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DYTISCIDAE AND NOTERIDAE OF WISCONSIN (COLEOPTERA). II. DISTRIBUTION, HABITAT, LIFE CYCLE, AND IDENTIFICATION OF SPECIES OF DYTISCINAE'

William L. Hilsenhoff²

ABSTRACT

Twenty-one species of Dytiscinae were collected in Wisconsin over the past 30 years, including three species of Acilius, one species of Cybister, eight species of Dytiscus, five species of Graphoderus, two species of Hydaticus, and two species of Thermonectus. Species keys are provided for adults, and except for *Dytiscus* and *Cybister*, keys are also provided for larvae. Based on a study of 13,236 adults and 854 larvae, information on the distribution and abundance of each species in Wisconsin is provided along with notes on their habitat, life cycle, and identification.

Six genera and 21 species of Dytiscinae were collected in Wisconsin. These include the largest species of Dytiscidae, with adults ranging from nine to 42 mm in length. Because they are large, adults swim rapidly and are difficult to capture with a net. I collected most adult Dytiscinae with bottle traps, and while larvae were more readily captured with a net than adults, they too, were effectively captured with bottle traps (Hilsenhoff 1991). Collecting efforts, measurement of specimens, and general information about life cycles are summarized in Part I of this study (Hilsenhoff 1992). Part I also contains a generic key to adults and a map of Wisconsin with numbered counties that are grouped into nine areas; this map is often referred to below.

Based on 13,236 adults and \$52 lowes that could be identified to provide

Based on 13,236 adults and 853 larvae that could be identified to species, the general distribution and relative abundance of species of Dytiscinae is summarized in Table 1 for the nine areas of Wisconsin. Totals for collections that resulted from intensive studies in McKenna Pond (Hilsenhoff 1992) and the Leopold Memorial Reserve (Sauk County) are included separately in this table because of the large number of beetles that were collected. The latter includes monthly (March-October) net and trap collections from 16 ponds between May 1989 and May 1992, which are part of an ecological study of pond insects by Leonard Huebner. Dytiscidae collected by Huebner were not included in part I of this study (Hilsenhoff 1992), but will be included in this and subsequent parts. The 658 adult Dytiscinae that were collected with bottle traps from Horicon Marsh by Kevin Kenow during the summer months from 1983 through 1985 are reflected in totals for the south-central area (Table 1); most were Graphoderus and Hydaticus. He did not collect beetles during other months and no larvae were saved from his collections.

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Table 1. Numbers of Dytiscinae adults (A) and larvae (L) from nine areas of Wisconsin (Hilsenhoff 1992), McKenna Pond (McK), and Leopold Memorial Reserve (LMR) collected between 1962 and 1992.

	NW	NC	NE	WC	С	EC	SW	SC	SE	McK	LMR	TOTAL
Acilius mediatus A	0	8	2	9	0	0	0	11	0	0	0	30
A. mediatus L	0	0	1	0	0	0	0	1	0	0	0	2
A. semisulcatus A	415	422	412	225	324	215	86	146	61	463	863	3632
A semisulcatus L	36	47	100	15	16	34	7	7	9	11	3	285
A. sylvanus A	43	50	62	15	52	89	136	56	10	101	760	1374
A. sylvanus L	1	2	0	0	6	3	21	5	2	2	4	46
Cybister fimbriolatus A	0	0	0	1	0	1	1	6	1	65	113	188
C. fimbriolatus L	0	0	0	0	0	2	0	0	0	10	0	12
Dytiscus alaskanus A	0	0	0	3	0	0	0	0	0	0	0	3
D. carolinus A	0	0	0	0	0	0	5	8	1	0	0	14
D. cordieri A	6	9	11	11	61	18	2	41	21	59	1	240
D. dauricus A	6	24	11	0	0	0	0	0	0	0	0	41
D. fasciventris A	29	85	45	29	67	46	63	101	49	1	32	547
D. harrisii A	20	14	3	5	28	8	0	3	1	1	0	83
D. hybridus A	13	7	1	41	26	30	36	57	29	180	360	780
D. verticalis A	148	110	29	63	40	32	35	52	17	22	194	742
Graphoderus fascicollis A	34	4	6	2	13	9	8	147	9	15	32	279
G. liberus A	389	64	152	24	51	3	0	47	36	61	77	904
G. liberus L	25	0	10	0	1	0	0	0	1	13	0	50
G. manitobensis A	0	0	0	0	2	2	3	21	0	21	5	54
G. manitobensis L	0	0	0	0	0	5	0	0	0	1	3	9
G. occidentalis A	10	0	4	3	2	7	3	109	3	19	21	181
G. perplexus A	61	31	69	24	49	10	7	139	24	1395	50	1859
G. perplexus L	7	16	27	3	2	6	0	3	1	107	1	173
Hydaticus aruspex A	256	144	248	142	162	99	143	173	63	189	123	1742
H. aruspex L	41	23	19	1	57	34	5	11	12	24	3	230
H. piceus A	4	0	2	0	5	25	157	103	25	27	17	365
H. piceus L	2	0	0	1	0	4	9	0	6	0	0	22
Thermonectus basillaris A	0	0	0	1	0	0	0	0	2	2	0	5
T. ornaticollis A	0	0	0	13	0	1	4	9	1	120	25	173
T. ornaticollis L	0	0	0	0	0	0	0	0	1	24	5	30

Below, under each genus, is a key to adults of species that occur or may occur in Wisconsin; a size-range for adults from Wisconsin is included for each species. A key to third instar larvae (larvae having lateral spiracles) is included, except for *Cybister* and *Dytiscus*. Usually second instar larvae can also be identified with these keys, but first instar larvae are structurally very different. Following the keys is information on distribution and abundance in Wisconsin, general range in North America, habitat, and identification. County records are represented by numbers on the map in part I (Hilsenhoff 1992); records based only on larvae are marked with an asterisk.

Acilius Leach, 1817

Four species occur in northeastern North America (Hilsenhoff 1975); only three were found in Wisconsin as a result of this study. It is possible that Acilius fraternus fraternus may also occur in Wisconsin, since it was reported by Wallis from four localities in Minnesota (Larson, 1973); however, none of these specimens could be located to verify Wallis' identifications. A male adult A. fraternus fraternus in the University of Wisconsin Insect Research Collection is labeled only "Wis." and "Collection of W.S. Marshall". This specimen, which was probably collected before 1925, may not have been collected in

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Wisconsin. Larvae of species collected from Wisconsin were identified by using available descriptions and circumstantial evidence such as relative abundance of larvae and adults, their distribution, and especially collections of adults and larvae from the same site. Inclusion of the larva of A. fraternus fraternus is based upon the description and figures of Wolfe (1980).

All species normally have a univoltine life cycle in Wisconsin. Adults overwinter in deeper ponds and margins of lakes and streams, but often fly to a wide variety of other habitats in early spring where they apparently mate and oviposit in late March and April, and then die. Most larvae develop in May (first and second instars) and June (third instar), and pupate in June. Most adults emerge in June and early July.

Key to Species of Adult Acilius in Wisconsin

1. Testaceous ventrally; 13.2-16.6 mm longsylvanus Black, or mostly black ventrally2 2(1). Smaller, 10.6-12.5 mm long; metatibia and tarsus black; males without tufts of hairs on inner ventral margin of 3 basal mesotarsal segments; females without elytral sulci and with a distinct M-mark on dorsum of Larger, > 12.5 mm long; metatibia and tarsus testaceous to rufous; males with tufts of golden hairs on inner ventral margin of 3 basal mesotarsal segments; females with elytral sulci or without a distinct 3(2). Metafemur testaceous with a small basal infuscation; second visible abdominal sternum usually with a pale lateral spot on each side; anterior pro- and mesotarsal claws of male longer and thicker than posterior claws; female elytra sulcate, longest sulci extending to basal seventh of elytra; 12.6-16.6 mm long.....semisulcatus Metafemur rufous to piceous, lighter apically; second visible abdominal sternum without pale lateral spots; pro- and mesotarsal claws of male not modified; female elytra, if sulcate, with longest sulci extending only to basal fourth of elytra; 13.4-16.0 mm long (Indiana speci-

Key to Species of Larval Acilius in Wisconsin

mens) fraternus fraternus

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Acilius fraternus fraternus (Harris, 1828)

Distribution and Abundance: Range: IA-MA-GA-AR. A. fraternus dismalus Matta and Michael, 1976 occurs farther south.

Habitat: Michael and Matta (1977) most often collected this species in shaded ponds and pools with some leaf litter.

Life Cycle: Unknown, but likely univoltine in the northern part of its

Identification: Adults are similar to A. semisulcatus, but are readily separated from that species by characters in the key. The M-mark on the head is very obscure; often it cannot be seen. The larva of A. f. fraternus, as described by Wolfe (1980), is similar to the larva of A. mediatus because the ligula is forked near the middle. However, the ligula in Wolfe's figure is more slender than in A. mediatus and the frontoclypeus of A. f. fraternus does not have the distinct, dark, anterior rectangle of A. mediatus.

Acilius mediatus (Say, 1823)

Distribution and Abundance: Uncommon statewide (Table 1). County records: 10, 12-13, 15, 18*, 19, 30-31, 57. Range: MN-NB-NC-MO. Habitat: All adults and larvae were collected from swamps or small, soft-

water ponds in areas above precambrian formations.

Life Cycle: A second instar larva was collected in early June; a third instar larva and a teneral adult were collected in late June; a slightly teneral adult was found August 10 in the extreme north. Most adults were collected in April, or from July through October. This indicates a univoltine life cycle as

described above for the genus.

Identification: Adults can be recognized in the field by their smaller size, dark coloration, and bold black and yellow fasciae across the apical third of the elytra. The second instar larva was collected from a site where 15 adults were collected on six dates and no other species of Acilius has been found. The ligula and markings on the head differed markedly from other Acilius larvae that I collected in Wisconsin; therefor I conclude it must be the larva of A. mediatus. Subsequently a third instar larva was collected from a Sphagnum habitat, which is typical for adults of this species. The head capsule width of the third instar larva was less than 0.5 mm, and narrower than in third instar larvae of A. semisulcatus and A. sylvanus.

Acilius semisulcatus Aubé, 1838

Distribution and Abundance: Very common in northern two-thirds, common in southern third (Table 1). County records: 1-27, 29-61, 63-72. Range: AK-NF-NJ-IL-AB

Habitat: Adults and larvae were collected most frequently from permanent ponds, but they also occurred in deeper marshes, margins of swamps, and

vernal ponds and marshes.

Life Cycle: Most adults were collected in March and April, and from late June to November; they were uncommon in May and early June. Second instar larvae were found from May 7 to June 27, third instar larvae from May 5 to July 24, and teneral adults from June 1 to August 21. Two larvae collected August 20-21 from cold northern swamps probably resulted from delayed development. The univoltine life cycle described for the genus is typical for this species. Two larvae were collected from a warm central-Wisconsin marsh in mid-August and two more from a flooded field in October; teneral adults were also collected in October. These records probably represent a partial second generation, which may occur in some years.

Identification: The testaceous metafemora with a small basal infuscation

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immediately distinguishes adults from other species with dark venters. Larvae are readily identified by the elongate ligula, which usually is branched between the apical third and apical sixth. I have two larvae from northern Wisconsin with their ligula branched near the middle, but their heads lack the dark anterior marks found in A. mediatus and A. f. fraternus and I believe they are A. semisulcatus. The brief larval description by Watts (1970) describes this species and not A. sylvanus, which in 1970 was considered to be a color variant of A. semisulcatus. Wilson's (1923) larval description is errone-

Acilius sylvanus Hilsenhoff, 1975

ous; he describes a Graphoderus larva.

Distribution and Abundance: Common statewide (Table 1). County records: 2-6, 8-11, 13, 16-25, 27-44, 45*, 46-52, 54-63, 66, 70-72. Range: MB-PQ-ME-NJ-IL

Habitat: The habitat is similar to that of A. semisulcatus, except adults and larvae were infrequently found in acid waters. Often adults of A. semi-

sulcatus and A. sylvanus occurred together.

Life Cycle: Second instar larvae were found from May 11 to July 13, third instar larvae from May 8 to July 13, and teneral adults from June 21 to August 10. Almost no adults were collected from late April to mid-June. This suggests a life cycle like that described for the genus.

Identification: The testaceous ventral surface of adults and lack of a distinct sub-apical fascia on the elytra are distinctive. The elongate branches of the ligula with distinct apical and sub-apical spines readily separate larvae

from other species.

Cybister Curtis, 1827

A single species of this southern genus occurs in the northern United States and Canada.

Cybister fimbriolatus (Say, 1823)

Distribution and Abundance: Uncommon in central and southern Wisconsin (Table 1). County Records: 26, 46, 48*, 51, 57-58, 60-61, 67. Range: MB-NS-FL-TX.

Habitat: Larvae and adults inhabit deeper water of open permanent

ponds.

Life Cycle: Adults were collected from April to November. Second instar larvae were found from June 5 to 21, third instars from June 23 to July 15, and teneral adults from August 17 to September 24. Adults overwinter, probably in deeper ponds, and oviposit in spring. Larvae develop in late spring and summer, and apparently pupate from late July into September. Adults emerge in late summer and early autumn to complete a univoltine life cycle.

Identification: Adults resemble small Dytiscus verticalis or large D. hybridus, but are distinctly widened at the apical third and have numerous tiny, green spots on the elytra. They lack a pale sub-apical fascia on the elytra, which occurs in D. verticalis, and almost always have a green prosternal process. The protarsal disc of males is angulate on the anterior margin, giving it a triangular shape when not expanded. Females have elongate, longitudinal aciculations laterally on the elytra. Larvae resemble those of Dytiscus because second and third instars are large and have a setal fringe on the last two abdominal segments. They are readily identified, however, because their urogomphi are vestigial and they possess long teeth on the labroclypeus. Wilson (1923) described the larva.

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Dytiscus Linnaeus, 1758

Roughley (1990) revised the world fauna, providing a wealth of information on identification, distribution, habitat, life history, and phylogeny. Part I of his revision deals only with adults; part II, which has not yet been published, will contain keys and descriptions of larvae. I was unable to identify larvae of some species, so my study of *Dytiscus* in Wisconsin is based only on adults. Eight species were collected and are keyed below along with *D. circumcinctus*, which also may occur in Wisconsin. Because they are large, adults were measured with a caliper instead of an ocular micrometer. The length of Wisconsin specimens was generally longer than reported by Roughley (1990).

Aquarium and field observations, along with collection records and date of occurrence of teneral specimens, indicate all species have a univoltine life cycle similar to that reported by Aiken and Wilkinson (1985) for *D. alaskanus*. Adults of Dytiscus overwinter in a variety of deeper aquatic habitats and disperse in spring as soon as these habitats become free of ice and air temperatures are sufficiently warm to permit flight. Adults mate very early in the spring and oviposit when their breeding habitat becomes free of ice, which may be from late March to early May, depending on habitat and latitude. Most adults apparently die after mating and oviposition, but some survive well into summer. Eggs of most species probably hatch from late April to late May, depending on water temperatures and date of oviposition. Larval development is completed from early June to early August, with much variation among and between species. At least 60% of adult Dytiscus were collected in March and April with bottle traps, often from overwintering habitats still partially covered with ice. The remaining adults were collected mostly from June through August; few were collected in May and after September. The scarcity of adults after September is probably due to movement into deeper water to overwinter and decreased activity, which makes them less vulnerable to trapping.

Key to Species of Adult Dytiscus in Wisconsin

2(1).	Metacoxal process rounded, never spinose; venter pale or dark 2 Metacoxal process distinctly spinose; venter mostly pale
3(2).	Larger, > 33 mm long; elytra with a sub-apical pale fascia4 Smaller, < 29 mm long; elytra without a sub-apical pale fascia5
4(3).	 Smaller, < 29 mm long; elytra without a sub-apical pale tascia Metacoxal plate and first visible abdominal sternum dark rufous, same color as rest of metasternum and venter; posterior margin of pronotum without a pale band; 33.4-38.6 mm long
	margin of pronotum with a pale band; 35.7-41.6 mm longharrisii
5(3).	Mesotarsus of male with median glabrous area dividing suckers; female without elytral sulci; venter dark rufous, without black fasciae; 24.4–28.8 mm long
1	Mesotarsus of male without glabrous area dividing suckers; female with elytral sulci; venter with black fasciae
	Metacoxal plate and first visible abdominal sternum pale, much lighter than infuscate mid-metasternum; anterior of pronotum with pale border; 24.8-28.5 mm long

color to metasternum; anterior of pronotum without a pale border; 7(1). Head narrowly pale along inner margin of eye; piceous marks on basal abdominal sterna absent or very narrow basal lines; 27.5-34.0 mm 8(7). Larger, 35.4-39.7 mm long; basolateral piceous marks extend at least

half distance to posterior margin on visible abdominal sterna 2 and

Smaller, 29.4-31.5 mm long; basolateral piceous marks usually do not extend half distance to posterior margin on visible abdominal sterna 2 and 3alaskanus

Dytiscus alaskanus J. Balfour-Browne, 1944

Distribution and Abundance: Very rare in west-central area (Table 1). County records: 25, 29. Range: AK-NF-NH-MN-WA+WY+CO.

Habitat: Wisconsin specimens were collected from emergent vegetation in large permanent ponds. This species is more abundant west and north of Wisconsin, where it inhabits permanent ponds and lakes (Roughley 1990).

Life Cycle: Aiken and Wilkinson (1985) studied the bionomics in north-

central Alberta. They reported a univoltine life cycle with overwintering adults, mating in April, and oviposition as soon as the lake was free of ice. First instar larvae appeared from mid-to late May, and peak numbers of third instar larvae occurred throughout July. In Wisconsin this sequence probably occurs earlier because of a warmer climate.

Identification: Adults could be confused with D. dauricus, but in Wisconsin they are distinctly smaller. In males, the penis (median lobe of aedeagus) in dorsal view is broad and evenly tapered to the apex (Fig. 1), while in D. dauricus (Fig. 2) and D. circumcinctus it is narrower and subapically sinuate to form an apical knob. In sulcate females, ridges on elytral intervals 8 and 9 meet to form a "V". These ridges do not meet in D. dauricus or D. circumcinctus. The size of black basolateral marks on visible abdominal sterna 2 and 3 varies in the three Wisconsin specimens from narrow to expanded almost halfway to the posterior margin, but the marks are distinct on the last visible sternum in all specimens. Dytiscus circumcinctus adults lack a black mark on the last visible abdominal sternum.

Dytiscus carolinus Aubé 1838

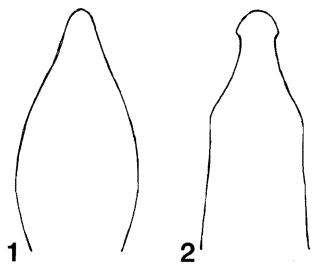
Distribution and Abundance: Rare in southern third (Table 1). County records: 52, 55, 57, 60, 72. Range: WI-MA-GA-AR.

Habitat: All except one adult were collected from ponds and sloughs associated with large rivers.

Life Cycle: Six of the seven collections were overwintering adults collected from March 17 to April 4. The seventh collection contained four adults, which were trapped June 23-25 in LaCrosse County; two were teneral, which indicates oviposition in early spring and completion of larval development by mid-June.

Identification: Adults are most similar to D. fasciventris, but can be separated from that species by characters in the key. Abdominal sterna are rufous with black fasciae; in D. fasciventris they are usually testaceous with black fasciae and when darker the first abdominal sternum and the metacoxal plate are always paler.





Figures. 1-2. Apical 2 mm of penis (dorsal view). 1. Dytiscus alaskanus. 2. D. dauricus.

Dytiscus circumcinctus Ahrens, 1811

Distribution and Abundance: Not yet found in Wisconsin. Range: AK-PQ-ME-NC-IA-ND-WA.

Habitat: Roughley (1990) reported that adults in western North America were found in a wide range of aquatic habitats.

Life Cycle: The life cycle is apparently univoltine, with adults overwinter-

ing in both terrestrial and aquatic habitats (Roughley 1990).

Identification: The lack of black abdominal markings, except for extremely narrow basal lines on visible abdominal sterna 1-3 (Roughley 1990), separates this species from D. alaskanus and D. dauricus in Wisconsin.

Dytiscus cordieri Aubé, 1838

Distribution and Abundance: Fairly common statewide (Table 1). County records: 3-6, 8, 10, 12, 14-15, 17, 19-25, 33-35, 37-39, 41-48, 50-51, 57-59, 61, 64, 67-68, 70-72. Range: AK-NB-NC-CO-CA.

Habitat: Adults were collected from open ponds and marshes.

Life Cycle: The life cycle is typical of that described above for the genus. It is completed somewhat earlier than in most other species, probably due to warmer water in its open breeding habitat. Teneral adults, along with many

mature adults, were collected from June 23 to August 2.

Identification: This is the only Dytiscus in Wisconsin in which adults are almost entirely testaceous ventrally. They lack the spinose metacoxal lobes of other medium to large Dytiscus that are mostly testaceous ventrally.

Dytiscus dauricus Gebler, 1832

Distribution and Abundance: Uncommon in northern third (Table 1). County records: 1-2, 4-5, 9-13, 15, 17-18, 20-22. Range: AK-LB-NH-SD-CO-AZ-CÁ.

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Habitat: Adults were collected from bogs, swamps, and a variety of

Life Cycle: Most adults were captured in traps in April and August; the remainder (five) were collected in June and July. Two teneral adults were

found in August, indicating a typical univoltine Dytiscus life cycle.

Identification: The very large size readily separates adults from those of D. alaskanus and most D. circumcinctus. All Wisconsin adults had basolateral marks on visible abdominal sterna 2 and 3 extending posteriorly to the middle of the segment or beyond, which would separate them from D. circumcinctus and most D. alaskanus. Other differences are discussed under D. alaskanus.

Dytiscus fasciventris Say, 1824

Distribution and Abundance: Common statewide (Table 1). County records: 2-6, 9-27, 29-42, 44-52, 54-61, 64, 66-68, 70-72. Range: YK-LB-NJ-IL-MN-MT-BC

Habitat: Adults were collected from a variety of ponds and marshes,

especially those with sedges (Carex, Eleocharis).

Life Cycle: The univoltine life cycle is typical of *Dytiscus*. Teneral adults were trapped from June 6 to August 10, especially from late June through July.

Identification: The combination of small size and testaceous venter with black basal fasciae on each segment is distinctive.

Dytiscus harrisii Kirby, 1837
Distribution and Abundance: Uncommon in northern two-thirds, rare in southern third (Table 1). County records: 2-13, 15-17, 20, 27, 29-39, 42, 44, 46,

48, 59, 61, 65. Range: AK-NF-PA-NE-ND-BC.

Habitat: Most adults were collected from a variety of ponds and marshes; two were collected from swamps, and two from the margin of rivers in October. All teneral adults (five from four sites) were trapped in sedge marshes or shallow ponds with sedge margins; I believe this is the larval habitat. Other than the two overwintering adults collected in October, I did not notice an association with streams as mentioned by Roughley (1990).

Life Cycle: Teneral adults were collected in central Wisconsin between June 23 and July 2, accounting for most adults collected in June and July. Because of the shallow, warm habitat in which larvae apparently develop,

they complete development earlier than most other Dytiscus.

Identification: Because of their large size, a subapical pale fascia on the elytra, and a mostly dark venter, adults can be confused only with D. verticalis. The pale first visible abdominal sternum, light mark on the anterior of each metacoxal plate, and broadly pale basal band on the pronotum easily separate adult D. harrisii from that species.

Dytiscus hybridus Aubė, 1838

Distribution and Abundance: Common in southern two-thirds, fairly common in northern third. County records: 1, 3-6, 8, 12-16, 20, 25-26, 28-32, 34-41, 44-58, 60-72. Range: AB-NB-SC-CO+OR

Habitat: Overwintering adults were collected from a variety of ponds and deeper marshes, but most teneral adults were found in shallow cattail (Typha)

marshes, which is likely their breeding habitat.

Life Cycle: The life cycle is typical of Dytiscus, with teneral adults being

collected between June 23 and August 1.

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Identification: The small size and uniformly dark venter of adults is a distinctive combination.

Dytiscus verticalis Say, 1823

Distribution and Abundance: Common statewide, especially so in northwest. County records: 1-23, 25-27, 29-40, 44-51, 53-55, 57-61, 65-68, 70-72. Range: MB-PE-VA-IN-MN

Habitat: Adults were collected from a variety of ponds, and less frequently from marshes and bogs. Most teneral adults were collected from shallow ponds with cattails along the margin; one was found in a sedge marsh.

Life Cycle: The relatively large number of adults collected in June suggests that overwintering individuals live longer than most other species and may continue to oviposit in late spring. Larval development was apparently later than in other species. All teneral adults were collected July 13 to August 20, except for one trapped in a sedge marsh on July 2.

Identification: The dark venter, large size, and sub-apical pale fascia on the elytra separate adults from all other dytiscids, except *D. harrisii*. Their separation is discussed under *D. harrisii*.

Graphoderus Dejean, 1833

All five North American species were collected. Wallis (1939) provided a key to male adults of North American species, which he concluded were distinct from species found in Europe, but he did not delineate their distribution. Lacking a recent revision, ranges of species within the United States are inadequately defined. Both adults and larvae of G. liberus differ significantly in many respects from the other four species, which are similar to one another. Male adults of these four species can be readily identified by the number of palettes on the mesotarsi; a table for separation of females was prepared by Tracy and Hilsenhoff (1982). The distinctive larva of G. liberus was described by Barman (1972) and that of G. perplexus (as zonatus) by Watts (1970), but the latter description was not helpful in separating G. perplexus larvae from those of the three similar species, which are undescribed. A study of Wisconsin larvae revealed characters by which third instar larvae of most species can be separated, but I was unable to separate larvae of G. fascicollis and G. occidentalis. A provisional key to larvae is provided below. Larvae (except G. liberus) were associated with adults by circumstantial evidence such as relative abundance, distribution within Wisconsin, date of occurrence, and presence of larvae and adults in the same site. Adults of G. fascicollis are most similar to those of G. occidentalis, while adults of G. manitobensis and G. perplexus are similar to each other. These relationships apparently also hold for the larvae. Numerous adults (359) of all species except G. liberus were collected in bottle traps from Horicon Marsh by Kevin Kenow from June through August, accounting for unusually high totals in the south-central area (Table 1).

Although all species of *Graphoderus* are predominantly univoltine, with adults overwintering in aquatic habitats, substantial differences in life cycles seem to exist between species. Overwintering adults of *G. fascicollis* and *G. occidentalis* apparently do not become active until later in the spring then *G. manitobensis* and *G. perplexus*, and thus oviposition and larval development is delayed. All of the species may have a partial second generation in some years.

Key to Species of Adult Graphoderus in Wisconsin

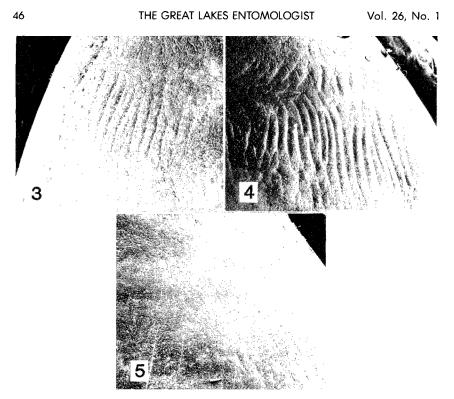
Key to Species of Larval Graphoderus in Wisconsin

Graphoderus fascicollis (Harris, 1828)

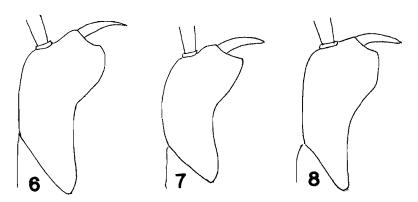
Distribution and Abundance: Fairly common statewide (Table 1). County records: 3-7, 9, 12, 15, 18-20, 25, 29, 34, 37-38, 40, 46-48, 50-51, 57-59, 61,

67-70, 72. Range: MN-PQ-ME-IN.

Habitat: Most adults were collected from small ponds containing cattails along at least one margin. Almost half of all adults were collected from Horicon Marsh, a very large marsh with numerous stands of cattails.



Figures. 3-5. SEM of lateral fourth of female pronotum. 3. Graphoderus perplexus. 4. G. manitobensis. 5. G. occidentalis.



Figures. 6-8. Right stipes of larva (ventral view). 6. $Graphoderus\ perplexus.\ 7.\ G.\ manitobensis.\ 8.\ G.\ fascicollis.$

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Life Cycle: Almost all third instar larvae believed to be *G. fascicollis* or *G. occidentalis* were collected June 7 to July 20; teneral adults were found June 25 to August 25, three-fourths of them in July. While adults were collected from March to October, 77% were found from June through August (excluding summer only collections from Horicon Marsh). I believe that most overwintering adults do not mate and oviposit until late May or June, with larval development being completed mostly in late June and July. One third instar larva that I believe is this species was collected October 5 in a flooded area; it probably represents a partial second generation.

Identification: Adults can be readily identified by the key. The area separating the anterior pronotal black band from the margin rarely may be rufotestaceous, but the posterior band is never separated from the margin as in G. perplexus. The three large and 22-24 small palettes on the protarsi and 12 palettes on the mesotarsi of males are diagnostic. In addition to characters in the key, larvae of this species and G. occidentalis have the inner apical margin of the stipes truncated (Fig. 8), which differs from the rounded inner apical

margin in G. perplexus (Fig. 6).

Graphoderus liberus (Say, 1825)

Distribution and Abundance: Common statewide, especially so in northern third (Table 1). County records: 1–20, 22–23, 25, 27, 30–31, 33–35, 38, 42, 44, 57–58, 61, 66, 68–70, 72. Range: NT-NF-FL-MN.

Habitat: Adults and larvae were collected mostly from margins of deeper ponds and small lakes. Larvae were found most frequently, but not exclu-

sively, in acidic habitats.

Life Cycle: Almost all third instar larvae were collected from June 7 to August 16; one was collected from McKenna Pond on September 15. Only 1% of adults were collected before May, but substantial numbers were collected from May through September. Unlike other Dytiscinae and other Graphoderus, adults were more readily collected with a net than with bottle traps (Hilsenhoff 1987). Reliance on bottle traps for collections in March and April and prolonged ice cover in the normal deepwater habitat probably account for low numbers found in early spring. This species apparently has a univoltine life cycle; adults overwinter in ponds and lakes, mate in early spring, and oviposit when the ice has thawed. Presence of third instar larvae in McKenna Pond from June 7 to August 6, 1976 suggests staggered oviposition, which may also account for the single larva found that year on September 15.

Identification: The longitudinal stripes on the larvae are distinctive. Adults can be easily recognized in the field by their shape, distinctive color, and very active behavior; they tend to "jump" when out of water and

disturbed.

Graphoderus manitobensis Wallis, 1933

Distribution and Abundance: Uncommon in southern half (Table 1). County records: 39-40, 46-47, 49, 52, 54, 57, 59, 61. Range: MB-WIIA. Habitat: Large sedge and cattail marshes or ponds in open areas.

Life Cycle: Twenty-one adults were collected from McKenna Pond April 3 to May 24; 20 were collected from Horicon Marsh June 13 to July 28 (only summer collecting). The remaining 13 adults were collected from various sites between April and early July. All adults, except one, were collected with bottle traps; none were found after July 28. Eight third instar larvae were collected June 10–30, with one second instar also present on the latter date. Another larva was found on September 10; it probably represents a partial second generation. Teneral adults occurred June 23 to July 14. Adults apparently

overwinter, probably in the breeding site, mate in early spring, and oviposit soon thereafter. Larvae develop in May and June and pupate; adults emerge

from mid-June to mid-July to complete a univoltine life cycle.

Identification: The 26-29 palettes on mesotarsi of adult males is diagnostic; three large and 25-30 small palettes occur on protarsi. Adult females, which were described by Tracy and Hilsenhoff (1982), have a more pronounced corrugated macrosculpture on the pronotum (Fig. 4) than other similar species. They most resemble females of G. occidentalis because both anterior and posterior black pronotal bands are contiguous with the margin, but in G. occidentalis the corrugated macrosculpture is obsolete and the metasternal wing is much wider. The metasternal wing in G. manitobensis is very narrow (0.33 mm), narrower than in almost all G. perplexus and much narrower than in G. fascicollis and G. occidentalis. Larvae resemble those of G. perplexus, but the inner margin of the stipes is gradually widened to the apex (Fig. 7) and not abruptly widened as in the other three species of Graphoderus with similar larvae (Figs. 6, 8). The sclerite on the larval prosternum is rectangular, and not narrowed anteriorly as in G. perplexus. In mature larvae it is slightly longer than wide, while in mature G. perplexus larvae it is about twice as long as wide, but this character varies somewhat with the age of the larva.

Graphoderus occidentalis Horn, 1883

Distribution and Abundance: Uncommon statewide; 81% of adults collected from Horicon Marsh and McKenna Pond (Table 1). County records: 3, 6-7, 19-20, 24-25, 29, 37, 43-44, 46, 48, 50, 57-59, 61, 67, 70-71. Range: YK-PQ-NY-WI-ND-UT.

Habitat: Adults were collected from a variety of ponds. The fact that half of the adults were collected from Horicon Marsh by Kevin Kenow suggests that this large, predominantly cattail marsh is a preferred habitat. Unfortu-

nately, larvae from Horicon Marsh were not saved.

Life Cycle: Teneral adults were collected June 28 to August 15, which suggests a life cycle like that described for G. fascicollis. One teneral adult was collected October 3, indicating a partial second generation in some years.

was collected October 3, indicating a partial second generation in some years.

Identification: The 2 large and 12–13 small palettes on protarsi and lack of palettes on mesotarsi of males, and the obscure corrugated sculpturing on the pronotum of females (Fig. 5), separate adults of this species from those of similar Graphoderus. Because the black anterior band on the pronotum is contiguous with the anterior margin (in pinned specimens the area near the margin may appear rufopiceous), adults most resemble those of G. manitobensis; separation of females is discussed under that species. Two larvae that may be this species have 40 or fewer spines on the last abdominal sternum compared with 46 or more in larvae believed to be G. fascicollis, but this character is variable and no other differences between these larvae and those believed to be G. fascicollis were found.

Graphoderus perplexus Sharp, 1882

Distribution and Abundance: Common statewide (Table 1). County records: 1-8, 11-15, 17-21, 23, 25, 27-29, 31, 34-44, 46-47, 48*, 50, 52, 54, 57-59, 61, 64, 66-67, 69-72. Range: AK-NF-AR-UT

Habitat: Adults and larvae were found in a variety of ponds, most of them being relatively shallow and vegetated with cattails, bur-reed (*Sparganium*), and sedges. About 75% of all adults were collected from McKenna Pond (Table 1), a relatively shallow 0.8 h pond containing cattails and bur-reed.

Life Cycle: Seventy percent of adults were collected from March through May. Adults obviously overwinter in ponds, mate in early spring, and oviposit

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in April. In McKenna Pond, first instar larvae were collected May 1, and small third instar larvae were found as early as May 5, with large third instar larvae appearing by May 15. Peak numbers of third instar larvae were collected in late May and early June; a few were found as late as July 21 in the north. Third instar larvae of other species of *Graphoderus* were not found before June 7. Teneral adults were collected from June 7 to July 23, to complete a univoltine life cycle. In 1977 (after a drought in 1976), McKenna Pond was completely dry by July, but flooded July 17–18 after heavy rain; on August 4 several second instar and two third instar larvae were collected. In 1980 and 1981 single third instar larvae were collected from McKenna Pond in early September and a teneral adult was found November 5, 1981. Teneral adults were collected elsewhere on August 15 and September 21. These late-occurring larvae and the teneral adults probably represent a partial second generation.

Identification: Adults can be readily distinguished by characters in the key. The corrugation of the pronotum of females, while readily seen (Fig 3), is not pronounced as it is in *G. manitobensis* (Fig. 4). The 3 large and 25-35 small palettes on protarsi and 14-15 palettes on mesotarsi of males is diagnostic. Larvae are most similar to those of *G. manitobensis*, but the shape of the stipes differs as described in the key. Larvae of *G. perplexus* and *G. manitobensis* can be readily separated from those of *G. fascicollis* and *G. occidentalis* by couplet 2 of the key and by conspicuous darkening at the base of spines on the last abdominal sternum, which is not evident in the latter two species.

Hydaticus Leach, 1817

Roughley and Pengelly's (1981) study of *Hydaticus* in North America provides the most recent key and descriptions for adults of the five species. Two species occur in the western Great Lakes region and are commonly found in Wisconsin. Larvae resemble smaller larvae of *Dytiscus*, but lack lateral ringes on the urogomphi and have two projecting lobes on the labium (Figs. 9, 10). Although only the larva of *H. aruspex* has been described (Watts 1970, as *H. stagnalis*), a study of larvae collected in Wisconsin enabled me to identify both species and to develop a key to third instar larvae.

The life cycle differs from other Dytiscinae, except *Thermonectus*, because adults overwinter in terrestrial habitats. Galewski (1964) reported that *Hydaticus* was one of four genera of European dytiscids that overwinters as adults in forest litter. Although I found four adults in aquatic habitats as early as late March, substantial numbers were not collected before the last 10 days of April. Temperatures sufficiently warm to thaw overwintering sites and permit flight frequently occur in Wisconsin as early as the last half of March.

Key to Species of Adult Hydaticus in Wisconsin

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Key to Species of Larval Hydaticus in Wisconsin

Anterior projections of labium pronounced, about a long as distance between their tips, and separated by a U-shaped emargination (Fig. 9); 4-8 small spines on genae on each side of gular areaaruspex
 Anterior projections of labium short, length much less than half distance between their tips, and separated by a shallow emargination (Fig. 10); no groups of small spines on genaepiceus

Hydaticus aruspex Clark, 1864 (= H. modestus Sharp, 1882)

Distribution and Abundance: Very common statewide (Table 1). County records: 1-45, 46*, 47-59, 61, 63-64, 65*, 66-68, 70-71, 72*. Range: AK-NF-NJ-MO-CA.

Habitat: Adults and larvae were collected from Sphagnum bogs and swamps, sedge and cattail marshes, and from a wide variety of temporary and

permanent ponds.

Life Cycle: Overwintering adults fly from terrestrial sites to breeding habitats in early spring, with mating and oviposition occurring throughout April. Most larvae develop in May and June, with 70% of larvae having been collected in June. Third instar larvae were collected May 11 to October 8, with significant numbers found in August and September. This suggests at least a partial second generation in late summer. Less than 2% of the adults were collected from aquatic habitats after August, which indicates that they fly to terrestrial overwintering sites in late summer or early autumn.

Identification: Adults and larvae of the two species are readily identified by characters in the key. Adults of *H. aruspex*, which have 3 elytral patterns, can be readily recognized in the field. Male adults of *H. aruspex* have fasciate and non-fasciate elytra. In non-fasciate males, elytra are black with a lateral yellow border; in fasciate males, the pattern is similar except that there is a pale sub-basal fascia. In addition to these patterns, female adults often have about six longitudinal yellow vittae on each elytron. All patterns occur in Wisconsin, with the fasciate pattern in males and vittate pattern in females predominating.

Hydaticus piceus LeConte, 1863

Distribution and Abundance: Common in southern third to rare in northern third (Table 1). County records: 1, 3, 6, 21, 24, 26*, 38-41, 44-45, 47-52, 54-61, 64, 66-68, 70-72. Range: AB-NS-NJ-MO.

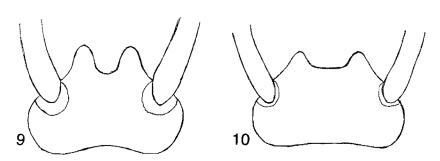
Habitat: Adults and larvae were found in permanent ponds and marshes,

especially those with cattails and bur-reed.

Life Cycle: Adults were collected from April 8 to August 18; most were collected before July. Most larvae were found June 5-30; two were found August 10-12. Overwintering adults apparently enter ponds in April, mate, and oviposit. Larvae develop in May and June, with apparently at least a partial second generation in late July and August.

Identification: In size, shape, and general coloration adults superficially resemble *Rhantus sinuatus*, *Agabus erichsoni*, and several species of *Ilybius*, but they can be immediately recognized by their solid rufopiceous color with a

somewhat lighter head and pronotum.



Figures. 9-10. Labium of larva (ventral view). 9. Hydaticus aruspex. 10. H. piceus.

Thermonectus Dejean, 1837

Dejean initially named this genus *Thermonetus* in 1833, but later (1837) changed the spelling (Nilsson et al 1989). In anticipation that the earlier spelling ultimately will be suppressed by the International Commission of Zoological Nomenclature, I will continue to use *Thermonectus*. The genus was revised in North America by McWilliams (1969), but the revision has not been published, except for descriptions of two new species in the southwestern United States and Mexico (Goodhue-McWilliams 1981). Only two species occur in the Great Lakes region; both were found in Wisconsin. Larvae of both species were described by Wilson (1923); his description of *T. basillaris* was relied upon for its inclusion in the larval key.

The life cycle is apparently univoltine, with adults overwintering in terrestrial habitats, which they do not leave until late spring or early summer. Larval development is rapid, as documented below for *T. ornaticollis*.

Key to Species of Adult Thermonectus in Wisconsin

Key to Species of Larval Thermonectus in Wisconsin

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Thermonectus basillaris (Harris, 1829)

Distribution and Abundance: Very rare in west-central area and southern third (Table 1). County records: 31, 61, 67, 70. Range: WI-MA-FL-CA-MO.

Habitat: Two adults were collected from McKenna Pond when it was a permanent pond; another was found in a temporary, cattail-sedge pond, and a fourth occurred in the margin of a spring. All were collected between August 3 and October 19.

Life Cycle: The life cycle is probably similar to that of *T. ornaticollis*.

Identification: Adults of the two species are readily separated by the key. The only larvae I have seen are those of *T. ornaticollis*; they differ significantly from the larva described and figured by Wilson (1923) for *T. basillaris*.

Thermonectus ornaticollis (Aubé, 1838)

Distribution and Abundance: Uncommon in southern two-thirds (Table 1). County records: 25–26, 28–29, 48, 51, 53–54, 57–58, 60–61, 71*, 72. Range: ND-VT-FL-AZ-WY.

Habitat: Adults were collected from ponds in open areas, which contained a variety of vegetation or lacked vegetation. Larvae were collected from

recently flooded areas that had been dry.

Life Cycle: Adults were collected June 14 through October 6, third instar larvae July 1 through August 18, and teneral adults August 18 to September 30. Since all types of habitats, including temporary ones, were sampled extensively in April and May with traps and nets, I assume that adults were absent from these habitats before June. In McKenna Pond, which was sampled at weekly intervals after ice-out in 1980 and 1981, adults were first collected June 14, 1980 and June 16, 1981; 20 (3/4 \$\epsilon\) were collected on the latter date. Adults apparently oviposit in recently flooded areas, and larvae complete development within a month in late spring and summer. Rapid development was documented in McKenna Pond, which was dry in July 1977 until flooded by a six-inch rainfall the night of July 17–18. On July 21 one female adult was collected, and on August 4 nine male adults, one second instar larva, and 23 third instar larvae were collected. On August 18, three teneral and 51 mature adults were collected along with one third instar larva. I believe that adults overwinter in terrestrial sites where they remain until warm late spring or summer rains inundate temporary lentic habitats and margins of more permanent ones. Adults then fly to these habitats and oviposit. Eggs hatch within a few days (Wilson 1923) and larvae complete development within a few weeks.

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