Revision of the subfamily Hydrodytinae Miller (Coleoptera: Dytiscidae) with description of a new genus

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The New World subfamily Hydrodytinae Miller is revised. Two genera are recognized, Hydrodytes Miller and Microhydrodytes gen. n. Hydrodytes contains three known species, H. opalinus (Zimmermann), H. dodgel (Young) and H. inacculus (Guignot). Microhydrodytes contains a single known species, M. elachistus sp. n. Keys are provided to the genera and species in the subfamily. Important morphological features are illustrated for diagnosing the species and a phylogenetic hypothesis is proposed for all species.

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Introduction
A recent cladistic analysis of morphological characters of the family Dytiscidae indicated that several species previously placed in the genus Agaporrhomorphus Zimmermann actually form a group that is sister to the subfamily Hydroporinae (Miller 2001b) based mainly on characters from the female genitalia. Rather than sinking these taxa into Hydroporinae, a group well supported by numerous distinctive synapomorphies, a new subfamily, Hydrodytinae, was erected to include them (Miller 2001b). The remaining species in the genus Agaporrhomorphus have now been revised in a separate paper (Miller 2001a).

The subfamily Hydrodytinae, as characterized here, includes two genera (one new) and four species (one new). The species are very small in size, and are all Neotropical or southeastern Nearctic (Florida). Very little is known of the biology of the group. However, as noticed by Young (1989), it is of interest that all but one species are known only from females, possibly indicating that males are at least difficult to collect or perhaps even absent altogether in those species. Hydrodytes opalinus (Zimmermann) has been collected from a water hole in a forest, and H. dodgel (Young) has been collected from a river and a large lake using a dip net (Epler 1996), but all other specimens examined are from light traps. Guéorguiev (1968) included the two species known at the time in his key to Agaporrhomorphus. Other than this the members of the group have received limited taxonomic treatment. The discovery of a species in Florida (Young 1989) represented a northern extension of the known range for the group, which displays a biogeographic pattern typical of other dytiscids such as Megadytes Sharp, Pachydrus Sharp, Lacocotyes Régimbart and Derovatellus Sharp. These genera, and Hydrodytes, are widespread elements of the Neotropical fauna and occur as far north as southern Florida.

Because of the apparent sister-group relationship between this small group of Neotropical dytiscids and the Hydroporinae, which represents one of the largest radiation of Hydradephaga, Hydrodytes species are potentially useful for a variety of questions regarding evolution, biogeography and conservation of dytiscids. Natural history information about members of this group is sorely needed.

Material and methods
Material. – Specimens were examined from the Cornell University Insect Collection, Ithaca, NY (CUIC), the Florida State Collection of Arthropods, Gainesville, FL (FSCA) and my per-
sonal collection (KBMC). Type specimens were borrowed from the Zoologische Staatssammlung des Bayerischen Staates, Munich, Germany (ZSBS).

**Measurements.** - Measurements were made using an ocular scale on a Wild M3C dissecting microscope. Measurements provided include TL = total length and GW = greatest width. The ratio TL/GW is also provided to give an indication of shape. The number of specimens measured was limited by the number of intact specimens available, but when enough were available, 20 were measured.

**Classification system.** - Certain members of the systematic community have recently advocated abandoning the currently used classification system of ranks that originated with Linnaeus and replacing it with a so-called 'phylogenetic systematics' (e.g. Cantino et al. 1999; de Queiroz & Gauthier 1990; de Queiroz & Gauthier 1992). I thoroughly reject the outrageous argumentation presented by promoters of this flawed philosophy of classification. There is no valid scientific, philosophical or practical reason for abandoning the Linnaean system of ranks and a multitude of reasons for maintaining it (Dominguez & Wheeler 1997; Nixon & Carpenter 2000). For example, although naming a particular clade at a particular rank has no objective, scientific basis, when used in a cladistic classification ranks are valuable (at the very least) for easily communicating exclusivity. That is, in a system of naming only monophyletic groups using ranked names it can be concluded immediately that a taxon that is at the same rank as another is not nested within it, and vice versa. Names under a rankless system would be unable to provide this information with the same level of simplicity, and a rankless system has a wealth of other flaws (Dominguez & Wheeler 1997; Nixon & Carpenter 2000). The results of the
analysis presented here conform to the Linnaean classification phylogeny in a traditional hierarchical system of formal ranks as governed by the International Code of Zoological Nomenclature, the principle of formally naming only monophyletic groups (Hennig 1966) and consistency with the traditional use of various names within Dytiscidae.

HYDRODYTINAE Miller, 2001


Diagnosis. - Scutellum visible; pro- and mesotarsi distinctly pentameric in both sexes; prothorax and prosternal process not declivitous and without medial tubercle; genocoxa with prolonged anterior apodeme (Fig. 7-14); metathoracic wing broad, vein M4 attaining oblongum cell, subcostal binding patch distinct (Fig. 6); median lobe asymmetrical (Fig. 3) and size small (< 4.0 mm). A single synapomorphy discovered is the characteristic shape of the female rami which are distinctly sinuate in all species examined (Fig. 7-10).

Key to the genera of Hydrodytinae

1. Dorsal surface without opalescent sheen, with small, distinct punctures on elytra; size smaller (< 2.2 mm); antennomeres very short and broad (Fig. 1) ..........Microhydrodytes gen. n.
2. Dorsal surface with an opalescent sheen, without punctation or with punctures small and indistinct; size larger (> 2.5 mm); antennomeres long and slender ..........Hydrodytes Miller

Microhydrodytes Miller, gen. n.

(Fig. 1, 7, 11)

Type species. - Microhydrodytes elachistus Miller, new species, by original designation.

Etymology. - This genus is named elachistus from the Greek for 'small' in reference to the very small size of the single known specimen.

Material examined. - Holotype, ♀ in FSCA labeled, ‘BRASIL: Matto Grosso, Jarcare-Parque Nat. Xingu xi.65 BLT MAlvarenga e WCA Bokerma/HOLOTYPE Microhydrodytes elachistus Miller, 2000 [red label with double black line border].’

Diagnosis. - Very small (< 2.2 mm); surface of elytron covered with distinctive, small punctures, not opalescent; antennomeres very short and broad (Fig. 1).

Description. - Measurements. n = 1. TL = 2.11 mm, GW = 1.07 mm, TL/GW = 1.97.

Coloration. Head, pronotum and elytron red-brown, slightly lighter laterally on pronotum and elytron. Ventral surfaces red-brown; antennae, palpi and legs yellow.

Sculpture and structure. Head with fine network of microreticulation forming isodiametric cells, medially with few, fine punctures. Antennomeres short and broad, nearly moniliform. Pronotum with sculpture similar to head; lateral bead obscured at anterior end, lateral margin nearly straight; anterolateral margin of pronotum inflated. Elytron with fine microreticulation as on head and pronotum, with evenly distributed, slightly longitudinal, fine punctures, more dense and more rounded near apex. Prosternum medially strongly carinate; prosternal process flat, apex rounded, extending in emargination of mesosternum nearly to level of hind margins of mesocoxae, lateral margins broadly beaded. Mesosternum and metacoxa covered with fine microreticulation of long, narrow cells.

Female genitalia (Fig. 7, 11). Bursa relatively short, robust; spermathecal duct broad, moderately short; spermatheca robust (compressed in sin-
Single specimen examined); fertilization duct elongate, moderately broad, coiled; common oviduct robust, moderately broad, elongate; rami sinuate, robust; gonocoxa elongate, lateral margin broadly sinuate, apically with two elongate setae, anterior apodeme slightly sinuate; laterotergite narrow in ventral aspect, relatively unmodified; gonocoxo- sternite posteriorly broadly rounded with large field of short setae, anterior lobe narrow.

Discussion. — Young (1989) mentioned this small species when describing H. dodgei. It is known from only a single female specimen. Usually, modern dytiscid workers refrain from describing new taxa from single specimens, especially if the specimen is a female. Often, species delimitations are based mainly on male genitalia. However, this species is very distinctive and clearly represents an undescribed species best placed in a new genus.
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3.77 mm ($\bar{x} = 3.64$), GW = 1.46-1.74 mm ($\bar{x} = 1.61$ mm), TL/GW = 2.07-2.45 ($\bar{x} = 2.26$).

Habitus. Body elongate oval, lateral margins evenly and broadly rounded; dorsoventrally moderately flattened.


Sculpture and structure. Head impunctate to very finely punctate; pronotum and elytron with very shallow, indistinct punctures sparsely distributed. Lateral pronotal margin with very fine bead nearly obscured, especially anteriorly. Prosternum medially strongly carinate; prosternal process medially strongly convex, lateral margins distinctly beaded, apex bluntly rounded. Metasternum smooth, impunctate, anterior emargination for reception of prosternal process moderately deep, distinctly V-shaped, anterior lobes pointed. Metacta and abdominal sternum smooth, without surface structure.

Male genitalia (Fig. 2-4). Median lobe in lateral aspect evenly rounded along ventral margin, slightly sinuate along dorsal margin, apex acutely pointed (Fig. 2); in ventral aspect broad, right side distinctly concave medially, apex broadly rounded (Fig. 3). Lateral lobe in lateral aspect very slender, straplike, with elongate apical segment, with apex narrowly rounded and with small cluster of slender setae, dorsal margin with sparse, elongate series of setae medially (Fig. 4).

Female genitalia (Fig. 8, 12). Bursa broad posteriorly, tapering anteriorly; spermatheca duct very long, moderately narrow throughout length; spermatheca sub-spherical; fertilization duct very narrow, elongate; ramius slender, elongate, sinuate; gonocoxa elongate-rounded, slightly narrower posteriorly, with surface sculpture of irregular series of longitudinal, parallel lines, apically with two elongate setae, anterior apodeme moderately long; latetergite slender, elongate; gonocoxosternite sub-triangular, posterior apex narrowly rounded.

Sexual dimorphism. Male with posterior mesotarsal claw basally more strongly curved and with apical portion distinctly sinuate (Fig. 5), other mesotarsal claw and protarsal claws unmodified.

Variation. Specimens from Trinidad (FSCA) are much lighter in color (yellow-brown) and have a light yellow band at the base of the elytra.

Distribution. This species is known from Brazil, Honduras and Trinidad.
Discussion. — Because I have not seen the type specimen, there is potentially some doubt about the attribution of the name *H. inaculatus* to this species. However, Guignot's (1957) description, particularly of the male genitalia, has convinced me that his species and the one described here are the same.

This is the only species of the subfamily that is known from males. As with the other species in the subfamily, most of the specimens examined were collected at lights. The species is sister to the pair *H. opalinus* + *H. dodgei* (Fig. 15), though this is based on relatively weak evidence (see discussion under *H. opalinus*).

**Hydrodytes opalinus** (Zimmermann, 1921)

(Fig. 6, 9, 13)

*Agapororhopus* opalinus Zimmermann 1921: 204;
Blackwelder 1944: 77; Guérin-Meneville 1968: 37.

*Hydrodytes opalinus*; Miller 2001b: 77.

Material examined. — Lectotype (here designated to fix the assignment of this name with this species); ♀ in ZSB, labeled, “Brazilien/ Mato-Grosso Corumbá Type [green circular disc, handwritten] / Agaporomorphus opalinus / LECTOTYPE / Agaporomorphus opalinus Zimmermann, 1921 designated by KB Miller, 2001 [red label with double black line border].” Paralectotypes: 4 ♀ in ZSB, labeled same as lectotype, but without fourth label above.

Other material: BOLIVIA: Dpto Beni, 67 km NW Trinidad, blacklight, 18 July 1998, K.B. Miller (12, KBMC); BRAZIL: Mato Grosso, Cuiaba (Cuiaba) Exp. Stat., blacklight, 11 May 1972, W.H. Whitcomb (1, FSCA); Mato Grosso, Jacare, F.N. Xingu, blacklight, November 1965, Alvarenga and Werner (3, FSCA); Para, Belem, 9 July 1969, P. and P. Spangler (1, FSCA); HONDURAS: Cayo District, Mile 66-Western Highway, blacklight, 10 July 1969, W. and D. Hasse (2, FSCA); PERU: Madre de Dios, Río Tambopata Res., 16 January 1987, J.V. McHugh and Q.D. Wheeler (1, CUIC); Yarinacocha, Dept. Loreto 48 (Pucallpa), light, 3 December 1961, B. Malkin (1, FSCA); SURINAM: Carolina Ck. 10 km from Zanderij, waterhole in forest, 18 September 1962, B. Malkin (1, FSCA); MOINGO, Boven, Cottica R., 17 May 1927 (1, CUIC); TRINIDAD: Mayaro, 28 April 1929, Darlington (1, FSCA); VENEZUELA: Barinas, Rio Caparo, 21 May 1987 (3, FSCA); Miranda, Panaquiere, blacklight, 22 February 1982, J.H. Frank (6, FSCA).

Diagnosis. — Size relatively small (TL = 2.60-3.10 mm); spermathecal duct elongate, strongly twisted near spermatheca and bursa short (Fig. 9); males unknown.

Description. — Measurements. n = 20. TL = 2.60-3.10 mm (x = 2.87), GW = 1.15-1.48 mm (x = 1.35 mm), TL/GW = 1.96-2.34 (x = 2.14).

Habitus. Elongate, slender, laterally evenly and broadly rounded along body margin in dorsal aspect; dorsoventrally moderately flattened.

Coloration. Dorsal surfaces brown to dark brown, pronotum and base of elytron lighter yellow-brown; all dorsal surfaces with distinct opalescent (multicolored) sheen. Palpi and antennae yellow. Legs yellow; metatibia and metasternum brown. Other ventral surfaces brown to yellow-brown.

Sculpture and structure. Head, pronotum and elytron with very shallow, indistinct punctures. Lateral pronotal margin with fine beak. Prosternum medially distinctly carinate; prosternal process medially convex, lateral margins distinctly beaded, apex narrowly rounded. Metasternum smooth, impunctate, anterior emargination for reception of prosternal process relatively deep, V-shaped, anterior lobes sharply pointed. Metacoxa and abdominal sterna smooth, without surface structure. Metathoracic wing broad, vein M4 attaining oblongum cell, subcubital binding patch distinct (Fig. 6).

Male genitalia. Male unknown.

Female genitalia (Fig. 9, 13). Bursa long, moderately narrow; fertilization duct moderately broad, elongate, strongly coiled; spermatheca spherical, small; fertilization duct very slender, elongate; rami long, sinuate; gonocoxa elongate oval, apically with two elongate setae; anterior apodeme relatively short; gonocoxosternite subtriangular, posterior apex narrowly rounded.

Variation. A specimen from Trinidad (FSCA) is very light yellow. Two specimens from Brazil (FSCA) are larger and more slender and have the dorsal surfaces dark brown. These specimens do not appear to have significant differences in other characters (including female genitalia) from other specimens.

Distribution. — *Hydrodytes opalinus* is relatively widespread in northern South America and apparently occurs at least as far north as Honduras.

Discussion. — This widespread species may be a complex of species since specimens vary in size and coloration. However, only females were examined, and these all have similar genitalia and other characters. Most of the specimens examined were collected at lights except one from Surinam which was collected from a waterhole in the forest. The species is sister to *H. dodgei* (Fig. 15). However, this is based at this time only on the
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common absence of examined males in these two species, though the two species are superficially similar, as well. While the absence of males has certainly not been firmly corroborated, the fact that a relatively large number of specimens of these two species have been examined without seeing a single male leads me to believe that the character has some merit. This species is similar to *H. dodgei* in size and other external characters, but differs in having a longer and more twisted spermathecal duct and a shorter bursa copulatrix (Fig. 9-10).

**Hydrodtyes dodgei** (Young, 1989)

(Fig. 10, 14)


*Hydrodtyes dodgei*; Miller 2001: 77.

**Material examined.** — Paratypes, 11 in FSCA with following data: USA: Florida, Alachua Co., Gainesville, blacklight, 15 September 1972, WH Pierce (7); Columbia Co., Osceola Nat. Forest Field Station, blacklight, 22 September 1976, J.R. Wiley (1); Gainesville, Doyle Conner Bldg., blacklight, 28-31 August 1972, P.W. Head (2); Marion Co., 9 mi SSW Osula, blacklight, 16 September 1975, J.R. Wiley (1).

**Diagnosis.** — Size relatively small (TL = 2.71-2.92 mm); spermathecal duct relatively short and moderately twisted near spermatheca and with bursa very long (Fig. 10); males unknown.

**Description.** — Measurements. n = 12. TL = 2.71-2.92 mm (X = 2.80). GW = 1.26-1.45 mm (X = 1.34 mm). TL/GW = 1.98-2.17 (X = 2.09).

Habitus. Moderately elongate, slender, laterally evenly and broadly rounded along body margin in dorsal aspect; dorsoventrally moderately flattened.

Coloration. Dorsal surfaces brown, pronotum and base of elytron lighter yellow-brown; all dorsal surfaces with distinct opalescent (multicolored) sheen. Palpi and antennae yellow. Legs yellow; metatibia and metatarsomeres brown. Other ventral surfaces brown to yellow-brown.


Male genitalia. Males unknown.

Female genitalia (Fig. 10, 14). Bursa very long, moderately broad; spermathecal duct slender, elongate, not strongly coiled; spermatheca broad, elongate and medially expanded, strongly twisted; fertilization duct very slender, elongate; vagina broad; rami long, slender, strongly sinuate; gonocoxae elongate, apically slightly narrowed, apically with several short setae; laterotergite elongate, slender in ventral aspect; gonocoxosternite rounded.

Variation. Slight variation in color of dorsal surfaces, but otherwise relatively invariant.

**Distribution.** — This species is known only from southern Florida.

**Discussion.** — The holotype of this species was not examined, but numerous paratypes (FSCA) were. This species is sister to *H. opalinus* (Fig. 15). See the discussion under that species.

**Cladistic analysis**

Few discrete characters were identified for clarification of relationships between these taxa, but the characters found for grouping taxa were easily configured into the most parsimonious arrangement. The following five characters were used in the cladistic analysis of species of Hydrodtyinae. Outgroup states were coded for members of *Copelatus* (Copelatinae) and *Laccornis* (Hydroporinae). A character matrix is presented in Tab. 1.

1. Anterior apodeme on gonocoxa; (0) absent, (1) present.
2. Gonocoxal rami; (0) not characteristically sinuate, (1) sinuate.
3. Dorsal surface; (0) not opalescent, (1) opalescent.
4. Dorsal punctuation; (0) reduced, absent, (1) present, distinctive.
5. Males; (0) absent, (1) present.

**Results.** — A single most parsimonious cladogram was discovered with complete character congruence and a length of 5 (Fig. 15). Although character 1 is uninformative for those taxa included in the analysis, the absence of anterior apodemes on the gonocoxae of dytiscid taxa other than Hydrodtyinae and Hydroporinae (Miller 2001b) leads me to map the character as a synapomorphy of these two subfamilies.
Figure 15. Single most parsimonious cladogram depicting relationships between species of Hydrodytinae. Mapped characters are non-homoplasious (length = 5, CI = 1).

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References


Table 1. Matrix of taxa and characters for cladistic analysis of Hydrodytinae and outgroup taxa.

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