribe is characterised by the combination of the following synapomorphies: (1) the apices of the gonocoxae are obliquely bifid (Fig. 9) and (2) the apex of the pygidium is narrowed and abruptly upcurved at the apex (Fig. 8A, B). Other distinctive plesiomorphic or homoplasious characters present in this tribe include: (1) the protarsus attached near the apex of the protibia (Fig. 6B), (2) the apex of the protibia with multiple stout spines (without one larger, curved spine) (Fig. 6B), (3) without a distinct setal fringe along the protibia (Fig. 6B), (4) without a setal fringe at the apex of the medial metacoxal lobe (Fig. 4B), (5) with the

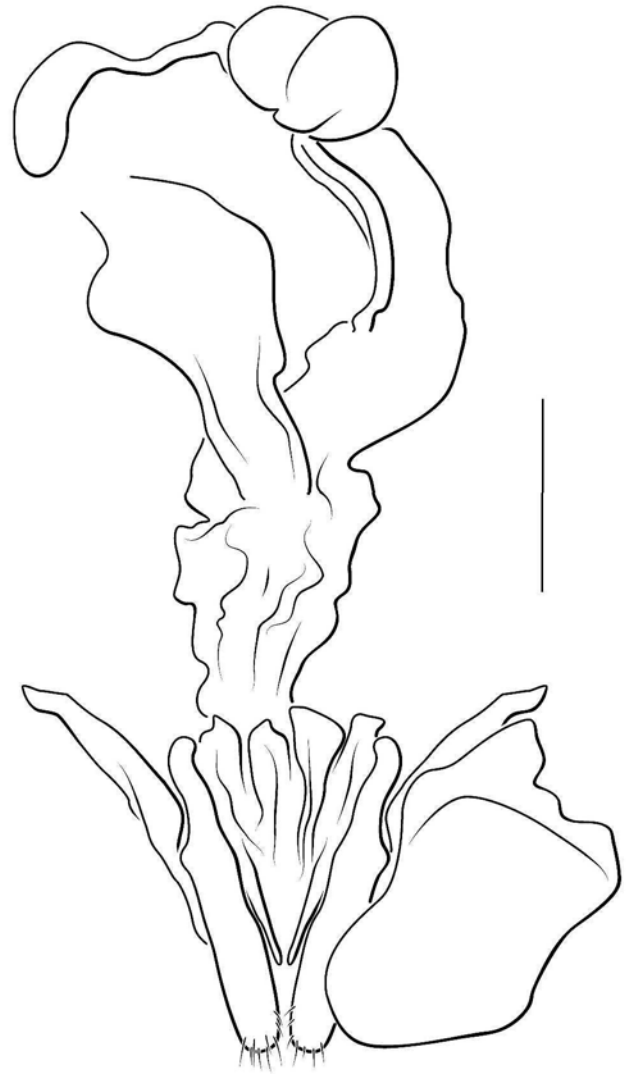


Figure 11 Female genitalia, ventral aspect, *Tonerus wheeleri*. Scale bar = 0.25 mm.

dorso-apical angle of the protibia distinct (Fig. 6B) and (6) with a distinct series of small teeth laterally on the gonocoxa (Fig. 9).

Relationships. This tribe is sister to the other Noterinae except Tonerini (Figs 20, 21).

Comments. This tribe (numerous species in a single genus) have long been thought to be plesiomorphic based in large part on the configuration of the protibia which lacks a large curved spine, has a distinctive dorso-apical angle, and the protarsus attached near the apex of the protibia (Fig. 6B). This analysis reconfirmed that *Neohydrocoptus* is sister to most groups of Noteridae (with the exception of Phreatodytinae, Notomicrinae and *Tonerus* Figs 20, 21).



Figure 12 Female genitalia, ventral aspect, *Pronoterus* sp. Scale bar = 0.25 mm.

***Neohydrocoptus* Sâto, 1972**
(Figs 4B, 6B, 8A, B, 9)

Neohydrocoptus Sâto, 1972

Hydrocoptus auctorum, nec Motschulsky, 1853 (Coleoptera: Dytiscidae).

Type species. *Neohydrocoptus bivittus* Motschulsky, 1859 by original designation.

Diagnosis. This is the only member of this tribe and is characterised by its diagnostic combination (see above).

Distribution. *Neohydrocoptus* is found in India and Africa.

Comments. Members of this group are found throughout south and south-east Asia and Africa. They are often dorsally punctate and marked with longitudinal stripes.

Tribe Pronoterini Nilsson, 2005

Pronoterini Nilsson, 2005

Type genus. *Pronoterus* Sharp, 1882.

Diagnosis. This tribe is characterised by the presence of a fringe of setae at the apex of the medial metacoxal lobe (Fig. 4B), the apically pointed gonocoxae (Fig. 9), and characters of the front leg including lack of a setal fringe on

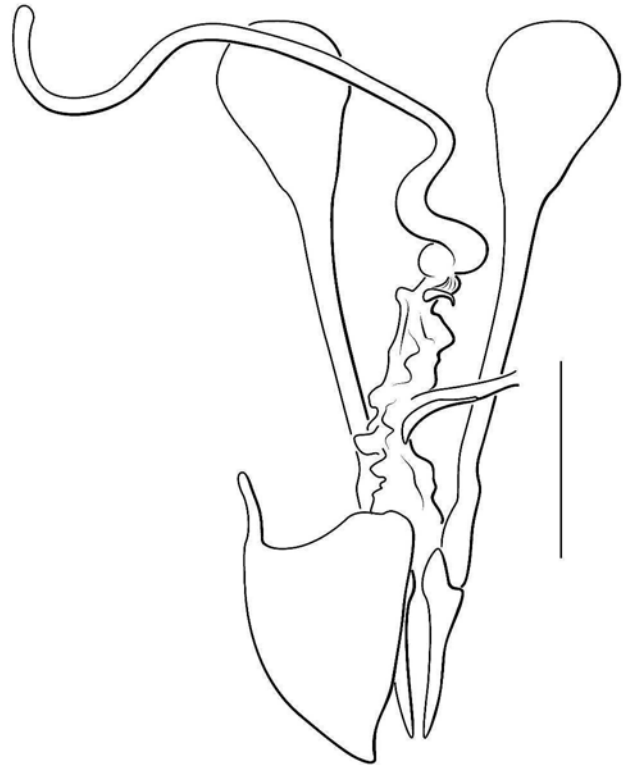


Figure 13 Female genitalia, ventral aspect, *Mesonoterus crassicornis*. Scale bar = 0.25 mm.

the protibia, multiple spines at the apex of the protibia, and distinct apical protibial angles (Fig. 6B). This group also has the largest retractable ‘claw’ on abdominal tergum VIII (Figs 8C, D).

Relationships. This tribe is sister to the tribe Noterini (Figs 20, 21).

Comments. This tribe appears to be intermediate between the more plesiomorphic members of the Noteridae and the apomorphic and more homogeneous Noterini. Only a single New World genus with relatively few species is placed in this tribe.

***Pronoterus* Sharp, 1882**
(Figs 4C, 6D, 8C, D, 13)

Pronoterus Sharp, 1882

Type species. *Pronoterus punctipennis* Sharp, 1882 by monotypy.

Diagnosis. This is the only genus in this tribe and is characterised by its diagnostic combination (see above).

Distribution. Members of this group are found only in southern and eastern North America and South America.

Tribe Noterini Thomson, 1860

Noterides Thomson, 1860

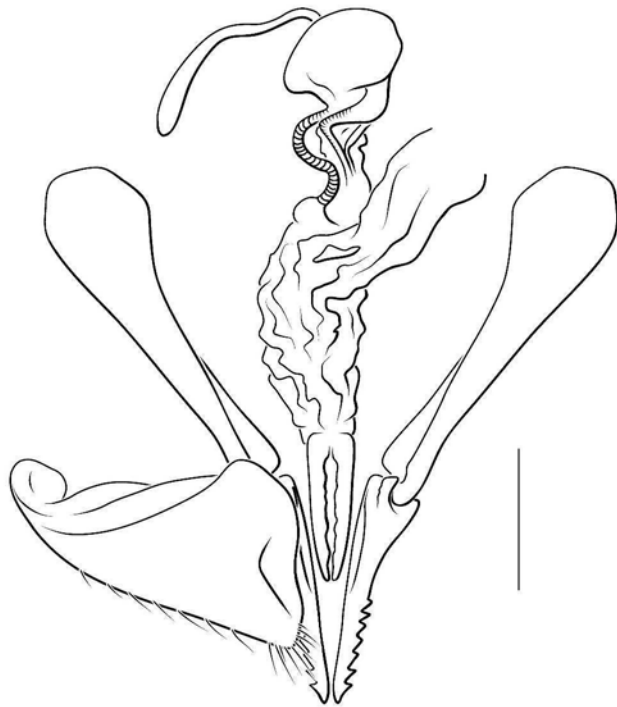


Figure 14 Female genitalia, ventral aspect, *Noterus clavicornis*. Scale bar = 0.25 mm.

Eunoterinae Belkaceme, 1991, unavailable, not based on a genus name.

Hydrocanthini Sharp, 1882; Nilsson, 2005 (synonym).

Suphisini Sharp, 1882; Nilsson 2005 (synonym).

Type genus. *Noterus* Clairville, 1806.

Diagnosis. This tribe is characterised by several synapomorphies including: (1) an enlarged, curved, prominent protibial spur (Figs 6E–K) (relatively small and not strongly curved in *Mesonoterus* (Fig. 6E)), (2) the dorso-apical angle of the protibia rounded (Figs 6E–K) and (3) a distinct setal fringe present along the protibia (Figs 6E–I, K; secondarily lost in *Suphis* Fig. 6J).

Relationships. This tribe is sister to the Pronoterini (Figs 20, 21) with high support (Fig. 20). Relationships between the genera, and monophyly of some genera within Noterini are not strongly supported, however (Fig. 20). Although the classification within this group is modified based on these results, it seems clear that additional data may be needed to better resolve these relationships. Nevertheless, these results represent the most comprehensive to date and several changes are made to the classification based on them.

Comments. Members of this tribe are the most commonly collected in the Noteridae and include a range of taxa united by similarities mainly in the front legs. With the exception of *Mesonoterus*, which historically has been placed in the Notomicrini *sensu auctorum*, there has been little variation in recognition of this group as a monophyletic taxon.

***Mesonoterus* Sharp, 1882**

(Figs 4D, 6E, 8E, 14)

Mesonoterus Sharp, 1882

Type species. *Mesonoterus laevicollis* Sharp, 1882 by monotypy.

Diagnosis. *Mesonoterus* are noterines without many apomorphies and with numerous plesiomorphies. They have the following combination of characters: (1) a reduced apical angle of the protibia (Fig. 6E), (2) a distinct setal fringe present along the protibia (Fig. 6E), (3) a distinct protibial spur that is smaller and less strongly curved than other members of the tribe (Fig. 6E), (4) the protarsus originating near the apex of the protibia (Fig. 6E), and (5) a modification of the last abdominal tergum which is apically narrowed with a fringe of setae and a stout medial spinous process (Fig. 8E).

Relationships. *Mesonoterus* is sister to the rest of Noterini (Figs 20, 21). Although support values for this relationship are not high, the features on which this is based are convincing (see comments below, Fig. 20).

Distribution. *Mesonoterus* includes four species found in the southern Nearctic and Neotropical regions.

Comments. This genus is a member of the Noterini since it has the characteristic apomorphies of that tribe including the reduced apical angle of the protibia (Fig. 6E), the distinct setal fringe along the protibia (Fig. 6E), and a distinct protibial spur (Fig. 6E). However, the protibial spur is smaller and less strongly curved than other members of the tribe (Fig. 6E) and the protarsus originates near the apex of the protibia (Fig. 6E) instead of from the side. Because of this, the genus is phylogenetically intermediate in its character combination between groups like *Pronoterus* and *Neohydrocoptus* and the remaining Noterini (Figs 20, 21). Few discrete synapomorphies were discovered for the genus with the exception of the unusual shape of the last abdominal tergum (Fig. 8E) which appears to be correlated with an elongate spinous process at the apex of the 6th abdominal sternum.

***Synchortus* Sharp, 1882**

Synchortus Sharp, 1882

Type species. *Hydrocanthus asperatus* Fairmarie, 1869 by subsequent designation of Guignot (1946).

Diagnosis. Specimens of this genus were not available for examination for this study. The genus appears to be similar to *Noterus* and *Mesonoterus* in having the prosternal process relatively narrow and apically rounded but also having a distinctly enlarged protibial spur (Belkaceme, 1991; Beutel *et al.*, 2006). *Synchortus* differs from *Mesonoterus* by lacking a cluster of setae on the apex of the medial metacoxal lobe (Belkaceme, 1991; Beutel *et al.*, 2006) making it most similar to *Noterus*. According to Pederzani (1995) the genus differs from *Noterus* in the degree of impression of the stria at the anterior margin of the pronotum, a feature that was found in this study to be

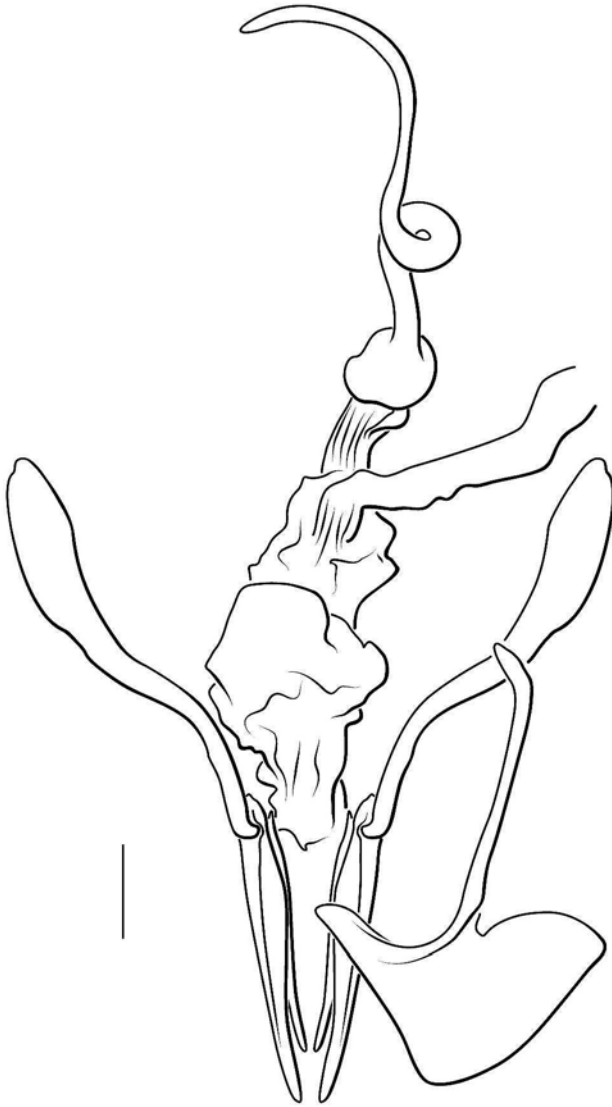


Figure 15 Female genitalia, ventral aspect, *Siolius* sp. Scale bar = 0.25 mm.

unreliable in *Hydrocanthus* and other genera in which it has been used to delimit groups. According to Beutel *et al.* (2006) adults of *Synchortus* differ from those of *Noterus* in having an elongate slender sensorial field at the apex of the apical labial palpomeres whereas *Noterus* has this field rounded (Char. 3), and *Noterus* has the posterior protibial spur present whereas it is absent in *Synchortus* (Char. 18) (Fig. 20).

Distribution. Members of this genus are Afrotropical.

***Noterus* Clairville, 1806**
(Fig. 6F,K, 15)

Noterus Clairville, 1806

Type species. *Dytiscus crassicornis* Müller, 1776, by monotypy.

Diagnosis. This genus is characterised within Noterini by the following: (1) the anterior metatibial spur is not serrate, (2) the metacoxal setal fringe is absent, (3) the prosternal process is relatively narrow and apically rounded, (4) the posterior protibial spur is present, (5) the anteromedial margin of the prosternum has a distinct hooklike process and (6) the apical sensorial field on the labial palp is rounded.

Relationships. *Noterus* is sister to the Noterini except *Mesonoterus* (Figs 20, 21), though support for this relationship is relatively low (Fig. 20).

Distribution. Members of this genus are Palaearctic.

Comments. By virtue of the occurrence of its members in Europe, this taxon has been known better and longer than most in the family. Among Noteridae it has the best known morphology (Belkaceme, 1991), life history (Balfour-Browne & Balfour-Browne, 1940), and larval stages (Ruhnau, 1985).

***Renotus* Guignot, 1936**

Renotus Guignot, 1936

Type species. *Hydrocanthus deyrollei* Sharp, 1882 by original designation.

Diagnosis. Among those noterid genera with a broad, truncate prosternal process, this genus is characterised by the lack of a close linear series of long setae at the anteroapical angle of the metafemur. There is a series of setae along the metafemur, but these are not in a closely spaced series at the anteroapical angle as they are in other taxa such as *Hydrocanthus* (Fig. 7). Superficially the single species in this group is similar to *Noterus*, but differs from that taxon by the presence of a very broad prosternal process. Balfour-Browne (1969) regarded the genus as similar to South American *Siolius*, and it often comes out near that genus in analyses (Belkaceme, 1991; Beutel *et al.*, 2006).

Relationships. *Renotus* is sister to the Noterini except *Mesonoterus* and *Noterus* (Figs 20, 21), though branches subtending these relationships are not high (Fig. 20).

Distribution. This genus includes only a single African species.

***Siolius* Balfour-Browne, 1969**
(Fig. 12)

Siolius Balfour-Browne, 1969

Type species. *Siolius bicolor* Balfour-Browne, 1969 by original designation.

Diagnosis. *Siolius* is characterised by having (1) a very broad prosternal process, (2) a close linear series of long setae at the anteroapical angle of the metafemur, (3) smooth pronotal margins and (4) relatively short laterotergites that extend posteriorly well beyond the base of the gonocoxae (Fig. 12).

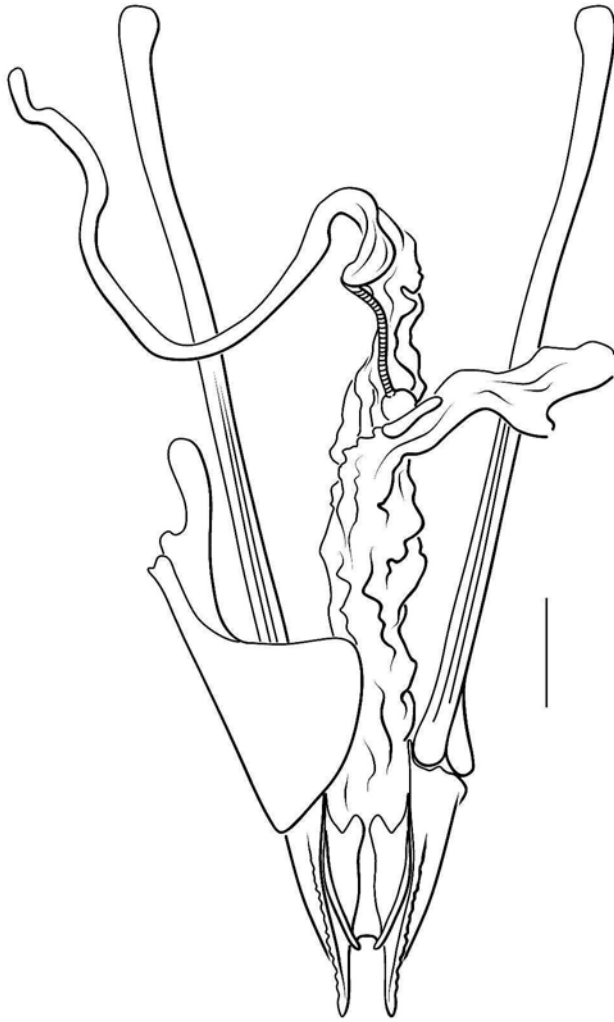


Figure 16 Female genitalia, ventral aspect, *Suphis cimicoides*. Scale bar = 0.25 mm.

Relationships. *Siolius* is in an unresolved relationship with two other clades, *Suphis* + (*Liocanthyrus* + *Suphisellus*) and *Canthydrus* + *Hydrocanthus* (Figs 20, 21). None of the relationships in this portion of the tree are strongly supported (Fig. 20) attesting to the considerable similarity among the genera of Noterini.

Distribution. Members of this genus are Neotropical.

Comments. This genus shares a number of apomorphies with other members of Noterini, but the female genitalia have features that make them appear more plesiomorphic including the short laterotergites that extend posteriorly along the gonocoxae (Fig. 12), though these features are independently derived (Fig. 20). Three species are currently known in this Neotropical genus, though there appear to be at least several undescribed species including the two examined for this analysis. It has not been revised since it was described by Balfour-Browne (1969).

Suphis Aubé, 1836

(Figs 4G, 6J, 16)

Suphis Aubé, 1836

Colpius LeConte, 1861; Spangler and Folkerts, 1973 (synonymy).

Type species. *Suphis*: *Suphis cimicoides* Aubé, 1836 by monotypy; *Colpius*: *Colpius inflatus* LeConte, 1863 by subsequent monotypy.

Diagnosis. This is one of the most distinctive taxa in the Noteridae. Its members are extremely robust and dorsally convex. In addition, the protarsal spur is very large and curved (Fig. 6J), the protibial setal fringe is secondarily reduced (Fig. 6J, 20) and the noterid platform does not extend onto the metaventricle (though this is secondarily derived, Figs 4G, 20).

Relationships. *Suphis* is sister to *Liocanthyrus* + *Suphisellus* (Figs 20, 21), though support for this is relatively low (Fig. 20).

Distribution. Members of this group are found in the Neotropical and southern Nearctic regions.

Comments. *Suphis* are typically very robust, broad, and dorsally convex. The anterior portion of the prosternum is extremely narrow, the mesocoxae are very broad with the noterid platform does not extend onto the metaventricle (Fig. 4G). Although sharing the essential characteristics of the tribe, the front legs are modified from the typical features of its members (Fig. 6J). The species (all Neotropical and southeastern Nearctic) were revised by Grosso (1994).

Liocanthyrus Guignot, 1957, new status

Canthydrus (*Liocanthyrus*) Guignot, 1957

Type species. *Canthydrus angustus* Guignot, 1957, by original designation.

Diagnosis. *Liocanthyrus* can be recognised by the following diagnostic combination within Noterini: (1) the prosternal process is broad, (2) the protarsus is attached along the side of the protibia instead of apically, (3) there is a single, large, curved apical tibial spur, (4) the anterior metatibial spur is not serrate, (5) the prosternum has a distinct line of stiff setae on each side of the middle and (6) the lateral bead of the pronotum is relatively broad and is not serrate.

Relationships. *Liocanthyrus* is sister to *Suphisellus* (Figs 20, 21), although with relatively low support (Fig. 20).

Distribution. As currently defined, the genus includes only four Neotropical species.

Comments. This genus was described as a subgenus of *Canthydrus* Sharp. *Canthydrus* as traditionally defined is not monophyletic in this analysis, however, with the single included species of *Liocanthyrus* sister to *Suphisellus* and *Canthydrus* sister to *Hydrocanthus* (Figs 20, 21). Because of evident polyphyly of *Canthydrus sensu lato* and the availability of a

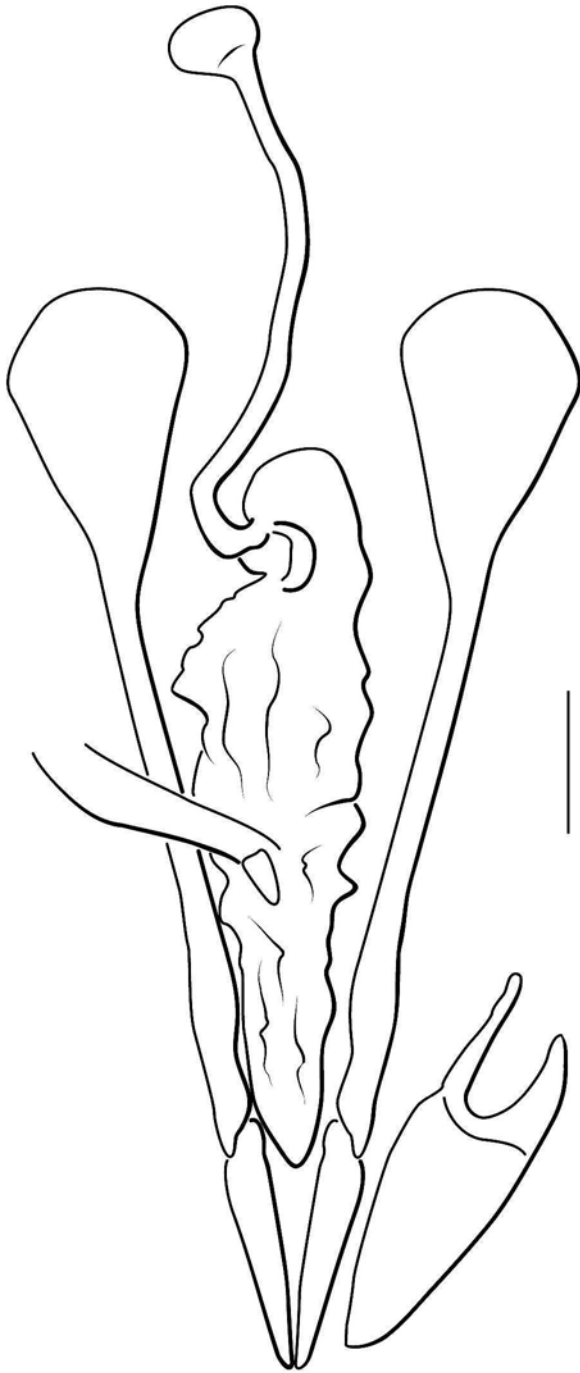


Figure 17 Female genitalia, ventral aspect, *Suphisellus* sp. Scale bar = 0.25 mm.

name, *Liocanthyrus* Guignot, 1957 is elevated from subgenus to genus rank (**new status**).

***Suphisellus* Crotch, 1873**
(Figs 3B, 4E, 6H, 17)

Suphisellus Crotch, 1873

Suphisellus Zimmermann, 1921, preoccupied.



Figure 18 Female genitalia, ventral aspect, *Canthydrus luctuosus*. Scale bar = 0.25 mm.

Type species. *Suphisellus* Crotch: *Noterus bicolor* Say, 1830 by subsequent designation of Leech, 1948; *Suphisellus* Zimmermann: *Suphisellus variicollis* Zimmermann, 1921 by subsequent designation of Leech, 1948, preoccupied by Crotch, 1873.

Diagnosis. This genus has the same diagnostic combination as *Liocanthyrus* (see above) except *Suphisellus* has the lateral bead narrow and there is a crease along the lateral margin at the posterolateral angle extending to about the middle of the side of the pronotum (Fig. 3B). *Liocanthyrus* lacks this crease and has the lateral bead relatively broad.

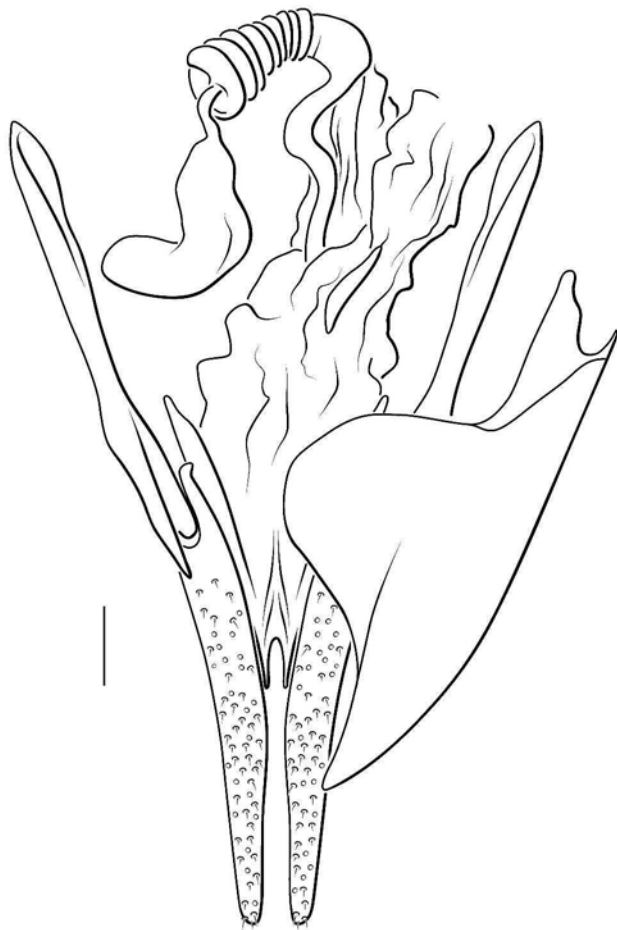


Figure 19 Female genitalia, ventral aspect, *Hydrocanthus iricolor*. Scale bar = 0.25 mm.

Relationships. *Suphisellus* is sister to *Liocanthyrus* (Figs 20, 21).

Distribution. This large group is found in the Nearctic and Neotropical regions.

Comments. Despite the considerable diversity in size, shape and morphological features in this genus, the combination of a narrow lateral bead with a fine crease along the lateral margin at the posterolateral angle (Fig. 3B) is a consistent character state uniting this genus. The group is restricted to North and South America, and in most respects appears quite similar to *Liocanthyrus*. They are frequently brightly marked with fasciae, stripes or maculae.

***Canthydrus* Sharp, 1882**
(Figs 6G, 18)

Canthydrus Sharp, 1882

Type species. *Hydrocanthus guttula* Aubé, 1838, by subsequent designation of Guignot (1946).

Diagnosis. Members of *Canthydrus* have the following diagnostic combination within Noterini: (1) the prosternal process is broad, (2) the protarsus is attached along the side of the protibia instead of apically (Fig. 6G), (3) there is a single, large, curved apical tibial spur (Fig. 6G), (4) the anterior metatibial spur is not serrate, (5) the prosternum is covered with conspicuous, stiff setae not organised into a series, and (6) the lateral bead of the pronotum is relatively broad.

Relationships. *Canthydrus* is sister to *Hydrocanthus* (Figs 20, 21), though with relatively low support.

Distribution. This is one of the largest and most diverse genera in the Noteridae with members occurring throughout much of Africa, Asia and Australia.

***Hydrocanthus* Say, 1823**
(Figs 3A, 4F, 5, 6I, 7, 19)

Hydrocanthus Say, 1823

Guignocanthus Young, 1985; Miller, 2001 (synonymy).

Hydrocanthus (*Sternocanthus*) Guignot, 1948.

Allocanthus Guignot, 1947, *nomen nudum*.

Type species. *Hydrocanthus*: *Hydrocanthus iricolor* Say, 1823 by monotypy; *Guignocanthus*: *Hydrocanthus ancus* Guignot, 1942 by original designation; *Sternocanthus*: *Hydrocanthus micans* Wehncke, 1883 by monotypy.

Diagnosis. *Hydrocanthus* is a somewhat heterogeneous group with the following diagnostic combination within Noterini: (1) the prosternal process is broad (Fig. 4F), (2) the protarsus is attached along the side of the protibia instead of apically (Fig. 6I), (3) there is a single, large, curved apical tibial spur (Fig. 6I), (4) the anterior metatibial spur is serrate (Fig. 7), (5) the lateral pronotal margins are serrate (Fig. 3A) and (6) the prosternum lacks a distinct line of stiff setae on each side of the middle (Fig. 4F).

Relationships. *Hydrocanthus* is sister to *Canthydrus* (Figs 20, 21).

Distribution. This taxon is widespread in North and South America and Africa.

Comments. The African species have historically been placed in the subgenus *Sternocanthus* Guignot based on the putative presence of a distinctly impressed submarginal line anteriorly on the pronotum. This character was surveyed across numerous New World and several African species, and there was no obvious difference in the degree of impression of the submarginal line or series of punctures in these taxa. There was no more variation between New World and African species than there was between species supposedly in the same subgenus. *Hydrocanthus* including *Sternocanthus* is supported relatively strongly in the cladistic analysis (Fig. 20). For these reasons, *Sternocanthus* Guignot, 1948 is hereby placed in synonymy with *Hydrocanthus* Say, 1823 (**new synonym**).

Key to the subfamilies, tribes and genera**of Noteridae**

1. Metacoxa and metaventrite fused laterally, suture obscured (Fig. 4A); size small to extremely small (< 1.7 mm).....Notomicrinae 2
 - Metacoxa and metaventrite not fused laterally, suture entire; size larger (> 1.8 mm) 3
2. Eyes absent; cuticle depigmented.....*Speonoterus*
 - Eyes present; cuticle not depigmented *Notomicrus*
3. Eyes absent; with long sensory hairs on pronotum and elytra; paramedian angle of anterior metacoxal wall absent Phreatodytinae *Phreatodytes*
 - Eyes present; without long sensory hairs on pronotum and elytra; paramedian angle of anterior metacoxal wall present Noterinae 4
4. Protibia with prominent, produced dorso-apical angle (Figs 6A–D); apical margin with several elongate spines, without one single apically curved spine (Figs 6A–D); without fringe of short setae along antero-dorsal margin (Figs 6A–D)..... 5
 - Protibia with dorso-apical angle rounded, not produced (Figs 6E–K); apically with single curved, elongate spine (Figs 6E–K); with fringe of short setae along antero-dorsal margin of pro- and mesotibia (Figs 6E–I, K; or only mesotibia in *Suphis*)..... Noterini 7
5. Apices of metacoxa without cluster of setae (Fig. 2, 4A, B, G); metafemur without apical-ventral margin with series of closely spaced setae; pro- and mesotarsomeres I not incrassate 6
 - Apices of metacoxa with cluster of setae (Fig. 4C–F); metafemur with apico-ventral margin with series of closely spaced setae; pro- and mesotarsomeres I incrassate, narrowed basally and expanded apically Pronoterini *Pronoterus*
6. Apex of prosternal process very broad and truncate (Fig. 2) Tonerini *Tonerus*
 - Apex of prosternal process narrow (Fig. 4B) Neohydrocoptini *Neohydrocoptus*
7. Prosternum medially with prominent series of stiff setae (Fig. 4E)..... 8
 - Prosternum medially without series of stiff setae or with numerous setae covering entire surface 9
8. Pronotum with lateral bead narrow with fine crease at posterolateral angle extending anteriorly to about middle of pronotum (Fig. 3B).....*Suphisellus*
 - Pronotum with lateral bead broad, without fine crease at posterolateral angle *Liocanthyrus*
9. Posterior metatibial spur serrate (Fig. 7)..... 10
 - Posterior metatibial spur not serrate..... 11
10. Prosternum medially nearly glabrous, without extensive setae *Hydrocanthus*
 - Prosternum medially with extensive field of prominent setae *Canthydrus*
11. Protibial fringe absent (Fig. 6J); prosternum narrow (Fig. 4G); noterid platform not extending onto metaventrite (Fig. 4G); body robust, dorsally extremely convex.....*Suphis*
 - Protibial fringe present; prosternum broad; noterid platform extending onto metaventrite; body elongate, not extremely convex dorsally 12
12. Apex of metacoxal lobe without cluster of setae..... 13
 - Apex of metacoxal lobe with cluster of setae (Fig. 4D) 14
13. Posterior protibial spur absent; apical sensorial field on labial palpus elongate, slender.....*Synchortus*
 - Posterior protibial spur present; apical sensorial field on labial palpus rounded.....*Noterus*
14. Protibial spur slender, only slightly curved (Fig. 6E); protarsus attached near the apex of protibia (Fig. 6E) *Mesonoterus*
 - Protibial spur robust, broad, strongly curved; prostarsus attached to protibia distinctly 15
15. Metafemur with distinct linear series of closely approximated setae at anteroventral angle.....*Siolius*
 - Metafemur with series of setae along entire anteroventral margin, but without distinct linear series at anteroventral angle *Renotus*

List of the subfamilies, tribes and genera of Noteridae

- Noteridae Thomson, 1860
- Phreatodytinae Uéno, 1957
 - Phreatodytes* Uéno, 1957
 - Notomicrinae Zimmermann, 1919
 - Notomicrus* Sharp, 1882
 - Speonoterus* Spangler, 1996
 - Noterinae Thomson, 1860
 - Tonerini Miller, **new tribe**
 - Tonerus* Miller, **new genus**
 - Neohydrocoptini Zalat, Saleh, Angus and Kaschef, 2000
 - syn. Hydrocoptini auctorum, nec Branden, 1885
 - Neohydrocoptus* Sato, 1972
 - Pronoterini Nilsson, 2005
 - Pronoterus* Sharp, 1882
 - Noterini Thomson, 1860
 - syn. Eunoterinae Belkaceme, 1991
 - syn. Hydrocanthini Sharp, 1882
 - syn. Suphisini Sharp, 1882
 - Mesonoterus* Sharp, 1882
 - Suphis* Aubé, 1836
 - syn. *Colpius* LeConte, 1861
 - Noterus* Clairville, 1806
 - Renotus* Guignot, 1936
 - Siolius* Balfour-Browne, 1969
 - Hydrocanthus* Say, 1823
 - syn. *Guignocanthus* Young, 1985
 - syn. *Sternocanthus* Guignot, 1948
 - Canthydrus* Sharp, 1882
 - Liocanthyrus* Guignot, 1957, **new status**
 - Suphisellus* Crotch, 1873
 - hom. *Suphisellus* Zimmermann, 1921
 - Synchortus* Sharp, 1882

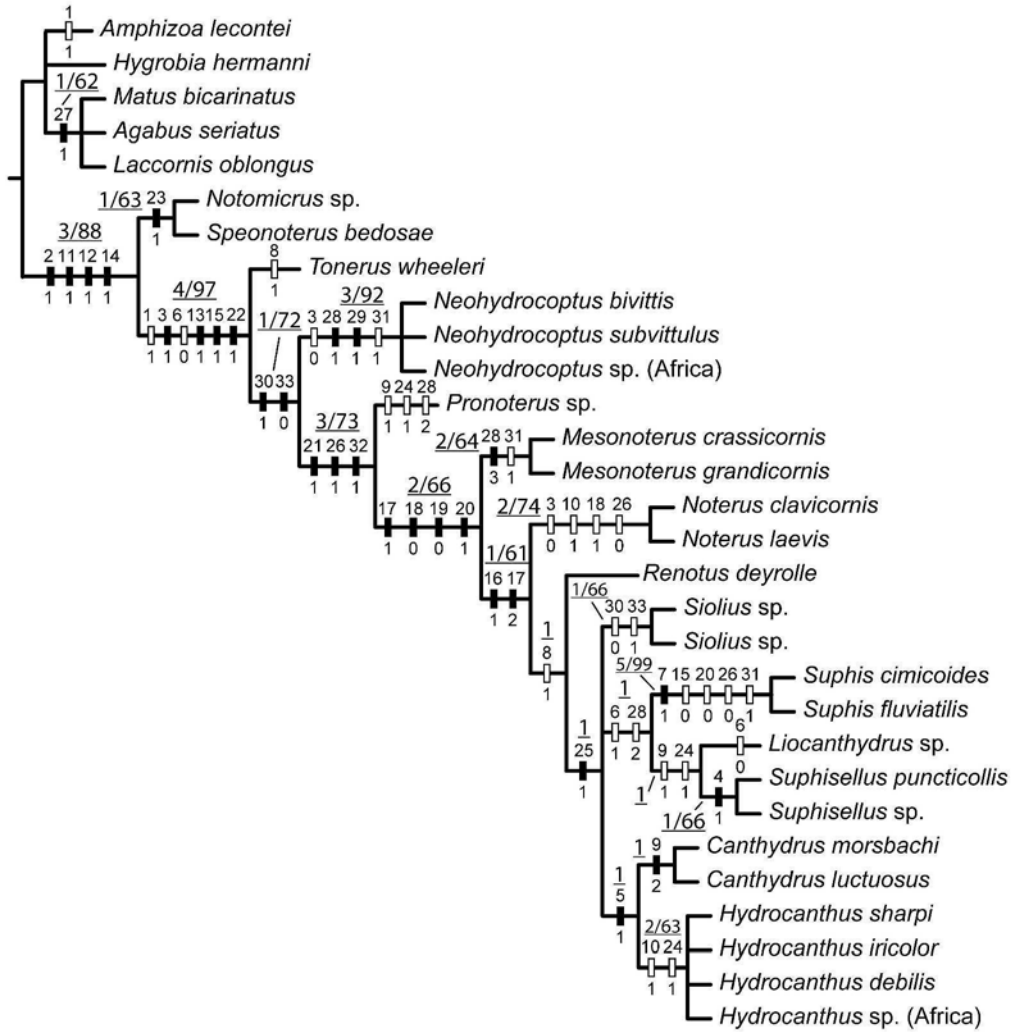


Figure 20 Single tree resulting from parsimony analysis of Noteridae based on morphological characters (length = 57, CI = 64, RI = 92) with characters mapped using fast optimisation in WinClada. Filled hatchmarks indicate unique character state transformations, open hatchmarks indicate homoplasious transformations or reversals. Numbers above hatchmarks are character numbers. Numbers below hatchmarks are character state numbers (derived at that branch). Underlined numbers are Bremer branch support values and bootstrap values (shown when greater than 50%).

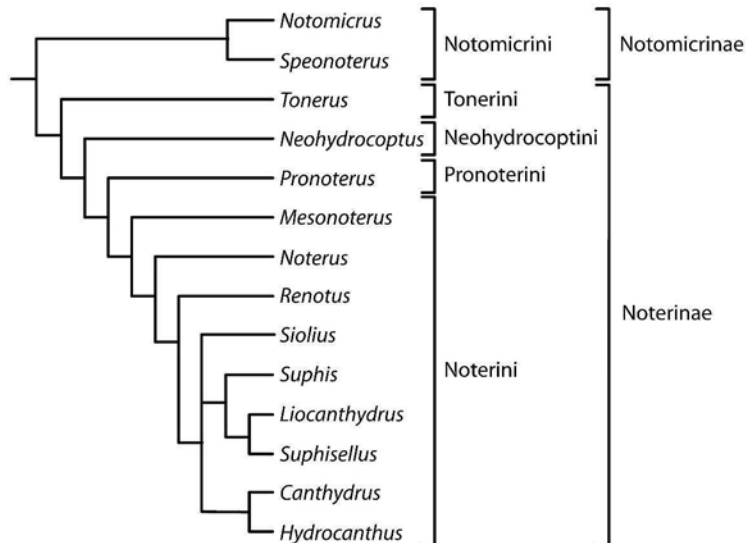


Figure 21 Summary tree of parsimony analysis of Noteridae genera showing relationships among and classification of genera, tribes and subfamilies (*Phreatodytes* and *Synchortus* not included).



Figure 22 *Tonerus wheeleri*, habitus. Scale bar = 1 mm.

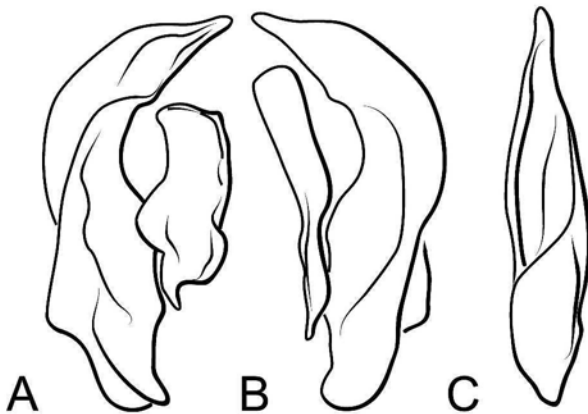


Figure 23 *Tonerus wheeleri*, male genitalia. A – Male median lobe and right lateral lobe, right lateral aspect. B – Male median lobe and left lateral lobe, left lateral aspect. C – male median lobe, ventral aspect.

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References

- BALFOUR-BROWNE, F. 1961. The metendosternite in the Coleoptera. *Journal of the Linnean Society of London, Zoology* **44**, 337–354.
- BALFOUR-BROWNE, F. & BALFOUR-BROWNE, J. 1940. An outline of the habits of the water-beetle, *Noterus capricornis* Herbst (Coleopt.). *Proceedings of the Royal Entomological Society of London, Ser. A* **15**, 105–112.
- BALFOUR-BROWNE, J. 1969. A new genus of Noteridae (Coleoptera: Noteridae, Noterini). *Proceedings of the Royal Entomological Society of London, Ser. B* **38**, 5–6.
- BELKACEME, T. 1991. Skelet und Muskulatur des Kopfes und Thorax von *Noterus laevis* Sturm. Ein Beitrag zur Morphologie und Phylogenie der Noteridae (Coleoptera: Adephaga). *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)* **462**, 1–94.
- BEUTEL, R.G., MALKE, M. & STEINER, W.E. 2006. The systematic position of Meruidae (Coleoptera, Adephaga) and the phylogeny of the smaller aquatic adephagan beetle families. *Cladistics* **22**, 102–131.
- BEUTEL, R.G. & ROUGHLEY, R.E. 1987. On the systematic position of the genus *Notomicrus* Sharp (Hydradephaga: Coleoptera). *Canadian Journal of Zoology* **65**, 1898–1905.
- BREMER, K. 1994. Branch support and tree stability. *Cladistics* **10**, 295–304.
- BURMEISTER, E.-G. 1976. Der ovipositor der Hydradephaga (Coleoptera) und seine phylogenetische Bedeutung unter besonderer Berücksichtigung der Dytiscidae. *Zoomorphologie* **85**, 165–257.
- DETTNER, K. 2005. Noteridae Thomson, 1857. In: KRISTENSEN, N.P. & BEUTEL, R.G., Eds., *Handbook of Zoology, Vol. IV. Arthropoda: Insecta. Part 38. Coleoptera, Vol. 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. Walter De Gruyter, Berlin, pp. 72–81.
- FRANCISCOLO, M.E. 1979. *Coleoptera. Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae*. E. Calderini, Bologna.
- GOLOBOFF, P. 1995. NONA. Published by the author, Tucumán, Argentina.
- GROSSO, L.E. 1994. Revision de las especies Neotropicales del genero *Suphis* Aubé, con la description de *S. ticky* n. sp. (Coleoptera – Noteridae). *Acta Zoologica Lilloana* **42**, 225–238.
- GUIGNOT, F. 1946. Génotypes des Dytiscoidea et des Gyrinoidea. *Revue Française d'Entomologie* **13**, 112–118.
- MILLER, K.B. 2001. On the phylogeny of the Dytiscidae (Coleoptera) with emphasis on the morphology of the female reproductive tract. *Insect Systematics and Evolution* **32**, 45–92.
- NILSSON, A.N. 2005. Family Noteridae (Coleoptera, Adephaga). In: NILSSON, A.N. & VAN VONDEL, B.J., Eds., *Amphizoidea, Aspidytiidae, Haliplidae, Noteridae and Paelobiidae (Coleoptera, Adephaga)*. *World Catalog of Insects. Vol. 7*. Apollo Books, Stenstrup, pp. 87–153.
- NILSSON, A.N. & VAN VONDEL, B.J. 2005. *Amphizoidea, Aspidytiidae, Haliplidae, Noteridae and Paelobiidae (Coleoptera, Adephaga)*. Vol. 7. Apollo Books, Stenstrup.
- NIXON, K.C. 2002. WinClada. Published by the author, Ithaca, NY.
- PEDERZANI, F. 1995. Keys to the identification of the genera and subgenera of adult Dytiscidae (*sensu lato*) of the world (Coleoptera Dytiscidae). *Atti della Accademia Roveretana Degli Agiati* **4**, 5–83.
- RIBERA, I., HOGAN, J.E. & VOGLER, A.P. 2002. Phylogeny of hydradephagan water beetles inferred from 18S rRNA sequences. *Molecular Phylogenetics and Evolution* **23**, 43–62.
- ROUGHLEY, R.E. 2001. Noteridae C.G. Thomson, 1857. In: ARNETT, R.H. & THOMAS, M.C., Eds., *American Beetles. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, Boca Raton, pp. 147–152.

- ROUGHLEY, R.E. & LARSON, D.J. 2001. Dytiscidae Leach, 1815. In: ARNETT, R.H. & THOMAS, M.C., Eds., *American Beetles, Archostemata, Myxophaga, Adepaga, Polyphaga: Staphyliniformia*. CRC Press, Boca Raton, pp. 156–186.
- RUHNAU, S. 1985. Zur Morphologie und Biologie der praeimaginalen Stadien des Wasserkafers *Noterus crassicornis* (Muller, 1776) (Coleoptera, Hydradephaga, Noteridae). Diplom-Arbeit, Tu.
- SPANGLER, P.J. 1996. Four new stygobiotic beetles (Coleoptera: Dytiscidae; Noteridae; Elmidae). *Insecta Mundi* **10**, 241–259.
- UÉNO, S.I. 1996. New phreatobiotic beetles (Coleoptera, Phreatodytidae and Dytiscidae) from Japan. *Journal of the Speleological Society of Japan* **21**, 1–50.
- YOUNG, F.N. 1978. The New World species of the water-beetle genus *Notomicrus* (Noteridae). *Systematic Entomology* **3**, 285–293.