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Author(s): Kelly B. Miller

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REVIEW OF THE GENUS *CYBISTER* CURTIS, 1827 (COLEOPTERA: DYTISCIDAE: DYTISCINAE: CYBISTRINI) IN NORTH AMERICA

KELLY B. MILLER

Department of Biology and Museum of Southwestern Biology
University of New Mexico
Albuquerque, NM 87131, U.S.A.
kbmiller@unm.edu

ABSTRACT

The genus *Cybister* Curtis (Coleoptera: Dytiscidae) in the Nearctic region is reviewed including taxonomic history, keys to species, diagnoses, illustrations, distributions, and natural history. Three species are recognized in the genus. *Cybister explanatus* LeConte, 1852 (= *Cybister explanatus laevicollis* Zimmermann, 1919; = *Cybister explanatus fuscus* Zimmermann, 1919) is found from southern Oregon through California and Nevada and through western Mexico to Chiapas. *Cybister occidentalis* Aubé, 1838 is found in Cuba, the Bahamas, and extreme southern Florida. *Cybister fimbriolatus* (Say, 1823) (= *Cybister dissimilis* Aubé, 1838; = *Cybister flavocinctus* Aubé, 1838 **new synonymy**; = *Cybister ellipticus* LeConte, 1852 **new synonymy**; = *Cybister cavicollis* Sharp, 1887 **new synonymy**; = *Cybister crotchi* Wilke, 1920) is found from southeastern Canada west to Ontario and North Dakota south through eastern North America to Florida and the Bahamas (Bahimi Island), west through the southern United States to Arizona and southern California and south throughout Mexico to the Yucatán. Lectotypes are designated for *C. ellipticus* and *C. explanatus*.

Key Words: taxonomy, nomenclature, diving beetles, key to species, synonymy, lectotypes

The genus *Cybister* Curtis (Coleoptera: Dytiscidae) includes a large number of species (~100, Nilsson 2001) with members that are medium to extremely large (~50 mm) in size. *Cybister* includes some of the largest of all water beetles and, as such, some of the largest freshwater invertebrate predators. They are important components of aquatic systems throughout most of the world, but are less abundant and less species rich in the Holarctic and Neotropical regions where they are largely replaced by *Dytiscus* L. and *Megadytes* Sharp, respectively. In the New World, the Neotropical and Nearctic species do not appear to be closely related (Miller *et al.* 2007). Instead, the Nearctic species are more closely related to Asian and African clades of *Cybister* (Miller *et al.* 2007).

North American *Cybister* were placed in the subgenus *Nealocomerus* Brinck based on the presence in males of an apparent stridulatory device formed by the base of the metafemur and a series of ridges on the medial surface of the metacoxae (Fig. 1, Brinck 1945). Although this appears to be a convincing synapomorphy for North American *Cybister* (Miller *et al.* 2007), the genus is not well known in much of the world and it is not known how generally distributed this feature might be. The Nearctic taxa are monophyletic (Miller *et al.* 2007), but the clade is nested within other groups of *Cybister* (Miller *et al.* 2007) and, because of this, *Nealocomerus* was synonymized with *Cybister s. str.* by Miller *et al.* (2007).

Nearctic *Cybister* are commonly encountered, but their taxonomy has been confused and unclear, and an examination of the literature and specimens in several collections has indicated need for clarification of the species limits and nomenclature. Specimens in western North America, especially south into Mexico, are particularly difficult to assign to one of the several currently recognized species since many of these have not been assessed since their original descriptions. It is an interesting feature of dytiscid systematics that often the species largest in body size are among the most poorly known taxa, whereas many of the smaller dytiscids have been revised using modern methods. The goal of this project is to clarify the species taxonomy and nomenclature associated with *Cybister* in North America. Several additional species are known from South America (Trémouilles 1984; Trémouilles and Bachmann 1980), but they do not appear to be closely related to the North American taxa (Miller *et al.* 2007) and are not included in the current treatment.

MATERIALS AND METHODS

Several hundred specimens were examined. Specimens of *Cybister* are large and difficult to ship, so no attempt was made to borrow and examine specimens comprehensively from many collections. However, two large collections, the United States National Collection of Insects

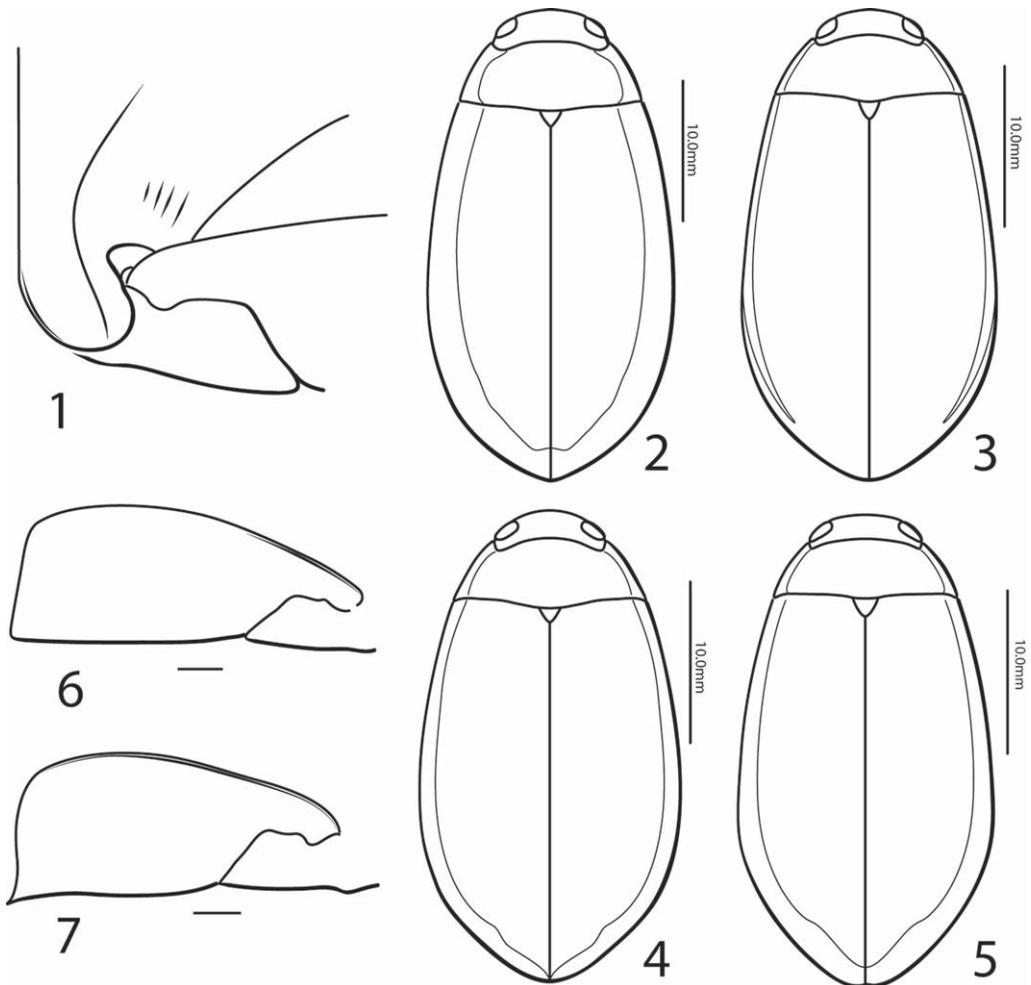
(USNM, Smithsonian Institution) and the University of Kansas Biodiversity Institute Insect Collection (SEMC) have many specimens from throughout the range of the species, sufficient for reviewing the diversity of the species, and these were examined in detail. Specimens from the K. B. Miller Collection were also examined. Online images of type specimens in the Museum of Comparative Zoology, Harvard University (MCZC), are available at insects.oeb.harvard.edu/mcz/ for *Cybister crotchi* Wilke, *Cybister ellipticus* LeConte, and *Cybister explanatus* LeConte, and these were examined. Because of some confusion as to the identity of the types of *C. explanatus*, specimens in the type series were borrowed from

the MCZC. The holotype of *Cybister cavicollis* Sharp was examined by R. Braga (personal communication) on a visit to the Natural History Museum, London.

Measurements were made with a digital caliper to the nearest 0.1 mm. No attempt was made to randomly sample specimens. Instead, the largest, smallest, widest, and narrowest specimens were targeted for measurements to ascertain the ranges of variation in total length (TL) and greatest width (GW).

TAXONOMY AND CHARACTERS OF NORTH AMERICAN *CYBISTER*

North American species of *Cybister* are together monophyletic based on the common presence in

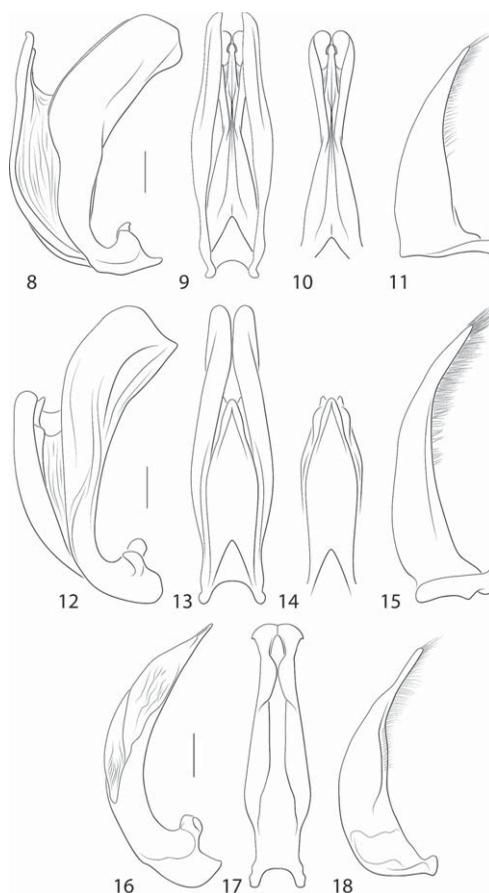


Figs. 1–7. *Cybister* species. 1) *C. fimbriolatus*, male, base of left metacoxa, metatrochanter, and metafemur showing position of stridulatory ridges on the metacoxa; 2) *C. fimbriolatus*, California; 3) *C. fimbriolatus*, Florida; 4) *C. occidentalis*, Bahamas; 5) *C. explanatus*, California; 6) *C. fimbriolatus*, right metatrochanter and metacoxa; 7) *C. explanatus*, right metatrochanter and metacoxa.

males of a stridulatory device (Larson and Pritchard 1974) comprised of a short series of ridges (3–4) near the coxal cavity which interfaces with a ridge on the base of the metafemur (Fig. 1, Miller *et al.* 2007). This was the basis of the subgenus *Nealocomerus* (Brinck 1945), but the group was found to be nested within other clades of *Cybister* and use of the subgenus name was abandoned (Miller *et al.* 2007). Within the clade, species are very similar in external appearance. Historically, much has been made of fairly subtle or seemingly continuous variation in several features in the group.

Coloration has been considered important since specimens range from dorsally green to copper to nearly black and ventrally reddish brown to nearly black. This coloration varies considerably within species and populations (as with many other species of diving beetles). The width of the lateral yellow stripe on the pronotum and elytron varies from wide, including the entire elytral margin, and extending posteriorly to the apex of the elytra (Fig. 2) to narrow, apically separated from the lateral margin, and not extending to the apex of the elytra (Fig. 3). Many specimens of *Cybister fimbriolatus* (Say) from Florida and other areas of the southeast are nearly black dorsally and ventrally and have a narrow lateral yellow stripe (Fig. 3), whereas many specimens (also regarded here as *C. fimbriolatus*, see below) from the western USA and into Mexico are green to brown dorsally, brown ventrally, with the lateral yellow margin very broad and extending to the apex of the elytra (Fig. 2). Coloration is variable among and within populations, and in a more thorough survey of this variation it was not found to be useful as a basis of species delimitation. Body shape has also been regarded as important with specimens in some populations seemingly more parallel-sided and other populations apparently broader or laterally more broadly rounded (*e.g.*, Young 1953), but this does not seem to be the case based on actual measurements of numerous specimens. This impression of more parallel sides in specimens that are actually the same relative width and shape may instead be a function of the broader, somewhat more parallel lateral yellow stripes in western populations which give the appearance of a more parallel body shape (Fig. 2). Length to width ratios are, in fact, the same throughout the North American species. Similarly, one purported characteristic of *Cybister occidentalis* Aubé compared with *C. fimbriolatus* is location of greatest body width. In *C. occidentalis*, the greatest width has been regarded as at the posterior two-thirds of the body versus more near the middle (Young 1953, 1954). This also does not appear to be a reliable character with position of greatest width actually quite similar across the group and

the majority of specimens of all species widest near the posterior two-thirds (Figs. 2–5). *Cybister occidentalis* females purportedly have a single metatarsal claw, whereas female members of *C. fimbriolatus* supposedly have two claws, one smaller than the other (Young 1953). This, however, is variable in all specimens of North American *Cybister*, with most female specimens having two claws, one small and vestigial, but a few specimens having a single claw, as in males. Finally, despite previous emphasis on sexual sculpturing



Figs. 8–18. *Cybister* species, male genitalia. **8)** *C. fimbriolatus*, median lobe, right lateral aspect; **9)** *C. fimbriolatus*, median lobe, ventral aspect; **10)** *C. fimbriolatus*, ventral sclerite of median lobe, ventral aspect; **11)** *C. fimbriolatus*, right lateral lobe, right lateral aspect; **12)** *C. occidentalis*, median lobe, right lateral aspect; **13)** *C. occidentalis*, median lobe, ventral aspect; **14)** *C. occidentalis*, ventral sclerite of median lobe, ventral aspect; **15)** *C. occidentalis*, right lateral lobe, right lateral aspect; **16)** *C. explanatus*, median lobe, right lateral aspect; **17)** *C. explanatus*, median lobe, ventral aspect; **18)** *C. explanatus*, right lateral lobe, right lateral aspect.

as a species-level character (Young 1953, 1954), the extent of female sculpturing on the dorsal surface of the pronotum and elytron is variable in each species from nearly absent to extensive, and is not useful for species delimitation.

The only known reliable characters to delimit species in North American *Cybister* are the shape of the apicoventral apex of the metafemur and the male genitalia. In specimens of *C. explanatus*, the apicoventral apex of the metafemur (Figs. 6, 7) has a distinctive, acuminate angle (Fig. 7), whereas other species vary from right-angled to somewhat rounded (Fig. 6). The shape of the male genitalia, in particular, is very consistent within species, and very different among species (Figs. 8–18), and this is used here as the primary system for species determination. Based on these features, only three species are recognized within the North American members of *Cybister* (= “*Cybister fimbriolatus* group”).

KEY TO THE NORTH AMERICAN SPECIES OF *CYBISTER*

1. Apicoventral angle of metafemur acuminate, sharply pointed (Fig. 7); male median lobe slender, apically laterally expanded and truncate, but without extremely large marginal lobes enclosing ventral sclerite (Figs. 16, 17)..... *C. explanatus*
- 1'. Apicoventral angle of metafemur right-angled to slightly rounded, not acuminate or sharply pointed (Fig. 6); male median lobe broad with extremely large marginal lobes enclosing ventral sclerite (Figs. 8, 9, 12, 13)..... 2
2. Male median lobe with ventral sclerite short and broad, extending just beyond half length of median lobe (Figs. 12–14), median lobe shape as in Figs. 12, 13; distributed in Cuba, Bahamas, and extreme southern Florida, USA (Fig. 19)..... *C. occidentalis*
- 2'. Male median lobe with ventral sclerite long and narrow, extending to near apex of median lobe (Figs. 8–10), median lobe shape as in Figs. 8, 9; widespread, from south-eastern Canada south to Florida and Bahamas west to California south through Mexico (Fig. 19)..... *C. fimbriolatus*

Cybister fimbriolatus (Say, 1823)

Figs. 1–3, 6, 8–11, 19

Dytiscus fimbriolatus Say, 1823: 91. Aubé 1838: 69 (as a synonym of *C. dissimilis* Aubé, 1838: 69). *Cybister dissimilis* Aubé, 1838: 69. Melsheimer 1853: 29 (as a synonym of *C. fimbriolatus*); Sharp 1882b: 48 (as a synonym of *C. fimbriolatus*);

Zimmermann 1920: 259 (as a synonym of *C. fimbriolatus*); Wilke 1920: 250 (as a synonym of *C. fimbriolatus*); Blackwelder 1944: 80 (as synonym of *C. fimbriolatus*). Secondary homonym of *Dytiscus dissimilis* Rossi, 1792.

Cybister flavocinctus Aubé, 1838: 78. Sharp 1882b: 48; Chevrolat 1841: 5; Zimmermann 1920: 259.

New synonymy.

Cybister ellipticus LeConte, 1852: 202. Melsheimer 1853: 29; Fall 1901: 54; Wilke 1920: 250 (as a synonym of *C. fimbriolatus*); Zimmermann 1920: 259; Leech 1948: 412; Leech and Chandler 1956: 323; Larson *et al.* 2000: 833.

New synonymy.

Cybister fimbriolatus. Melsheimer 1853: 29; Crotch 1873: 398; Sharp 1882a: 715, 1887: 759; Wickham 1895: 152; Roberts 1905: 106; Zimmermann 1920: 259; Wilson 1923: 277 (natural history and larval description); Blackwelder 1944: 80; Folkerts 1967: 27 (natural history); Johnson and Jakanovich 1970: 111 (natural history); Yasuzumi *et al.* 1971: 476 (micro-morphology); Johnson 1972: 23 (flight behavior); Poinar and Petersen 1978: 20 (parasites); Ideker 1979: 41 (natural history); Barman and White 1995: 159 (natural history); Shepley-James *et al.* 2009: 189 (larval description); Larson *et al.* 2000: 832.

Cybister olivieri sensu Crotch, 1873: 399 (not Crotch, 1872: 205).

Cybister cavicollis Sharp, 1887: 759. Blackwelder 1944: 80. **New synonymy.**

Cybister crotchi Wilke, 1920: 246.

Cybister (Nealocomerus) cavicollis. Brinck 1945: 13.

Cybister (Nealocomerus) crotchi. Brinck 1945: 13.

Cybister (Nealocomerus) elipticus [sic]. Brinck 1945: 13.

Cybister (Nealocomerus) fimbriolatus. Brinck 1945: 13.

Cybister (Nealocomerus) flavocinctus. Brinck 1945: 13.

Cybister (Nealocomerus) fimbriolatus crotchi. Young 1953: 7, 1954: 120.

Cybister (Nealocomerus) fimbriolatus fimbriolatus. Young 1953: 9, 1954: 120.

Cybister fimbriolatus crotchi. Michael and Matta 1977: 43; Larson *et al.* 2000: 832.

Cybister fimbriolatus fimbriolatus. Michael and Matta 1977: 43; Larson *et al.* 2000: 832.

Diagnosis. The apicoventral angle of the metafemur is nearly right-angled and often slightly rounded (Fig. 6) but not acuminately produced (Fig. 7). There are also extremely large marginal lobes on the median lobe of the aedeagus in males (Figs. 8, 9). The species is similar to *C. occidentalis*, and the two can only be definitively separated by characteristics of the male median lobe. In

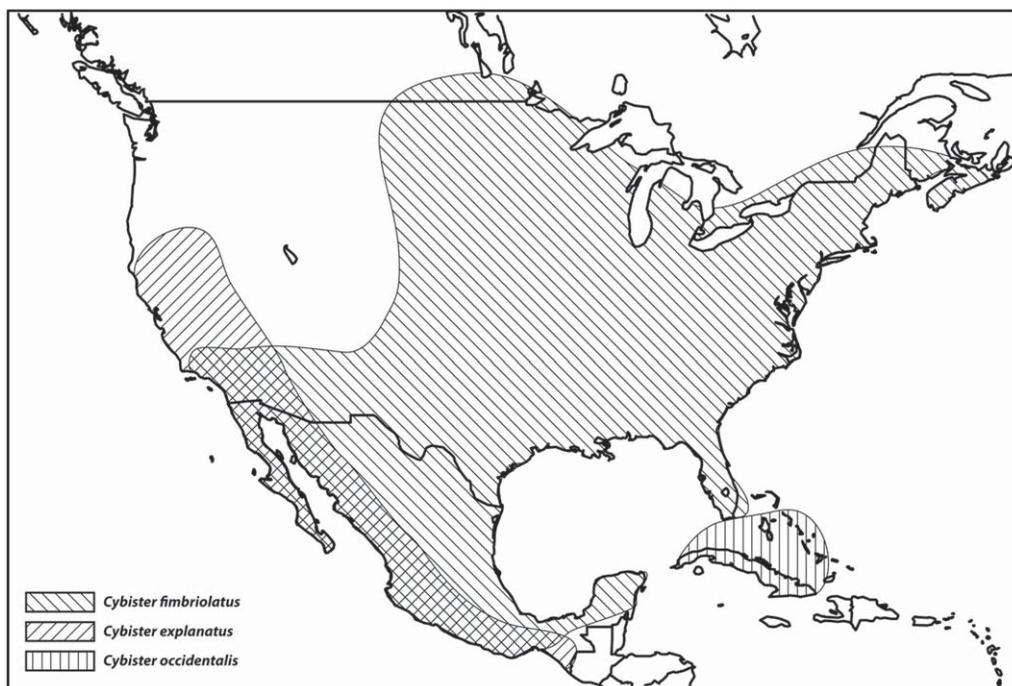


Fig. 19. Distribution of *Cybister* species in North America and Mexico.

C. fimbriolatus, the ventral sclerite is long and relatively slender, extending to near the apex of the median lobe (Figs. 8–10). In *C. occidentalis*, the ventral sclerite is much shorter and broad, ending well short of the apex of the median lobe (Figs. 12–14). There are other shape differences in the median lobes between the two species, as well, with the apex of the median lobe in *C. fimbriolatus* broadly triangular and lobed apicodorsally (Fig. 8) but in *C. occidentalis* apically broadly convex and angulate apicodorsally (Fig. 12).

Measurements. TL = 25.5–33.1 mm, GW = 12.9–17.3 mm, TL/GW = 1.8–2.0.

Variation. Members of this group are variable in coloration, size, shape, extent of female microsculpturing, number of female metatarsal claws, and number of ridges in the male metacoxal stridulatory device. Dorsal color varies from nearly black to green. The lateral yellow stripe on the pronotum and elytron varies from very wide and extending to the apex of the elytron (Fig. 2) to relatively narrow and short, not extending to the elytral apex and, in some cases, separated from the lateral elytral margin (Fig. 3). The ventral color varies from nearly black to nearly red, in some cases, depending in part on how teneral the specimen is. Total length ranges from about 26–33 mm. Most female specimens have a field of short “scratches” on the sides of the

pronotum and the elytron basally and laterally, but the extent of the field is variable with some specimens having this microreticulation absent or nearly so. All males have a single metatarsal claw like other *Cybister*, but females usually have a small, vestigial second claw, though it is more distinctive and longer on some specimens than others, and it is absent on some specimens. Finally, the male metacoxal stridulatory structure is comprised of a short series of ridges with some specimens having three and others having four.

Young (1953, 1954) made a careful study of the species in eastern North America and identified these varying features. His conclusion was that the populations in the Bahamas and coastal areas from Louisiana east to Florida and north to Pennsylvania (Fig. 3) have 1) the male stridulatory ridges on the metacoxa usually three (four in other populations), 2) the female microsculpture on the elytron less dense and less broadly distributed than other populations, 3) the marginal yellow stripe on the pronotum and elytron narrower and shorter than the broader and longer stripe on other populations, and 4) size smaller (26.0–32.0 mm vs. 28.0–33.0 mm in other populations). Despite these differences, Young (1953, 1954) discovered considerable overlap and introgression of these characteristics and, so, recognized two subspecies, *C. fimbriolatus crotchii*

in the southeast (Fig. 3) and *C. fimbriolatus fimbriolatus* in the rest of its distribution (Fig. 4). Use of these subspecies is abandoned here (see below).

Members of the species in the western part of its range south into Mexico (previously placed in *C. ellipticus*, *C. cavicollis* and *C. flavocinctus*, see below) seem to be somewhat more parallel-sided with broader yellow stripes (Fig. 2). A careful examination of specimens along with measurements indicates that the seemingly more parallel habitus is something of an illusion, perhaps created by the generally broader lateral stripes in many specimens. These features, however, are variable even within this geographic area. Importantly, the male genitalia are extremely consistent in shape throughout the range of the species (Figs. 8–11).

Taxonomy. The main source of the numerous names attributable to this species is the intra-specific variation in size, coloration, shape and female microsculpturing along with wide geographic distribution. Six species-group names are associated with the species, with several of these historically regarded as either subspecies or varieties at various times. All of these names were based on variation that was discovered to fit well within the observed overall variation of the species throughout the range. Surprisingly little variation was observed in male genitalia among any specimens, including those individuals and populations that tend to have size or color variation or are from widely divergent geographic localities. All of these names are, therefore, referred to a single species.

Say's (1823) syntypes of *Dytiscus fimbriolatus* (type locality = "USA") are probably lost, but there is little doubt about the attribution of the name *C. fimbriolatus* (Say) to this species, and, following Article 75.3 of the Code, a neotype is not needed and not designated here.

Aubé (1838) described two species: *C. dissimilis* from the "USA" (type locality = "États-Unis") and *C. flavocinctus* from Mexico (type locality = "Mexique"). *Cybister dissimilis* was synonymized by Melsheimer (1853) and this was followed by Sharp (1882a) and others. Although the syntypes were not examined, it is clear from the description and others' interpretations that *C. dissimilis* refers to the same species as *C. fimbriolatus*. *Cybister flavocinctus* is purportedly more parallel-sided with a more distinctive lateral yellow band than many *C. fimbriolatus* (Aubé 1838), but these characteristics are consistent with the range of variation of *C. fimbriolatus*. Sharp (1882b) regarded *C. flavocinctus* as "...excessively close to some of the varieties of *Dytiscus fimbriolatus*..." Although the types of *C. flavocinctus* were not examined, Sharp's (1882b) evaluation that the

species is a junior synonym of *C. fimbriolatus* is followed here.

Cybister ellipticus LeConte was described for specimens that were purportedly more green, have a broader lateral yellow band, and are more parallel-sided than typical *C. fimbriolatus* (LeConte 1851–1852) (type locality = USA, California, Colorado River valley (indicated as "vallem fluminis Colorado" on the label). Sharp (1882b) thought the species was very close to *C. fimbriolatus*, and others have regarded them as synonyms in the past (e.g., Wilke 1920). LeConte (1851–1852) seemingly had multiple specimens of this species on which he based his description. A single male specimen in the MCZC is labeled as the type, and this specimen is selected as the lectotype to stabilize nomenclature in the group. It is labeled, "[gold disc]/ T. ellipticus Cal. Lec. [handwritten]/ Type 6087 [red label]." Based on the description, examination of photographs of this type at insects.oeb.harvard.edu/mcz/, and the conclusion that the specimen fits well within the range of variation of *C. fimbriolatus*, *C. ellipticus* LeConte clearly refers to the same species as *C. fimbriolatus*, and is regarded here as a junior synonym, following Wilke (1920).

Young (1953) discussed the derivation of the names *Cybister olivieri* and *Cybister crotchii*. Crotch (1872) first proposed the name *Cybister olivieri* for a species illustrated by Olivier (1795) under the name *Dytiscus costalis* F. but regarded by Crotch as distinct from that species. Crotch (1873) later designated a type specimen (type locality = "USA, Florida," in the MCZC) for *C. olivieri*, but this designation was invalid because the illustrated specimen is the type. Olivier's (1795) species is a cybistrine from French Guiana and Suriname, so is likely a species of *Megadytes*, not *Cybister*, and is currently placed in that genus (Wilke 1920; Young 1953; Nilsson 2001). Wilke (1920) believed that Crotch's species concept required a new name and, therefore, proposed *Cybister crotchii* Wilke by indication to Crotch (1873). The type specimen of *C. crotchii* (= *C. olivieri sensu* Crotch 1873, not Crotch 1872) is in the MCZC and photographs were examined at insects.oeb.harvard.edu/mcz/. It is labeled, "Fla./ olivieri 2 [handwritten]/ M.C.Z. Type 25443 [red label, number handwritten]." It seems clear that the name *C. crotchii* belongs to the same species as *C. fimbriolatus* (e.g., see Young 1953). Although regarded as a subspecies in the past (e.g., Young 1953), this seems undesirable given that many specimens within the purported range of *C. fimbriolatus crotchii* do not conform to the purported character combination of the subspecies, and specimens well outside that range are similar or exhibit other types of variation. For this reason, use of subspecies names within *C. fimbriolatus* is abandoned here.

Sharp (1887) described the species *Cybister cavicollis* from a single female specimen that has reduced dorsal sexual sculpturing, but otherwise is typical of Mexican populations of *C. fimbriolatus*. The female holotype specimen is in the Natural History Museum, London, and was examined by R. Braga (personal communication). The type locality is "Mexico, near the city [Mexico City]," well within the distribution of *C. fimbriolatus* (Fig. 19). Based on the description and this examination of the types, it seems clear, that with other species based on southwestern North American specimens, this name refers also to *C. fimbriolatus* and is recognized as a junior synonym here.

Distribution. This is the most broadly distributed of the three species of *Cybister* in North America, ranging from southeastern Canada to North Dakota and Ontario and throughout the eastern United States south through Florida and to the Bahamas (Bimini Island) (Fig. 19). The species also extends west through the southern United States to Arizona and southern California and south throughout Mexico to the Yucatán (Fig. 19). There is currently no evidence the species breeds in Canada, however, and specimens collected there may have dispersed from farther south (Larson *et al.* 2000).

Natural history. *Cybister fimbriolatus* is found in a variety of habitats, but primarily larger water bodies such as ponds, lake margins, and ditches with emergent vegetation. Specimens often come to lights. Their feeding habits as predators have been investigated by Ideker (1979) and Johnson and Jakinovich (1970). Flight behavior has been studied by Johnson (1972). A nematode, *Drilomermis leioderma* Poinar and Petersen, was described from *C. fimbriolatus* (Poinar and Petersen 1978). Larvae were described by Wilson (1923) and Shepley-James *et al.* (2009).

Cybister occidentalis Aubé, 1838

Figs. 4, 12–15, 19

Cybister occidentalis Aubé, 1838: 67. Chevrolat 1863: 202; Sharp 1882a: 733; Zimmermann 1920: 263; Blackwelder 1944: 80; Epler 1996: 3:39, 2010: 5.51.

Cybister (Nealocomerus) occidentalis. Young 1953: 7, 1955: 121; Brinck 1945: 13.

Diagnosis. This species is uniquely characterized by the nearly right-angled (Fig. 6) to slightly rounded (Fig. 7) apicoventral angle of the metafemur combined with the presence of extremely large marginal lobes on the median lobe of the aedeagus in males (Fig. 12–14). This species differs from *C. explanatus* in having the apicoventral angle of the metafemur nearly right-angled and

often slightly rounded (as in Fig. 6) rather than acuminate produced (Fig. 7) and the presence of extremely large marginal lobes on the median lobe of the aedeagus in males (Fig. 12–14). *Cybister occidentalis* can only be confidently separated from *C. fimbriolatus* by characteristics of the male median lobe. In *C. fimbriolatus*, the ventral sclerite is long and relatively slender, extending to near the apex of the median lobe (Figs. 8–10). In *C. occidentalis*, the ventral sclerite is much shorter and broader, ending well short of the apex of the median lobe (Figs. 12–14).

Measurements. TL = 27.6–33.7 mm, GW = 14.4–18.2 mm, TL/GW = 1.8–1.9.

Variation. The main variation within this species is in size, though it is not extreme (30–34 mm). Also, some specimens have the lateral yellow stripes on the elytra shorter, not extending to the apex of the elytra.

Taxonomy. Aubé (1838) described this species based on specimens from Cuba (type locality = "Cuba, Havana"). The type specimen was not examined, but there can be little doubt as to the identity of this species from Cuba.

Distribution. This species is found mainly in the Bahamas and Cuba (Fig. 19). The species has also been collected from Big Pine Key from extreme southern Florida (Young 1953, 1954; Epler 2010). Turnbow and Smith (1983) recorded the species also from Crisp County, Georgia. This is some distance outside the expected range of the species, and Young (1954) did not find the species anywhere else in the southeastern mainland, suggesting that this record could be erroneous.

Natural History. This species is found in ponds and ditches (Young 1953, 1954).

Cybister explanatus LeConte, 1852

Figs. 5, 7, 16–19

Cybister explanatus LeConte, 1852: 202. Crotch 1873: 399; Sharp 1882a: 734, 1887: 759; Zimmermann 1920: 259; Blackwelder 1944: 80; Leech 1948: 413; Hatch 1953: 239; Leech and Chandler 1956: 323.

Cybister explanatus laevicollis Zimmermann, 1919: 243. Zimmermann 1920: 259 (as a variety of *C. explanatus*); Blackwelder 1944: 80 (as variety of *C. explanatus*).

Cybister explanatus fuscus Zimmermann, 1919: 242. Zimmermann 1920: 259 (as a variety of *C. explanatus*); Blackwelder 1944: 80 (as a variety of *C. explanatus*);

Cybister (Nealocomerus) explanatus. Brinck 1945: 13.

Cybister (Nealocomerus) fuscus. Brinck 1945: 13.

Diagnosis. *Cybister explanatus* is easily distinguished externally from all other New World

Cybister by the acuminate and sharply pointed anteroventral angle of the metafemur in both sexes (Fig. 7). Males have the median lobe (Figs. 16, 17) more slender, apically broadly rounded in ventral aspect, and lacking the large marginal lobes that enclose the ventral sclerite in *C. fimbriolatus* and *C. occidentalis* (Figs. 8–10, 12–14). The male lateral lobe is more slender and straplike apically (Fig. 18) compared with the other two species (Figs. 11, 15). Many specimens have some yellow coloration along the anterior and posterior margins of the pronotum. Females usually have sexual sculpturing (fields of fine scratches) on the pronotum, bases of the elytra, and, often, on the base of the head. This sculpturing is variable in the species, with many specimens having no sculpturing on the elytra.

Measurements. TL = 24.5–29.0 mm, GW = 13.0–15.2 mm, TL/GW = 1.8–1.9.

Variation. This species tends to be less variable than others throughout its range, with most variation in size and coloration. The lateral stripe of yellow on the pronotum and elytron is somewhat variable in width and length. The dorsal coloration varies from green to brown-black. The ventral coloration varies from brown to black, some of which appears to be due to how teneral is the specimen.

Taxonomy. LeConte (1851–1852) seemingly had multiple specimens of *C. explanatus* since he indicated multiple collecting localities. There are three specimens in the LeConte Collection (MCZC) attributed to *C. explanatus*. One is a male of *C. fimbriolatus* labeled with “Cala” (determined as *C. ellipticus* by J. Zimmermann). Another is a male *C. explanatus* labeled “Cal” and the last is a female *C. explanatus* labeled “[gold disc]/ T. explanatus S.D. & Sac. Lec. [handwritten]/ Type 6088 [red label].” The red type label on the female was added later, and does not constitute a lectotype designation, and no lectotype has yet been selected. Of the three specimens, the *C. fimbriolatus* specimen is not a suitable lectotype since it would upset stability of the name. Also, LeConte described *C. ellipticus* (= *C. fimbriolatus*, see above) in the same paper as *C. explanatus*, and this specimen is more likely to be part of the syntype series for that species (he would have been unlikely to misidentify it). Of the two other specimens, the female has the gold disc characteristic of specimens collected in California by LeConte and included in the same paper (LeConte 1851–1852). Although LeConte did describe species labeled “Cal,” these are generally in later papers. Although a male lectotype might be preferable given that most diving beetle classification is based on males, the female specimen is unambiguously *C. explanatus* (it has acuminate posterolateral angles of the metafemur), and the male specimen, though also clearly

C. explanatus, may not be part of the syntype series. For these reasons, the female specimen is selected as the lectotype to promote stability of the concept of this species. The type locality for the species was listed as San Diego and the Colorado and Sacramento Rivers (LeConte 1851–1852). The lectotype does not help clarify this since it is just labeled as both “S.D. & Sac.”

The types for *C. explanatus laevicollis* Zimmermann nor *C. explanatus fuscus* Zimmermann (presumably in the Zoologische Staatssammlung, Munich) were not examined. Their type localities are each “Mexico.” Each of these were described as “varieties” or subspecies of *C. explanatus* based on variation in color and microsculpture (Zimmermann 1919), though Brinck (1945) recognized *C. fuscus* at the species rank. However, the variation of each of these fits well within the range of variation of *C. explanatus* throughout its distribution, and their status as species or subspecies is abandoned here.

Distribution. *Cybister explanatus* occurs from extreme southern Oregon through California and western Nevada and through western Mexico to Chiapas (Fig. 19).

Natural history. *Cybister explanatus* specimens are found in a variety of habitats, but mainly larger ponds and lakes. They often come to lights. Specimens likely attributable to this species (curiously, without the heads) were found in prehistoric human coprolites in a Nevada cave (Roust 1967), indicating their historical use as human food, this seemingly despite the prothoracic chemical defensive compounds produced by these dytiscids. Many other components (e.g., fish, mussels) of the coprolites were found to be characteristic of the Humboldt Sink (Roust 1967), suggesting the aquatic beetles probably also came from that site.

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