CLASSIFICATION, DISTRIBUTION, AND PHYLOGENY OF NORTH AMERICAN (NORTH OF MEXICO) SPECIES OF *GYRINUS* MÜLLER (COLEOPTERA: GYRINIDAE)

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ABSTRACT

The species of *Gyrinus* Müller from North America (north of Mexico) are revised; 40 species are assigned to *Gyrinus*. *Gyrinus rugosus* is described as new from California. Separate keys are provided for males and females. Information is provided about type specimens and taxonomic notes, sexual dimorphism, habitat information, and Nearctic distribution. Five new synonyms are recognized: *G. frosti* Fall and *G. floridensis* Ochs are junior synonyms of *G. gibber* LeConte, *G. hatchi* Wallis is junior synonym of *G. ventralis* Kirby, *G. punctellus* Ochs is junior synonym of *G. bifarius* Fall, and *G. instabilis* Fall is junior synonym of *G. aeratus* Stephens. Lectotypes are designated for: *G. pectoralis* LeConte, *G. minutus* Fabricius, *G. rockinghamensis* LeConte, *G. confinis* LeConte, *G. dichrous* LeConte, *G. maculiventris* LeConte, *G. aquiris* LeConte, and *G. ventralis* Kirby. A neotype is designated for each of *G. parcus* Say, *G. analis* Say, *G. obtusus* Say. *G. limbatus* Say is listed as a nomen inquirendum. The occurrence of *G. marinus* Gyllenhal and *G. aeratus* Stephens in the Nearctic Region is verified. In the eastern half of North America, the most speciose region is in the northeast United States; in western North America it is in British Columbia.

The phylogenetic position of *Gyrinus* in Gyrinidae is investigated by using characters in Hatch (1925), Ochs (1926–27), Balfour-Browne (1950), Brinck (1955), and Larsén (1966), with *Spanglerogyrus* Folkerts (Spanglerogyinae) as the outgroup. Most data indicate that, within Gyrininae, Orectochilini is the sister clade to Gyrinini and Enhydrini. A phylogenetic hypothesis for Nearctic species of *Gyrinus* is also constructed; this phylogenetic analysis is highly polychotomous but four groups are suggested. Monophyly of these groups is primarily established by abdominal coloration and aedeagal structure. Two subgroups based on leg and tarsal claw coloration are proposed within the third and fourth clades.

INTRODUCTION

More than 100 years ago, Sharp (1868) considered gyrinids to be one of the most interesting groups of beetles found in England. Owing to their remarkable structural adaptation to aquatic environments and peculiar behavioral patterns gyrinids have received considerable attention since the 1950s.

The genus *Gyrinus* Müller has a worldwide distribution but is most diverse in the Nearctic Region (table 1); 40 species are recorded in this study in North America north of Mexico. The first comprehensive study of Nearctic *Gyrinus* was provided by LeConte (1868). Régimbart (1883) later listed 77 species of *Gyrinus* worldwide, noted synonyms, and discussed distributions. Sharp (1914) was the first to include figures and to emphasize and illustrate the importance of the genitalia in identification. Sharp (1882) also studied Central American gyrinids which later were revised by Ochs (1949). Ochs' revision lists three species that also were found in southern U.S.: *G. parcus, G. plicifer,* and *G. cosobrinus.*

The most recent revision of Nearctic species of *Gyrinus* was by Fall (1922). He constructed a key based on features of male genitalia, color, elytral sculpture, and body form. Hatch (1925, 1926) studied structure, phylogeny, and ecology of gyrinids.

More recent taxonomic studies of the Nearctic fauna are regional: Pacific Northwest (Hatch, 1953), Florida (Young, 1954), Maine (Malcolm, 1971), California (Leech and Chandler, 1956), Alabama (Folkerts, 1978), and North and South Carolina (Sanderson, 1982). While these are useful local studies, they do not address the extensive complications involving intraspecific geographic variation. Even after Fall's revision (1922), identification of Nearctic species remains difficult for the following reasons: (1) insufficient numbers of specimens of certain species were available to Fall when he assessed geographic variation. This problem was magnified even more because he based some of his major subdivisions on these variable characters (e.g., color of thoracic segments, hypomera, epipleura, and body size), (2) species descriptions were detailed but not always consistent, (3) the figures of male genitalia often were not drawn in sufficient detail to show the differences among very similar species, (4) eight new species have been described since his work (*G. gehringi* Chamberlain, *G. dubius* Wallis, *G. hoppingi* Leech, *G. hatchi* Wallis, *G. instabilis* Fall, *G. obtusus* Say, *G. punctellus* Ochs, and *G. floridensis* Ochs), and finally (5) two names recognized by Fall are

considered synonyms herein: *G. frosti* (junior synonym of *G. gibber*), and *G. instabilis* (junior synonym of *G. aeratus*).

The objectives of this study are to: (1) review literature on gyrinid natural history to provide a basis for future life history and field studies, (2) provide an updated workable key for both sexes of each species to allow accurate identification, (3) construct detailed, comprehensive, and consistent species descriptions which include information on variation so that the species can be comprehensively defined, (4) document distributions to determine patterns of diversity and variation, (5) propose a phylogenetic hypothesis for genera of Gyrinidae in order to assess the position of *Gyrinus* in Gyrinidae, and (6) propose a phylogenetic hypothesis for the species of *Gyrinus* in North America.

NATURAL HISTORY

Reproduction/Development

Copulation. Adult gyrinids mate on the water surface from March through early summer (Dalgliesh, 1912). Copulation lasts one to two minutes, but males of *Gyrinus* often remain on females for an entire day (Zaitsev, 1953).

Egg-Laying. Oviposition begins two to three days after copulation and may last up to three days. Eggs are white and oval in shape; they are laid in irregular rows or clusters just below the water surface on submerged vegetation or submerged parts of emergent vegetation. Occasionally eggs are found above the water line, but these eggs desiccate (Hatch, 1925). The incubation period is generally 10–17 days for species of *Gyrinus* (Hatch, 1925).

Larval Development. Gyrinid larvae hatch synchronously and crawl about the empty egg shells and adjacent material for several hours before dispersing (Wilson, 1923). They subsequently pass through three instars in 30–40 days. Balfour-Browne (1950) observed that some species of British gyrinids have an extended breeding season, because larvae of different ages were seen from March through September. Brinck (1955) reported that in South Africa the larva of a species of *Aulonogyrus* occurred throughout the year, but emergence occurred only in the summer.

Pupation and Cocoon Formation. Mature gyrinid larvae crawl from the water and construct their cocoons on emergent vegetation. Cocoons are oval and approximately 6.4 mm long and 3.2 mm wide (Butcher, 1930). Gyrinid larvae make cocoons from a variety of substances such as sand grains, small fragments of rocks, seed and flower heads, and bits of wood. These materials are glued together with oral secretions. Balfour-Browne (1950) stated that the appearance and color of the cocoon depend on the material and the amount of gluelike oral secretion used.

Gyrinus pupate on a variety of vertical surfaces. Butcher (1930) found *Gyrinus* cocoons 60–90 cm above the water, attached lengthwise to *Scirpus* and *Typha* stems. Goodlife (*in* Balfour-Browne, 1950) collected cocoons of specimens of *G. natator* 45–70 cm above the ground, attached to *Juncus* and other grasses approximately 90 cm from the water's edge.

How do gyrinids make cocoons? Wilson (1923) claimed that larvae cling to grass stems with the sickle-shaped hooks of the tenth abdominal segment and construct the pupal case around their bodies. However, Butcher (1930) stated that larvae first form a large ball of material and then work themselves into the mass to form the cocoon. Further observations on this interesting behavior are needed.

Adults. Pupation and eclosion apparently occur mainly from August to September and the adult stage overwinters. Adults probably live one to two years (Zaitsev, 1953).

Abundance

Robert (1955) and Morrissette (1979) collected the greatest number of species of *Gyrinus* from May through September in Quebec. We corroborated their conclusion by randomly selecting approximately 1000 specimens from our material and examined dates of capture (see table 3). About 75 percent of the specimens we analyzed were captured between May and October. It appears that gyrinids are most plentiful or at least most commonly collected toward the end of

summer when they begin to congregate (this is discussed below).

Feeding

Adult Feeding. There is disagreement as to whether adult gyrinids are herbivores, predators, or scavengers. Most evidence indicates that adults do not have specialized diets and feed primarily on living or dead animal matter floating on the water surface (Westwood *in* Miall, 1895; Dalgliesh, 1912; Hatch, 1925; Balfour-Browne, 1944; Wood, 1962). However, phytophagy may be induced if no suitable animal prey are available (Balfour-Browne, 1950).

Larval Feeding. Gyrinid larvae are carnivorous, but the exact method of digestion is not known conclusively. The mandibles are grooved, suggesting that gyrinid larvae digest externally (Zaitsev, 1953; Hatch, 1925; Sharp, 1882). Hatch (1925) presumed that gyrinid larvae ingest the contents of their prey through their canaliculate mandibles.

Balfour-Browne (1950) suspected internal digestion. He specifically mentioned that food was macerated in the buccal cavity, then strained through the hairs inside the mouth. The exact mechanism of ingestion is not known and Balfour-Browne's observation of maceration and straining requires further investigation.

Habitat

Whirligig beetles occur in most freshwater habitats including ponds, streams, lakes, bogs, swamps, and roadside ditches. Hatch (1925) stated that *Gyrinus* generally occurs in lentic habitats. Brinck (1955) however found South African species of *Gyrinus* in shaded portions of small and swiftly flowing streams. Wilson (1923) believed that the occurrence of *Gyrinus* on rivers was temporary and that they were more common on ponds adjacent to rivers.

We observed that the most common habitats of members of *Gyrinus* in New Jersey were the margins of shallow creeks with emergent vegetation and stone, gravel, or sand substrate. Specimens were found most often in the shelter of backwaters and under overhanging roots of stream edge trees; however, we sometimes found specimens in midstream, particularly if emergent vegetation was present there. Usually if *Gyrinus* scattered into the open waters of creeks, they returned quickly to the marginal areas after making a series of jerking movements.

In order to determine habitat types for *Gyrinus* in North America, we analyzed habitat information from locality labels. We found approximately 1000 specimens with adequate label information that we could confidently and consistently divide into one of the three broadly defined habitat types: lentic, lotic, and bog. Under lentic habitat we categorized: lakes, ponds, pools, canals, sloughs, marshes, swamps, and reservoirs. Rivers, streams, brooks, creeks, and springs were classified as lotic. The third habitat type was bog. Results indicate that *Gyrinus* were collected slightly more often in lentic habitats (56.6%) (table 2).

Resting Sites of Adult Gyrinids. Folkerts and Donavan (1973) observed that stream-dwelling *Gyretes* and *Gyrinus,* as adults, climb out of the water and cling to emergent twigs or other material to rest. They suggested that the importance of this behavior might be either protection from predators, energy conservation, or thermoregulation. Not all gyrinids use resting sites; for example, generally larger-size members of *Dineutus* have not been observed to leave the water surface to rest.

Predators of Gyrinidae

Gyrinids are most susceptible to predation in the larval stage. Forbes (1888) observed that gyrinid larvae were eaten by many fish such as sheephead or croaker (*Aplodinotus grunniens* Rafinesque), long-eared sunfish (*Lepomis megalotis* Rafinesque), smallmouthed black bass (*Micropterus dolomieu* Lacepede), common red horse (*Moxostoma aureolum* Le Sueur), large-scaled red horse (*Moxostoma macrolepidotum* Le Sueur), common shiner (*Notropis cornutus* Mitchill), and white crappie (*Pomoxis annularis* Rafinesque). Pearse (*in* Wilson, 1923) discovered that gyrinid larva accounted for 6 percent of the total food of black bullhead (*Ameiurus melas* Rafinesque), 2.5 percent for German carp (*Cyprinus carpio* Linnaeus), and 11.2 percent for Iowa darter [*Etheostoma exile*

(Girard)]. Adult gyrinids are relatively free from predation because they exude a distasteful defensive secretion when disturbed (see below). Heinrich and Vogt (1980) did not find any gyrinids in the stomachs of 49 yellow perch [*Perca favescens* (Mitchill)], 20 rock bass [*Ambloplites rupestris* (Rafinesque)], 30 large-mouth bass [*Micropterus salmoides* (Lacepede)], or 30 pumpkinseeds [*Lepomis gibbosus* (Linnaeus)]. Their laboratory observations of captured fish showed that they occasionally ingested adult gyrinids, but in a short time the beetles were regurgitated. Nevertheless, there are a few reports of adult gyrinids occurring in fish stomachs. Forbes (1888) found fragments of gyrinid beetles in gut contents of marbled bullhead (*Ameirurus nebulosus marmoratus* Le Sueur) and bluegill (*Lepomis macrochirus* Rafinesque). Wilson (1923) stated that birds are the primary enemies of gyrinids. However, McAtee (*in* Wilson, 1923) examined 2398 mallard ducks stomachs, and found 130 dytiscids, 99 hydrophilids, 25 haliplids, but only 9 gyrinids.

Parasites of Gyrinidae

Gyrinids pupate terrestrially and pupal parasites are most common. Because pupal cell construction requires considerable time, parasitic Hymenoptera and Diptera are able to locate the larvae most efficiently during this phase (Wilson, 1923). The first North American records of parasites of *Gyrinus* that we are aware of were those of Wickham (1894). He associated the pupal parasite *Cyrtogaster dineutus* Ashmead, a chalcid wasp, with individuals of an unnamed *Dineutus*. Wickham (1894) reported *Gausocentrus gyrini* Ashmead (an ichneumonid) as a parasite of *Gyrinus*. Cushman (1930) recorded *Hemiteles hungerfordi* Cushman (an ichneumonid) as a parasite of *Gyrinus*.

Invertebrates other than insects also parasitize gyrinids. Wood (1962) found protozoans belonging to *Tokophyra* on the swimming legs and ventral abdominal segments of specimens of *Dineutus assimilis* Kirby. Huldén (1983) reported occurrence of the ectoparasitic fungi *Laboulbeniales* on specimens of *G. aeratus, G. marinus,* and *G. minutus* Fabricius. Lanciani (1979) and Svensson (1985) showed that parasitic water mites (*Eylais* spp.) lowered the survival rate of adult gyrinids.

Defense

Adult gyrinids defend themselves against predators primarily by chemical, physical, and structural means. Protection from predators in spring and early summer is critical due to high adult mortality during the overwintering period (Smith, 1926; Svensson, 1985). Several structural adaptations are protective. Gyrinids can visually detect enemies or prey from above and below the surface with their divided eyes (Hatch, 1925; Young, 1954; Carthy and Goodman, 1964; Bennett, 1967; Tucker, 1969; Benfield, 1972). Gyrinids also are able to perceive approaching predators by detecting deflected surface waves with the Johnston's organ located in the pedicel of the antennae (Benfield, 1972). Tucker (1969) claimed that, except for some noctuid moths, gyrinids are the only insects that use any kind of echolocation.

Gyrinid swimming modifications constitute the best propulsion mechanism known among aquatic invertebrates and perhaps the entire animal kingdom (Nachtigall, 1974). This swimming ability enables them to escape predators. Swimming speeds approach 53 cm/sec in specimens of *Dineutus carolinus* LeConte (Tucker, 1969) and a remarkable 100 cm/sec in *Gyrinus natator* (Nachtigall, 1974).

However, the most effective defense mechanism of gyrinids is probably chemical. Miall (1895) noticed a milky fluid released from all joints, especially the fore and hind edges of the thorax. He stated that this fluid had the odor of cockroaches. Benfield (1972) described the odor of the defensive chemical released by specimens of *Dineutus discolor* Aubé as similar to ripe fruit. Benfield (1972) clearly showed that individuals of *Dineutus discolor* released a secretion from pygidial glands, which deterred predation by blue gill (*Lepomis macrochirus* Rafinesque) and rainbow trout (*Salmo gairdneri* Richardson). If fish food was coated with the beetle's secretions, that food also was rejected.

Various defensive chemicals have been isolated, identified, and synthesized (Mein-

wald et al., 1972; Schildknecht et al., 1972; Wheeler, 1972; Miller et al., 1975; Newhart and Mumma, 1978; Dettner, 1979). The defensive secretions of gyrinids are composed of four norsesquiterpenes (gyrinidal, gyrinidione, gyrinidone, isogyrinidal), an aliphatic aldehyde, and an alcohol (Dettner, 1979). Gyrinidal comprises 50 percent of the defensive secretions; it is probably the precursor for the other norsesquiterpenes. Miller et al. (1975) showed the average relative composition of norsesquiterpenes in specimens of *D. assimilis* and *D. nigrior* Roberts to be: 48 percent gyrinidal, 36 percent gyrinidione, 7 percent gyrinidone, and 6 percent isogyrinidal. Gyrinidal is found in specimens of *G. ventralis* Kirby, *G. natator, G. minutus, G. substriatus* Stephens, *G. frosti* Fall, *D. assimilis, D. horni* Roberts, and *D. serrulatus* (Meinwald et al., 1972; Schildknecht et al., 1972; Newhart and Mumma, 1978). Besides the norsesquiterpenes, 3-methyl butanol is found in *G. natator* (Schildknecht et al., 1972); the pygidial glands contained 2.5 mg of this aliphatic aldehyde (Blum, 1981). 3-methyll-butanol also is found in pygidial glands of *G. natator* (Schildknecht et al., 1972).

The function of the pygidial glands has been studied intensively. The pygidial secretions of gyrinids (sesquiterpenes) probably act as a deterrent to predation and may even be toxic to predators. Relative toxicity is probably a function of dosage (Miller et al., 1975). Alternatively, Vulinec (1987) suggested that these chemicals may serve as surfactants enabling gyrinids to propel themselves across the water surface more easily.

Dettner (1985) demonstrated fluctuations in the level of defensive chemicals throughout the summer and correlated this with the age structure of the population. Dettner concluded that levels of defensive chemicals during midsummer were low because of a predominance of young individuals at that time.

Aggregative Behavior

Adult gyrinids characteristically congregate. Aggregations may be composed of a single species, but frequently are multispecies swarms. As early as 1868, LeConte reported the formation of multispecific aggregations of North American gyrinids. He identified six species of *Gyrinus* collected from the same habitat in the Charles River in Massachusetts. Fall (1922) identified seven species of *Gyrinus* from a large swarm on Lake Quannipowitt at Wakefield in Massachusetts as: *G. ventralis* Kirby, *G. confinis* LeConte, *G. sayi* Aubé, *G. dichrous* LeConte, *G. pernitidus* LeConte, *G. aquiris* LeConte, and *G. rockinghamensis* LeConte. Frost (1928) captured specimens of several species of *Gyrinus* together on different days in the Little Androscoggin River in Paris, Maine. These were later identified by Fall (1922) as *G. affinis* Aubé, *G. fraternus* Couper, and *G. sayi.* Wallis (*in* Fall, 1922) caught *G. minutus, G. confinis,* and *G. bifarius* LeConte together at several sites in Manitoba. We collected *G. marginellus* Fall, *G. lecontei* Fall, and *G. analis* Say from a small swarm in Whippany River in New Jersey.

Robert (1955) collected *Gyrinus* from seven different localities on Lake Brochet, Quebec, during May through July in 1953, and in May and June in 1954. He found *G. pectoralis, G. sayi, G. aeratus,* and *G. affinis* together in 25 out of 28 collections. *G. pectoralis* was dominant in all but one of these collections. He also collected specimens from several physiographically different lakes. The species composition varied for each. For example, he found *G. fraternus, G. impressicollis,* and *G. confinis* in fluvial eutrophic lakes; *G. pectoralis, G. aeratus,* and *G. gehringi* in glacial eutrophic lakes; and *G. pugionis, G. latilimbus,* and *G. lecontei* in dystrophic lakes.

During several collecting trips in New Jersey, we commonly observed *Dineutus* and *Gyrinus* in the same swarm. Hatch (1925) observed scattered *Gyrinus* in a swarm of *Dineutus,* which included a mixture of *Dineutus nigrior* and *D. horni.* Folkerts and Donavan (1973) observed that *Gyrinus pachysomus* Fall and *Gyretes iricolor* Young occupied the same site. Brinck (1955) found three species pairs commonly occurring together in Sweden: *Gyrinus caspius* Menetries and *G. paykulli* Ochs, *G. natator* and *G. substriatus,* and *G. aeratus* and *G. marinus.*

Although gyrinids form multispecies complexes in some habitats, the importance of interspecific competition in the life history of these beetles has not been investigated ex-

tensively. Brinck (1955) is one of the few who has studied interspecific competition among gyrinids. In Sweden, he was convinced that no competition occurred among the adults of different species. He assumed that cannibalistic tendencies of larvae reduced the size of the larval population and that this reduced competition in the adult stage. Results of Istock's (1965) experiments are consistent with Brinck's assumption. He demonstrated that competition was most intense during larval stages for three overlapping species of *Dineutus*.

Istock (1965) suggested the following additional factors influencing competition among individuals of *Dineutus horni, D. nigrior,* and *D. assimilis*: (1) Species interaction. When larvae of *D. horni* and *D. nigrior* occurred together, the amount of food per larva was critical. When prey abundance was reduced incrementally in co-occurring populations of *D. nigrior* and *D. horni, D. horni* became cannibalistic at a higher prey density than did *D. nigrior.* Therefore, larvae of *D. horni* could outcompete those of *D. nigrior* when prey density was declining. (2) Seasonality. Members of *D. nigrior* had a seasonal advantage due to an earlier onset of breeding. Coupled with the small amount of space in which larvae disperse, this resulted in locally high densities of *D. nigrior* initially. (3) Temperature. A 5°C reduction in temperature reversed the outcome of competition between *D. nigrior* and *D. assimilis.* For example, at 30°C, *D. horni* excludes *D. nigrior* quickly, but at 25°C *D. horni* excludes *D. nigrior* (if *D. horni* is initially higher in numbers).

Brinck (1955) further observed that oxygen requirements varied among larvae of different species. As oxygen concentration declined, some larvae stopped feeding sooner than others. Salt tolerance was variable among species. For example, in coastal pans of South Africa, *G. vicinus* occurred only when salt content of the water was low (0.01%) while other species occurred in high salt concentrations.

The multispecies complexes of *Gyrinus* may consist of hundreds of individuals, and in such complexes food might be a limiting factor. In lakes and ponds, we did not find much food on the water's surface. Food availability appears even more critical in lotic situations. According to Heinrich and Vogt (1980), however, specimens of *D. horni* are nocturnal and their foraging sites are different from their resting sites.

The functional significance of aggregation in gyrinids is discussed by several authors. The role of aggregation may be defensive (Benfield, 1972; Heinrich and Vogt, 1980; Vulinec, 1987). Heinrich and Vogt (1980) showed that single gyrinids were more rapidly captured by fish than gyrinids in groups even though aggregations themselves would seem to be more noticeable to predators. Nikolsky (1963) stated that when a predator attacks shoaling fish, they immediately disperse, disorienting the predator; this mechanism may also apply for gyrinids. Benfield (1972) claimed that aggregation functions to advertise repugnant defensive secretion (aposematic displacement). However, Heinrich and Vogt (1980) believed that the role of aggregation did not include advertisement of chemical defenses since swarms do not continuously release these chemicals in large quantities unless attacked.

MATERIALS AND METHODS

Adult *Gyrinus* were borrowed from 32 museums throughout the United States, Canada, and Europe. The following museums lent *Gyrinus* for this study.

AMNH American Museum of Natural History, L. H. Herman
ANS Academy of Natural Sciences Philadelphia, D. Azuma
BMNH British Museum (Natural History), M. J. D. Brendell
CAS California Academy of Science, D. H. Kavanaugh
CM Carnegie Museum of Natural History, J. Rawlins
CNN Canadian National Collection, A. Smetana
CSU Colorado State University, B. C. Kondratieff
FEM Frost Entomological Museum, K. C. Kim
FMNH Field Museum of Natural History, J. S. Ashe

FS	Forschungsinstitut Senckenberg, R. zur Strassen
FSCA	Florida State Collection of Arthropods, R. Woodruff
IRSB	Institut Royal des Sciences Naturelles de Belgique, L. Baert
JBWM	J. B. Wallis Entomological Museum, R. E. Roughley
KSB	University of Kansas, State Biological Survey of Kansas, B. Coler
LACM	Natural History Museum Los Angeles County, C. L. Hogue
LSU	Louisiana State University, C. B. Barr
MCZ	Museum of Comparative Zoology, Harvard University, A. F. Newton
MEM	Mississippi Entomological Museum, T. L. Schiefer
ND	University of North Dakota, P. B. Kannowski
OSU	Oregon State University, J. D. Oswald
PU	Purdue University, A. Provonsha
SMEK	University of Kansas, Snow Entomological Museum, P. D. Ashlock
UCD	University of California Davis, R. O. Schuster
UM	University of Michigan, M. F. O'Brien
UN	University of Nebraska, B. C. Ratcliffe
UNH	University of New Hampshire, D. S. Chandler
USNM	National Museum of Natural History, P. J. Spangler
UW	University of Wisconsin, S. Krauth
WSU	Washington State University, R. S. Zack
YU	Yale University, C. L. Remington
ZMH	Zoologiska Institution, O. Bistrom
ZMUC	Zoologisk Museum, O. Martin

Dissection. Reliable identification usually requires examination of male genitalia. To extract male genitalia, male *Gyrinus* were first relaxed in near boiling water and then genitalia were extracted by inserting a hooked needle into the abdominal opening. If necessary, genitalia were cleared in 10 percent KOH at near boiling temperature for 30–60 sec or overnight at room temperature. Aedeagus and parameres were stored in a drop of glycerin in a microvial or glued to a point which was pinned beneath the specimens. Ten percent of the total number of male specimens from each locality were dissected.

SEM Study. Each examined structure was dissected, coated with a gold-palladium alloy, and analyzed with an Hitachi S-510 Scanning Electron Microscope.

Body Measurements. Ten specimens of each sex for each species were selected for measurements. To determine range of size, the smallest and largest individuals were included in each sample. The following measurements were made: (1) overall body length (from head to tip of abdomen), and (2) greatest body width (basal portion of elytra).

All measurements are in millimeters.

Maps. The geographic distributions for all North American species of *Gyrinus* are shown on maps 1–14. Label information is recorded for each species according to the following format: state, county, city or town, specific habitat, and date. Localities were mapped for all species but only for those specimens we personally identified.

Color Determination. Despite variability, color of the abdominal segments, epipleura, hypomera, and legs sometimes are useful in recognition of species of *Gyrinus.* However, consistently determining, comparing, and recording color was difficult. Initially, we attempted to use the Naturalists' Color Guide (Smith, 1975). However, many of the colors of the specimens of *Gyrinus* did not match these standards. Therefore, we developed a series of color standards by setting aside actual specimens (deposited in AMNH) that represented a set of colors that we could consistently use as references. The six color categories are: (1) black, (2) black-red, (3) brown, (4) dark brownish red, (5) light reddish brown, and (6) orange or yellow.

Species Descriptions. Descriptions of species are presented in the form of tables (table 12). This method is useful as it facilitates easier character comparison among taxa. It is also readily available for further computer analysis, and it reduces the total pages of traditional descriptions.

Criteria for Species. We utilized the evolutionary species concept (Simpson, 1961; elaborated by Wiley, 1981). However, "everyday" recognition of specimens involves recognition of character gaps and similarity. It is difficult to distinguish the distinctiveness of a gap necessary to justify species status. Different criteria using different kinds and numbers of structural characters have been used to show a gap distinct enough to separate populations at the species level. Erwin's (1970) criterion was based on genitalic dif-

ferences with the addition of an external character. Whitehead (1972) accepted a genitalic difference as being a sufficient criterion for determination of such a gap. Wolfe (1984), on the other hand, believed that any one structural character potentially was sufficient for the determination of such a gap. In this study, male genitalia are used as the primary criterion for delimiting species of *Gyrinus*; however, two species, *G. opacus* and *G. hoppingi* are not separable by genitalic differences. Elytral microreticulation is used to distinguish specimens of these species.

Evaluating structural gaps is especially difficult if populations are allopatric. However, the "validity" of a structural gap sometimes can be supported by distributional information. For example, sympatric populations are considered distinct species if there is no character intergradation among the individuals. For allopatric species, of course, there can be no intergradation. The basic criteria that we used for judging allopatric species were the minimum differences that we accepted for sympatric species.

SYSTEMATICS

We follow the higher classification of gyrinids provided by Folkerts (1979). He divided Gyrinidae into two subfamilies: Gyrininae Régimbart and Spanglerogyrinae Folkerts. Separation of these subfamilies is based primarily on position of dorsal and ventral eyes, shape of mesotibia, metatibia, and body length. Four tribes are placed in Gyrininae: Gyrinini Régimbart, Enhydrini Régimbart, Orectochilini Régimbart, and Heterogyrini Brinck. The three genera placed in Gyrinini are *Gyrinus* Müller, *Aulonogyrus* Motschulsky, and *Metagyrinus* Brinck (*Paragyrinus* Ochs). Heterogyrini with a monotypic genus *Heterogyrus* Legros is recorded only from Madagascar. Five genera assigned to Enhydrini are: *Enhydrus* Leporte, *Dineutus* MacLeay, *Andogyrus* Ochs, *Macrogyrus* Régimbart, and *Porrorhynchus* Régimbart. Three genera are included in Orectochilini: *Orectochilus* Lacordaire, *Orectogyrus* Régimbart, and *Gyretes* Brullé. Spanglerogyrinae is monotypic with *Spanglerogyrus* Folkerts.

A preliminary list of species numbers, based on five regions of the world, for each genus is provided in table 1. Although this list is generally based on older literature (pre-1950), general trends are recognized. Species of Gyrinidae are the most numerous in Africa. The number of species of *Gyrinus* is highest in northern North America and lowest in Central America and West Indies.

KEY TO THE NEARCTIC (NORTH OF MEXICO) GENERA OF THE FAMILY GYRINIDAE

[Adapted from Folkerts (1979) and Sanderson (1982)]

1. Meso- and metatibia about 4 times as long as broad; dorsal and ventral compound eyes narrowly separated, almost contacting laterally; body length less than 3 mm ..... *Spanglerogyrus* Folkerts
- Meso- and metatibia about as long as broad; dorsal and ventral compound eyes distinctly separated; body length more than 3 mm 2
2. Last abdominal segment elongate, elytra pubescent on sides ..... *Gyretes* Brullé
- Last abdominal segment rounded, elytra not pubescent on sides 3
3. Scutellum invisible, elytra with 9 indistinct striae ..... *Dineutus* MacLeay
- Scutellum visible, elytra with 11 distinct striae ..... *Gyrinus* Müller

HISTORICAL REVIEW OF *GYRINUS*

TYPE SPECIES: *Dytiscus natator* Linnaeus, 1758.

The genus has been attributed to several authors: Linnaeus, 1762 (Guignot, 1947; Zaitsev, 1953), Geoffroy, 1762 (Ahlwarth, 1910; Guignot, 1931–33; Leech, 1948; Hatch, 1953, and Régimbart, 1883, 1902–03), Müller, 1764 (Silfverberg, 1978; Holmen, 1987), and Linnaeus, 1767 (Brinck, 1955; Fransiscolo, 1979). Linnaeus described the first gyrinid as *Dytiscus natator*. Geoffroy (1762)

TABLE 1
Number of Species of 11 Genera of Gyrinidae by Zoogeographic Region
Data from Leng (1920), Hatch (1925), Ochs (1926–27), Blackwelder (1944), and Brinck (1952, 1955, 1977, 1980)

	Nearctic	Neotropical	Australia	Eurasia	Africa	TOTAL
Spanglerogyrus	1	0	0	0	0	1
Orectochilus	0	0	0	83	1	84
Orectogyrus	0	0	0	8	207	215
Gyretes	9	70	0	0	0	79
Aulonogyrus	0	0	1	4	43	48
Gyrinus	46	39	5	30	10	130
Enhydrus	0	4	0	0	0	4
Dineutus	14	16	2	5	23	60
Porrorhynchus	0	0	0	5	0	5
Andogyrus	0	6	0	0	0	6
Macrogyrus	0	5	8	6	0	19
TOTAL	70	140	16	141	284	651

placed *Dytiscus natator* Linnaeus in a new genus, *Gyrinus*. Geoffroy's generic names, however, were rejected because he did not use binomial names consistently. After Geoffroy, Müller (1764) made the name available with a short description. Although Müller did not associate the genus with any species name, according to International Commission of Zoological Nomenclature (Code, 69 a ii), he is the author of the genus (Silfverberg, 1978).

Régimbart (1883) divided *Gyrinus* into two groups, one possessing a medial longitudinal carina on the scutellum, the other possessing a smooth scutellum. Zaitsev (1907) first named these groups. He applied the name *Gyrinulus* to species with a scutellar carina (*G. minutus* and *G. rockinghamensis*), and *Gyrinus* s. s. to the remainder. Hatch (1925) described some of the South American species under a third subgenus, *Neogyrinus*, which he diagnosed by an obsolescence of discal elytral striae.

Ochs (1935) described a fourth primarily Neotropical subgenus, *Oreogyrinus*. However, *G. parcus*, the type species of this subgenus, extends from North Dakota to Chile. He distinguished this subgenus from *Gyrinus*, *Gyrinulus*, and *Neogyrinus* by the more distinctly impressed striae and punctation of the elytra in members of *Oreogyrinus*. Ochs (1949) subsequently and more completely diagnosed adults of *Oreogyrinus* as possessing the following features: black ventral surface, strictly marginal 11th stria, posteriorly broadened elytral margin, and presence of a more or less noticeable apical plica. Although we are skeptical about the validity of the above subgenera, the species-level phylogenetic evidence that we present below neither supports nor rufutes their validity. We have elected not to use the names herein until further phylogenetic study more strongly supports their use.

GENERIC DESCRIPTION OF NEARCTIC ADULTS OF *GYRINUS*

Among all gyrinids, Nearctic *Gyrinus* are recognized by the following characters.

Head. Prognathus head capsule with dorsal and ventral pair of eyes separated by slightly less than one dorsal eye width, in lateral view. Dorsal eyes separated dorsally by approximately 1.75 eye widths. Ventral pair of eyes a little more widely separated than dorsal pair. Depression located at anteromedial edge of each dorsal eye.

Labrum. Subequal in length to postclypeus. A dorsoanterior, transverse, dense row of setae located just posterior to anterior edge; ventral surface with a broad, triangularly shaped, dense patch of long slender spines. Postclypeus variously rugous; posterior edge marked by only subtle transverse suture. Frontal ridge extending posteriorly on each side to anterior ventral portion of eye, eventually becoming contiguous with ventral edge of eye.

Postclypeus (Clypealia). With short series of long setae along ventral edge, just anterior to antennal insertion. Ventrally a transverse, impressed line extending one-third of posterior width of submentum on each side; medial one-quarter of each impressed line becoming posteriorly directed. Gular sutures absent.

Labium. Submentum extended laterally on each side as a broad lobe; an irregular, longitudinal series of setae present on posterior medial portion with a large, quadrate emargination in which mentum is located. Mentum with one oblique impressed line extending posteriorly from point of each labial insertion. Labial palps three-segmented, basal segment anteromedially cleft, apical segment with a single patch of sparsely distributed sensilla. Anterodorsal surface of labium obliquely oriented and concave; numerous short, stout spines located in dorsal and lateral portions.

Maxilla. Cardo and stipes with widely spaced, long, apicolateral setae along dorsolateral edge. Galea present, composed of one palpomere, inserted just anterior to maxillary palp. Maxillary palp with four palpomeres, basal palpomere not distinctly cleft basally, apical palpomere with one apical patch of sparsely distributed placiform and conate sensilla. Lacinia scythelike in shape, tapering to a blunt point, oval sclerite evident basomedially. Edge of lacinia with a row of stout curved spines along dorsomedial and ventromedial edge; spines separated into an apical and basal group by a short gap. Basal sclerite with approximately 6 spines on dorsomedial edge and 10 on ventromedial edge.

Mandibles. Apically truncate, with one broadly triangular retinacular tooth; short transverse suture present just posterior to retinacular tooth. Each mandible with a ventromedial, curved row of dense setae extending entire length. Dorsolateral groove present. Epipharynx membranous, somewhat bulging on each side of middle, without a pair of distinct, discrete lobelike structures (which are evident in many dytiscids); densely microreticulate on each side of middle, with a few widely spaced, short and slender sensilla.

Antennae. Flagellum with seven antennomeres, apical segment three times longer than subapical segment; scape and pedicel greatly enlarged, scape cup-shaped, dorsomedially deeply emarginate to receive flagellum; pedicel enlarged and platelike, with dense row of setae along distal edge; flagellar sensilla densest on apical segment.

Prothorax. Pronotum with each anterolateral angle produced as subacute point; lateral edge with narrowly reflected portion, margined or not. Disk of pronotum with irregular subtle depressions, in most specimens somewhat transversely oriented. A transverse series of distinct punctures located on each side of pronotum just behind anterior edge extending from anterolateral corner to a point on pronotal disk approximately behind medial edge of eye; punctures approximately parallel to anterior pronotal edge. Prosternum behind gular region narrow (subequal to length of labrum), and laterally expanding as a lobe; distinct sutures not evident between proepisternum and proepimeron. Prosternum separated from propleuron by distinct notopleural suture. Propleuron broad, width approximately equal to width of ventral eye, posternal process distinctly evident, length (from anterior edge of prosternum) approximately equal to length of maxillary palp, extending to mesosternum; procoxa contiguous posteriorly.

Mesothorax. Scutellum visible; anterior edge of mesonotum posteroventrally produced as a pair of parallel long and slender apodemes. Mesosternum with an oblique, transverse row of punctures on each side, posterolateral edges obliquely tapering to a midpoint between mesocoxae and narrowly separating mesocoxae, slightly emarginate at posterior apex; mesosternal suture extending anteriorly from posterior apex for approximately one-half the length of mesoternum. Suture between mesosternum and mesepimeron present but indistinct. Mesocoxa roughly triangular, mesocoxal lobes less distinct than metacoxal lobes, mesocoxa with a medial longitudinal row of setae.

Metathorax. Metasternum extending anteriorly between mesocoxae as a rather long and narrow lobe and contacting posteromedial portion of mesosternum; anterolaterally extended as a long, very narrow sclerite, distal portion of lateral extension of metaster-

num gradually expanded. Metepisternum with an evident circular depression and metepisternal ostiole present or not. Metacoxa greatly enlarged, platelike and laterally expanded, posterolateral corner contacting elytral epipleura, metacoxal lines extending anteriorly, laterally extended portion approximately parallel to anterior margin of coxa but not reaching distal coxal edge; a posteromedial longitudinal series of setae evident on each coxa between coxal lobes.

Elytron. Not extending to tip of abdomen, leaving most of tergum 8 exposed. Elytron with 11 striae, and lateral edge reflexed outward forming a narrow elytral margin of variable width. Hypomeron excavated in anterior portion to receive folded prolegs, excavation contiguous with obliquely oriented concavity of prosternum, mesosternum, and metepisternum.

Abdomen. True abdominal sternum 1 not visible; abdominal sterna 2–3 almost completely divided by posterior extension of metacoxae (fig. 149); sterna 4–7 subequal in length, sterna 7 and 8 without medial row of setae. Sternum 8 not markedly prolonged, posterolaterally fringed with a distinct row of setae. Abdominal tergum 1 scarcely sclerotized, terga 2–5 becoming progressively more sclerotized, terga 6–8 dorsally entirely sclerotized.

Front Leg. Not markedly expanded or modified for swimming; natatorial setae absent. Profemur with anterior row of widely spaced, long and slender spines, dorsal surface with two roughly parallel, irregular rows of spines, a few widely spaced longer spines evident in most specimens. Dorsal surface of protibia with medial row of longitudinally oriented short spines, a second longitudinal row situated just anteriorly, this anterior row composed of short spines with a few larger spines interspersed. A row of short dense spines along entire dorsomedial edge with a few, long and slender spines widely interspersed; another more abbreviated row of short dense spines in distal one-quarter of protibia, anterodistal apex of tibia with dense transverse series of spines. Protarsus not markedly modified for swimming, arolium of protarsus evident, but only one-quarter of length of protarsal claw. Tarsus with a dense row of short spines ventromedially; spines present dorsomedially, but longer than ventromedial spines and clustered at proximal angle of each tarsomere.

Middle Leg. All segments markedly broadened and modified for swimming. Natatory setae present on anterior edge of femur, tibia, and fifth tarsomere; natatory setae of tibia and tarsomere broadened into bladelike structures. Anterior and posterior edge of tibia and posterior edge of tarsus densely set with short spines. Tarsomeres 1–3 each posteriorly extended, forming a lobelike structure, tarsomere 4 elongate (subequal in length to tibia), somewhat broadened but without posteriorly directed lobelike extension. Tarsomere 5 short, approximately one-quarter length of tarsomere 1, claws slightly larger than tarsomere 5, evenly articulate, equal in length. Large bladelike arolium present, equal in length to claws.

Hind Leg. Similar in shape and modification to midleg but slightly less broadened and modified. Natatory setae as on mesoleg but additionally present on posterior and posteroproximal edge of tibia and tarsomere 1, respectively. Posterodistal corner of tibia with two enlarged spines.

Male Genitalia. Aedeagus approximately equal in length to parameres. Parameres broadly fused to aedeagus basoventrally, fused area forming a platelike structure that covers basal one-third of aedeagus, apex of parameres broadly rounded or truncate and with dense fringe of long setae. Aedeagus variously shaped at apex, but consistently symmetrical bilaterally. Basal plate with a posteriorly extended process at each posterodorsal, lateral corner.

Female Genitalia. Genital valves somewhat elongate and rectangularly shaped, medial and lateral edge with short, thin, densely placed spines. Valvifer present, firmly articulated to posterolateral corner of genital valve; genital valve and valvifer subequal in length. Apex of valvifer with dense, long setae.

Proventriculus. Consists of eight longitudinally oriented lobes: four larger lobes alternating with four reduced lobes. Each larger lobe with a medial ciliate ridge; posteriorly with a somewhat anteriorly projected, thinly sclerotized, rectangular valvelike structure.

Each smaller lobe rather convex and with shorter ciliate ridge, posteriorly with a thinly sclerotized bladelike structure which projects between rectangular valves of larger lobes.

Sexual Dimorphism. Most obvious sexually dimorphic features involve protarsal structure, elytral microreticulation, and body size. In males, protarsomeres expanded, slightly broader than maximum width of tibia; ventral surface covered with modified sensilla, each sensilla apically shaped like small suction cups; usually in rows of five to seven. In approximately half of species, elytron of females more distinctly microreticulate than in males; microreticulation of males sometimes more transversely oriented than in females. In all but one species (*G. impressicollis*) females longer than males.

CLASSIFICATION OF NEARCTIC SPECIES OF *GYRINUS*

CHARACTERS AND CHARACTER STATES USED IN ANALYSIS

Although genitalic characters are almost always used as the primary character for identification, elytral microreticulation, micropunctation, abdominal coloration, shape of pronotal transverse impressed line, and size of metepisternal ostiole also are used extensively.

ELYTRON

MICROPUNCTATION AND MICRORETICULATION

Two kinds of elytral punctures are evident: (1) large punctures found in striae, and (2) minute micropunctures found on the elytral surface between the striae. Strial punctures are large, pitlike, and without an associated sensillum; there are 11 striae composed of this type of puncture (figs. 27–32, 148). Micropunctures are approximately $1/10$ to $1/40$ the size of strial punctures, and are distributed rather evenly on the dorsal surfaces of the head, pronotum, and elytra.

Four categories of micropunctation based on density were recognized. (1) Dense. Micropunctures separated by only three to five micropuncture widths (e.g., *G. pectoralis,* fig. 70. (2) Moderately dense. Micropunctures separated by five to eight micropuncture widths (e.g., *G. analis,* fig. 55, and *G. sayi,* fig. 61). (3) Sparse. Micropunctures separated by eight or more puncture widths (e.g., *G. ventralis,* fig. 74. (4) Very Sparse. In specimens of some species, e.g., *G. maculiventris* (fig. 51), and *G. marginellus,* micropunctation is so sparse and fine that it is not evident with a light microscope; however, it is always noticeable at higher magnification of SEM.

Microreticulation occurs in all members of *Gyrinus*; but at times is only evident with SEM (200× or more). The microreticulate network occurs in a variety of patterns. The variations were categorized into six groups. 1) Scalelike. Consists of rounded sculpticells arranged in an overlapping pattern that gives a scalelike appearance; these sculpticells are approximately as long as they are wide (e.g., *G. rockinghamensis,* fig. 41). (2) Polygonal. Network of lines forms sculpticells that are four- to six-sided irregular polygons (e.g., *G. dubius,* fig. 62). (3) Moderately Transverse. Sculpticells are four to five times wider than they are long (e.g., in *G. gibber,* fig. 46. (4) Distinctly Transverse. Reticular sculpticells are 8 to 10 times wider than long (e.g., in *G. gehringi,* fig. 48). (5) Oblique Microstriae. Specimens of one species, *G. affinis,* have thick, short, fissurelike scratches (oblique microstriae, fig. 47) uniformly covering the dorsal surfaces of the pronotum and elytra. (6) Not Evident. Microreticulation is so lightly impressed that it is evident only at higher magnifications (e.g., *G. maculiventris,* fig. 51).

Reticulation varies across the elytral surface. Commonly, microreticulation is least impressed anteromedially, especially proximate to the elytral suture (fig. 148, area 1). Microreticulation is most uniformly and consistently evident in dorsolateral areas of the elytron (fig. 148, area 2) and this is where "standardized microreticulation" was determined for use in the species descriptions and the key.

It is important to note that shape of microreticular sculpticells usually changes grad-

ually toward the lateral and posterior portions of each elytron (fig. 148, area 3). For example, specimens with "typically" transverse microreticulation in area 2 usually had a scalelike pattern in area 3. However, there are exceptions to this general trend: (1) microreticular pattern is very uniform throughout the elytral surface in *G. sayi, G. gibber, G. opacus,* and (2) in *G. rugosus,* area 3 is abruptly and very distinctly microreticulated while areas 1 and 2 have a distinctly smooth elytral surface.

Sexual Dimorphism in Elytral Microreticulation. Previous gyrinid taxonomists described sexual dimorphism in members of *Gyrinus* based primarily on the fact that female specimens are at least somewhat duller than male specimens. Four categories of sexual dimorphism were recognized in terms of the distinctiveness of female microreticulation. (1) Distinctly Sexually Dimorphic (figs. 52–59). Male specimens, when examined at 50×, have no microreticulation evident or microreticulation only slightly noticeable posteriorly (fig. 148, area 3) on elytron. If noticeable posteriorly, the microreticular pattern usually is in the form of very fine transverse lines. Conversely, female specimens, when examined at 50×, have microreticulation distinctly impressed and usually scalelike or polygonal (except in *G. woodruffi* which has moderately transverse microreticulation) e.g., *G. analis, G. woodruffi, G. latilimbus, G. parcus*). (2) Moderately Sexually Dimorphic (figs. 60–63). Males possess consistently evident microreticulation, but female microreticulation is always more distinctly impressed. Variation in shape of microreticular sculpticells is evident in some specimens, but less distinctly so than in those of category 1 above. For example, female *G. dubius* have microreticular sculpticells that are polygonal while the patterns of male specimens is moderately transverse. (3) Slightly Sexually Dimorphic (figs. 66–69). Males and females have similar microreticular patterns (usually transverse); however, female microreticulation is slightly more impressed (e.g., *G. lecontei, G. ventralis*). (4) Not Sexually Dimorphic. Both males and females have evident microreticulation with insignificant difference in distinctness and/or form of microreticular sculpticells (*G. borealis,* fig. 43).

Elytral Striae

The size of punctures of the elytral striae gradually becomes larger toward the elytral margin. Among specimens of a few species, punctures in striae 7–11 are conspicuously larger than are those of striae 1–6 (e.g., *G. pachysomus,* figs. 38, 39, *G. borealis,* fig. 40, and *G. elevatus,* fig. 34). When punctures of striae are larger laterally, these striae also tend to be more impressed or groovelike than their more sutural counterparts; therefore in the species indicated above, striae 7–11 are not only larger, but also are distinctly more impressed than are striae 1–6. Elytral striae 1–11 are equally impressed only in female *G. parcus* (fig. 32).

Position of 11th Stria. The 11th stria is located close to the outer margin of elytron and extends from the basal edge almost to the apex. It is usually characterized by a variably evident arch located along the basal one-third of the elytron (figs. 21–23). Four basic categories were recognized based on shape and position of the 11th stria relative to the outer margin of elytron. (1) Entirely Marginal. The 11th stria is located at the reflection of the outer margin of elytron throughout its length with, at most, a very subtle anterior arch. Specimens of only one species, *G. parcus,* are in this category (figs. 24, 152). (2) Posteriorly Marginal. The 11st stria is close to elytral margin, only in the apical half. This character state occurs in specimens of only two species, *G. opacus* and *G. maculiventris.* (3) Apically Marginal. Specimens are placed in this category if the 11th stria is located at (e.g., *G. pachysomus,* fig. 21) or just above (e.g., *G. gibber,* fig. 23) the elytral marginal inflection in only the apical third. (4) Remote. The 11th stria is remote from the outer margin of elytron even in the apical third (e.g., *G. aeneolus,* fig. 30, and *G. rugosus,* fig. 25).

Pronotal Transverse Impressed Line

A transverse impressed line is located on each side of pronotum. Each pronotal line originates at the outer lateral edge, runs parallel to and just behind the anterior pronotal edge, and ends approximately even with the

medial edge of the eye. In *G. minutus, G. rockinghamensis,* and *G. analis* this line is almost uniformly parallel to the anterior edge (figs. 8, 10, 151). However, in three species, *G. latilimbus* (figs. 7, 9, 150), *G. elevatus,* and *G. pernitidus,* the pronotal transverse impressed line is distinctly curved, and these species can be separated, in part, by that characteristic. The pronotal transverse impressed line is variably anteriorly concave such that it is medially more distant from the anterior pronotal edge than from either end.

Metepisternal Ostiole

The size of the metepisternal ostiole varies from not evident to very large. For species descriptions, we recognize three sizes of metepisternal ostiole. However, the distinction between the three categories is gradual; therefore only the two most distinct character states (i.e., largest and not evident) were used in the key. The metepisternal ostiole is consistently not visible in specimens of only two species (*G. gibber,* fig. 18 and *G. rugosus*). The metepisternal ostiole is largest in *G. borealis, G. elevatus, G. marginellus, G. pachysomus,* and *G. woodruffi* (figs. 11–14). As stated above, intermediate sizes exist but are not used in the key. It is interesting to note that specimens of species with the largest metepisternal ostioles also share a number of other characters such as a distinctly convex body, very shiny elytra, and uniformly reddish ventral surfaces.

Male Genitalia

The most important aedeagal character states pertain to overall shape (in dorsal and lateral views), apical width, and degree of longitudinal dorsal convexity. Despite species-specific diagnostic attributes in aedeagal structure, several general morphotypes can be discerned. (1) Needlelike. The aedeagus abruptly tapers in apical half or third in both dorsal and lateral views (e.g., in *G. borealis, G. plicifer, G. elevatus,* figs. 77–84). (2) Apically Broadened. The apex of the aedeagus is broadened and in lateral view it exceeds or almost so the apical width of parameres (e.g., in *G. gibber,* fig. 139, and *G. ventralis,* fig. 142). (3) Dorsally Convex. The aedeagus is drastically and angulately convex dorsally, so that it appears "roof-shaped" (e.g., in *G. opacus,* fig. 132, and *G. hoppingi,* fig. 135). (4) Enlarged and Cup-Shaped. Only the specimens of one species, *G. impressicollis,* are in this category. Members of this species have extremely large, broadened parameres which together form a cup-shaped structure (figs. 143, 144). (5) Notched. The aedeagal apex is slightly broadened posteriorly, but is narrowed apically where it is notched medially; this occurs in two species: *G. minutus* (fig. 145) and *G. rockinghamensis* (fig. 146). (6) Basally Broadened. Specimens of several species have a slight or moderately broadened aedeagal base. However, in two species (*G. pugionis,* fig. 75, and *G. borealis,* fig. 78), the basal region is drastically broadened, so much so that the lateral edge extends out as a shelf that is somewhat sinuate in lateral view.

There are a number of other important male genitalic characters. The presence of a very distinct longitudinal medial carina that reaches to the tip of the aedeagus is characteristic of male *G. pernitidus* (figs. 127, 128). *G. confinis* (fig. 126) also have a medial longitudinal carina, but it does not extend to the tip of the aedeagus. In *G. ventralis,* the male genitalia are laterally distinctly truncate with the posterior margin medially pointed (fig. 142). This median projection at the apex also is present but less distinct in *G. fraternus* (fig. 141), *G. marginellus* (figs. 137, 138), and especially in *G. gibber* (fig. 139). Finally, the male genitalia of *G. marginellus* (figs. 137, 138), *G. fraternus* (fig. 141), *G. latilimbus* (fig. 129), and *G. ventralis* (fig. 142) have a slightly convex dorsal surface in the apical third. On the other hand, members of *G. gibber* (figs. 139, 140) and to a lesser degree those of *G. confinis* (figs. 125,126) have a distinctly concave dorsal shape (almost spatulate in *G. gibber*) in the apical third of the genitalia.

Coloration of Ventral Surfaces

Abdominal and thoracic coloration is an important taxonomic character, but it is sometimes difficult to evaluate the states at the species level because of geographic variation. Two extreme examples are: (1) *G. minutus* in which the mesosternum and meta-

sternum vary from yellowish to light reddish [specimens from Michigan to northwestern Canada seem to have darker (light brown) thoracic sterna], (2) *G. plicifer* from New Mexico which has a brownish-red ventral surface; specimens from Baja California have a very conspicuous orange ventral surface, while specimens from California and Oregon have light reddish sterna. Aside from geographic variation, the color pattern may change with age, environmental conditions, and killing and relaxation procedures (Ochs, 1926–27; Balfour-Browne, 1950; Wood, 1962; Zimmerman, 1970).

Because of the above problems, whenever possible, we gave priority to the use of structural characters in the key. However, it was still necessary to use ventral coloration, especially for identification of females. Most problems were circumvented by emphasizing the color of abdominal sterna 4–7 instead of the color of all ventral surfaces. There are four basic categories based on coloration of abdominal sterna 4–7: (1) uniformly reddish or yellowish (e.g., *G. ventralis, G. fraternus*), (2) uniformly black or dark brown (e.g., *G. sayi,* fig. 153, *G. dubius*), (3) medially black becoming reddish or abruptly orange on the sides (e.g., *G. pugionis,* fig. 156, and *G. maculiventris,* fig. 155), (4) medially dark brown or black becoming gradually reddish brown to reddish on the sides (e.g., *G. lecontei,* fig. 154).

KEY TO MALES OF NEARCTIC SPECIES OF *GYRINUS*

1. Mesosternum with anterior margin trilobed, each lobe distinctly broadly convex (fig. 3); tarsal claws distinctly black or blackish brown; aedeagus in figures 119, 120; body length 4.3–5.1 mm ..... *pectoralis* LeConte, p. 24
– Mesosternum with anterior margin less distinctly trilobed, medial and lateral projections more angulate (fig. 4), tarsal claws either black, blackish brown, or light reddish 2
2. Scutellum with longitudinal, medial, basal carina (fig. 6); body length ≤4.9 mm; dorsal surface at 40× with distinctly scalelike microreticulation (figs. 6, 41, 44); mesoternum in anterior half with evidently medial, longitudinal depression (fig. 5); aedeagus in dorsal view with apex medially notched (figs. 145, 146) 3
– Scutellum without a longitudinal carina; body length ≥3.8 mm; dorsal surface at 40× without distinct scalelike microreticulation; mesosternum in anterior half flat, even slightly convex, not longitudinally depressed (figs. 3, 4); aedeagus in dorsal view with apex lacking a medial notch 4
3. Elytron with 11th stria in apical third, close to outer margin (fig. 26); color of abdominal sterna 4–7 black or blackish brown (in some specimens sides orange), mesosternum, metasternum, epipleuron, and hypomeron orange; aedeagus at apex medially more distinctly notched (fig. 147); body more oval (L/W = 2.2), body length 3.3–4.9 mm ..... *minutus* Fabricius, p. 24
– Elytron with 11th stria in apical third, further from outer margin (fig. 22); ventral surface uniformly yellowish brown or reddish brown; aedeagus at apex medially more shallowly notched (fig. 145); body narrower (L/W = 2.0), body length 3.4–3.9 mm ..... *rockinghamensis* LeConte, p. 28
4. Pronotum and elytron with dense, minute, oblique microstriae (fig. 47); abdominal sterna 4–7 uniformly and entirely black, sternum 8, epipleuron, and hypomeron abruptly and conspicuously orange; aedeagus in apical third distinctly and abruptly narrowed (fig. 85); body length 5.6–6.4 mm ..... *affinis* Aubé, p. 28
– Pronotum and elytron not with oblique microstriae; abdominal sternal coloration, aedeagal structure, and body length various 5
5. Elytron with 11th stria marginal or almost marginal throughout its length (figs. 24, 152); elytral striae 6–11 noticeably impressed, almost groovelike (fig. 32); body distinctly convex (L/H = 2.58); body length, 4.3–5.0 mm; aedeagus in figure 121 ..... *parcus* Say, p. 33
– Elytron with 11th stria at most marginal only in posterior half, in anterior region moderately to distinctly elevated or arched (as in figs. 19–23, 150, 151); elytral striae 6–11 not impressed (figs. 35, 37), or at most impressed through 8–11 (figs. 38, 40); body convexity and length various 6
6. Tarsal claws distinctly darkened, either black, blackish brown, or blackish red 7
– Tarsal claws not darkened, either orangish or light reddish 9
7. Body length = 7.0–7.8 mm; protarsal claws

shorter than 5th protarsomere (fig. 2); genitalia bizarrely modified, aedeagus and parameres large, broad, and forming a cup-shape structure (figs. 143, 144) .... *impressicollis* Kirby, p. 36

– Body length <7 mm; protarsal claws equal to or longer than 5th protarsomere (as in fig. 1); aedeagus not as above 8

8. Aedeagus in dorsal view gradually narrowing and slightly convex, narrowly rounded at apex (figs. 99, 100); body length 5.2–6.0 mm ..... *wallisi* Fall, p. 36

– Aedeagus in dorsal view slightly more constricted in the middle, more distinctly convex, tapering to a point at apex (fig. 101); body length, 6.0–6.5 mm .... *marinus* Gyllenhal, p. 37

– Aedeagus in dorsal view parallel sided, dorsally flattened in apical third, aedeagal apex and lateral lobes subtruncate (figs. 102, 103); body length, 4.7–5.4 mm .... *aeratus* Stephens, p. 38

9. Aedeagus distinctly and abruptly constricted so as to form a dorsoventrally flattened apical projection (figs. 88, 89, 93); color of ventral surfaces reddish, at most abdominal sterna medially lightly infuscate 10

– Aedeagus not as above; color of ventral surfaces various in color 11

10. Constricted portion of aedeagus longer (fig. 93); elytral microreticulation evident only posteriorly, micropunctation sparse (as in fig. 74) ..... *obtusus* Say, p. 39

– Constricted portion of aedeagus shorter (figs. 88, 89); elytral microreticulation evident uniformly, micropunctation dense .... *bifarius* Fall, p. 40

11. Aedeagus in dorsal and lateral view abruptly narrowed in apical one-quarter to one-third so much so that pointed and acute apex appears almost needlelike, apex only one-quarter to one-sixth width of parameres (figs. 75–84); metepisternal ostiole always very large (figs. 11–14) 12

– Aedeagus not as abruptly narrowed, apex ≥one-third width of parameres; metepisternal ostiole various in size (figs. 11–18) 15

12. Elytron with distinct subapical convexity (fig. 33); elytral surface shiny without evident microreticulation; color of abdominal sterna and legs reddish; body distinctly convex (L/H = 2.45); distributed in western North America; aedeagus in figs. 80–82 .... *plicifer* LeConte, p. 42

– Elytron without distinct subapical convexity (as in figs. 34, 35); elytral microreticulation, body convexity, color of abdominal sterna and legs various; distributed in eastern North America 13

13. Body length 4.7–5.0 mm, shape narrower (L/W = 2.02), and distinctly convex (L/H = 2.62); elytron shiny, without evident microreticulation, outer margin narrow (as in fig. 36); pronotum medially with transverse, impressed line distinctly sinuately curved (as in figs. 7, 9, 150); ventral surfaces reddish; aedeagus in figures 83, 84; distributed in southeastern North America .... *elevatus* Leconte, p. 43

– Body length ≥5.5 mm, shape broader (L/W = 1.7–1.8) and not as convex (L/H = 2.90–2.95); elytron with uniform and evident microreticulation in form of obliquely oriented moderately transverse sculpticells (fig. 43), outer margin wide (fig. 40); pronotum medially with transverse impressed line less evidently sinuately curved; color of abdominal sterna 4–7 black or black with laterally narrow reddish areas; distributed in northeastern North America 14

14. Punctures of elytral striae 8–10 larger and more deeply impressed than striae 1–7, striae 8–10 posteriorly converging more closely (as in fig. 40); color of abdominal sterna 4–7 uniformly black; aedeagus in figures 77–79 ..... *borealis* Aubé, p. 45

– Punctures of elytral striae 8–10 not larger and more impressed than striae 1–7, striae 8–10 posteriorly not converging (as in figs. 35–37); color of abdominal sterna 4–7 black with narrowly reddish areas on sides (fig. 156); aedeagus in figures 75, 76 .... *pugionis* Fall, p. 46

15. Aedeagus (at widest point in apical quarter) as wide as or slightly wider than parameres (at widest point in apical quarter) (figs. 136–142) 16

– Aedeagus (at widest point in apical quarter) at most subequal to width of parameres (at widest point in apical quarter) 20

16. Body length 3.9–4.5 mm, distinctly convex (L/H = 2.32); metepisternal ostiole extremely large (fig. 13); pronotum with transverse impressed line parallel to anterior margin (as in figs. 8, 10); aedeagus in figures 137, 138 ..... *marginellus* Fall, p. 46

– Body length >4.5 mm, not distinctly convex (L/H > 2.85); metepisternal ostiole much smaller or absent (as in figs. 15–18); pronotum medially with transverse, impressed line slightly or distinctly sinuately curved (as in figs. 7, 9) 17

17. Color of abdominal sterna 4–7 uniformly black, sternum 8 reddish; elytron with 11th

stria close to outer margin in apical third (fig. 20) 18

– Color of ventral surfaces uniformly reddish; elytron with 11th stria more remote from outer margin in apical third (as in figs. 25, 27, 35) 19

18. Elytron dull, with evident microreticulation in form of obliquely oriented moderately transverse sculpticells (fig. 46); metepisternal ostiole absent (fig. 18); legs bicolored, protibia, mesofemur, and metafemur infuscate; maximum height in lateral view anterior to midpoint of body length giving gibbous profile (fig. 20); aedeagus broad, in dorsal view distinctly concave in apical third (figs. 139, 140) .... *gibber* LeConte, p. 48

– Elytron shiny, without evident microreticulation; metepisternal ostiole medium-size (as in fig. 15); legs uniformly orange; body not gibbous in lateral view; aedeagus broad, in dorsal view slightly convex in apical third (fig. 136) ..... *piceolus* Blatchley, p. 49

19. Aedeagus with apex broadly truncate, anterolateral corners more angulate, medially slightly produced (fig. 142); elytron with a bronze sheen ..... *ventralis* Kirby, p. 49

– Aedeagus anterolaterally more rounded (fig. 141); elytron black ..... *fraternus* Couper, p. 51

20. Aedeagus (at widest point in apical quarter) at most subequal to parameres (at widest point in apical quarter) (figs. 125–135) 21

– Aedeagus (at widest point in apical quarter) at most half as wide as parameres (at widest point in apical quarter) (figs. 86–122) 26

21. Body length 4.0–4.3 mm; elytron with 11th stria in anterior half more distinctly impressed (fig. 150); pronotum medially with transverse, impressed line distinctly sinuately curved (figs. 7, 9, 150); color of ventral surfaces uniformly reddish; aedeagus slightly expanding, broadly angulate at apex, dorsally very slightly convex (fig. 129) ..... *latilimbus* Fall, p. 53

– Body length >4.9 mm; elytron with 11th stria in anterior half not distinctly impressed; pronotum medially with transverse, impressed line less sinuately curved, sometimes even parallel to anterior margin (as in figs. 8, 10); color of ventral surfaces various; aedeagus not as above 22

22. Elytron with dense micropunctation (as in fig. 73); aedeagus in apical third almost parallel sided, shallowly concave and with longitudinal medial carination not attaining tip, apex broadly rounded (figs. 125, 126); color of ventral surfaces reddish (in some specimens medially abdominal sterna 4–7 infuscate) ..... *confinis* LeConte, p. 54

– Elytron with sparse micropunctation; aedeagus not as above, dorsally slightly flat or distinctly convex, longitudinally medially carinate, often appearing roof-shaped, apex angulate in mid-tip (figs. 127, 128, 130–135); color of mesosternum and metasternum never uniformly reddish, but black, brown, or reddish with black areas, abdominal sterna 4–7 black 23

23. Elytron with 11th stria in apical third remote from outer margin (fig. 25); outer margin of elytron posteriorly with numerous small rugae (fig. 25); metepisternal ostiole absent (fig. 18); dorsal surface shiny and bronzed, elytral microreticulation posteriorly and laterally (between striae 7–10) distinctly more visible (fig. 49); aedeagus in apical half gradually tapering to an acute point (figs. 130, 131); distributed in California and Oregon ..... *rugosus,* n. sp., p. 55

– Elytron with 11th stria in apical third close to outer margin (as in figs. 20, 21); outer margin of elytron posteriorly without numerous small rugae; metepisternal ostiole size small to medium; microreticulation absent or present but uniformly so; aedeagus more parallel sided or even slightly expanded apically (figs. 127, 128, 132, 135); distributed in eastern North America and throughout Canada 24

24. Body distinctly convex (L/H = 2.62); elytra shiny without evident microreticulation; pronotum medially with transverse, impressed line distinctly sinuately curved (as in figs. 7, 9); legs uniformly reddish; aedeagus in apical third only very slightly expanded in mid-tip sinuate (figs. 127, 128) ..... *pernitidus* LeConte, p. 56

– Body moderately convex (L/H > 2.95); elytral microreticulation distinctly to moderately evident (fig. 42); pronotum medially with transverse, impressed line slightly curved, almost parallel to anterior margin (as in fig. 8); legs bicolored, protibia, mesofemora, and metafemora infuscate; aedeagus longitudinally medially carinate and elevated, giving a roof-shaped appearance in apical third, broadly angulate at apex (figs. 132–135) 25

25. Elytron dull, with distinctly evident microreticulation (fig. 42, 45); distributed in northeastern U.S. and throughout Canada ..... *opacus* Sahlberg, p. 57

– Elytron shinier, elytral microreticulation similar in shape but more effaced; restricted to western Canada ... *hoppingi* Leech, p. 59

26. Elytron with 11th stria in apical third remote from outer margin (as in figs. 30, 31); body length small, 4.0–4.7 mm; elytron shiny, without evident microreticulation; pronotum with transverse, impressed line parallel to anterior margin (as in figs. 8, 10); aedeagus in apical quarter parallel sided, in dorsal view flat, at tip narrowly rounded (figs. 108–110) 27
– Elytron with 11th stria in apical third, close to outer margin (as in fig. 21); body length 3.8–7.0 mm; elytron with or without evident microreticulation; pronotum with transverse, impressed line various in position; aedeagus not as above 28
27. Outer margin of elytron very narrow, three times narrower than 11th interval at apex, not distinctly angulate (fig. 31); metepisternal ostiole very large (as in fig. 12); body length 4.1–4.7 mm; aedeagus at apex 2.5 times narrower than parameres (fig. 108) ..... *woodruffi* Fall, p. 59
– Outer margin of elytron wider, 1.5–2.0 times narrower than 11th interval at apex, more distinctly angulate (fig. 30), metepisternal ostiole smaller (as in fig. 15); body length 4.0–4.3 mm; aedeagus at apex almost 3 times narrower than parameres (figs. 109, 110) ..... *aeneolus* LeConte, p. 59
28. Body extremely convex (L/H = 2.34); metepisternal ostiole extremely large (fig. 14); punctures of elytral striae 8–10 distinctly large and more impressed than punctures of 1–7 (figs. 38, 39); color of abdominal sterna and legs uniformly reddish brown; elytron very shiny, without evident microreticulation; distributed in southeastern U.S.; aedeagus in figures 122–124 .... *pachysomus* Fall, p. 60
– Body not as convex (L/H > 2.95); metepisternal ostiole smaller (as in figs. 15, 14); punctures of elytral striae 8–10 not distinctly larger and more impressed than punctures of striae 1–7; color of legs and abdominal sterna various; elytron with or without evident microreticulation; aedeagus not as above 29
29. Body length small, 3.8–4.0 mm; elytron shiny, without evident microreticulation; abdominal segments 4–7 metallic black, remaining ventral surfaces uniformly and conspicuously orange (fig. 157); aedeagus very slender, gradually narrowing, but in apical half almost parallel sided, at apex narrowly rounded (figs. 86, 87) .... *dichrous* LeConte, p. 61
– Body length >4.3 mm; elytron with or without microreticulation; color of ventral surfaces various; aedeagal shape not as above 30
30. Aedeagus in apical third constricted and flat, medially weakly carinate, at apex acute, laterally curves up (figs. 111, 112); body length 4.3–5.0 mm; dorsal surface dull with aeneous luster; pronotum with transverse, impressed line parallel to anterior margin (figs. 8, 10, 151) ..... *analis* Say, p. 62
– Aedeagus not as above; body length ≥4.9 mm; dorsal surface dull or shiny; pronotum with transverse, impressed line various in position 31
31. Ventral surfaces bicolored, sides of abdominal sterna 4–7, sternum 8 entirely, epipleuron, hypomeron, and legs conspicuously and abruptly orange; mesosternum, metasternum, and medially abdominal sterna 4–7 metallic black (fig. 155); elytron with 11th stria in apical half approaching or almost located at outer marginal inflection; aedeagus tapering, laterally strongly compressed, in dorsal view carinate, tip acute (figs. 90, 91); body length 5.0–5.9 mm ... . *maculiventris* LeConte, p. 64
– Abdominal coloration not as above; elytron with 11th stria in apical third approaching or almost located at outer marginal inflection; aedeagus variably shaped 32
32. Body length 6.3–7.0 mm, ventral surfaces bicolored, abdominal sterna 4–7, mesosternum, metasternum black, epipleuron, hypomeron, legs, and 8th sternum conspicuously and abruptly orange; elytron without evident microreticulation, micropunctation coarse and dense (fig. 51); aedeagus in figure 118 ..... *pleuralis* Fall, p. 64
– Body length 4.9–6.4 mm; ventral surfaces not bicolored; elytron with or without microreticulation, micropunctation sparse or very minutely dense; aedeagus not as above 33
33. Color of abdominal sterna 4–7 uniformly black 34
– Color of abdominal sterna 4–7 either uniformly reddish or medially infuscate, becoming gradually reddish laterally ... 36
34. Elytron without evident microreticulation, or microreticulation only barely noticeable as extremely fine transverse lines; aedeagus in figures 104, 105; distributed only in western North America ..... *picipes* Aubé, p. 64
– Elytron with evident and uniform microreticulation in form of moderately transverse sculpticells (figs. 61, 63); distributed in eastern and northwestern North America 35
35. Legs bicolored, protibia, mesofemur, and me-

tafemur infuscate; elytral micropunctation minute and dense (fig. 63); distributed in western Canada; aedeagus in apical quarter dorsally distinctly flat, at apex narrowly rounded (figs. 106, 107) ..... *dubius* Wallis, p. 65

– Color of legs uniformly reddish; elytral micropunctation sparse and less dense (fig. 61); distributed in eastern and northern North America; aedeagus in apical third dorsally only very narrowly flat, at apex acute (figs. 92, 93) ..... *sayi* Aubé, p. 65

36. Color of ventral surfaces uniformly reddish; aedeagus in figures 96–98 ..... *gehringi* Chamberlain, p. 66

– Color of abdominal sterna 4–7 medially brown or black, sides gradually becoming reddish laterally; aedeagus not as above; distributed in eastern and western North America 37

37. Aedeagus tapering to a point, laterally strongly compressed, dorsally carinate, at apex acute (figs. 94, 95); body length 5.1–5.7 mm ..... *lecontei* Fall, p. 67

– Aedeagus in apical third almost parallel sided, laterally slightly compressed, dorsally not carinate, at apex very slightly angulate (figs. 113–117) 38

38. Aedeagal apex half as wide as apex of parameres (figs. 115–117); distributed in eastern North America ... *aquiris* LeConte, p. 68

– Aedeagal apex less than half as wide as apex of parameres (figs. 113, 114); distributed in western North America ..... *consobrinus* LeConte, p. 70

KEY TO FEMALES OF NEARCTIC SPECIES OF *GYRINUS*

1. Mesosternum with anterior margin trilobed, each lobe distinctly broadly convex (fig. 3); tarsal claws distinctly black or blackish brown; body length 5.5–5.7 mm ..... *pectoralis* LeConte, p. 24

– Mesosternum with anterior margin less distinctly trilobed, medial and lateral projections more angulate (fig. 4); tarsal claws either black, blackish brown, or light reddish; body length various 2

2. Scutellum with longitudinal, medial, basal carina (fig. 6); body length ≤4.4 mm; dorsal surface at 40× dull with distinctly scalelike microreticulation (figs. 6, 41, 44); mesosternum in anterior half with evident medial, longitudinal groove (fig. 5) 3

– Scutellum without a longitudinal carina; body length ≥4 mm; dorsal surface at 40× without distinct scalelike microreticulation; mesosternum in anterior half flat, even slightly convex, not longitudinally depressed (figs. 3, 4) 4

3. Elytron with 11th stria in apical third close to outer margin; (fig. 28 or as in fig. 23); color of abdominal sterna 4–7 black or blackish brown, in some specimens sides orange, mesosternum, metasternum, epipleuron, and hypomeron orange; body broader (L/W = 1.98), body length 3.7–4.4 mm ..... *minutus* Fabricius, p. 24

– Elytron with 11th stria in apical third more remote from outer margin (fig. 22); color of ventral surfaces uniformly yellowish brown or reddish brown; body narrower (L/W = 1.97), body length 3.5–4.3 mm ..... *rockinghamensis* LeConte, p. 28

4. Pronotum and elytron with dense, minute, oblique microstriae (fig. 47); color of abdominal sterna 4–7 uniformly and entirely black, sternum 8, epipleuron, and hypomeron abruptly and conspicuously orange; body length 6.8–7.0 mm ..... *affinis* Aubé, p. 28

– Pronotum and elytron never with oblique microstriae; color of abdominal sterna and body length various 5

5. Elytron with 11th stria marginal or almost marginal throughout its length (figs. 24, 152); elytral striae 1–11 noticeably impressed, intervals convex (fig. 32); body distinctly convex (L/H = 2.61), body length 4.7–5.5 mm; elytron at 50× with scalelike microreticulation (fig. 58) ..... *parcus* Say, p. 33

– Elytron with 11th stria at most marginal only in posterior half, in anterior region moderately to distinctly elevated or arched above elytral margin (figs. 19–23, 150, 151); elytral striae impressed at most 8 through 11 (as in figs. 38–40); body convexity and length various; elytron at 50× various in microreticulation 6

6. Tarsal claws (especially mid and hind tarsi) distinctly darkened, either black, blackish brown, or blackish red 7

– Tarsal claws not darkened, either orangish or light reddish 8

7. Body length 6.5–7.3 mm, broad (L/W = 1.70); elytron and pronotum dull with dense microreticulation, micropunctures not evident (fig. 64), outer margin wider, reflexed upward, therefore noticeably concave (fig. 29) ..... *impressicollis* Kirby, p. 36

– Body shorter, 5.8–6.5 mm, and narrower (L/W = 1.86), elytron with dense microreticulation and micropunctation; outer margin narrower, not concave ... *wallisi* Fall, p. 36,

aeratus Stephens, p. 38,
marinus Gyllenhal, p. 37

8. Elytron with a distinct subapical convexity (fig. 33); distributed in western North America ..... *plicifer* LeConte, p. 42
- Elytron without a distinct subapical convexity (as in fig. 35) 9

9. Metepisternal ostiole conspicuously large (fig. 12–14); body distinctly convex (L/H = 2.41); elytron shiny without evident microreticulation and micropunctation; color of ventral surfaces reddish or reddish brown (in some specimens metasternum darker); punctures of elytral striae 8–11 larger than punctures of 1–7 (as in figs. 34, 38) .. 10
- Metepisternal ostiole moderately large to small (figs. 15–18); body distinctly or moderately convex (L/H = 2.53–3.17); elytron shiny or dull, with or without evident microreticulation and micropunctation; color of ventral surfaces various; punctures of elytral striae 8–11 larger or same as punctures of 1–7 12

10. Body large, 5.7–6.8 mm, broad (L/W = 1.78); elytron with outer margin wider (especially posteriorly, figs. 38, 39); distributed in southeastern North America .... *pachysomus* Fall, p. 60
- Body shorter, 4.2–5.2 mm, narrower (L/W = 2.0); elytron with outer margin narrower (fig. 36); distributed in southern and eastern North America 11

11. Pronotum with transverse, impressed line sinuately curved, more remote along medial portion of anterior margin (as in figs. 7, 9, 150); elytron with 11th stria in apical third, close to outer margin (as in fig. 34); distributed from Florida to Texas .... *elevatus* LeConte, p. 43
- Pronotum with transverse, impressed line parallel to anterior margin (as in figs. 8, 10); elytron with 11th stria in apical third distinctly remote from outer margin (as in fig. 25); distributed in eastern North America ..... *marginellus* Fall, p. 46

12. Elytron with 11th stria in apical third or half remote from outer margin (as in figs. 19, 25, 27, 30, 31); color of ventral surfaces reddish or reddish brown (darker in some specimens of *rugosus*) 13
- Elytron with 11th stria in apical third or half close to outer margin (as in figs. 20, 21, 23, 28, 33, 34); color of ventral surface various 17

13. Elytron with 11th interval posteriorly rugose (fig. 25); metepisternal ostiole absent (as in fig. 18); elytron laterally with a subtle but evident bronze chagrin, dorsally microreticulation effaced but lateroposteriorly distinctly evident (fig. 49); distributed in western North America (Oregon and California) ..... *rugosus*, n. sp., p. 55
- Elytron with 11th interval posteriorly not rugose; metepisternal ostiole various in size; elytron sometimes laterally with bronze chargin, microreticulation evident or not 14

14. Body length 4.2–5.2 mm; metepisternal ostiole large to medium (as in figs. 11, 15); pronotum with transverse, impressed line parallel to anterior margin (as in fig. 151); color of ventral surfaces uniformly reddish to reddish brown (in some specimens metathoracic sternum darker) 15
- Body length 4.9–6.2 mm; metepisternal ostiole small (as in figs. 16, 17); pronotum medially with transverse, impressed line slightly curved (as in fig. 152); color of ventral surfaces uniformly orange or reddish (in some specimens abdominal sterna 4–7 medially brownish) 16

15. Elytron dull grayish with distinct and uniform microreticulation (fig. 56); metepisternal ostiole large (as in fig. 12); elytron with outer margin narrow, not distinctly angulate (fig. 31) ..... *woodruffi* Fall, p. 59
- Elytron shiny bronze without evident microreticulation; metepisternal ostiole medium (fig. 15); elytron with outer margin slightly wider, more distinctly angulate (fig. 30) .. .. *aeneolus* LeConte, p. 59

16. Elytron at 50× with distinctly evident microreticulation and dense micropunctation (figs. 35, 73); color of abdominal sterna 3–8 orange or reddish (in some specimens medially darker; distributed in northeastern, north, and western North America .... *bifarius* Fall, p. 40,
obtusus Say, p. 39,
confinis LeConte, p. 54
- Elytron at 50× without evident microreticulation, or microreticulation barely noticeable, micropunctation sparse or of extremely fine density (fig. 74); color of ventral surfaces always uniformly orange; distributed in northeastern North America .... *ventralis* Kirby, p. 49,
fraternus Couper, p. 51

17. Elytron at 50× with evident microreticulation (as in figs. 43, 46, 52) 18
- Elytron at 50× without evident microreticulation, or microreticulation only barely evident (as in figs. 51, 55, 74) 26

18. Body shorter, 4.5–4.7 mm; color of ventral surfaces and legs uniformly orange or light reddish; pronotum with transverse, im-

pressed line sinuately curved, more remote along medial portion of anterior margin (fig. 150); elytron dull, at 50× with scalelike microreticulation (fig. 52); elytron with 11th stria in anterior half impressed (fig. 150) ..... *latilimbus* Fall, p. 53

– Body longer, ≥5 mm; color of ventral surfaces dark brown or black; pronotum medially with transverse, impressed line usually slightly curved, sometimes even parallel to anterior margin (figs. 8, 10); elytron shiny or dull, at 50× microreticulation various; elytron with 11th stria in anterior half not impressed 19

19. Color of abdominal sterna 4–7 medially dark brown, sides very narrowly reddish (fig. 156); metepisternal ostiole large (as in fig. 11); elytral microreticulation at 50× obliquely and moderately transverse (as in fig. 43); body long, 6.4–6.8 mm, broad (L/W = 1.80) ..... *pugionis* Fall, p. 46

– Color of abdominal sterna uniformly dark brown or black; metepisternal ostiole ranges from large to absent; elytral microreticulation at 50× various; body length and width vary 20

20. Punctures of 8th, 9th, 10th, and 11th striae larger and more deeply impressed than punctures of striae 1–7 (fig. 40); metepisternal ostiole large (fig. 11); elytral microreticulation at 50× obliquely moderately transverse (fig. 43); body long, 5.9–6.2 mm, broad (L/W = 1.79) .. *borealis* Aubé, p. 45

– Punctures of 8th, 9th, 10th, and 11th striae not distinctly large and more impressed than punctures of striae 1–7 (as in figs. 35, 37); metepisternal ostiole from medium size to absent; elytral microreticulation at 50× varies in shape; body size varies 21

21. Color of legs uniformly reddish or orange 22

– Legs bicolored; protibia, mesofemora, and metafemora infuscate 24

22. Pronotum with transverse, impressed line parallel and close to anterior margin (figs. 8, 10, 151); dorsal surface with dull aeneous luster; elytral microreticulation at 50× scalelike (fig. 54); color of 8th abdominal sternum uniformly orange; body length 5.0–5.5 mm ..... *analis* Say, p. 62

– Pronotum medially with transverse, impressed line slightly curved (as in fig. 152); dorsal surface without aeneous luster, elytral microreticulation at 50× scalelike or obliquely moderately transverse (figs. 42, 46, 60, 62); color of 8th abdominal sternum reddish (partly infuscate in some specimens); body length 5.5–6.6 mm 23

23. Metepisternal ostiole invisible (fig. 18); elytral microreticulation in form of obliquely and moderately transverse sculpticells (fig. 46); maximum height in lateral view anterior to midpoint of body length giving gibbous profile (fig. 20); body length 5.5–6.2 mm ..... *gibber* Leconte, p. 48

– Metepisternal ostiole moderately large (as in fig. 15); elytral microreticulation scalelike (fig. 60); body not gibbous in lateral view; body length 5.8–6.6 mm .... *sayi* Aubé, p. 65

24. Metepisternal ostiole invisible (fig. 18); elytral microreticulation in form of obliquely and moderately transverse sculpticells (fig. 46); maximum height in lateral view anterior to midpoint of body length giving gibbous profile (fig. 20); distributed from Florida to Maine ..... *gibber* LeConte, p. 48

– Metepisternal ostiole moderately large (fig. 15); elytral microreticulation scalelike or polygon (figs. 42, 62); body not gibbous in lateral view (as in figs. 22, 23); distributed in Canada 25

25. Elytron shinier, microreticulation uniformly effaced ..... *hoppingi* Leech, p. 59

– Elytron duller, microreticulation distinctly evident, scalelike (figs. 42, 62) .... *opacus* Sahlberg, p. 57, *dubius* Wallis, p. 65

26. Color of ventral surfaces and legs uniformly orange or light reddish; body length 6.1–6.6 mm ..... *gehringi* Chamberlain, p. 66

– Color of ventral surfaces never uniformly reddish, abdominal sterna 4–7 uniformly black (fig. 153) or medially dark but laterally reddish (figs. 154, 155); body length various 27

27. Body length 6.8–7.0 mm; elytron with coarse and dense micropunctation (fig. 71); color of abdominal sterna 4–7, mesosternum, metasternum metallic black, anal sternum, epipleuron, hypomeron, and legs abruptly and conspicuously orange .... *pleuralis* Fall, p. 64

– Body length 4.0–6.7 mm; elytron with sparse micropunctation (as in figs. 53, 57); ventral coloration various 28

28. Body very short, 4.0–4.4 mm, and narrower (L/W = 1.99); color of abdominal sterna 4–7 metallic black, rest of ventral surfaces uniformly orange (fig. 157) .... *dichrous* LeConte, p. 61

– Body longer, >5.2 mm, wider (L/W = 1.8–1.9); color of ventral surfaces varies .. 29

29. Color of abdominal sterna 4–7 uniformly black 30

– Color of abdominal sterna 4–7 laterally red-

dish or orange, medially brownish or black 32

30. Color of mesosternum orange; pronotum medially with transverse, impressed line sinuately curved, more remote along median portion of anterior margin (as in figs. 7, 9, 150) ..... *piceolus* Blatchley, p. 49
- Color of mesosternum black; pronotum with transverse, impressed line various in shape 31

31. Body very convex (L/H = 2.5); pronotum medially with transverse, impressed line sinuately curved, more remote along medial portion of anterior margin; distributed in eastern North America ..... *pernitidus* LeConte, p. 56
- Body less convex (L/H = 2.9); pronotum medially with transverse, impressed line slightly curved; distributed in western North America ..... *picipes* Aubé, p. 64

32. Color of abdominal sterna 4–7 medially metallic black, at sides abruptly and conspicuously orange (in shape of a lateral spot at each margin of each sternum 4–7 [fig. 155]), mesosternum and metasternum black; elytron with 11th stria in posterior half close to outer margin ..... *maculiventris* LeConte, p. 64
- Color of abdominal sterna 4–7 medially infuscate, laterally becoming gradually reddish or yellowish, mesosternum and metasternum reddish to brownish; elytron with 11th stria in posterior third close to outer margin 33

33. Distributed in western North America ..... *consobrinus* LeConte, p. 70
- Distributed in eastern North America ..... *aquiris* LeConte, p. 68, *lecontei* Fall, p. 67

TAXONOMIC TREATMENT OF NEARCTIC SPECIES OF *GYRINUS*

The following format is used in the treatment of Nearctic species of *Gyrinus:* (1) diagnostic character combination, (2) type information and taxonomic notes, (3) sexual dimorphism of dorsal microsculpture, (4) habitat information, and (5) distribution. For the diagnostic character combination, the fewest characters were used that fully separated specimens of each species from all others. These characters are listed in order of taxonomic importance. The diagnoses work best for male specimens but are useful for many females. When specimens of species are very similar, tables are constructed for comparisons (tables 4–7). In this section species are treated in the order in which they occur in the male key.

Gyrinus pectoralis LeConte

Figures 2, 3, 70, 119, 120; Map 13

Gyrinus pectoralis LeConte, 1868: 370, 372. Régimbart, 1883: 174; 1902–03: 8. Leng, 1920: 82. Fall, 1922: 227, 294, 295. Criddle, 1929: 116. Robert, 1963: 12, 27, 36. Ferkinhoff and Gundersen, 1983: 24, 39, 40.

DIAGNOSIS: This species is easily separated from those of other North American species by their completely unique trilobed mesosternum (fig. 3). Other distinguishing character states are: (1) blackish tarsal claws, (2) dense micropunctation, (3) aedeagus in figures 119, 120, (4) body measurements: male length 4.3–5.1 mm, width 2.4–2.9 mm; female length 5.5–5.7 mm, width 2.8–3.2 mm.

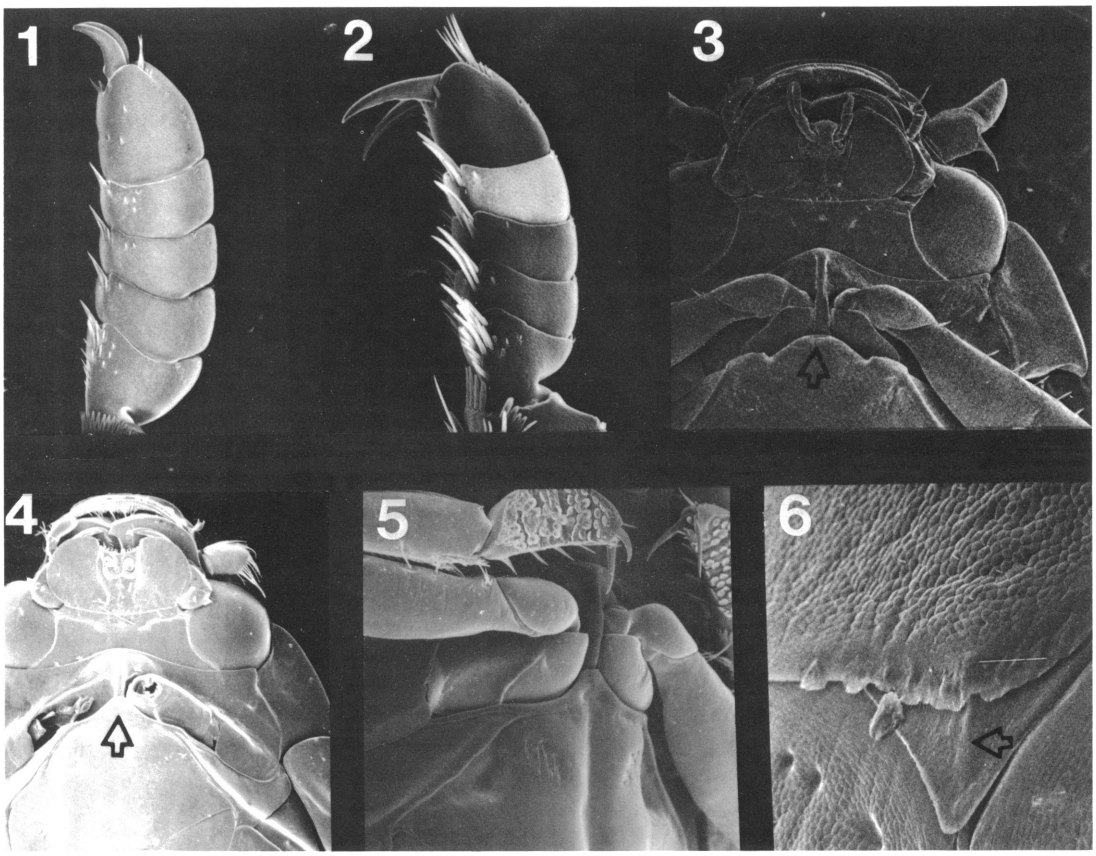
Gyrinus pectoralis is most similar to *G. aeratus* and *G. wallisi.*

TYPE INFORMATION AND TAXONOMIC NOTES: LeConte did not indicate how many specimens he based his description on. However, he indicated that they were from Lake Superior and Hudson Bay Territory (Fort Liard). We received eight specimens from the LeConte collection (MCZ) which we regard as syntypes. Fall (1922) did not clearly indicate one as lectotype. Therefore, we designated a male as lectotype. It is pinned and carries three labels: H.B. [handwritten]/ Ft.Liard [handwritten]/ pectoralis 3 [handwritten]. Aedeagus and parameres are on a point beneath the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: *G. minutus* is recollected with those of *G. picipes, G. wallisi, G. maculiventris, G. minutus, G. confinis,* and *G. bifarius* from the Piquitenay River, Manitoba (Frost *in* Fall, 1922). Robert (1955) and Morrissette (1979) both found *G. pectoralis* in mountain lakes in Quebec. Robert (1955) specifically mentioned that specimens were collected from the headwaters of the drainage basins of these lakes. Label information indicates that 69.6 percent of the collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 13. Records are from across Canada and the northern U.S.A.



Figs. 1–6. 1, 2. Protarsi of *Gyrinus*: **1,** *G. pectoralis* (40×); **2,** *G. impressicollis* (60×). 3–5. Mesosternum of *Gyrinus*: **3,** *G. pectoralis* (30×); **4,** *G. affinis* (30×); **5,** *G. rockinghamensis* (60×). 6. Scutellum of *G. minutus* 100×.

Gyrinus minutus Fabricius

Figures 6, 28, 146, 147; Map 1

Gyrinus minutus Fabricius, 1798: 65. Sahlberg, 1817: 48. Kirby, 1837: 81. Aubé, 1838: 683, 684. LeConte, 1868: 370, 372, 373. Sharp, 1868: 54, 55. Régimbart, 1883: 142, 143; 1902–03: 7. Ahlwarth, 1910: 21. Blatchley, 1910: 239. Sharp, 1914: 130, 131, 136. Leng and Mutchler, 1918: 97, 98. Leng, 1920: 82. Fall, 1922: 275, 276. Criddle, 1929: 115. Ochs, 1930: 136. Omer-Cooper, 1930: 65–66, 67. Balfour-Browne, 1938: 76, 85, 86; 1950: 342. Hatch, 1953: 242, 243. Zaitsev, 1953: 371. Young, 1954: 152. Brinck, 1960: 77, 79. Robert, 1963: 8, 27, 35. Gordon and Post, 1965: 27, 28. Ferkinhoff and Gundersen, 1983: 20, 27.

Gyrinus kirbyi Marsham, 1802: 100.

DIAGNOSIS: Specimens are separated from those of all other North American species by the following combination of characters: (1) scutellum with carina (fig. 6), (2) mesosternum grooved (as in fig. 5), (3) dorsal surface dull because of dense scalelike microreticulation (figs. 6, 41, 44), (4) abdominal segments 4–7 black, 8th segment, epipleuron, hypomeron, thoracic segments, and legs orange or reddish, (5) aedeagus in figures 146, 147, (6) body very short and narrow, body measurements: male length 3.3–4.9 mm, width 1.7–2.0 mm; female length 3.7–4.4 mm, width 2.0–2.3 mm.

Gyrinus minutus is most similar to *G. rockinghamensis*. Both species are distinguished from other North American representatives of *Gyrinus* by the presence of a carina on the scutellum and an apically notched aedeagus. However, specimens of these two species are easily confused. The most reliable nongenitalic character to separate them is the position of the 11th stria; it is closer to the elytral

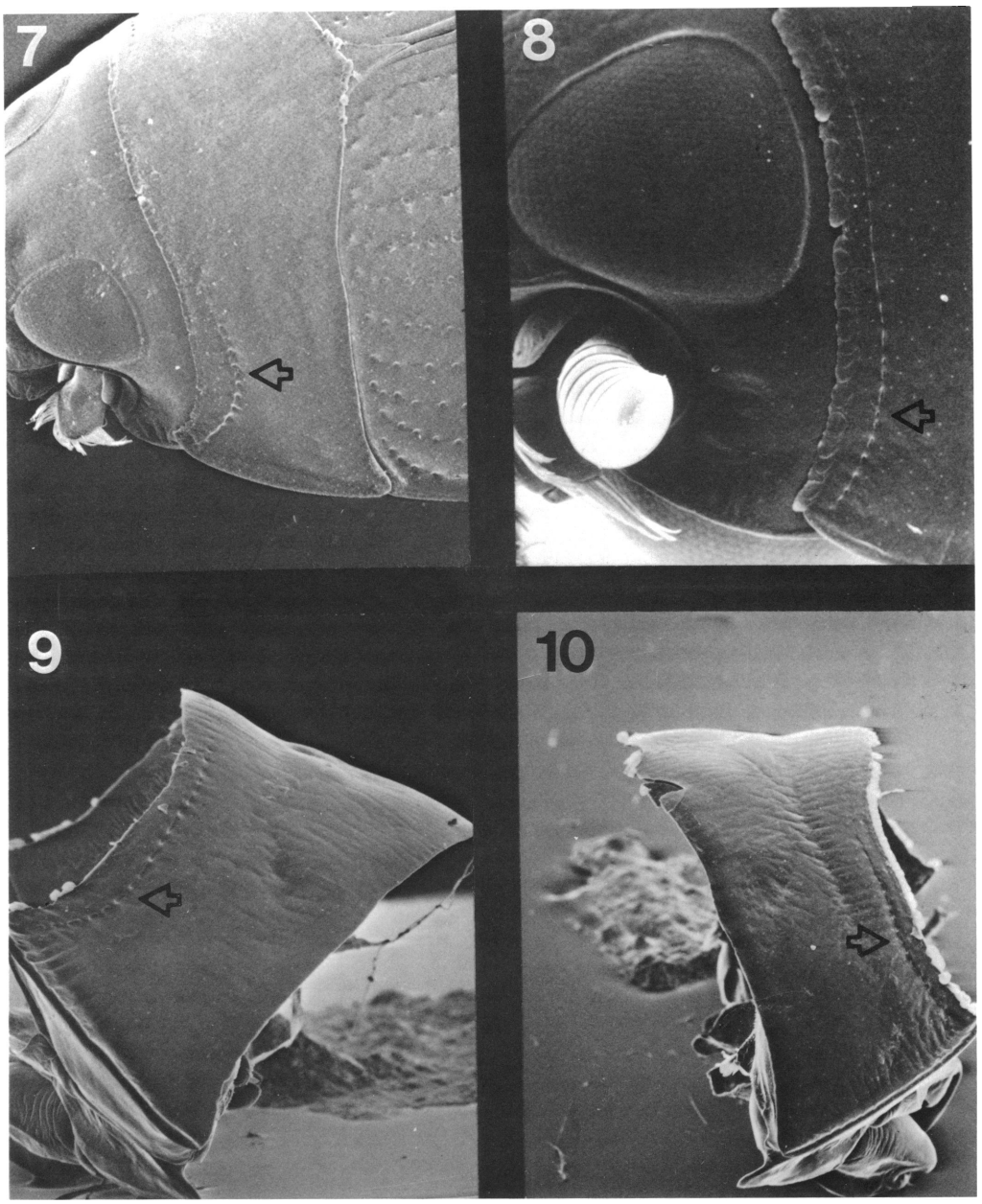
TABLE 2
Occurrence of Members of *Gyrinus* by Habitat Based on Analysis of Label Information of 936 Specimens
(Within each cell, top row is frequency and bottom row is percent)

SPECIES	BOG	LENTIC	LOTIC	Total
AENEOLUS	0 0.00	1 50.00	1 50.00	2
AERATUS	0 0.00	4 66.67	2 33.33	6
AFFINIS	0 0.00	60 58.82	42 41.17	102
ANALIS	0 0.00	11 28.95	27 71.05	38
AQUIRIS	0 0.00	4 80.00	1 20.00	5
BIFARIUS	0 0.00	9 25.71	26 74.29	35
BOREALIS	1 11.11	5 55.56	3 33.33	9
CONFINIS	0 0.00	22 91.67	2 8.33	24
CONSOBRINUS	0 0.00	22 34.40	42 65.60	64
DICHROUS	0 0.00	12 100.00	0 0.00	12
ELEVATUS	0 0.00	22 68.75	02 31.25	32
FRATERNUS	0 0.00	4 44.44	5 55.56	9
FROSTI	0 0.00	31 81.58	7 18.42	38
IMPRESSICOLLIS	0 0.00	5 83.33	1 16.67	6
LATILIMBUS	1 1.89	38 71.70	14 26.42	53
LECONTEI	1 3.33	18 60.00	11 36.67	30
LUGENS	0 0.00	47 65.28	25 34.72	72
MACULIVENTRIS	0 0.00	31 72.09	12 27.91	43
MARGINELLUS	0 0.00	1 7.69	12 92.31	13
MINUTUS	2 10.53	7 36.84	10 52.63	19
OPACUS	0 0.00	6 50.00	6 50.00	12
PACHYSOMUS	0 0.00	7 46.66	8 53.33	15
PARCUS	0 0.00	12 85.71	2 14.29	14
PECTORALIS	0 0.00	16 69.56	7 30.43	23
PICIPES	0 0.00	37 68.52	17 31.48	54
PLEURALIS	0 0.00	12 41.37	17 58.63	29
PLICIFER	0 0.00	15 20.27	59 79.73	74
PUGIONIS	1 4.17	21 87.50	2 8.33	24
ROCKINGHAMENSIS	0 0.00	7 46.67	8 53.33	15
VENTRALIS	0 0.00	32 80.00	8 20.00	40
WALLISI	0 0.00	8 66.67	4 33.33	12
WOODRUFFI	0 0.00	3 25.00	9 75.00	12
TOTAL	6 0.67	530 56.62	400 42.73	936 100.00

margin in the apical third in *G. minutus*. Although aedeagal structure is similar in both, there are differences. In *G. minutus* males the aedeagus is less expanded in the apical quarter, and the apex is more acute and deeply notched medially. Members of these species could be confused with those of *G. dichrous* because of very small body size, however species of *G. dichrous* do not have a scutellar carina. Table 4 summarizes several nongenitalic characters that distinguish these species.

TYPE INFORMATION AND TAXONOMIC NOTES: Two syntypes of *G. minutus*, one male and one female were received from the ZMUC. These two specimens are pinned on a white card. A pin with a red label is placed next to one of the specimens. Neither has any locality information. The male bears a label with the number 11 and the female bears a label with the number 71. We designate the male as the lectotype. The aedeagus was placed in a microvial attached beneath the specimen.

Because of the similarity of *G. minutus* and *G. rockinghamensis*, Régimbart (1902–03), and Balfour-Browne (1950) thought that *G. rockinghamensis* was a North American color variant of *G. minutus*, and synonymized these two species. Ochs (1930) and Young (1954) tentatively accepted species status for both *G. minutus* and *G. rockinghamensis* but with considerable reservation. On the other hand, LeConte (1868), Blatchley (1919), Fall



Figs. 7–10. Pronotum of *Gyrinus*: **7,** *G. latilimbus* (50×); **8,** *G. analis* (80×); **9,** *G. latilimbus* (60×); **10,** *G. analis* (50×).

(1922), Hatch (1925), and Omer-Cooper (1930) considered each definitely to be distinct at the species level. This taxonomic history is reviewed by Balfour-Browne (1950).

Gyrinus rockinghamensis is ventrally yellowish to yellowish brown and, based on this, is more similar to Palearctic *G. minutus* than to Nearctic *G. minutus* (which is more blackish abdominally). Although Nearctic *G. minutus* and *G. rockinghamensis* can be separated by abdominal coloration, the position of the 11th stria is sufficient for separation of *G. rockinghamensis* and Palearctic *G. minutus*.

TABLE 3

Frequency of Collections of Specimens of Nearctic *Gyrinus* by Season Based on Analysis of 936 Randomly Selected Specimens

(GEOAREA = geographic area, ECAN = Eastern Canada, FL = Florida, MIDAT = Mid-Atlantic, NE = Northeast U.S., SE = Southeast U.S.).

SPECIES	GEOAREA	JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
AENEOLUS	ECAN	0	0	0	1	0	0
	SE	0	1	0	0	0	0
AERATUS	ECAN	0	0	3	0	0	0
AFFINIS	ECAN	0	0	2	9	3	0
	NE	0	2	7	23	5	0
ANALIS	FL	1	0	0	1	3	0
	MIDAT	0	0	2	6	3	0
	SE	0	1	3	6	3	0
AQUIRIS	ECAN	0	0	0	1	0	0
	NE	0	0	2	0	1	0
BIFARIUS	ECAN	0	0	0	1	0	0
	MIDAT	0	0	1	0	0	0
	NE	0	1	0	2	1	0
BOREALIS	MIDAT	0	1	2	4	0	0
	NE	0	1	7	4	1	0
CONFINIS	MIDAT	0	0	0	1	0	0
	NE	0	2	6	7	2	0
CONSOBRINUS	MIDAT	0	0	0	1	0	0
DICHROUS	ECAN	0	0	0	1	1	0
	NE	0	1	1	9	0	0
ELEVATUS	FL	13	22	14	12	2	1
	SE	0	1	4	3	0	0
FRATERNUS	MIDAT	0	0	0	2	0	0
	NE	0	1	4	3	4	0
GEHRINGI	ECAN	0	0	2	2	0	0
	NE	0	0	1	0	0	0
GIBBER	ECAN	0	0	0	2	0	0
	FL	0	0	0	0	1	0
	MIDAT	0	0	0	1	0	0
	NE	1	3	3	21	2	0
	SE	0	3	0	0	0	0
IMPRESSICOLLIS	ECAN	0	0	1	3	0	0
	NE	0	0	0	3	0	0
LATILIMBUS	ECAN	0	0	2	0	1	0
	MIDAT	0	0	0	1	0	0
	NE	1	0	7	34	5	0
	SE	0	0	0	1	1	0
LECONTEI	ECAN	0	0	0	1	1	0
	MIDAT	0	0	1	1	0	0
	NE	0	7	9	16	4	0

TABLE 3—(*Continued*)

		JAN-FEB	MAR-APR	MAY-JUN	JUL-AUG	SEP-OCT	NOV-DEC
MACULIVENTRIS	MIDAT	0	1	0	0	3	0
	NE	0	3	6	12	3	0
	SE	0	0	1	0	0	0
MARGINELLUS	MIDAT	0	1	0	3	0	0
	NE	0	0	0	2	0	0
	SE	1	0	0	2	1	0
MINUTUS	ECAN	0	0	1	0	1	0
	FL	0	1	0	0	0	0
	MIDAT	0	0	1	0	0	0
	NE	0	2	5	8	0	0
	SE	0	0	1	1	0	0
PACHYSOMUS	FL	0	2	2	2	0	0
	SE	0	0	0	5	4	0
PARCUS	FL	1	0	0	0	0	0
	MIDAT	0	1	1	0	0	0
PECTORALIS	ECAN	0	0	0	1	0	0
	MIDAT	0	0	1	1	0	0
	NE	0	0	0	6	0	0
PERNITIDUS	MIDAT	0	1	2	0	0	0
PICEOLUS	ECAN	0	0	0	0	1	0
PICIPES	ECAN	0	0	0	1	0	0
PLEURALIS	MIDAT	0	0	0	0	1	0
	NE	0	1	0	0	0	0
PUGIONIS	ECAN	0	0	0	3	1	0
	MIDAT	0	0	0	0	1	0
	NE	0	2	9	20	4	1
ROCKINGHAMENSIS	FL	1	4	5	1	4	1
	MIDAT	0	1	11	7	2	1
	NE	0	0	1	2	0	0
	SE	0	0	2	2	0	0
SAYI	ECAN	0	0	5	8	0	0
	MIDAT	0	3	4	3	0	0
	NE	0	8	21	44	17	4
	SE	0	0	0	1	0	0
VENTRALIS	ECAN	0	0	0	3	0	0
	MIDAT	0	1	0	3	0	0
	NE	0	5	8	13	8	0
WALLIS	MIDAT	0	0	0	2	0	0
WOODRUFFI	FL	1	0	0	1	0	0
	MIDAT	0	0	3	3	3	0
TOTAL		20	89	172	331	98	8

Despite the difference in abdominal coloration of Palearctic and Nearctic populations of *G. minutus,* we are hesitant to differentiate Palearctic and Nearctic populations at the species or even subspecies level. Zaitsev (1953) indicated the presence of variation in abdominal coloration in Russian populations. More *G. minutus* need to be examined (especially from the Palearctic Region) before a final conclusion can be made.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: *G. minutus* is recorded from woodland pools (Blatchley, 1910), rocky pools (Sharp, 1914), peaty or semipeaty lakes (Robert, 1955; Morrissette, 1979), dystrophic habitats (Huldén, 1983b), and peat ringed bogs (Larson, 1983). However, Fall (1922) recorded this species from both lentic and lotic habitats. Label information indicates that 52.6 percent of the collections of specimens were from lotic habitats (table 2).

DISTRIBUTION: Map 1. Records are from Newfoundland to the Pacific coast, north to Alaska and south to Kansas.

Gyrinus rockinghamensis LeConte
Figures 5, 22, 41, 44, 145; Map 1

Gyrinus rockinghamensis LeConte, 1868: 370, 373. Régimbart, 1883: 142, 143; 1902–03: 7. Ahlwarth, 1910: 21. Blatchley, 1919: 316. Leng, 1920: 82. Fall, 1922: 275, 279. Ochs, 1930: 137. Omer-Cooper, 1930: 67. Balfour-Browne, 1950: 342. Young, 1954: 152–154. Sanderson, 1982: 10, 34.

DIAGNOSIS: Specimens of this species are separated from those of all other North American species by the following combination of characters: (1) scutellum with carina (fig. 6), (2) mesosternum grooved (fig. 5), (3) dorsal surface dull, with dense scalelike microreticulation (figs. 6, 41, 44), (4) ventral surfaces uniformly yellowish or orange, (5) aedeagus in figure 145, (6) body very short and narrow, body measurements: male length 3.4–3.9 mm, width 1.65–2.0 mm; female length 3.5–4.4 mm, width 1.7–2.2 mm.

G. rockinghamensis and *G. minutus* are the only North American species of *Gyrinus* with a carina on the scutellum and genitalia with notched apex. The most reliable nongenitalic character to separate these species are discussed above (see diagnosis of *G. minutus* and table 4).

TYPE INFORMATION AND TAXONOMIC NOTES: LeConte did not indicate how many specimens he based his description on. We received seven specimens from the LeConte collection (MCZ) which we regard as syntypes. Fall (1922) did not clearly indicate a lectotype. Therefore, we designated a male as the lectotype. It is glued on a point and carries the following labels: N.C./rockinghamensis 3 [handwritten].

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Young (1954) found this species in lakes, ponds, marshes, and roadside ditches in Florida. However, label information indicates that 53.3 percent of the collections were from lotic habitats (table 2).

DISTRIBUTION. Map 1. Records are most frequently from Florida and Alabama, but are also from New Jersey to Massachusetts.

Gyrinus affinis Aubé
Figures 4, 17, 47, 85; Map 6

Gyrinus affinis Aubé, 1838: 669, 670. LeConte, 1868: 369, 371. Régimbart, 1902–03: 7. Ahlwarth, 1910: 15. Blatchley, 1910: 238. Fall, 1922: 277, 293. Hatch, 1953: 242. Robert, 1963: 12, 19, 31. Ferkinhoff and Gundersen, 1983: 23, 37.

Gyrinus canadensis Régimbart, 1883: 159, 160.

DIAGNOSIS: *G. affinis* is easily separated from other North American species by the presence of oblique microstriae on the elytron and the thorax (fig. 47); otherwise *G. affinis* is most similar to *G. pleuralis.* Body measurements: male length 5.6–6.4 mm, width 3.1–3.8 mm; female length 6.8–7.0 mm, width 3.9–4.1 mm.

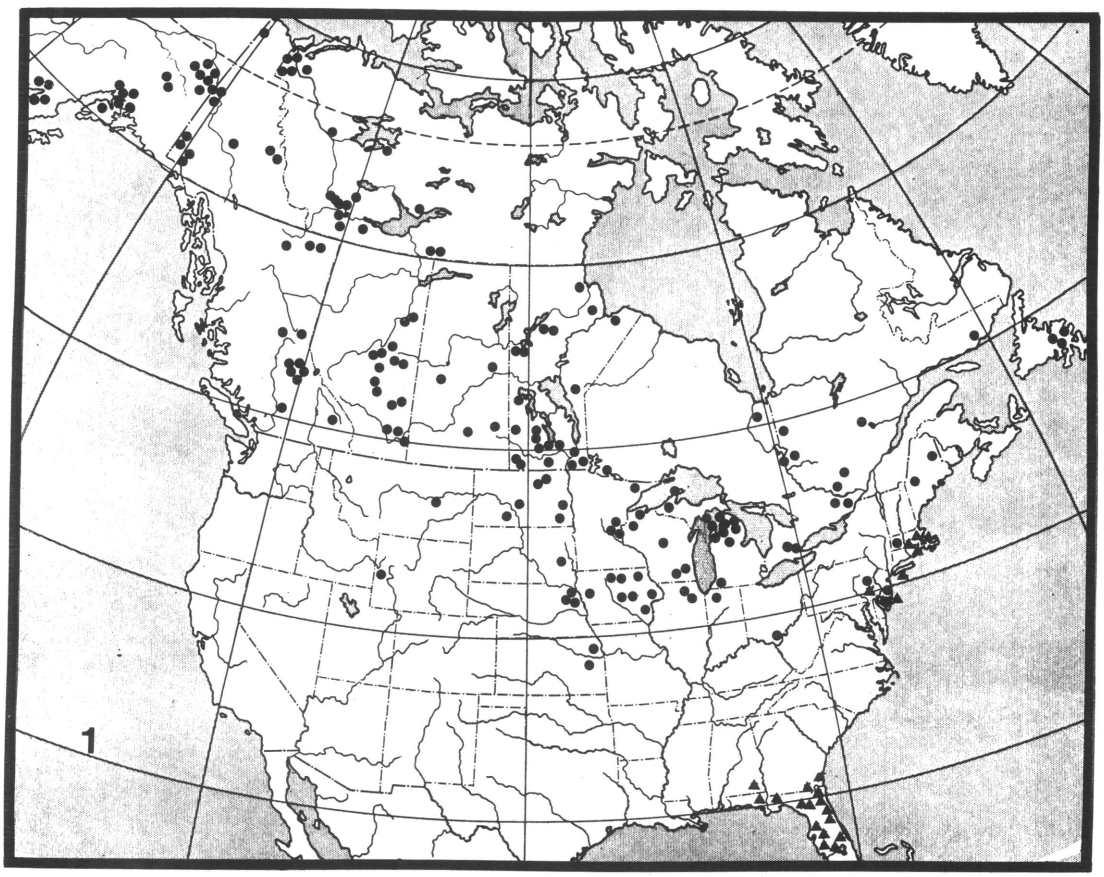
TYPE INFORMATION AND TAXONOMIC NOTES: Four female specimens (three from Quebec, and one from Pennsylvania) from IRSB were examined. The labels on the three specimens from Quebec very closely matched Régimbart's handwriting (by comparison to handwriting samples in Horn and Kahle, 1935). The label on the specimen from Pennsylvania matched Aubé's handwriting reasonably well. It is tempting to assume that

TABLE 4
Diagnostic Character States for Specimens of *Gyrinus dichrous, G. minutus, G. rockinghamensis*

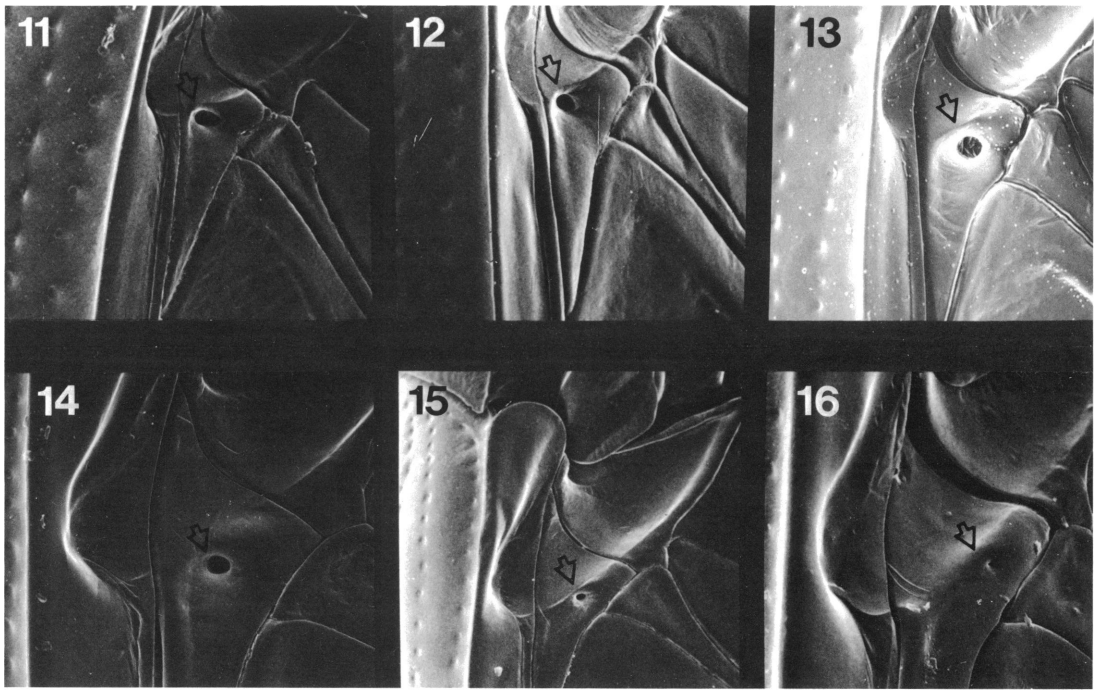
	dichrous	*minutus*	*rockinghamensis*
Scutellar carina	absent	present	present
Distinct elytral microreticulation	absent	present	present
Pronotal transverse line	curved	parallel	parallel
	remote	close	close
Abdominal segments 4–7 color	black	black	orange or yellowish
11th stria/elytral margin	close	close	remote

the Pennsylvania specimen was part of Aubé's original material. Unfortunately, the information Aubé provided with the original description only gives "Des Etats Unis d'Amerique" as type locality information. Because of these uncertainties we have not designated any of the above specimens as the lectotype. We will not designate a neotype until we are more certain that type material is not located at the Paris Museum.

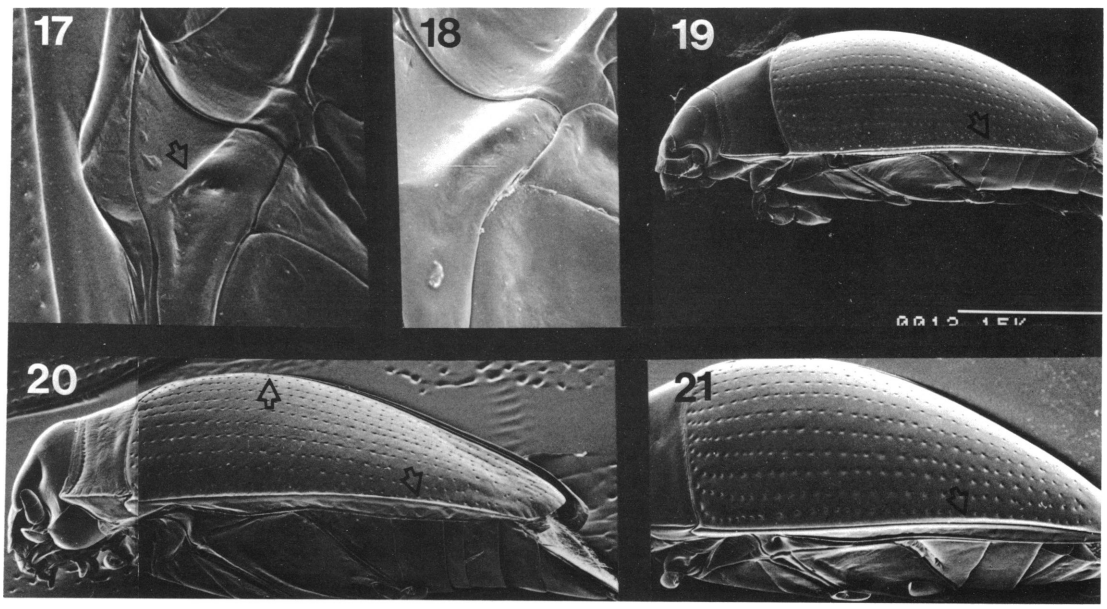
The description of *Gyrinus affinis* (Aubé, 1838) was vague and did not indicate specifically the presence of oblique striae that were considered so characteristic of this species by subsequent taxonomists. Also confusing was Aubé's indication that *G. affinis*



Map 1. Distribution in North America of *G. minutus* (●) and *G. rockinghamensis* (▲) based on species examined.



Figs. 11–16. Metepisternal ostiole of *Gyrinus*: **11,** *G. borealis* (80×); **12,** *G. elevatus* (60×); **13,** *G. marginellus* (80×); **14,** *G. pachysomus* (80×); **15,** *G. analis* (60×); **16,** *G. maculiventris* (80×).



Figs. 17–21. 17, 18. Metepisternal ostiole of *Gyrinus*: **17,** *G. affinis* (80×); **18,** *G. gibber* (100×). 19–21. Elytron of *Gyrinus,* lateral view: **19,** *G. marginellus* (20×); **20,** *G. gibber* (20×); **21,** *G. pachysomus* (20×).

was sexually dimorphic, a fact disputed by ourselves and Fall (1922). Aubé's description of *G. affinis* which stated "the surface is very finely reticulated in the male, smooth in the female" cannot be valid because there is no species of *Gyrinus* where females are not microreticulate and males are. It appears that Aubé's male and female belonged to different species.

Régimbart (1883: 160) redescribed *G. affinis* but he did not mention examining type material. His redescription of *G. affinis* differed substantially from that of Aubé's. Because Régimbart stated, "The elytron is finely but deeply micropunctated in both sexes, underneath completely black with the anal segment strongly metallic, and epipleuron and tarsi brightly red," we feel that *G. affinis* (sensu Régimbart) probably was *G. pleuralis* (sensu Fall, and Oygur and Wolfe).

To further complicate this issue, Régimbart described a new species, *G. canadensis,* which agrees with LeConte's, Fall's, and our concept of *G. affinis.* For example, Régimbart described *G. canadensis* in part as follows: "black underneath with the anal segment, epipleuron and tarsi brightly red. The elytron is covered with stripes closely together, transversely oblique, fine but well impressed." Because of this reference to oblique stripes we agree with Fall (1922) that *G. canadensis* is a junior synonym of *G. affinis.*

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Specimens of *G. affinis* have been collected from streams (Leech, 1938; Fall, 1922), and lakes (Fall, 1922). Robert (1955) and Morrissette (1979) indicated that specimens of *G. affinis* were found in stagnant waters. Label information shows that 58.8 percent of the collections were from lentic habitats (table 2).

DISTRIBUTION. Map. 6. Records are from Maine to the Pacific coast, north to Alaska and south to southern California.

Gyrinus parcus Say

Figures 24, 32, 59, 121, 152; Map 10

Gyrinus parcus Say, 1834: 448. Aubé, 1838: 701, 702. LeConte, 1868: 369, 371. Sharp, 1882: 50, 51. Régimbart, 1883: 178, 179; 1902–03: 8. Ahlwarth, 1910: 23. Leng and Mutchler, 1918: 97, 98. Fall, 1922: 277, 295. Blackwelder, 1944: 81. Ochs, 1949: 254, 263–267. Leech and Chandler, 1956: 421. Ferkinhoff and Gundersen, 1983: 24, 40.
Gyrinus parcus cognatus Ochs, 1949: 266.
Gyrinus parcus californicus Ochs, 1949: 267.
Gyrinus parcus elatus Ochs, 1949: 267.

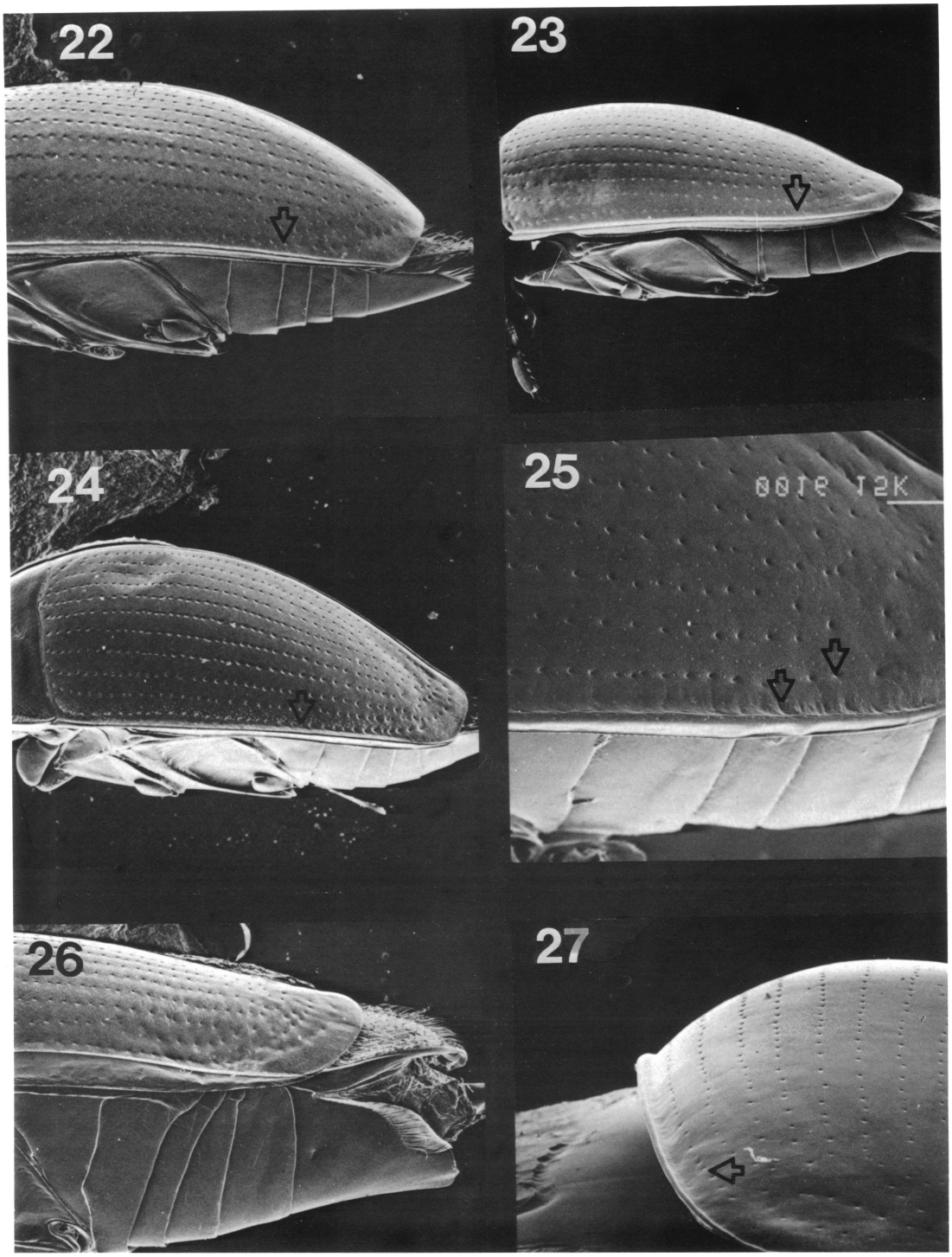
DIAGNOSIS: Specimens of this species are separated from those of other North American species of *Gyrinus* by the position of the 11th stria which is located in the elytral marginal inflection throughout its length (figs. 24, 151). Body measurements: male length 4.3–5.0 mm, width 2.4–2.7 mm; female length 4.7–5.5 mm, width 2.8–2.9 mm.

TYPE INFORMATION AND TAXONOMIC NOTES: Say's collection that included gyrinids is presumed lost. Therefore, a male specimen is designated as neotype. This specimen is deposited at AMNH. It is pointed and labeled as follows: Mexico, Nayarit, 8mi. east of Ixtlan del Rio on Hwy.15 Alt. ca. 400 ft, 7.1.66/ L. Bapista collection. Aedeagus and parameres are attached to the body.

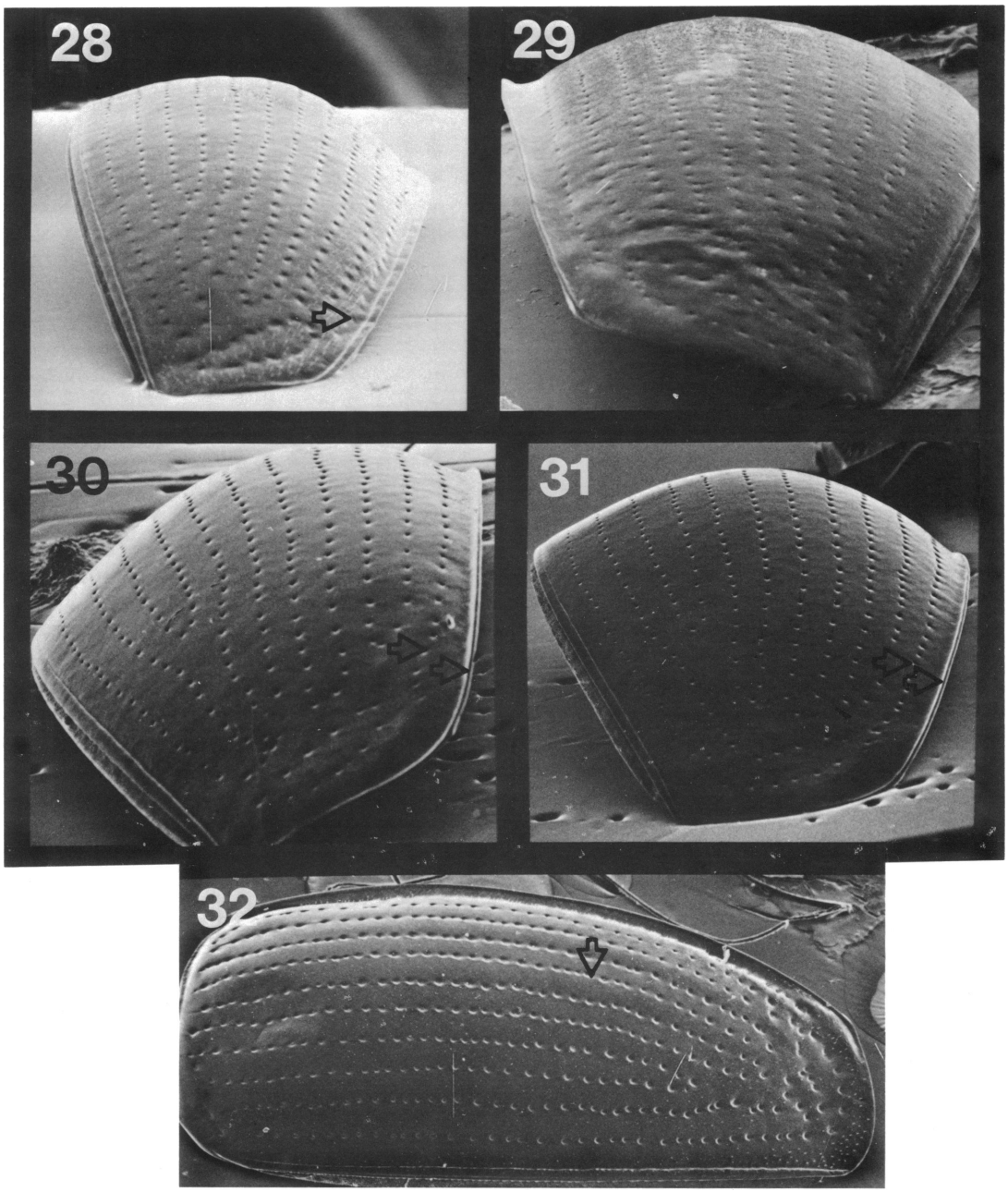
This is one of the most wide ranging and taxonomically complex gyrinid species in the New World. *Gyrinus parcus* s.l. extends from North Dakota to Chile. Aubé (1838) described a southern South American species, *G. chilensis.* Ochs (1949), synonymized that name with *G. parcus,* and described three subspecies and one form of *G. parcus* from southwestern U.S., Mexico, and Central America: *G. parcus agnatus* (Texas), *G. parcus cognatus* (Mexico), *G. parcus californicus* (California), and *G. parcus elatus* (Mexico–Central America). Later, Leech (1956) recorded *G. parcus californicus* from additional localities in southern California.

We examined specimens of *G. parcus* s.l. with a rather acute aedeagus from Arizona that did not fit any of Ochs' subspecies descriptions. Moreover, some individuals from Mexico had an even more acute aedeagus, a slight subapical elevation on the posterolateral side of each elytron, and widened elytral margins posteriorly. Based on specimens we have been able to examine, the subspecies described by Ochs do not seem valid; however, a final conclusion about this species complex will require examination of more specimens from Mexico and Central and South America than currently are available.

SEXUAL DIMORPHISM OF ELYTRAL MI-



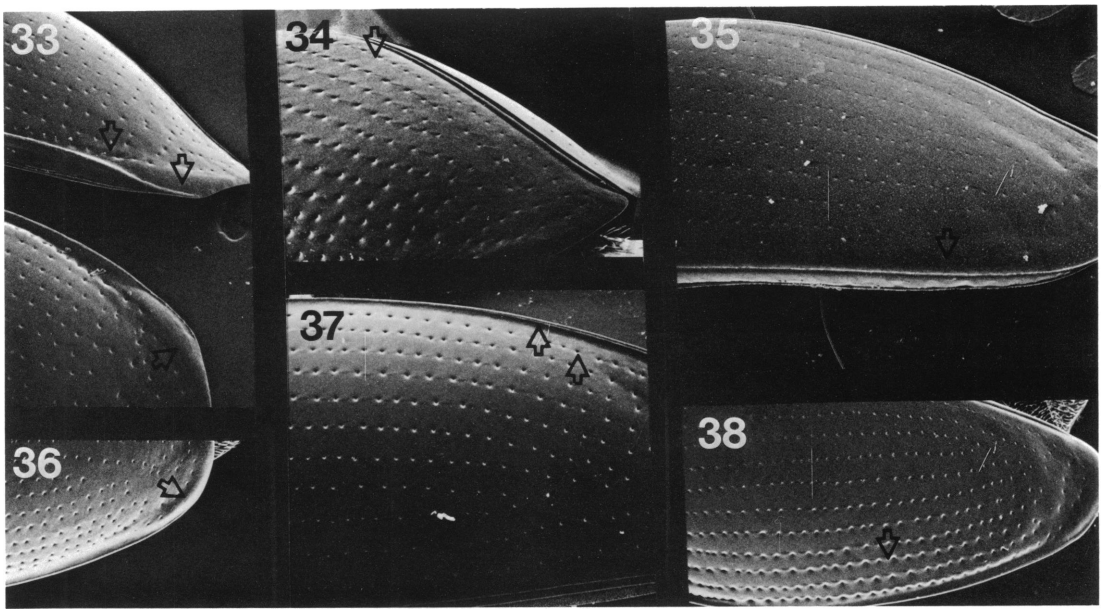
Figs. 22–27. Elytron of *Gyrinus,* lateral view: **22,** *G. rockinghamensis* (30×); **23,** *G. latilimbus* (20×); **24,** *G. parcus* (20×); **25,** *G. rugosus* (60×); **26,** *G. impressicollis* (30×); **27,** *G. bifarius* (30×).



Figs. 28–32. Elytron of *Gyrinus,* posterior view: **28,** *G. minutus* (40×); **29,** *G. impressicollis* (30×); **30,** *G. aeneolus* (40×); **31,** *G. woodruffi* (40×); **32,** *G. parcus* (30×).

CROSCULPTURE: Distinctly sexually dimorphic. Microreticulation in females is distinctly and uniformly scalelike. In males, microreticulation at most is evident only posteriorly as transverse lines. Additionally, all elytral striae (1–11) are distinctly impressed in females while only striae 6–11 are noticeably impressed in males.

HABITAT INFORMATION: Label information indicates that 85.7 percent of the collections



Figs. 33–38. Elytron of *Gyrinus,* dorsal view: **33,** *G. plicifer* (30×); **34,** *G. elevatus* (40×); **35,** *G. bifarius* (30×); **36,** *G. plicifer* (30×); **37,** *G. woodruffi* (40×); **38,** *G. pachysomus* (20×).

of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 10. Records are from North Dakota to Texas, and one from Florida.

Gyrinus impressicollis Kirby

Figures 1, 26, 29, 64, 65, 143, 144; Map 13

Gyrinus impressicollis Kirby, 1837: 79. Régimbart, 1883: 174, 175. Ahlwarth, 1910: 19. Fall, 1922: 278, 304. Robert, 1963: 12, 23, 33. Ferkinhoff and Gundersen, 1983: 23, 38, 39.

DIAGNOSIS: Specimens of this species are separated from those of all other North American species by the following combination of characters: (1) body exceptionally long, body measurements: male length 7.0–7.8 mm, width 3.9–4.5 mm; female length 6.5–7.3 mm, width 3.8–4.3 mm, (2) tarsal claws blackish, (3) protarsal claws shorter than fifth tarsomere (fig. 2), (4) aedeagus in figures 143, 144.

This species is unique and easily recognized by its extremely large size and bizarre genitalic structure.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype of *G. impressicollis* from the BMNH was examined. It is a male with genitalia entirely exposed. The specimen is glued on a white card and carries the following labels. Type [orange-circular label]/ Canada [handwritten]/ G. impressicollis Kirby.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Distinctly sexually dimorphic. Females have a uniform and very distinct polygonal reticulation, without noticeable micropunctation. In males, microreticulation is moderately distinct in the form of moderately transverse sculpticells. Micropunctation is dense.

HABITAT INFORMATION: Fall (1922) recorded specimens of this species from lotic (river) habitats. Morrissette (1979) indicated that *G. impressicollis* prefers fluvial lakes. Habitat information from labels indicates that 83.3 percent of collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 13. Records are from Michigan, Wisconsin, Quebec, Ontario, and Manitoba.

Gyrinus wallisi Fall

Figures 68, 69, 72, 99, 100; Map 13

Gyrinus wallisi Fall, 1922: 278, 302. Hatch, 1953: 242. Gordon and Post, 1965: 28, 29. Ferkinhoff and Gundersen, 1983: 26, 44.

DIAGNOSIS: Specimens of this species are separated from those of all other North American species by the following combination of characters: (1) tarsal claws blackish, (2) abdominal segments 4–7 uniformly black, (3) elytron with dense micropunctation (fig. 72), (4) aedeagus in figures 99, 100, (5) body measurements: male length 5.2–6.0 mm, width 2.8–3.4 mm; female length 5.6–6.5 mm, width 3.0–3.6 mm.

Based on nongenitalic characters, specimens of *G. wallisi* cannot be separated from their closely related Palearctic species, *G. marinus* and *G. aeratus* (see discussion under *G. marinus* and *G. aeratus*).

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is glued on a card, and carries the following labels: Piquitenay River, Manitoba. 7.27.17/ Type wallisi [handwritten]/ MCZ type 23989 [red label]/. Aedeagus and parameres are attached next to the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Label information shows that 66.7 percent of the collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 13. Records are from Alaska, across Canada and northern USA as far east as Quebec.

Gyrinus marinus Gyllenhal
Figure 101; Map 13

Gyrinus marinus Gyllenhal, 1808: 143. Sharp, 1914: 137. Régimbart, 1883: 172, 173. Ahlwarth, 1910: 19. Leng, 1920: 82. Ochs, 1930: 137. Omer-Cooper, 1930: 66, 68, 69. Balfour-Browne, 1938: 76, 84–86; 1950: 337, 338, 341, 358–365. Zaitsev, 1953: 365, 373, 381. Huldén, 1983b: 81; 1984: 189.
Gyrinus dorsalis Gyllenhal, 1808: 143.
Gyrinus aeneus Stephens, 1828: 95.

DIAGNOSIS: This species is separated from those of all other North American species by the following combination of characters: (1) tarsal claws blackish, (2) abdominal segments 4–7 black, (3) elytron with dense micropunctation, (4) aedeagus in figure 101, (5) body measurements: male length 6.0–6.5 mm, width 3.0–3.1 mm; female length 6.5 mm, width 3.5 mm.

Adult *Gyrinus marinus, G. aeratus,* and *G. wallisi* are very similar to each other. All three species are characterized by blackish tarsal claws, black abdominal segments, and dense micropunctation. Examination of the male genitalia is the only reliable way to recognize these three species; the aedeagus is dorsally more slender and tapering to a point in *G. marinus* (fig. 101), narrowly rounded in *G. wallisi* (figs. 99, 100), and narrowly truncate in *G. aeratus* (figs. 102, 103).

Palearctic populations of both *G. marinus* and *G. aeratus* are extremely variable, especially in elytral microsculpture (Sharp, 1914; Omer-Cooper, 1930; Zaitsev, 1953; Balfour-Browne, 1950). We also found that microreticulation of members of these species was extremely variable in North America. The elytron of most individuals has a shiny grayish sheen. However, the lateral sides of some specimens have a distinctly duller appearance because of dense microreticulation.

Color variation is most evident on the epipleuron, hypomeron, and the mesosternal segments: these vary from dark brown to yellowish. Gyllenhal (1808) described a remarkable color variant, *G. dorsalis,* which had a brown or reddish elytral surface. This brown dorsal coloration was also detected in some of the populations of *G. marinus* by Zaitsev (1953), in Russia. We have not seen *G. marinus* with such dorsal coloration in North America.

TYPE INFORMATION AND TAXONOMIC NOTES: The type is deposited in Zoological Museum in Uppsala; it was not examined. Gyllenhal described *G. marinus* in 1808. Subsequently Stephens (1828) described *G. aeneus.* Sharp (1914) synonymized *G. aeneus* under the name *G. marinus* Gyllenhal. He also recognized that *G. opacus* sensu Suffrian was actually *G. marinus* Gyllenhal (see discussion under *G. aeratus* Stephens).

Régimbart listed *G. marinus* from the United States (1883, 1902–03); however, these records were thought to be a mistake by Balfour-Browne (1950) and Brinck (1960). Our study verifies presence of *G. marinus* in northwestern North America.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Females usually have denser micropunctation and more uniform micro-

reticulation; however, these characteristics are variable (as discussed above) and sexual dimorphism sometimes is not very distinctly evident.

HABITAT INFORMATION: Habitat information is not available from North America. Balfour-Browne (1950) collected this species from peaty, brackish waters, and edges of lakes and rivers in England. In Russia, Zaitsev (1953) recorded *G. marinus* from stagnant, cool back waters of rivers. Holmen (1987) also found specimens of *G. marinus* in stagnant water and occasionally in the headwaters of streams.

DISTRIBUTION: Map 13. Records are from the Yukon Territories and Alaska.

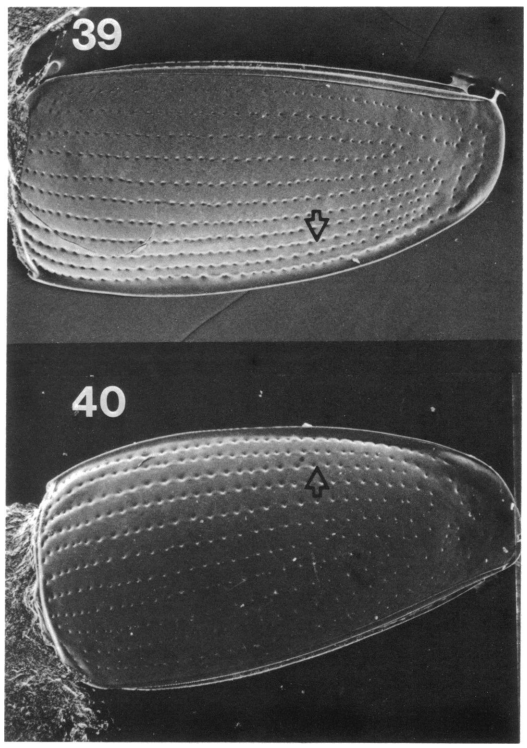
Gyrinus aeratus Stephens
Figures 102, 103; Map 13

Gyrinus aeratus Stephens, 1835: 395. Thomson, 1860: 116. Omer-Cooper, 1930: 66, 69. Guignot, 1933: 751. Brinck, 1938: 22. Balfour-Browne, 1950: 337, 341, 360–365. Zaitsev, 1953: 365, 373, 381. Huldén, 1983b: 81; 1984: 189.
Gyrinus aeneus Thomson, 1860: 116.
Gyrinus thomsoni Zaitsev, 1907: 122.
Gyrinus edwardsi Sharp, 1914: 131, 137.
Gyrinus instabilis Fall, 1931: 155, 156. NEW SYNONYMY.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) tarsal claws blackish, (2) abdominal segments 4–7 black, (3) elytron with dense micropunctation, (4) aedeagus in figures 102, 103, (5) body measurements: male length 4.7–5.4 mm, width 2.5–3.0 mm; female length 5.8–6.2 mm, width 3.0–3.3 mm.

Gyrinus aeratus is widely distributed (from England to Siberia) in the Palearctic Region; within the Nearctic Region it is found in Alaska and northwestern Canada. We compared several representatives of *G. aeratus* from the Palearctic Region with Nearctic specimens and found no differences substantial enough to suggest separate species status.

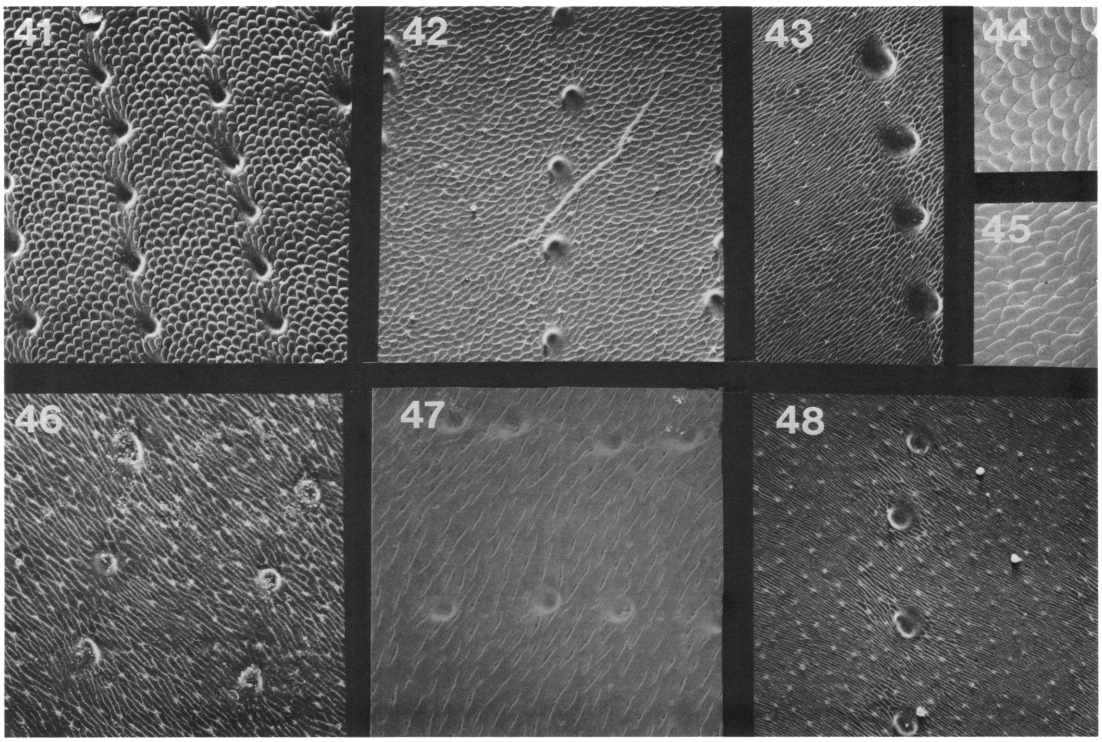
G. aeratus is very similar to *G. marinus* and *G. wallisi* in external structure. The only reliable character to distinguish *G. aeratus* and *G. marinus* is the shape of male genitalia (see comments under *G. marinus*). The variation in microreticulation and ventral coloration makes the females of *G. aeratus* extremely difficult to separate from females of *G. marinus* and *G. wallisi*. However, *G. aeratus* is generally smaller and narrower than *G. marinus* and *G. wallisi*. Also, the abdominal segments and metasternum usually are darker than those of *G. marinus*.



Figs. 39, 40. Elyton of *Gyrinus*, dorsal view (20×): **39**, *G. pachysomus*; **40**, *G. borealis*.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype of *G. aeratus* is deposited at BMNH. This male specimen is pinned on a white card and carries the following labels: Holotype [red, circular label]/ Gyrinus aeratus Step. Type [handwritten], J. Balfour-Browne Det. [handwritten].

Stephens (1835) described *G. aeratus*. Zaitsev (1907) named a species as *G. thomsoni*. Brinck (1938) discovered that *G. thomsoni* Zaitsev was a junior synonym of *G. aeratus* Stephens. Furthermore, *G. aeratus* consistently was misidentified by European taxonomists as *G. opacus* due to Suffrian's (1855 *in* Sharp, 1914; Brinck, 1938; Balfour-Browne, 1950) misinterpretation of *G. opacus* Sahlberg. This confusion was noticed by



Figs. 41–48. Elytral microsculpture of *Gyrinus*: **41,** *G. rockinghamensis* (200×); **42,** *G. opacus* (200×); **43,** *G. borealis* (200×); **44,** *G. rockinghamensis* (400×); **45,** *G. opacus* (400×); **46,** *G. gibber* (200×); **47,** *G. affinis* (200×); **48,** *G. gehringi* (200×).

Sharp (1914); however, he did not realize that *G. opacus* sensu Suffrian was *G. aeratus* Stephens and therefore described it as new species, *G. edwardsi*. Brinck (1938) synonymized *G. edwardsi* Sharp with *G. aeratus*.

Occurrence of this species in North America actually was indicated by Guignot (1933, 1947) and Zaitsev (1907); however, Balfour-Browne (1950) and Brinck (1960) believed that Guignot and Zaitsev must have confused *G. aeratus* with *G. opacus* Sahlberg. Fall (1931) described *G. instabilis* from Circle, Alaska. We examined the types of *G. instabilis* Fall and consider that name a junior synonym of *G. aeratus*.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Females are usually more distinctly and finely microreticulate and densely punctate. However, sexual dimorphism is variably evident because of the variation in microreticulation and micropunctation in both sexes.

HABITAT INFORMATION: Robert (1955) and Morrissette (1979) indicated that specimens of *G. aeratus* were found on the surface, and often at the borders, of relatively deep lakes with thick sediment beds. Holmen (1987) collected specimens of *G. aeratus* in oligotrophic lakes and at the edge of a large stream in Fennoscandia and Denmark. Although label information is scarce, 66.7 percent of the collections of specimens were from lentic habitats (table 2).

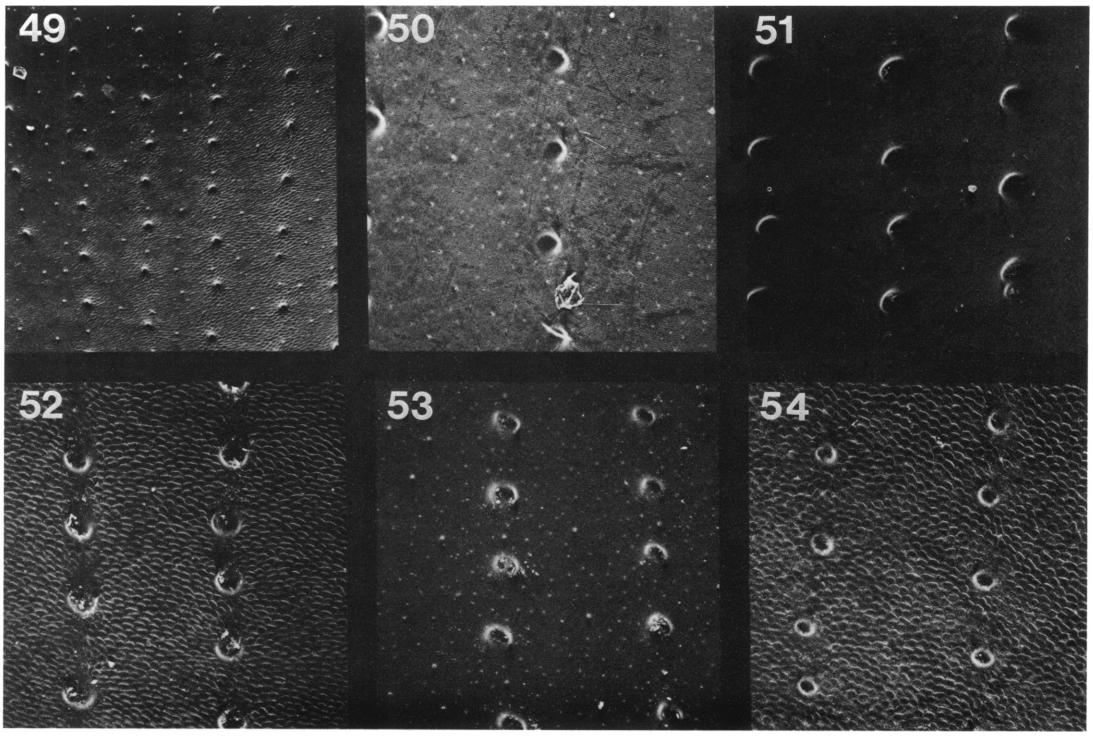
DISTRIBUTION: Map 13. Records are from Ontario to Alaska and south to New York.

Gyrinus obtusus Say

Figure 93; Map 11

Gyrinus obtusus Say, 1834: 447. Régimbart, 1883: 171. Ahlwarth, 1910: 23. Ochs, 1929: 103; 1949: 259, 260. Blackwelder, 1944: 81.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) aedeagus constricted in apical third (fig. 93), (2)



Figs. 49–54. Elytral microsculpture of *Gyrinus*: **49,** *G. rugosus* (100×); **50,** *G. lecontei* (200×); **51,** *G. maculiventris* (200×); **52,** female *G. latilimbus* (200×); **53,** male *G. latilimbus* (200×); **54,** female *G. analis* (200×).

ventral surfaces uniformly reddish or orange, sometimes darker medially, (3) elytron bronze, (4) 11th stria remote from outer margin of elytron in apical third, (5) body measurements: male length 4.8–5.7 mm, width 2.8–3.2 mm; female length 5.5–6.3 mm, width 3.2–3.6 mm.

G. obtusus and *G. bifarius* are the only North American gyrinids which have a distinctly constricted aedeagus apically. However, the shape of the constricted portion differs; it is longer and less constricted at its base in males of *G. obtusus*. In addition, males of *G. bifarius* have denser elytral micropunctation and more uniformly evident elytral microreticulation. In the males of *G. obtusus*, the elytron is shiny with microreticulation only evident in the apical portion of the elytron. In the females, scalelike elytral microreticulation is distinctly evident dorsomedially. Finally, the body form is different, being more distinctly convex in *G. obtusus*.

TYPE INFORMATION AND TAXONOMIC NOTES: Say's collection, which included the gyrinids, is presumed lost. Therefore we designated a male specimen as neotype. This specimen is deposited at AMNH. It is pinned and labeled as follows: 14 mi N. Durango Mex., VII.9.52, J.D. Lattin Collector.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Distinctly sexually dimorphic. Females have a distinctly evident scalelike microreticulation which is not noticeable on lateral and distal parts of the elytron, and between first and second elytral striae. Males have an overall shinier dorsal surface with moderately transverse microreticulation only noticeable posteriorly.

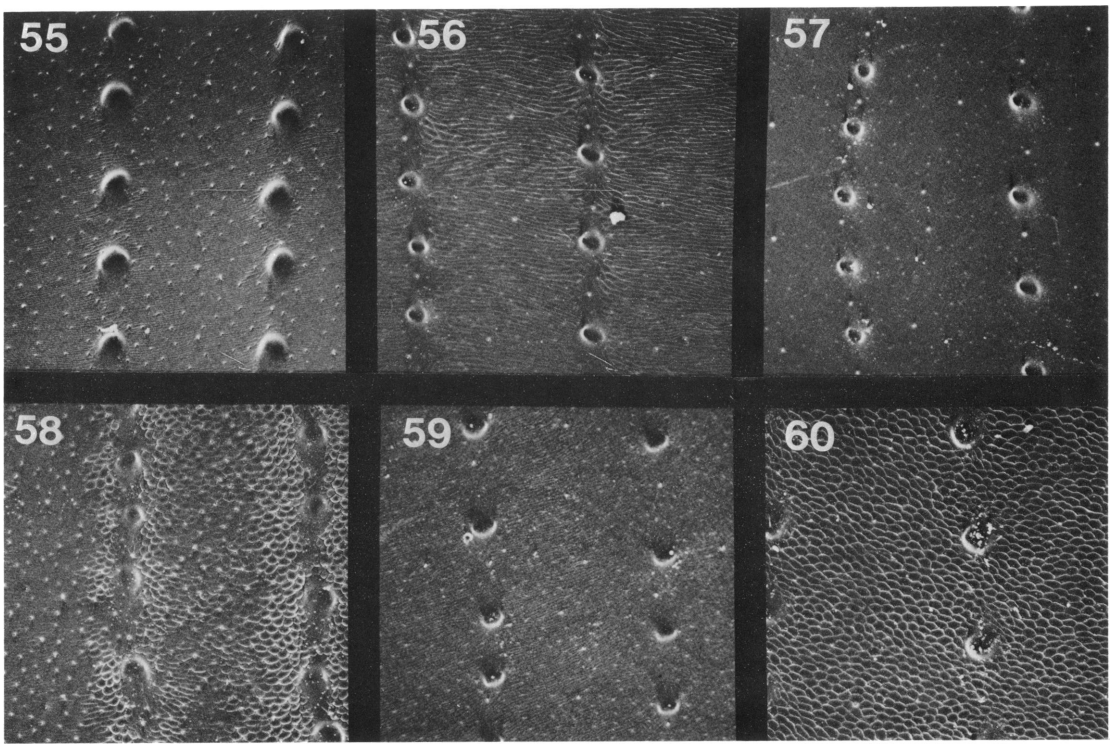
HABITAT INFORMATION: Not available.

DISTRIBUTION: Map 11. All previous records of this species are from Mexico (Ochs, 1949). In the USA we only recorded specimens of this species from New Mexico.

Gyrinus bifarius Fall

Figures 27, 35, 73, 88, 89; Map 11

Gyrinus bifarius Fall, 1922: 276, 286, 287. Criddle, 1929: 115, 116. Ochs, 1930: 137. Hatch,



Figs. 55–60. Elytral microreticulation of *Gyrinus,* sexual dimorphism (200×): **55,** male *G. analis*; **56,** female *G. woodruffi*; **57,** male *G. woodruffi*; **58,** female *G. parcus*; **59,** male *G. parcus*; **60,** female *G. sayi.*

1953: 240. Robert 1963: 12, 20, 32. Ferkinhoff and Gundersen, 1983: 22, 23.

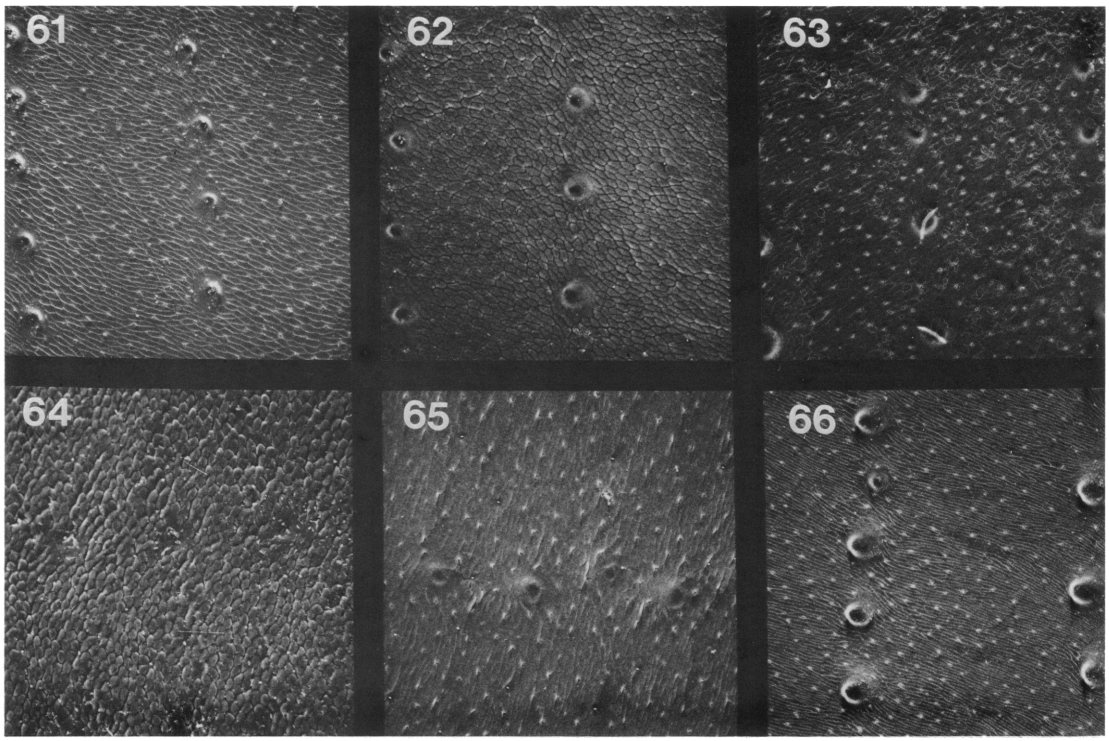
Gyrinus punctellus Ochs, 1949: 258, 259. NEW SYNONYMY.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron with dense micropunctation and microreticulation, (2) ventral surfaces uniformly yellowish or orange, sometimes darker medially, (3) 11th stria remote from outer margin of elytron in apical third (fig. 35), (4) aedeagus in figures 88, 89, (5) body measurements: male length 4.2–5.8 mm, width 2.3–3.0 mm; female length 5.9–6.5 mm, width 2.9–3.6 mm.

Gyrinus bifarius is confused most easily with *G. confinis.* Although *G. confinis* is usually larger, examination of aedeagal structure is necessary for a confident identification.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is mounted on a point and carries the following labels: Paris Me 8.29.17/ type bifarius [handwritten]/MCZ Type 23980 [red label]/. Aedeagus and parameres are glued on a small card beneath the specimen.

Specimens of *G. bifarius* from across North America revealed considerable degrees of gradual variation in elytral microreticulation, elytral micropunctation, and aedeagal size. Specimens from eastern North America generally possess less distinct microreticulation and micropunctation than do those from western North America; however, both characteristics occasionally vary within a locality, especially in southwestern North America. Aedeagal size varied randomly throughout the range of *G. bifarius.* Ochs (1949) described western populations as a new species, *G. punctellus.* We have been unable to obtain the holotype of *G. punctellus*; however, we were able to examine a paratype (FS). We are convinced, based on the amount of variation in *G. bifarius,* that *G. punctellus* is a junior synonym of *G. bifarius.*



Figs. 61–66. Elytral microreticulation of *Gyrinus,* sexual dimorphism (200×): **61,** male *G. sayi*; **62,** female *G. dubius*; **63,** male *G. dubius*; **64,** female *G. impressicollis*; **65,** male *G. impressicollis*; **66,** female *G. lecontei.*

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Moderately sexually dimorphic. In females, microreticulation is moderately distinct as transverse sculpticells. Reticulation in males is also transverse but less distinctly impressed.

HABITAT INFORMATION: Robert (1955) indicated that *G. bifarius* commonly is found in lakes which empty their water into larger lakes. Morrissette (1979) collected specimens from different lakes and rivers. Label information indicates that 74.3 percent of the collections of this specimen were from lotic habitats (table 2).

DISTRIBUTION: Map 11. Records are from Maine to California, north to the Northwest Territories and south to southern Arizona.

Gyrinus plicifer LeConte

Figures 33, 36, 80–82; Map 10

Gyrinus plicifer LeConte, 1852: 209; 1868: 368–371. Régimbart, 1883: 153, 156; 1902-03: 7. Fall, 1901: 13, 55; 1922: 276, 278, 288. Ahlwarth, 1910: 24. Criddle, 1929: 115. Blackwelder, 1944: 81. Leech, 1948: 420, 421. Ochs, 1949: 253. Hatch, 1953: 240.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron with distinct subapical convexity (fig. 33), (2) very shiny without noticeable microreticulation and micropunctation, (3) body convex, (4) metepisternal ostiole large (as in fig. 11), (5) abdominal segments 4–7 uniformly reddish, (6) aedeagus in figures 80–82, (7) body measurements: male length 6.5–5.6 mm, width 2.3–2.5 mm; female length 5.0–6.3 mm, width 2.7–3.4 mm.

TYPE INFORMATION AND TAXONOMIC NOTES: The type series consists of five specimens and is in the LeConte collection at MCZ. One female carries a label (S.D.). That specimen was uniquely indicated by Fall and that indication constituted a lectotype des-

TABLE 5
Diagnostic Character States for Specimens of *Gyrinus aeneolus, G. woodruffi, G. marginellus, G. elevatus, G. latilimbus*

	aeneolus	*woodruffi*	*marginellus*	*elevatus*	*latilimbus*
Pronotal transverse	parallel	parallel	parallel	curved	curved
Metepisternal ostiole	medium	large	large	large	medium
11th stria/elytral margin	remote	remote	remote	close	close
Elytral margin	narrow	narrow	narrow	narrow	wider
Elytral inflection	angled	not angled	angled	not angled	angled
Convexity	not convex	not convex	convex	convex	not convex
Elytral color laterally	bronze	black	bronze	black	black
Sexual dimorphism	♀ shiny	♀ dull	♀ shiny	♀ shiny	♀ dull

ignation. It is glued on a point and carries the following labels: tan circular tag./ Type 6106/ plicifer [handwritten] S.D.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Fall collected this species from the small streams in the mountains and foothills of southern California (1901). Label information indicates that 79.7 percent of collections of specimens are from lotic habitats (table 2).

DISTRIBUTION: Map 10. Records are from British Columbia south to Texas, and east to Oklahoma.

Gyrinus elevatus LeConte
Figures 12, 34, 83, 84; Map 9

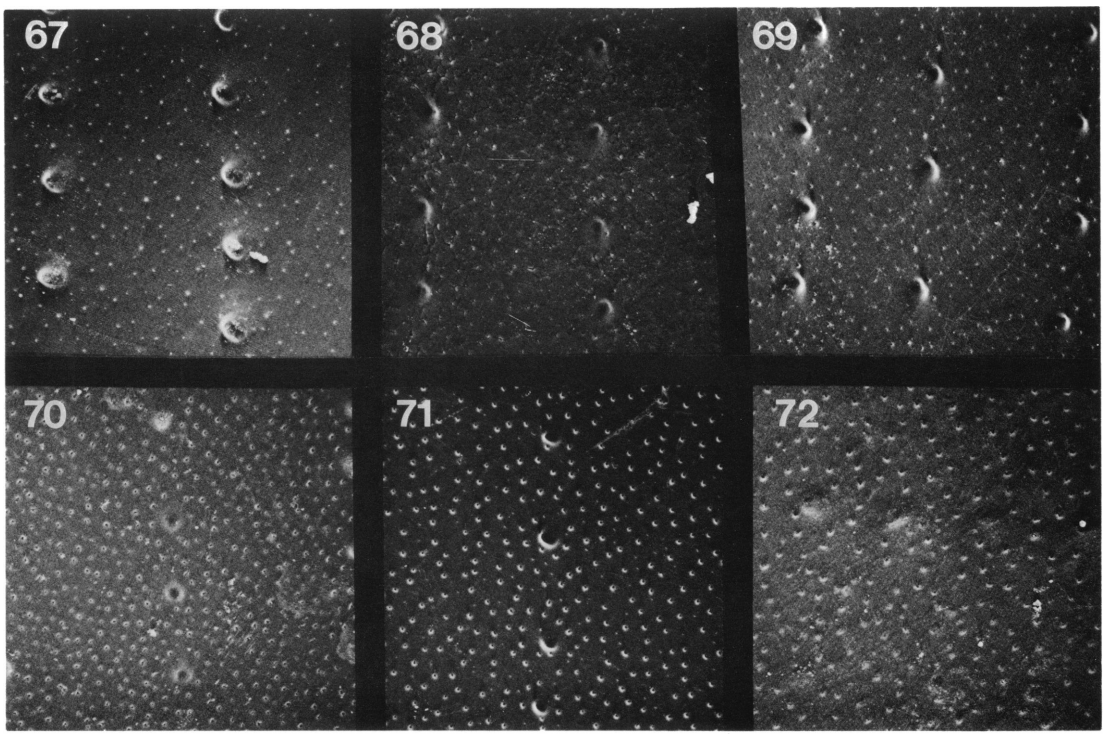
Gyrinus elevatus LeConte, 1868: 368, 370, 371. Régimbart, 1883: 150, 151; 1902–03: 7. Leng, 1920: 82. Ahlwarth, 1910: 18. Blatchley, 1910: 238, 239; 1919: 316. Fall, 1922: 276, 288, 289. Ochs, 1930: 136. Young, 1954: 152, 154. Folkerts, 1978: 347. Spangler, 1981: 147. Sanderson, 1982: 10: 36.
Gyrinus cubensis Régimbart, 1883: 151.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) metepisternal ostiole large (fig. 12), (2) elytron shiny without noticeable microreticulation and micropunctation, (3) pronotal transverse impressed line curved and distant from anterior pronotal margin (as in figs. 7, 9), (4) ventral surfaces reddish or light reddish brown, (5) aedeagus in figures 83, 84, (6) body length short and convex, body measurements: male length 4.7–5.0 mm, width 2.3–2.5 mm; female length 4.8–5.3 mm, width 2.4–2.6 mm.

Adult specimens of *G. elevatus, G. marginellus, G. aeneolus, G. woodruffi,* and *G. latilimbus* are similar. Although genitalic examination is not absolutely required for separation, confusion is possible because of their small size and lightly colored ventral surfaces. The most reliable nongenitalic characters are shown comparatively in table 5.

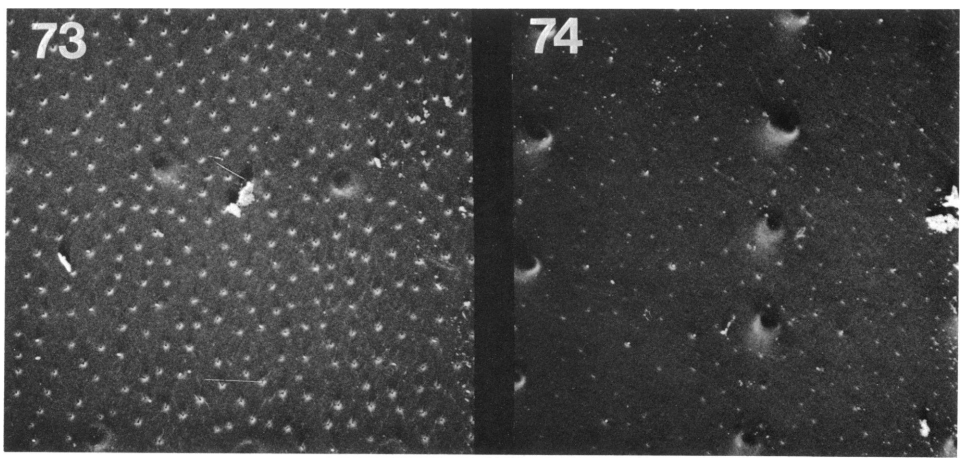
TYPE INFORMATION AND TAXONOMIC NOTES: LeConte (1868) indicated that his description was based on one specimen from New York numbered "1829"; therefore, that specimen can be regarded as the holotype. A specimen with that label and matching LeConte's description was examined from the LeConte collection at MCZ. It is pointed and carries the following labels: 1829 N.Y. [handwritten]/ ventralis Kirby [handwritten]/ Type 6099 [red label]/ G. elevatus Lec. [handwritten]. The aedeagus and parameres are glued next to the specimen. There is a second specimen placed with LeConte's type; apparently this second specimen (which is *G. ventralis*) subsequently was added to LeConte's series. The label on the type specimen indicates that it was collected from New York. However, all other examined locality information indicates that *G. elevatus* does not occur north of Georgia. Therefore, the type locality information probably is incorrect as previously noted by Ochs (1930), Fall (1922), and Spangler (1981).

Considerable confusion exists concerning the taxonomic status of *G. limbatus* and *G. elevatus.* Say described *G. limbatus* from Florida and Georgia (1825). His description is brief and vague. *Gyrinus limbatus* Say was placed as a synonym of *G. aquiris* by Aubé (1838) and Régimbart (1883), and as a syn-

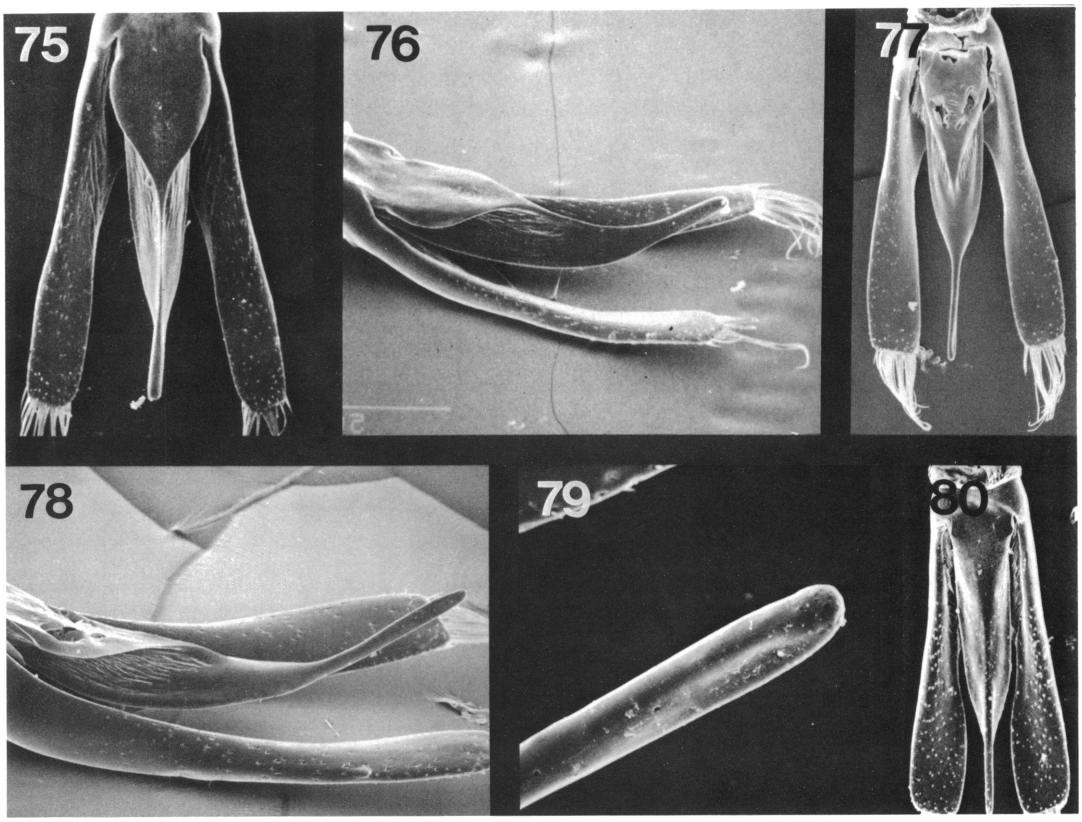


Figs. 67–72. Elytral microreticulation of *Gyrinus,* sexual dimorphism (200×): **67,** male *G. lecontei*; **68,** female *G. wallisi*; **69,** male *G. wallisi*; **70,** female *G. pectoralis*; **71,** male *G. pleuralis*; **72,** male *G. aeratus.*

onym of *G. ventralis* by Leng (1920). Régimbart's redescription for *G. limbatus* fits *G. elevatus.* Ahlwarth (1910), Fall (1922), Ochs (1930), and Young (1954) also believed that *G. limbatus* was a synonym of *G. elevatus* LeConte. Since there is not enough information in the description to allow designation of a neotype and/or to synonymize this species with *G. elevatus,* we regard *G. limbatus* as a nomen inquirendum.



Figs. 73, 74. Elytral microreticulation of *Gyrinus,* sexual dimorphism (200×): **73,** male *G. bifarius*; **74,** male *G. ventralis.*



Figs. 75–80. Male genitalia of *Gyrinus*: **75,** dorsal view, *G. pugionis* (60×); **76,** lateral view, *G. pugionis* (60×); **77,** dorsal view, *G. borealis* (60×); **78,** lateral view, *G. borealis* (80×); **79,** apical view, *G. borealis* (400×); **80,** dorsal view, *G. plicifer* (50×).

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Young (1954) stated that this was a primarily lentic species that was found occasionally in sandy-bottomed streams. Label information indicates that 68.8 percent of collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 9. Records are from Florida north to Georgia and west to eastern Texas.

Gyrinus borealis Aubé

Figures 11, 40, 43, 77–79; Map 3

Gyrinus borealis Aubé, 1838: 692, 693. LeConte, 1868: 369, 372. Régimbart, 1883: 176; 1902–03: 8. Ahlwarth, 1910: 16. Blatchley, 1910: 238, 240, Leng 1920: 82. Fall, 1922: 277, 295, 296. Ochs, 1930: 137. Sanderson, 1982: 10: 36. Ferkinhoff and Gundersen 1983: 24, 42.
Gyrinus corpulentus Régimbart 1883: 178.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) punctures of elytral striae 8–11 more impressed and larger than punctures of striae 1–7 (fig. 40), (2) metepisternal ostiole large (fig. 11), (3) elytron with uniformly evident microreticulation (fig. 43), (4) abdominal segments 4–7 uniformly black, (5) aedeagus in figures 77–79, (6) body long and broad, body measurements: male length 5.5–6.1 mm, width 3.1–3.4 mm; female length 5.9–6.2 mm, width 3.2–3.6 mm.

G. borealis is confused most easily with *G. pugionis*. Even the aedeagi are similar with the basal region of the aedeagus of each species so broadened that the lateral edges extend out as a shelf. However, specimens of the former usually are separated by the uniformly black abdominal segments 4–7 (i.e., reddish areas absent on the sides of abdom-

inal segments 4–7), and more impressed punctures of 8th, 9th, 10th, and 11th elytral striae.

TYPE INFORMATION AND TAXONOMIC NOTES: We have been unable to locate types of *G. borealis* at IRSB. However, type material may be at the Paris Museum.

Fall (1922) examined a "type" of *G. corpulentus* Régimbart and considered it to be "exactly the *G. borealis* of LeConte." We examined a single cotype of *G. corpulentus* which was sent from BMNH. The specimen was a female with the 8th, 9th, 10th, and 11th elytral striae distinctly impressed, large body, and dark brown abdominal surface. These characteristics closely match our concept of *G. borealis* Aubé and we agree with Fall's synonymy.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Label information indicates that 55.6 percent of collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 3. Records are from Maine west to Indiana and south to Virginia.

Gyrinus pugionis Fall
Figures 75, 76, 156; Map 3

Gyrinus pugionis Fall, 1922: 277, 296, 297. Robert, 1963: 12, 28, 36. Ferkinhoff and Gundersen, 1983: 24, 41.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) abdominal segments 4–7 medially black with sides narrowly reddish (fig. 156), (2) metepisternal ostiole large (as in fig. 11), (3) elytron with uniformly evident microreticulation (as in fig. 43), (4) aedeagus in figures 75, 76, (5) body long and broad, body measurements: male length 5.6–6.2 mm, width 3.1–3.3 mm; female length 6.4–6.8 mm, width 3.5–3.8 mm.

G. pugionis is very similar to *G. borealis* (see discussion under *G. borealis*).

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is pinned and carries the following labels: Saugus. Mass/ Essex Co./ type pugionis [handwritten]/ MCZ Type 23988 [red label]/. Aedeagus and parameres are attached to the body.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Robert (1955) and Morrissette (1979) both found *G. pugionis* in peaty or semi-peaty lakes. Robert specifically mentioned that this species invades narrow streams leaving these lakes. Label data indicate 87.5 percent of the collected specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 3. Records are from Maine to Minnesota, south to southern Michigan.

Gyrinus marginellus Fall
Figures 13, 19, 137, 138; Map 10

Gyrinus marginellus Fall, 1922: 276, 283, 284. Criddle, 1929: 115. Folkerts, 1978: 347. Sanderson, 1982: 10: 36. Robert, 1963: 10, 26, 35. Ferkinhoff and Gundersen, 1983: 21, 30.

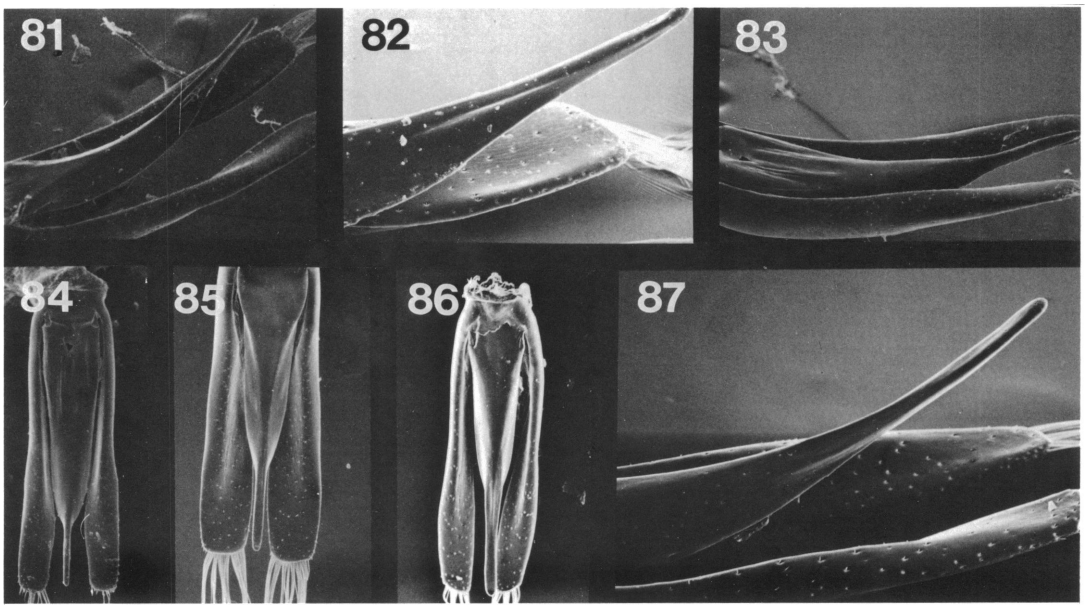
DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) 11th stria remote from outer margin of elytron in apical third (fig. 19), (2) elytron shiny without evident microreticulation and micropunctation, (3) metepisternal ostiole very large (fig. 13), (4) ventral surfaces reddish or reddish brown, (5) aedeagus in figures 137, 138, (6) body short, narrow, and convex; body measurements: male length 3.9–4.5 mm, width 2.1–2.2 mm; female length 4.2–4.4 mm, width 2.1–2.3 mm.

G. marginellus is easily confused with the following small-size species: *G. woodruffi, G. aeneolus, G. elevatus.* Table 5 provides nongenitalic characters to separate these species.

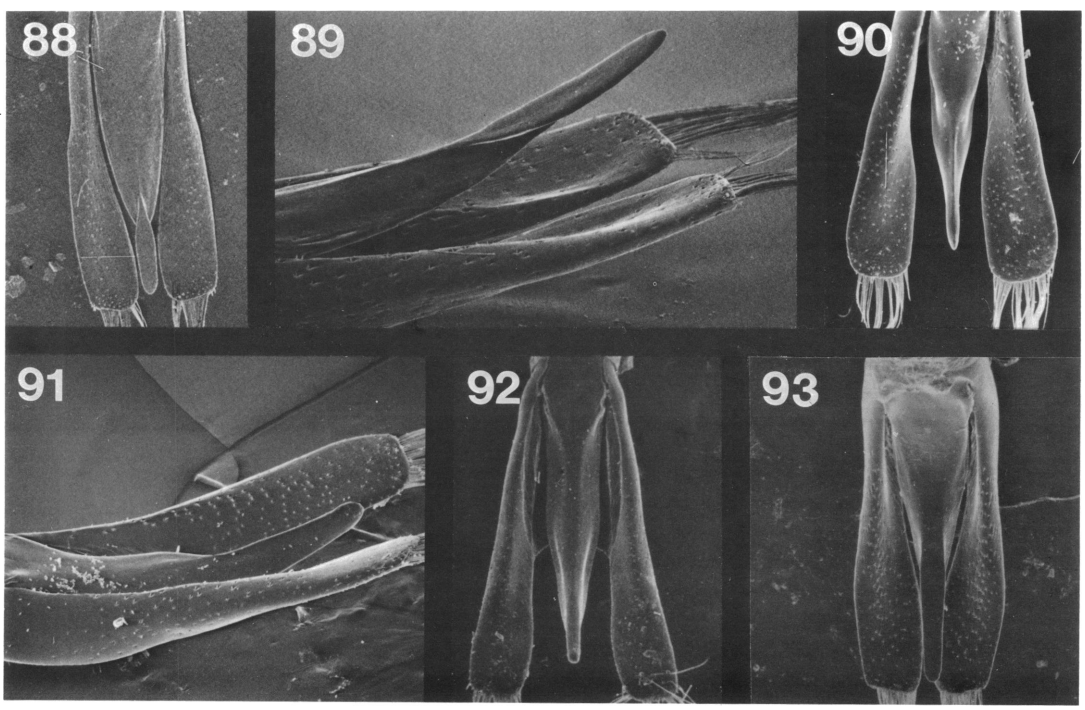
TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is mounted on a point and carries the following labels: 1908 Lakehurst NJ 4.26/ Wm T. Davis collection/ type marginellus [handwritten]/ MCZ Type 23985 [red label]/ G. aquiris Lec. [handwritten]/. Aedeagus and parameres are attached to the body.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

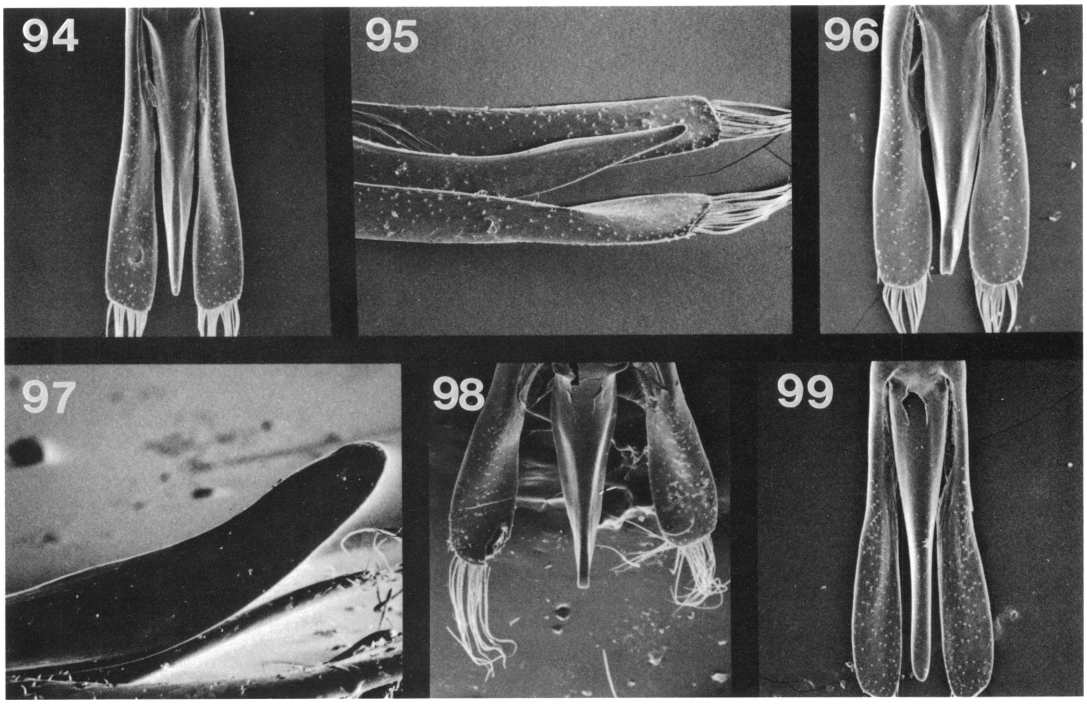
HABITAT INFORMATION: Morrissette (1979) found specimens of *G. marginellus* in clear rivers with gravel or clay bottoms. In New Jersey, we commonly found *G. marginellus* at the margins of streams with moderate cur-



Figs. 81–87. Male genitalia of *Gyrinus*: **81,** lateral view, *G. plicifer* (60×); **82,** lateral view, tip *G. plicifer* (150×); **83,** lateral view, *G. elevatus* (80×); **84,** dorsal view, *G. elevatus* (60×); **85,** dorsal view, *G. affinis* (50×); **86,** dorsal view, *G. dichrous* (60×); **87,** lateral view, *G. dichrous* (150×).



Figs. 88–93. Male genitalia of *Gyrinus*: **88,** dorsal view, *G. bifarius* (60×); **89,** lateral view, *G. bifarius* (150×); **90,** dorsal view, *G. maculiventris* (60×); **91,** lateral view, *G. maculiventris* (80×); **92,** dorsal view, *G. sayi* (60×); **93,** dorsal view, *G. obtusus* (60×).



Figs. 94–99. Male genitalia of *Gyrinus*: **94,** dorsal view, *G. lecontei* (50×); **95,** lateral view, *G. lecontei* (80×); **96,** dorsal view, *G. gehringi* (60×); **97,** lateral view, *G. gehringi* (150×); **98,** apical view, *G. gehringi* (60×); **99,** dorsal view, *G. wallisi* (50×).

rent and rocky/stony substrates. There usually was no vegetation at the stream's edge. Label data indicate that 92.3 percent of specimens were collected from lotic habitats (table 2).

DISTRIBUTION: Map 10. Records are from New Hampshire south to Virginia and east to Michigan. One record is from Alabama.

Gyrinus gibber LeConte

Figures 18, 20, 46, 139, 140; Map 5

Gyrinus gibber LeConte, 1868: 370, 372. Régimbart, 1883: 175. Leng, 1920: 82.
Gyrinus frosti Fall, 1922: 278, 303, 304. Young, 1954: 153, 156, 157. Robert, 1963: 14, 22, 33. Sanderson, 1982: 10: 36. Ferkinhoff and Gundersen, 1983: 25, 45. NEW SYNONYMY.
Gyrinus floridensis Ochs, 1929: 123. NEW SYNONYMY.

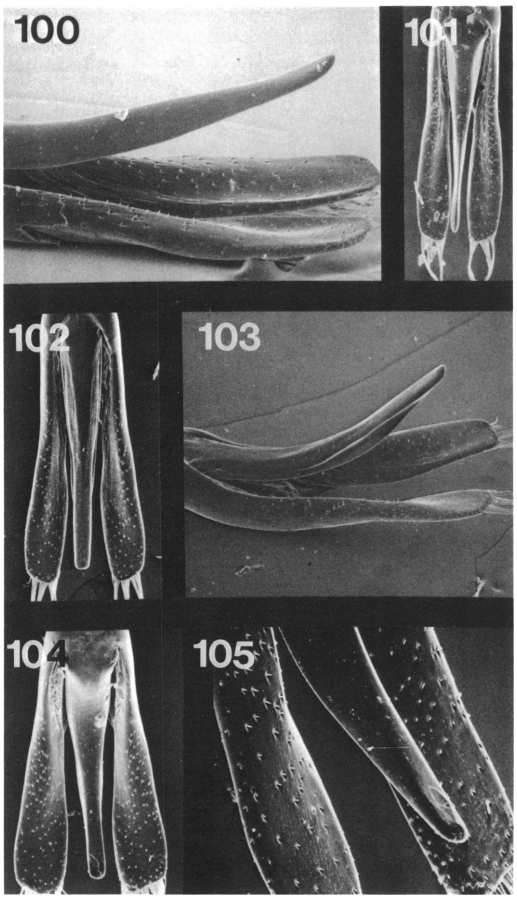
DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron dull, with evident microreticulation (fig. 46), (2) abdominal segments 4–7 black, 8th red, (3) metepisternal ostiole not visible (fig. 18), (4) aedeagus in figures 139, 140, (5) body measurements: male length 4.7–5.6 mm, width 2.8–3.1 mm; female length 5.5–6.2 mm, width 3.1–3.6 mm.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the LeConte collection at MCZ. It is pinned and carries the following labels: N.C./ Type 6107/ Gyrinus gibber Zimm. [handwritten].

LeConte (1868) described a female specimen from North Carolina as *G. gibber*. Horn (*in* Fall, 1922) synonymized *G. gibber* with *G. analis*. Although Fall (1922) used *G. gibber* in his key, he was doubtful about its status. He suggested that *G. gibber* might be a synonym of *G. frosti,* but not *G. analis*.

We agree that it is not a synonym of *G. analis*. The only difference we found between the type of *G. frosti* and the type of *G. gibber* is that the latter is more convex when viewed laterally. However, this characteristic is quite variable and we regard *G. frosti* as junior synonym of *G. gibber*.

Gyrinus floridensis was described from



Figs. 100–105. Male genitalia of *Gyrinus*: **100,** lateral view, *G. wallisi* (60×); **101,** dorsal view, *G. marinus* (40×); **102,** dorsal view, *G. aeratus* (50×); **103,** lateral view, *G. aeratus* (60×); **104,** dorsal view, *G. picipes* (60×); **105,** apicolateral view, *G. picipes* (150×).

Florida by Ochs (1929). He stated that *G. floridensis* was similar to *G. frosti,* but that specimens of the former were broader, larger, and more convex. Young (1954) and Ferkinhoff and Gundersen (1983) suspected that *G. floridensis* was not distinct from *G. frosti* at the species level. We have examined the holotype (CM) and the four paratypes (three from CM, and one from FS) and concluded that *G. floridensis* is a synonym of *G. gibber.*

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Specimens of *G. gibber* were found in lakes in Florida by Young (1954). Robert (1955) and Morrissette (1979) collected specimens from the lakes and drainage of fluvial lakes, respectively. Label information indicates that 81.6 percent of specimens were collected from lentic habitats (table 2).

DISTRIBUTION: Map 5. Records are from Florida to Louisiana, north to New Brunswick, Canada.

Gyrinus piceolus Blatchley
Figure 136; Map 4

Gyrinus piceolus Blatchley, 1910: 238, 240. Wallis, 1926: 50. Fall, 1922: 297; 1931: 154, 155. Young, 1953: 118. Robert, 1963: 12, 28, 36. Ferkinhoff and Gundersen, 1983: 23, 38.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron without microreticulation and micropunctation, (2) abdominal segments 4–7 uniformly black, (3) aedeagus in figure 136, (4) body measurements: male length 4.5–5.2 mm, width 2.5–2.7 mm; female length 5.5 mm, width 2.8 mm.

G. piceolus usually cannot be separated from *G. pernitidus* without genitalic examination. However, *G. piceolus* has the width of the elytral margin uniform throughout its length, a less convex body, and a lighter mesosternum.

TYPE INFORMATION AND TAXONOMIC NOTES: We received the lectotype from the Blatchley collection at PU. The specimen is glued to a point and carries the following labels: Lake Co.Ind.W.S.B. 5.5.07/ Type [red label]/Purdue Blatchley Collection/"resembles both affinis and aeneolus. Had with the latter, but undersurface black" [handwritten]/Lectotype Gyrinus piceolus Blatchley. Des: W.S.Blatchley 1930 [red label]/. Aedeagus and parameres are glued on a point beneath the specimen.

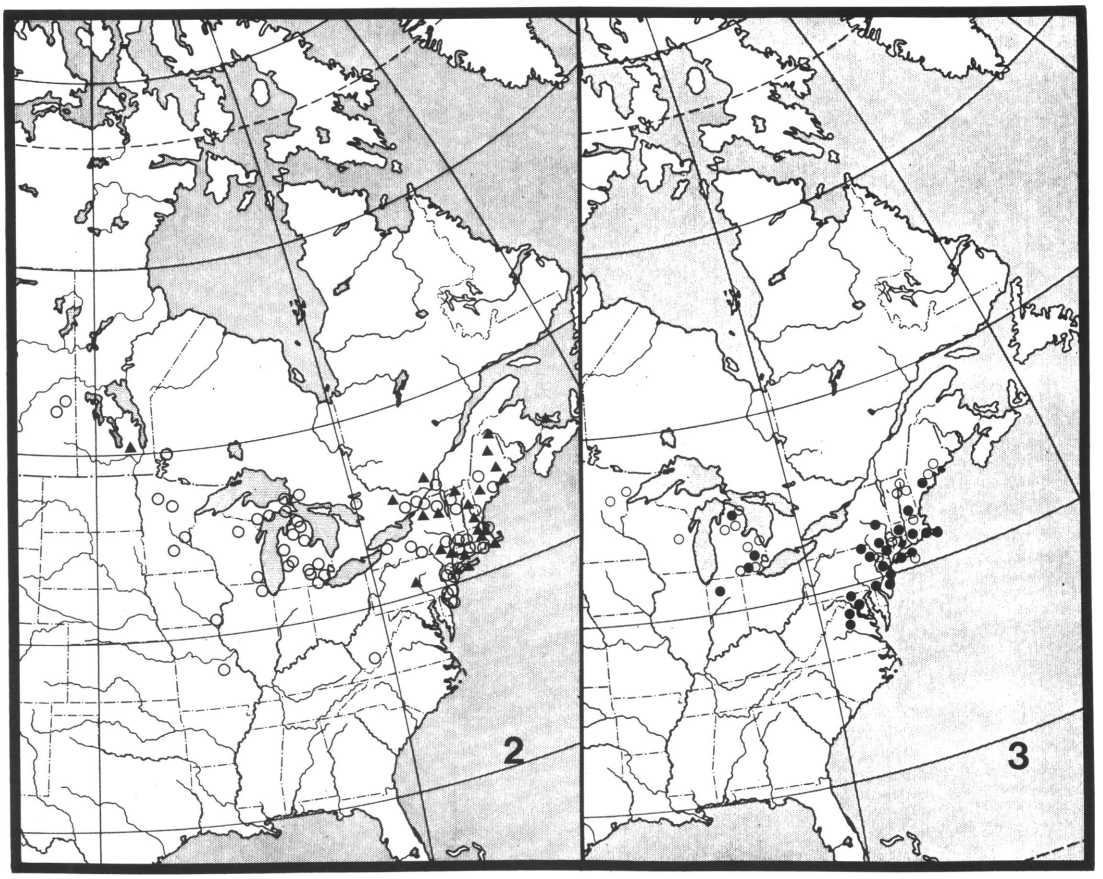
SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Not available.

DISTRIBUTION: Map 4. Known only from Indiana.

Gyrinus ventralis Kirby
Figures 74, 142; Map 2

Gyrinus ventralis Kirby, 1837: 80. Aubé, 1838: 672, 673. Régimbart, 1883: 151, 152; 1902–03: 7. Ahlwarth, 1910: 25. Blatchley, 1919: 238, 239. Leng, 1920: 82. Fall, 1922: 276, 279, 280.



Map 2. Distribution in North America of *G. fraternus* (▲) and *G. ventralis* (O) based on species examined.

Map 3. Distribution in North America of *G. pugionis* (O) and *G. borealis* (●) based on species examined.

Criddle, 1929: 115. Ochs, 1930: 136. Fall, 1931: 154. Robert, 1963: 10, 29, 37. Ferkinhoff and Gundersen, 1983: 22, 31.

Gyrinus hatchi Wallis, 1926: 93. NEW SYNONYMY.

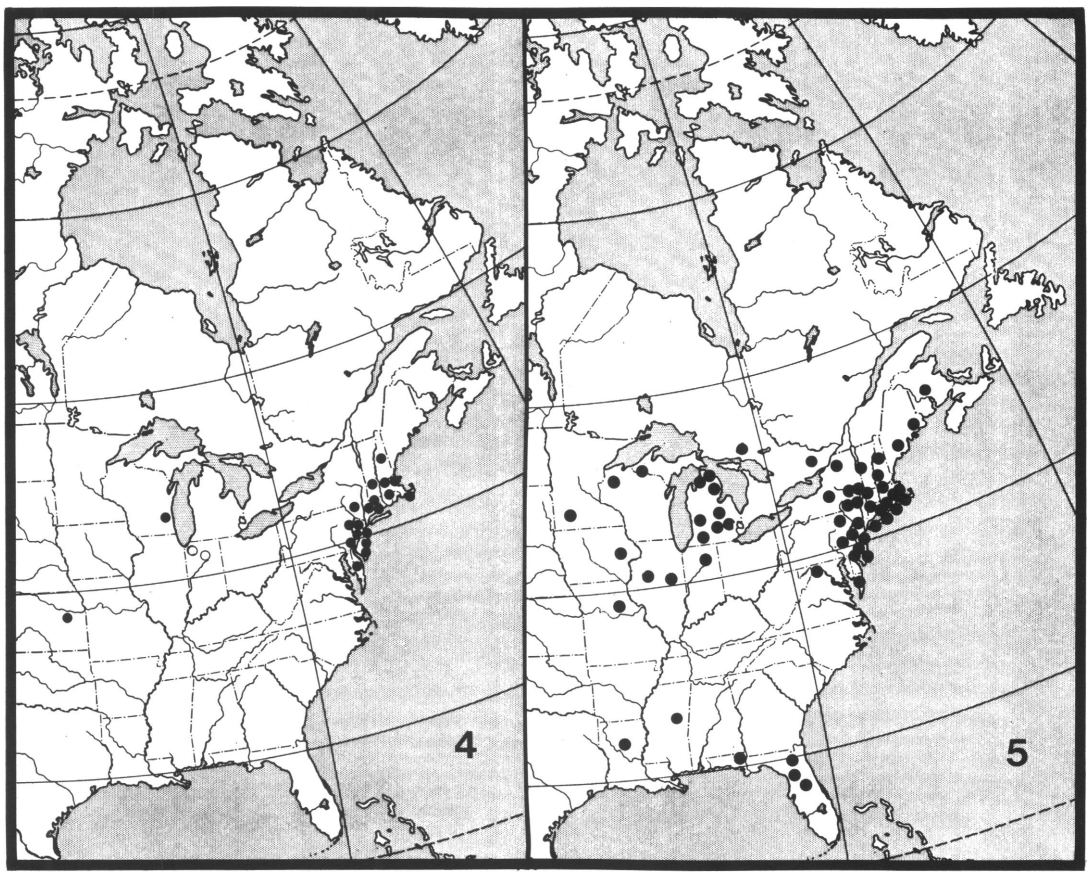
DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) 11th stria remote from outer margin of elytron in apical third, (2) ventral surfaces uniformly reddish or yellowish brown, (3) elytron without evident microreticulation, (4) aedeagus in figure 142, (5) body measurements: male length 4.9–5.7 mm; width 2.7–2.8 mm; female length 5.2–5.9 mm, 2.9–3.2 mm.

G. ventralis and *G. fraternus* cannot be separated based on nongenitalic characters. The aedeagus is apically broadened in the two species; however, it is laterally more truncate in *G. ventralis* (fig. 141 vs. 142).

TYPE INFORMATION AND TAXONOMIC NOTES: There are two syntypes of *G. ventralis* deposited at BMNH. We examined only one which we designated as the lectotype. The specimen we studied was pinned; the male genitalia were dissected and attached to a point beneath the specimen. It carries the following labels: Type [orange-circular label]/ namer [handwritten]/ G. ventralis Kirby.

Fall (1922) indicated that LeConte (1868) and Régimbart (1883) incorrectly applied the name *G. ventralis* Kirby to what was at that time an undescribed species. Fall named the undescribed species *G. lecontei* in his revision (1922).

Wallis described *G. hatchi* from Michigan



Map 4. Distribution in North America of *G. piceolus* (O) and *G. pernitidus* (●) based on species examined.

Map 5. Distribution in North America of *G. gibber* (●) based on species examined.

(1926) and considered it similar to *G. ventralis*. Based on our comparison of the holotype of *G. hatchi* (from CNC) with the lectotype of *G. ventralis*, we consider these names synonyms.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Slightly sexually dimorphic. Females have more lightly impressed microreticulation posteriorly than do males.

HABITAT INFORMATION: *Gyrinus ventralis* is recorded from a lake by Fall (1922). Morrissette (1979) indicated that *G. ventralis* prefers fluvial lakes. Label information indicates that 80 percent of the collections of specimens were from lentic habitats (table 2).

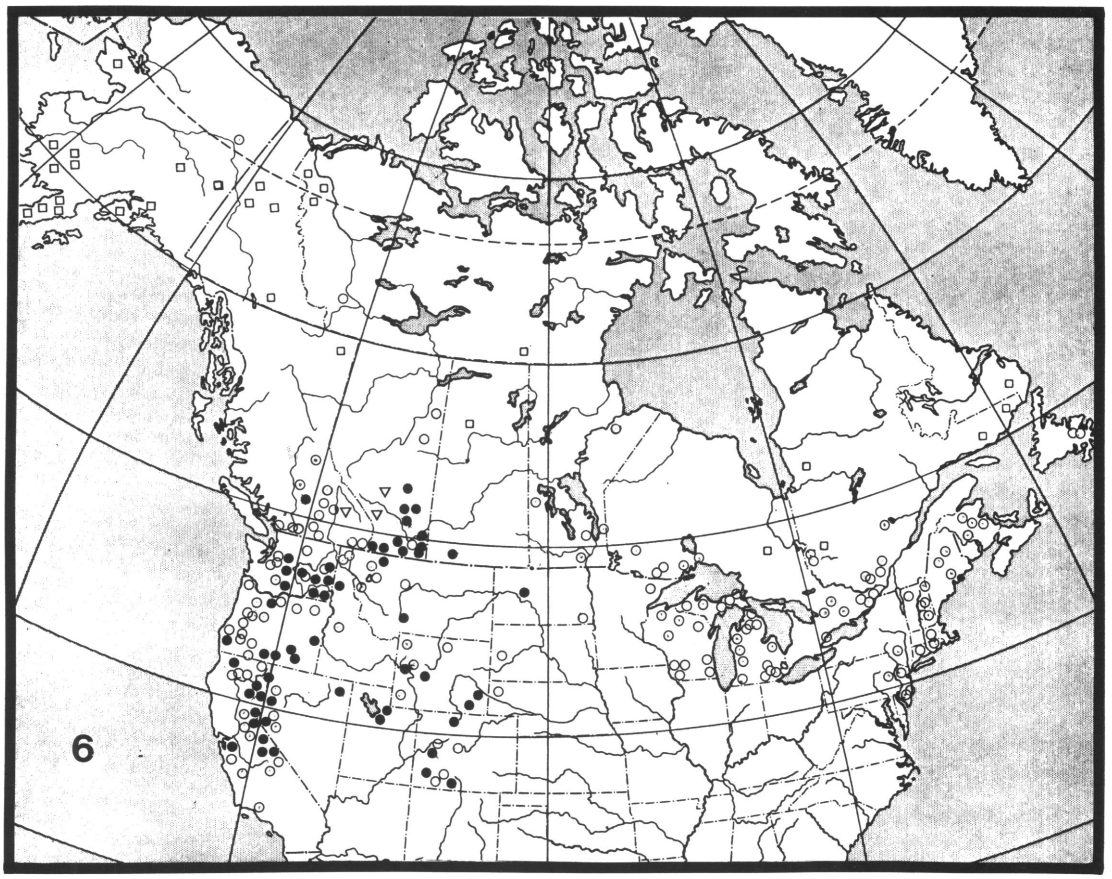
DISTRIBUTION: Map 2. Records are from Maine to Saskatchewan, and south to West Virginia.

Gyrinus fraternus Couper

Figure 141; Map 2

Gyrinus fraternus Couper, 1865: 60, 61. LeConte, 1868: 368, 370. Régimbart, 1883: 147, 148; 1902–03: 7. Ahlwarth, 1910: 18. Blatchley, 1910: 238, 239. Fall, 1922: 276, 280. Wallis, 1926: 93. Criddle, 1929: 115. Fall, 1931: 154. Robert, 1963: 10, 22, 23. Ferkinhoff and Gundersen, 1983: 22, 32.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) 11th stria remote from outer margin of elytron in apical third, (2) ventral surfaces uniformly reddish, (3) elytron without evident microreticulation, (4) metepisternal ostiole small (as in fig. 16), (5) aedeagus in figure 141, (6)



Map 6. Distribution in North America of *G. affinis* (○), *G. pleuralis* (●), *G. opacus* (□), and *G. hoppingi* (▽) based on species examined.

body measurements: male length 4.9–5.8 mm, width 2.7–2.9 mm; female length 5.8–6.2 mm, width 2.9–3.3 mm.

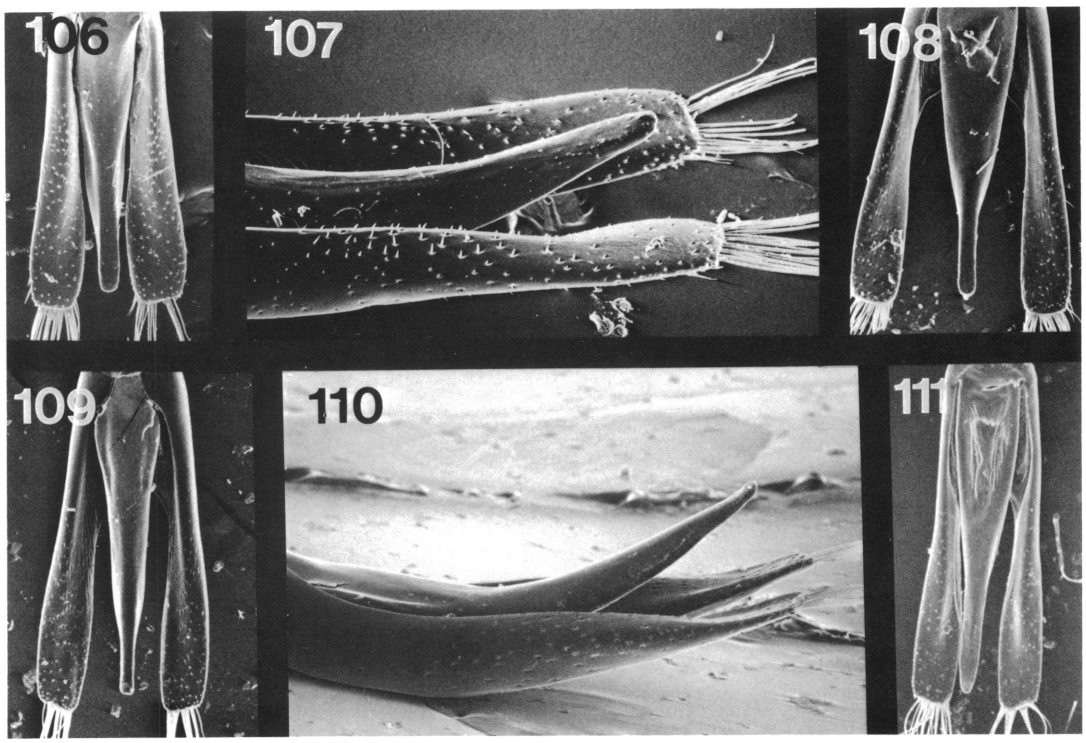
G. fraternus and *G. ventralis* cannot be separated reliably based on nongenitalic characters. In *G. fraternus* the aedeagus is apicolaterally rounded, but it is angulate in *G. ventralis*. Additionally, *G. ventralis* has a more distinct apicomedial projection which is much less evident in *G. fraternus*.

TYPE INFORMATION AND TAXONOMIC NOTES: Becker (1974) indicated a recent discovery of Couper's types at the Seminaire de Quebec, Quebec City but he did not find any specimens in Couper's collection labeled as *G. fraternus*. He thought that one female specimen with a lightly colored underside and labeled with a small green disk could be *G. fraternus*; because of the extreme similarities between the females of *G. fraternus* and *G. ventralis*, he was unsure about this identification. We have been unable to obtain this specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Couper (1865) indicated the common occurrence of specimens of this species in ponds near Quebec. Frost (*in* Fall, 1922) collected specimens from large swarms occurring in small rivers and lakes in Massachusetts. Robert (1955) found specimens of *G. fraternus* in lakes. Morrissette (1979) stated that *G. fraternus* prefers clear fluvial lakes with muddy bottoms. Label information indicates that 55.6 percent of collections of specimens were from lotic habitats (table 2).

DISTRIBUTION: Map 2. Records are from Maine south to Pennsylvania and west to southern Manitoba.



Figs. 106–111. Male genitalia of *Gyrinus*: **106,** dorsal view, *G. dubius* (50×); **107,** lateral view, *G. dubius* (100×); **108,** dorsal view, *G. woodruffi* (60×); **109,** dorsal view, *G. aeneolus* (60×); **110,** lateral view, *G. aeneolus* (100×); **111,** dorsal view, *G. analis* (50×).

Gyrinus latilimbus Fall

Figures 7, 9, 23, 52, 53, 129, 150; Map 12

Gyrinus latilimbus LeConte, 1868: 368, 370. Fall, 1922: 276, 285. Criddle, 1929: 115. Brinck, 1960: 79. Robert, 1963: 10, 24, 34. Gordon and Post, 1965: 28. Ferkinhoff and Gundersen, 1983: 20, 27, 28.

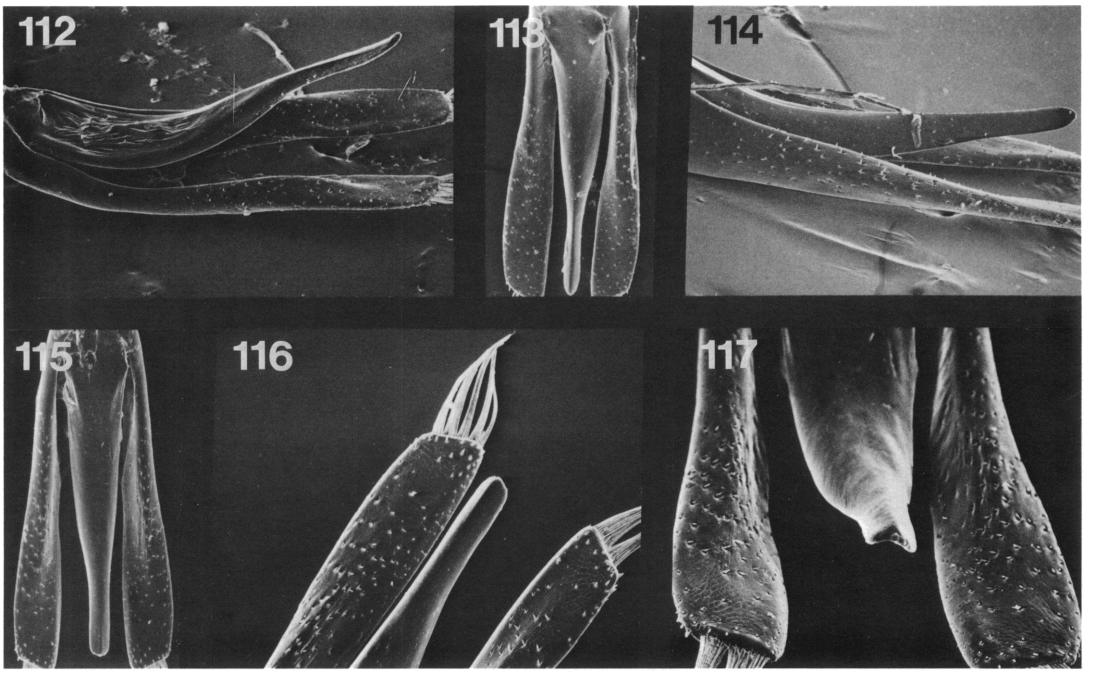
DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) ventral surfaces uniformly reddish, (2) 11th stria distinctly impressed anteriorly (fig. 150), (3) pronotal transverse impressed line distinctly curved (figs. 7, 9, 15), (4) elytron without microreticulation, (5) aedeagus in figure 129, (6) body small, body measurements: male length 4.0–4.3 mm, width 2.2–2.4 mm; female length 4.5–4.7 mm, width 2.3–2.6 mm.

Because of the similarity in size and abdominal coloration, *G. latilimbus* can be confused with *G. aeneolus, G. woodruffi,* and/or *G. marginellus.* The best character to distinguish *G. latilimbus* is the 11th stria which is more distinctly impressed anteriorly and closer to the elytral margin posteriorly. Other characters which help distinguish *G. latilimbus* are provided in table 5.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is pointed and carries the following labels: Tyngsboro Ms./ type latilimbus [handwritten]/ MCZ type 23983 [red labels]/. Aedeagus and parameres are glued on a point beneath the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Distinctly sexually dimorphic. Reticulation of females is uniformly and distinctly scalelike while males do not have any evident microreticulation.

HABITAT INFORMATION: Specimens of *G. latilimbus* are recorded from a river by Fall (1922). Robert (1955) and Morrissette (1979) indicated that *G. latilimbus* was found in small deep lakes near dense emergent vegetation,



Figs. 112–117. Male genitalia of *Gyrinus*: **112,** lateral view, *G. analis* (100×); **113,** dorsal view, *G. consobrinus* (60×); **114,** lateral view, *G. consobrinus* (100×); **115,** dorsal view, *G. aquiris* (60×); **116,** dorsolateral view, *G. aquiris* (100×); **117,** apical view, *G. aquiris* (150×).

i.e., *Carex* and *Scirpus*. Label information indicates that 71.1 percent of collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 12. Records are from Maine to Washington, north to British Columbia and south to Pennsylvania.

Gyrinus confinis LeConte
Figure 125, 126; Map 11

Gyrinus confinis LeConte, 1868: 368, 370. Régimbart, 1883: 147; 1902–03: 7. Ahlwarth, 1910: 17. Fall, 1922: 276, 278. Criddle, 1929: 115, 116. Ochs, 1930: 136. Robert, 1963: 12, 21, 32. Ferkinhoff and Gundersen, 1983: 22, 32, 33.

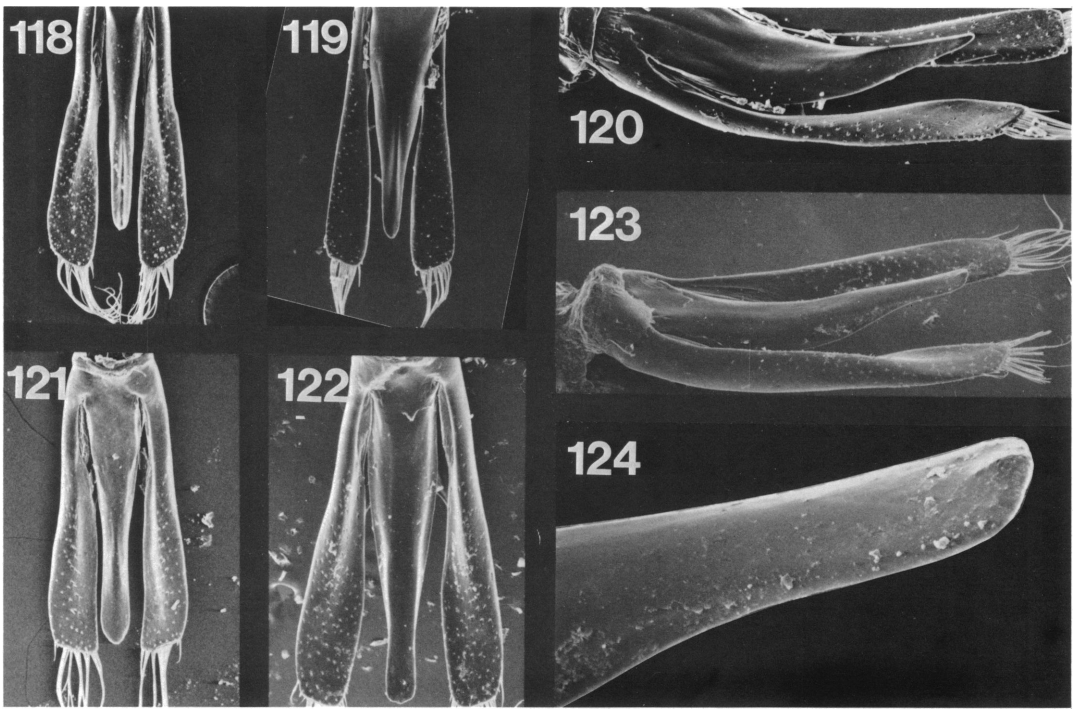
DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron with dense micropunctation and microreticulation (as in fig. 73), (2) metepisternal ostiole small (as in fig. 16), (3) 11th stria remote from outer margin of elytron in apical third, (4) ventral surface uniformly orange or yellowish, sometimes darker medially, (5) aedeagus in figures 125, 126, (6) body measurements: male length 5.0–6.1 mm, width 2.9–3.0 mm; female length 5.6–6.7 mm, width 2.9–3.5 mm.

G. confinis is most easily confused with *G. bifarius,* and aedeagal examination is necessary for conclusive identification.

TYPE INFORMATION AND TAXONOMIC NOTES: The type series consists of 15 specimens and is in the LeConte collection at MCZ. Fall (1922) did not clearly indicate a lectotype. We designated a male specimen as lectotype. It is glued to a point and carries the following labels: H.B.T./ confinis 15 [handwritten].

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Moderately sexually dimorphic. In females, microreticulation is moderately distinct as transverse sculpticells. Reticulation in males is also transverse but evidently less impressed.

HABITAT INFORMATION: Fall (1922) recorded this species from a river. Robert (1955) and Morrissette (1979) indicated that *G. confinis* mostly was found in running water. However, label information indicates that 99 percent of the collections of specimens were from lentic habitats (table 2).



Figs. 118–124. Male genitalia of *Gyrinus*: **118,** dorsal view, *G. pleuralis* (40×); **119,** dorsal view, *G. pectoralis* (60×); **120,** lateral view, *G. pectoralis* (80×); **121,** dorsal view, *G. parcus* (60×); **122,** dorsal view, *G. pachysomus* (60×); **123,** lateral view, *G. pachysomus* (60×); **124,** apical view, *G. pachysomus* (200×).

DISTRIBUTION: Map 11. Records are from Maine to British Columbia, north to Saskatchewan and south to New Jersey.

Gyrinus rugosus, new species
Figures 25, 49, 130, 131; Map 9

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) 11th interval rugose posteriorly (fig. 25), (2) 11th stria remote from outer margin of elytron in apical third (fig. 25), (3) elytral microreticulation only evident laterally and posteriorly, (4) metepisternal ostiole not visible (as in fig. 18), (5) aedeagus in figures 130, 131, (6) body measurements: male length 5.0–5.2 mm, width 2.7–2.9 mm; female length 5.4–5.9 mm, width 2.8–3.1 mm.

This species is separated from all other Nearctic species of *Gyrinus* by presence of minute rugosity between the posterior portions of 11th striae and the elytral margin (fig. 25). The male genitalia are distinctly different from those of any other species of north American *Gyrinus* (fig. 130).

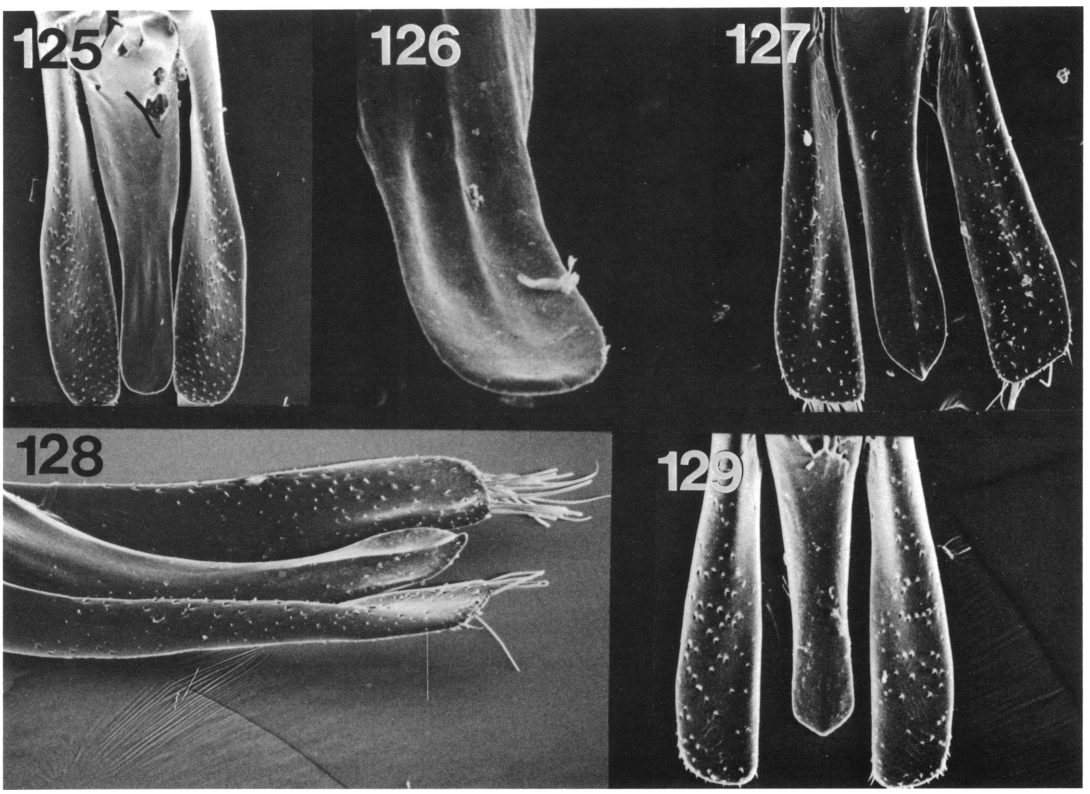
TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male and deposited at AMNH. It is mounted on a point and carries the following label: USA California, Sonoma Co, Monte Rio, 23 July 1908, PE Blaisdell coll. Allotype: same locality as holotype; paratypes (5): same locality as holotype.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Distinctly sexually dimorphic. In females, microreticulation is distinctly uniform and scalelike. In males, microreticulation is distinctly discontinuous; it is not noticeable anteriorly and discally, but it is distinctly visible and moderately transverse laterally.

ETYMOLOGY: From the Latin, *rugosus,* in reference to the small wrinkles noticeable posterolaterally on the elytron.

HABITAT INFORMATION: Not available.

DISTRIBUTION: Map 9. Records are from Oregon and California.



Figs. 125–129. Male genitalis of *Gyrinus*: **125,** dorsal view, *G. confinis* (60×); **126,** apical view, *G. confinis* (200×); **127,** dorsal view, *G. pernitidus* (80×); **128,** lateral view, *G. pernitidus* (100×); **129,** dorsal view, *G. latilimbus* (100×).

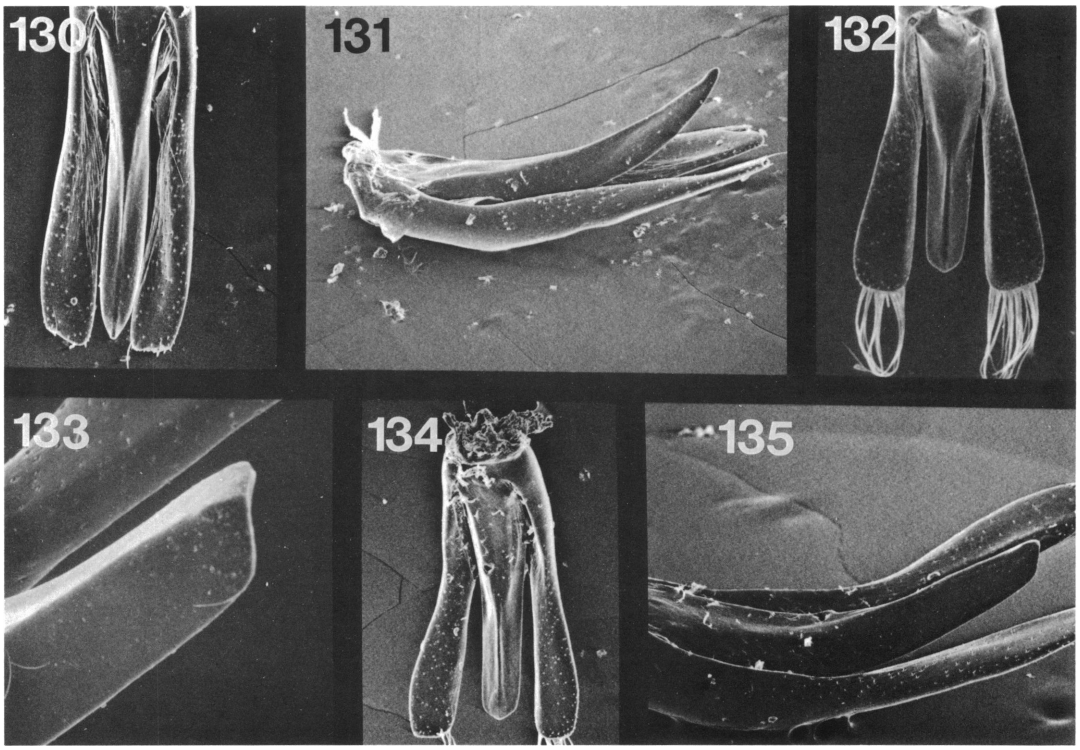
Gyrinus pernitidus LeConte
Figures 127, 128; Map 4

Gyrinus pernitidus LeConte, 1868: 396, 372. Régimbart, 1883: 169, 170; 1902–03: 8. Ahlwarth, 1910: 24. Leng and Mutchler, 1918: 97. Fall, 1922: 277, 297, 298; 1931: 154. Sanderson, 1982: 10: 36.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body convex, (2) pronotal transverse impressed line curved and remote from anterior pronotal margin (as in figs. 7, 9), (3) elytal microreticulation and micropunctation not evident, (4) abdominal segments 4–7 uniformly black, (5) aedeagus in figures 127, 128, (6) body measurements: male length 4.8–5.2 mm, width 2.5–2.7 mm; female length 5.0–5.5 mm, width 2.6–2.9 mm.

TYPE INFORMATION AND TAXONOMIC NOTES: LeConte (1868) indicated that the type of *G. pernitidus* is a single female from Georgia. There are two females of *G. pernitidus* in the LeConte collection (MCZ). None of these specimens have locality information. However, LeConte indicated that he associated another female of this species which was sent to him by Harris as No. 242. One of the females in the collection has this number attached to it; therefore, we believe the other female is the holotype. It is pinned and carries the following labels: a circular orange tag/ MCZ Type 6105 [red label]/ G. pernitidus Lec. [handwritten].

The type locality given in LeConte (1868) specifically refers to Georgia, but we are doubtful that this species occurs that far south. The names, *G. piceolus* and *G. pernitidus* were synonymized by Fall (1922), but removed from synonymy in Fall (1931). We have examined types of both species (see above). There are substantial genitalic differences and consistent but subtle external structural dif-



Figs. 130–135. Male genitalia of *Gyrinus*: **130,** dorsal view, *G. rugosus* (60×); **131,** lateral view, *G. rugosus* (60×); **132,** dorsal view, *G. opacus* (60×); **133,** apical view, *G. opacus* (200×); **134,** dorsal view, *G. hoppingi* (50×); **135,** lateral view, *G. hoppingi* (80×).

ferences in body convexity and the width of elytral margin. Additionally, the mesosternal color of *G. pernitidus* is darker than that of *G. piceolus*. Unfortunately, there are too few *G. piceolus* to conclusively evaluate the reliability of color difference.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Not available.

DISTRIBUTION: Map 4. Records are from New Hampshire south to New Jersey, with two midwestern records, one from Wisconsin and the other from Kansas.

Gyrinus opacus Sahlberg

Figures 42, 45, 132, 133; Map 6

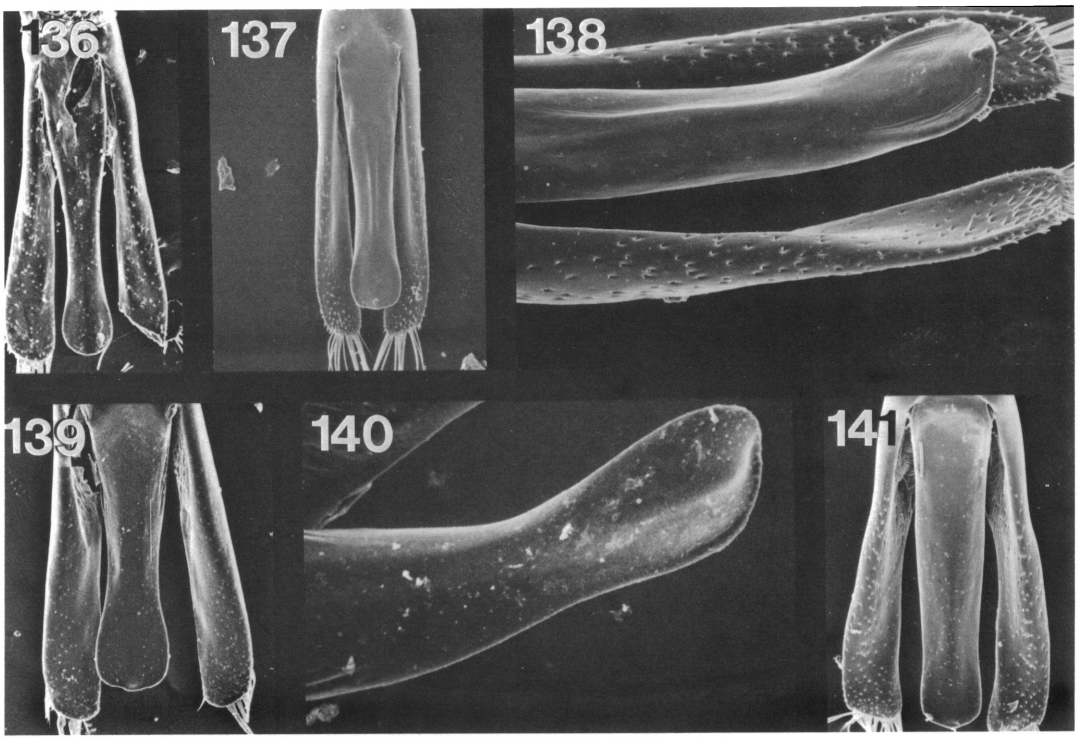
Gyrinus opacus Sahlberg, 1817: 47. Sharp, 1868: 55, 59. LeConte, 1868: 369, 372. Régimbart, 1883: 172; 1902–03: 8. Ahlwarth, 1910: 23. Sharp, 1914: 131, 135–138. Leng, 1920: 82. Fall, 1922: 301, 302. Leech, 1938: 60. Balfour-Browne, 1950: 363–366. Hatch, 1953: 241. Brinck, 1960: 77–79. Robert, 1963: 14, 27, 35. Ferkinhoff and Gundersen, 1983: 26, 46.

Gyrinus opacus var. *lecontei* Omer-Cooper, 1930: 65–68.

Gyrinus hoppingi Leech, 1938: 59, 60. Balfour-Browne, 1950: 321, 364. Hatch, 1953: 241. Brinck, 1960: 78.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) 11th stria located very close to outer margin of elytron in apical half, (2) elytron dull, with dense and uniform microreticulation (figs. 42, 45), (3) abdominal segments 4–7 uniformly black, (4) aedeagus in figures 132, 133, (5) body measurements: male length 4.8–5.7 mm, width 2.8–3.0 mm; female length 5.5–6.1 mm, width 2.9–3.1 mm.

TYPE INFORMATION AND TAXONOMIC NOTES: We received the holotype from the Sahlberg collection in ZMH. It is a female specimen and is glued on a card and carries



Figs. 136–141. Male genitalia of *Gyrinus*: **136,** dorsal view, *G. piceolus* (50×); **137,** dorsal view, *G. marginellus* (60×); **138,** apical view, *G. marginellus* (200×); **139,** dorsal view, *G. gibber* (60×); **140,** apical view, *G. gibber* (200×); **141,** dorsal view, *G. fraternus* (60×).

the following labels: G.opacus Sahlb.typ. vidi D.C. 22.11.1914 [handwritten] /Fenn.austr. Sahlb./Mus. Zool.Hifors Spec.typ. No. 138. Gyrinus opacus Sahlb.[handwritten]/Loan No c86-108n3 Zool.Mus.Helsinki.

The circumboreal distribution of *G. opacus* has been emphasized by many authors (Hatch, 1925; Omer-Cooper, 1930; Balfour-Browne, 1950; Brinck, 1960). Omer-Cooper (1930) described some populations of *G. opacus* from Iceland as a distinct "variety" (*G. opacus lecontei*) because specimens had more effaced elytral microreticulation. Because of homonymy she later renamed this taxon as *G. opacus blairi.* Leech (1938) described *G. hoppingi* from British Colombia and indicated that although *G. hoppingi* was very similar to *G. opacus,* the former always had more indistinct elytral microreticulation. Balfour-Browne (1950) did not think the microreticular difference was sufficient and synonymized *G. hoppingi* with *G. opacus.* Brinck (1960) believed that *G. hoppingi* deserved subspecific status.

We have examined the types of both species and numerous *G. opacus* from throughout its range. On *G. opacus,* microreticulation always is more distinct. Also, there is usually a noticeable lateral aeneous luster that is absent from *G. hoppingi.* Finally, the 11th stria is more completely marginal in the apical half on *G. opacus* than it is on *G. hoppingi.* Because we have seen no intergrades, we consider *G. opacus* and *G. hoppingi* to be distinct at the species level.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Balfour-Browne (1950) frequently collected *G. opacus* from peat pools. Larson (1983) stated that *G. opacus* was found in coastal barrens and alpine pools in Newfoundland. Holmen (1987) collected *G. opacus* from stagnant water, especially in peatholes and marshes of Fen-

noscandia and Denmark. The label information indicates that 50 percent of the collections of specimens of this species were from lentic habitats (table 2).

DISTRIBUTION: Map 6. Records are from Newfoundland to Alaska. There are no records from the U.S. south of Canada.

Gyrinus hoppingi Leech
Figures 134, 135; Map 6

Gyrinus hoppingi Leech, 1938: 59, 60. Hatch, 1953: 241. Balfour-Browne, 1950: 321, 364. Brinck, 1960: 78.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron with uniformly effaced microreticulation, (2) abdominal segments 4–7 uniformly black, (3) aedeagus in figures 134, 135, (4) body measurements: male length 4.9–5.5 mm, width 2.4–2.8 mm; female length 5.9–6.1 mm, width 2.5–2.9 mm.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in CNC. The specimen is pointed and carries the following labels: Trinity Valley 17.IX.37 B.C. Hugh B. Leech/ Tributary to Vance creek [handwritten]/ Holotype Gyrinus hoppingi [red label]/ Holotype Gyrinus hoppingi No 4302 Leech [red label]. Aedeagus and parameres are attached to the body.

This species is very close to *G. opacus*; see discussion under that species for more details.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Slightly sexually dimorphic. Female microreticulation is uniformly evident and transverse. In males, microreticulation is only evident laterally and posteriorly as extremely fine transverse sculpticells.

HABITAT INFORMATION: The type series was collected from a tributary to Vance Creek in British Columbia.

DISTRIBUTION: Map 6. Known only from British Columbia and Alberta.

Gyrinus woodruffi Fall
Figures 31, 37, 56, 57, 108; Map 9

Gyrinus woodruffi Fall, 1922: 276, 282, 283. Ochs, 1930: 137. Young, 1954: 152, 156.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body length short, convex, (2) metepisternal ostiole large (as in fig. 12), (3) elytron shiny, without noticeable microreticulation and micropunctation, (4) 11th stria remote from outer margin of elytron in apical third (fig. 31), (5) ventral surfaces uniformly reddish, (6) aedeagus in figure 108, (7) body measurements: male length 4.1–4.7 mm, width 2.1–2.3 mm; female length 4.8–5.2 mm, width 2.5–2.7 mm.

G. woodruffi is most similar to *G. aeneolus*. The differences are discussed below (see *G. aeneolus*). This species can also be confused with other small, ventrally light-colored species: *G. latilimbus, G. marginellus, G. elevatus*. Table 5 provides the most reliable nongenitalic characters to distinguish these five species.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in Fall's collection at MCZ. It is mounted on a point and carries the following labels: Staten Isl. N.Y. 6.14.19 H.B.W. [handwritten]/ type woodruffi [handwritten]/ MCZ type 23990 [red label]/. Aedeagus and parameres are on a point next to the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Distinctly sexually dimorphic. Reticulation of females is uniformly and distinctly scalelike. Males do not have any evident microreticulation.

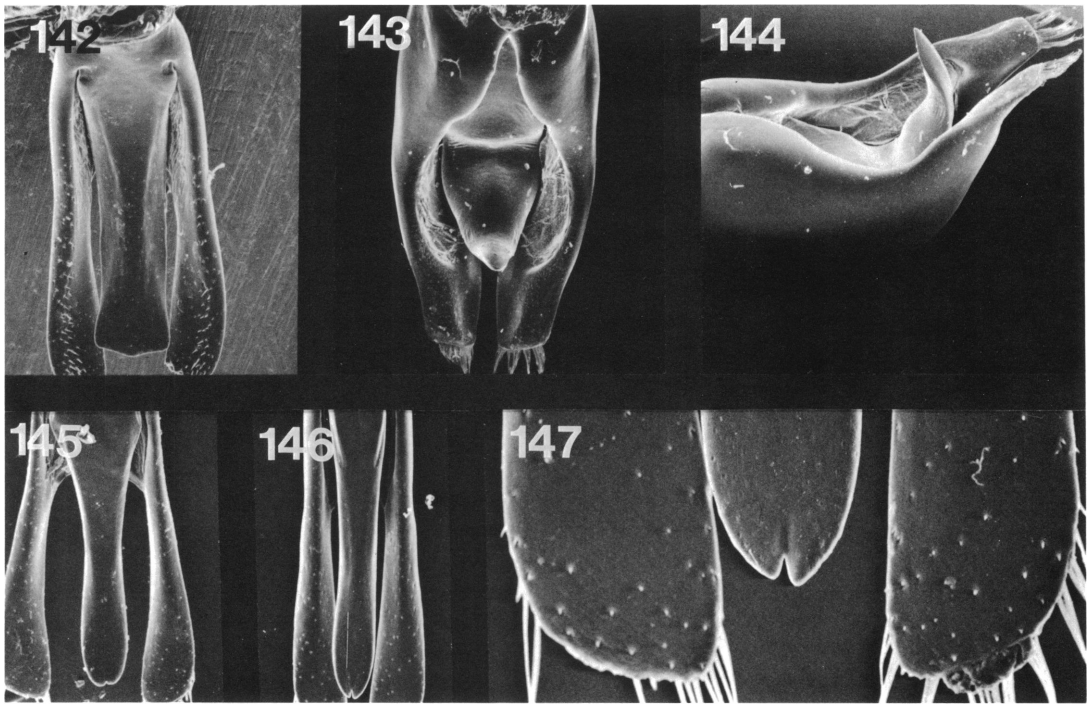
HABITAT INFORMATION: Young (1954) found specimens of this species primarily in streams. Label information indicates that 75 percent of collections were from lotic habitats (table 2).

DISTRIBUTION: Map 9. Records are from Florida west to eastern Texas and north to New York.

Gyrinus aeneolus LeConte
Figures 30, 109, 110; Map 9

Gyrinus aeneolus LeConte, 1868: 368, 370. Régimbart, 1883: 148, 149; 1902–03: 7. Ahlwarth, 1910: 14. Blatchley, 1910: 238, 239. Fall, 1922: 276, 282. Criddle, 1929: 115. Ochs, 1930: 136. Robert, 1963: 10, 18, 31. Sanderson, 1982: 10: 34, 36. Ferkinhoff and Gundersen, 1983: 21, 29, 30.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron without noticeable microreticulation and mi-



Figs. 142–147. Male genitalia of *Gyrinus*: **142,** dorsal view, *G. ventralis* (80×); **143,** dorsal view, *G. impressicollis* (30×); **144,** lateral view, *G. impressicollis* (30×); **145,** dorsal view, *G. rockinghamensis* (100×); **146,** dorsal view, *G. minutus* (80×); **147,** apical view, *G. minutus* (300×).

cropunctation, (2) abdominal sterna 4–7 uniformly light brownish, (3) 11th stria remote from outer margin of elytron in apical third (fig. 30), (4) elytron bronzed, (5) aedeagus in figures 109, 110, (6) body measurements: male length 4.0–4.3 mm, width 2.2–2.3 mm; female length 4.5–4.9 mm, width 2.4–2.7 mm.

G. aeneolus can be confused most easily with *G. woodruffi.* However, male *G. aeneolus* have the aedeagus at the apex noticeably narrower (fig. 109) and the elytral marginal inflection is much more distinctly pronounced (fig. 30). This species can also be confused with *G. latilimbus, G. marginellus,* and *G. elevatus.* Table 5 provides the best nongenitalic characters to separate members of these species.

TYPE INFORMATION AND TAXONOMIC NOTES: LeConte (1868) specifically stated that his description was based on one specimen. That specimen is a female and is in LeConte's collection at MCZ. It is pinned and has the following labels: circular tan tag/ MCZ Type 6097 [red label]/ *G. aeneolus* Lec. [handwritten].

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Blatchley (1910) collected specimens of this species from a low meadow pond near Bass Lake in Indiana. Label information indicates that 50 percent of collections were from lentic habitats (table 2).

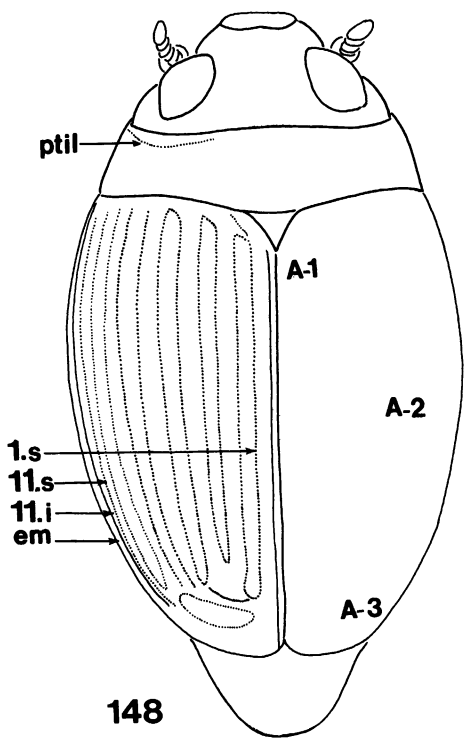
DISTRIBUTION: Map 9. Records are from New Brunswick west to Alberta, and south to Texas.

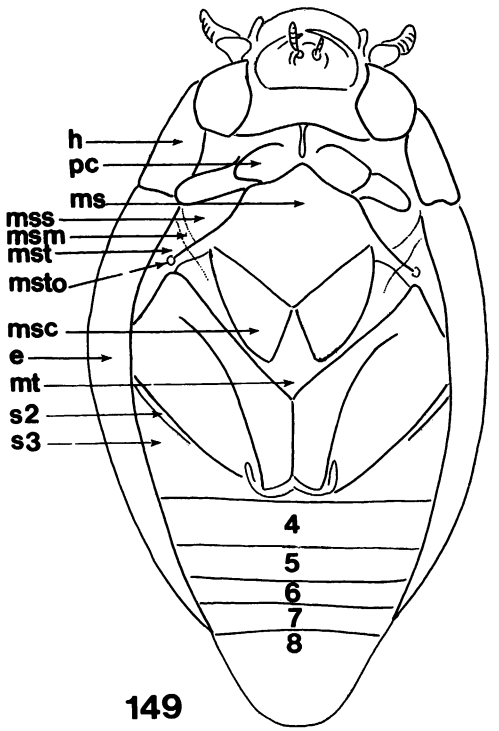
Gyrinus pachysomus Fall

Figures 14, 21, 38, 39, 122–124; Map 12

Gyrinus pachysomus Fall, 1922: 276, 288. Young, 1954: 152, 155. Sanderson, 1982: 36.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body extremely convex and broad, body measurements: male length 5.5–6.2 mm, width 3.0–3.2 mm; female length 6.0–6.9 mm, width 3.1–3.6 mm, (2) metepisternal ostiole very large (fig. 14), (3) 11th stria located in outer





Figs. 148, 149. **148.** Dorsal view of *Gyrinus*: PTIL = pronotal transverse impressed line, EM = elytral margin, 11th I = 11th interval, 11th S = 11th stria, 1st S = 1st stria. **149.** Ventral view of *Gyrinus*: PC = procoxal cavity, H = hypomeron, MS = mesosternum, MSS = mesepisternum, MSM = mesepimeron, MST = metepisternum, MSTO = metepisternal ostiole, MSC = mesocoxa, E = epipleuron, MT = metasternum, S2 = second sternum, S3 = third sternum.

marginal inflection of elytron in apical quarter (fig. 21), (4) elytron without noticeable microreticulation, (5) punctures of striae 8–10 distinctly larger than those of striae 1–7 (figs. 38, 39), (6) aedeagus in figures 122–124.

Specimens can only be confused with those of *G. plicifer,* from which they are easily separated by the absence of an apical convexity.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is mounted on a point and carries the following labels: Southern Pines/ A.H.Manee NC V.5.1915/ type pachysomus [handwritten]/ MCZ Type 23986 [red label]/. Aedeagus and parameres are glued next to the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Young (1954) found specimens of this species more often in lotic than lentic habitats. Label information indicates that 53.3 percent of collections of specimens were from lotic habitats (table 2).

DISTRIBUTION: Map 12. Records are from Florida to Texas and north to North Carolina.

Gyrinus dichrous LeConte

Figures 86, 87, 157; Map 12

Gyrinus dichrous LeConte, 1868: 368, 371. Régimbart, 1883: 150; 1902–03: 7. Ahlwarth, 1910: 18. Blatchley, 1910: 238, 239. Fall, 1922: 276, 284. Criddle, 1929: 115. Ochs, 1930: 136. Robert, 1963: 10, 21, 32. Ferkinhoff and Gundersen, 1983: 20, 27, 28.

Gyrinus fraterculus Notman, 1919: 131.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body length short, body measurements: male length

3.8–4.0 mm, width 2.2–2.4 mm; female length 4.0–4.5 mm, width 2.5–2.6 mm, (2) elytron without microreticulation, (3) mesosternum, metasternum, epipleuron, hypomeron, and legs uniformly orange or yellow, abdominal segments 4–7 black, (4) aedeagus in figures 86, 87.

Specimens can only be confused with those of *G. minutus* and *G. rockinghamensis*. Members of *G. dichrous* are easily separated from the latter two by the aedeagal apex which is not notched and by several reliable nongenitalic characters provided in table 4.

TYPE INFORMATION AND TAXONOMIC NOTES: The type series consists of six specimens, one of which was *G. aeneolus*. LeConte indicated that the type locality was "New England." Therefore, we designated the specimen that was collected in Massachusetts as the lectotype. The lectotype is pinned and carries the following labels: Mass/ MCZ Type 6098 [red label]/ G. dichrous Lec.

Notman (1919) described *G. fraterculus* and indicated that specimens closely resemble those of *G. dichrous*. However, the characters he used were variable and not sufficient to distinguish the two species. We agree with Fall (1922) that *G. fraterculus* (spelled "fratellus" by Fall, 1922) is a junior synonym of *G. dichrous*.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

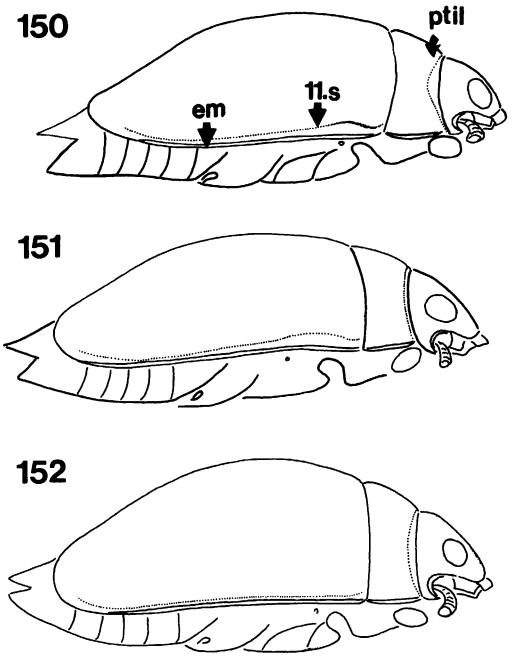
HABITAT INFORMATION: Fall recorded this species from a lake. Robert (1955) indicated that *G. dichrous* was mostly collected from eutrophic lakes. Morrissette (1979) found a few *G. dichrous* in clear, deep lakes. Label information indicates that *G. dichrous* occurs exclusively in lentic habitats (table 2).

DISTRIBUTION: Map 12. Records are from Maine to west Ontario, south to southern New Jersey.

Gyrinus analis Say

Figures 8, 10, 16, 54, 55, 111, 112, 152; Map 8

Gyrinus analis Say, 1825: 108. Kirby, 1837: 81. Aubé, 1838: 697, 698. LeConte, 1868: 370, 372. Régimbart, 1883: 170; 1902–03: 8. Ahlwarth, 1910: 15. Blatchley, 1910: 238, 240. Fall, 1922: 279, 300, 301; 1922: 278, 300. Ochs, 1930: 136. Young, 1954: 152, 155, 156. Robert, 1963: 14, 19, 31. Sanderson, 1982: 10: 36. Ferkinhoff and Gundersen, 1983: 25, 43, 44.

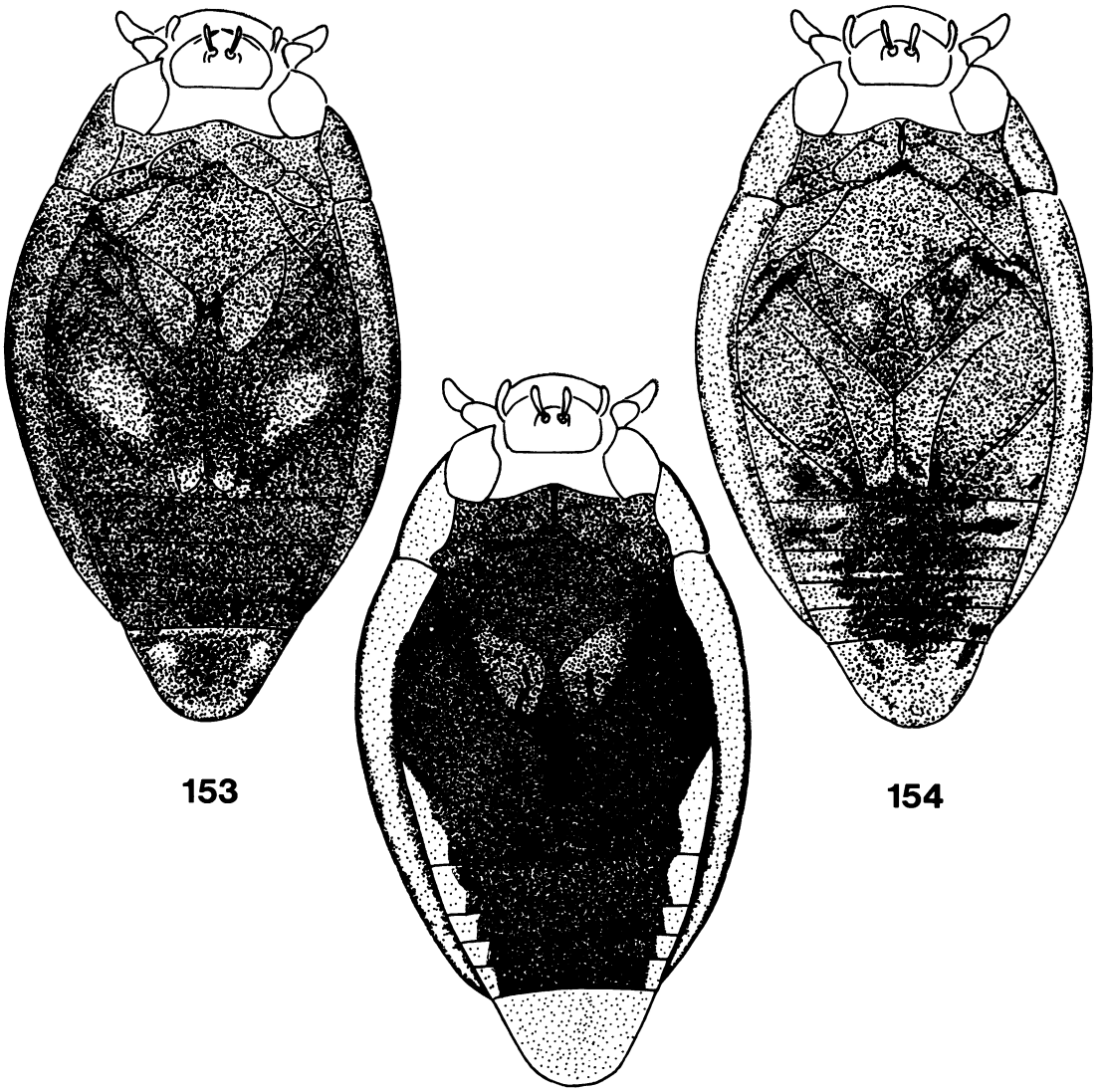


Figs. 150–152. Lateral view of *Gyrinus*: 11.s = 11th stria, ptil = pronotal transverse impressed line, em = elytral margin. **150,** 11th stria anteriorly impressed, pronotal transverse impressed line curved, *G. latilimbus*; **151,** 11th stria close to elytral margin posteriorly, pronotal transverse impressed line parallel, *G. analis*; **152,** 11th stria entirely marginal, *G. parcus*.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) pronotal transverse impressed line close and parallel to the anterior pronotal margin (figs. 8, 10), (2) elytron with barely noticeable microreticulation, (3) dorsal surface with dull aeneous luster, (4) ventral surface with abdominal segments 4–7 uniformly black, 8th segment orange or red, (5) aedeagus in figures 111, 112, (6) body measurements: male length 4.3–5.0 mm, width 2.4–2.7 mm; female length 5.0–5.5 mm, width 2.6–3.0 mm.

G. analis is distinguished from other species of North American *Gyrinus* primarily by the dull aeneous surface luster.

TYPE INFORMATION AND TAXONOMIC NOTES: Because Say's collection that included gyrinids is presumed lost, we designated a male specimen from New Jersey as the neotype. This specimen is deposited at the



Figs. 153–155. Ventral coloration of *Gyrinus*: **153,** *G. sayi*; **154,** *G. lecontei*; **155,** *G. maculiventris.*

AMNH. The neotype is pinned and labeled as follows: Olighants Mill, 28.4.1929, N.J., R.Sim. Aedeagus and parameres are attached to the body.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Distinctly sexually dimorphic. Females have evident, uniform, scale-like microreticulation; males have transverse microreticulation that is barely evident.

HABITAT INFORMATION: In Florida, *G. analis* was collected commonly from backwaters along the larger rivers and also from the smaller streams of Florida's western uplands (Young, 1954). Morrissette (1979) indicated that *G. analis* prefers slow moving portions of rivers. Label information indicates that 71.1 percent of collections of specimens were from lotic habitats (table 2).

DISTRIBUTION: Map 8. Records are from Florida west to Texas, north to Michigan.

Gyrinus maculiventris LeConte
Figures 16, 51, 90, 91, 155; Map 8

Gyrinus maculiventris LeConte, 1868: 368, 371. Régimbart, 1883: 154; 1902–03: 7. Ahlwarth, 1910: 19. Fall, 1922: 277, 292. Criddle, 1929: 115. Hatch, 1953: 241. Robert, 1963: 12, 26, 35. Gordon and Post, 1965: 27, 28. Ferkinhoff and Gundersen, 1983: 23, 36, 37.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) abdominal segments 4–7 medially black, but abruptly changing to orange laterally (fig. 155), (2) 11th stria located very close to outer margin of elytron in apical half, (3) elytron without evident microreticulation, (4) aedeagus in figures 90, 91, (5) body measurements: male length 5.0–5.9 mm, width 2.8–3.1 mm; female length 6.0–6.5 mm, width 3.1–3.4 mm.

Specimens are best recognized by their striking abdominal coloration (fig. 155). Another important distinguishing character is the position of the 11th stria which is positioned close to the outer margin of elytron in apical half.

TYPE INFORMATION AND TAXONOMIC NOTES: The type series consists of eight specimens, and is in the LeConte collection at MCZ. Two of the specimens are *G. aquiris,* and one is *G. consobrinus.* Fall (1922) did not clearly indicate a lectotype. Therefore, a male with the following data was designated as lectotype: a circular tan tag/ MCZ Type 6203 [red label]/ G. maculiventris Lec. [handwritten]. Aedeagus and parameres are glued on a small card beneath the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Label information indicates that 72.1 percent of collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 8. Records are from New Brunswick west to Alaska and south to West Virginia.

Gyrinus pleuralis Fall
Figures 71, 118; Map 6

Gyrinus pleuralis Fall, 1922: 277, 292, 293. Criddle, 1929: 115. Hatch, 1953: 242.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body long, body measurements: male length 6.3–7.0 mm, width 3.2–3.5 mm; female length 6.7–7.2 mm, width 3.4–3.8 mm, (2) abdominal segments 4–7 metallic black, 8th abdominal segment, epipleuron, hypomeron, and legs conspicuously and abruptly orange, (3) elytron with dense micropunctation (fig. 71), (4) aedeagus in figure 118.

G. pleuralis can be confused with *G. affinis* because the variation in body shape and color patterns overlap; however, the dense secondary punctation of *G. pleuralis* consistently will separate these two species.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is mounted on a point and carries the following labels: Laramie Wyo. H.F.W./ type pleuralis [handwritten]/ MCZ Type 23987 [red label]/. Aedeagus and parameres are glued on a card beneath the specimen.

SEXUAL DIMOSPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: *G. pleuralis* was recorded from a stream by Leech (1938). Habitat information from lables indicates that 58.6 percent of collections were from lotic habitats (table 2).

DISTRIBUTION: Map 6. Records are from Colorado west to central California and north to Alberta.

Gyrinus picipes Aubé
Figures 104, 105; Map 14

Gyrinus picipes Aubé, 1838: 694, 695. LeConte, 1868: 37, 369. Régimbart, 1883: 177, 178; 1902–03: 8. Ahlwarth, 1910: 24. Fall, 1922: 278, 298, 299. Criddle, 1929: 116. Robert, 1963: 14, 28, 38. Ferkinhoff and Gundersen, 1983: 25, 43.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron usually without noticeable microreticulation, (2) 11th stria close to outer margin of elytron in apical third, (3) abdominal segments 4–7 uniformly black, (4) aedeagus in figures 104, 105, (5) body measurements; male length 4.6–5.3 mm, width 2.6–2.9 mm; female length 5.6–6.2 mm, width 2.9–3.3 mm.

Gyrinus picipes are very similar to *G. sayi* and *G. dubius.* Table 7 summarizes the most

reliable nongenitalic characters for each species.

TYPE INFORMATION AND TAXONOMIC NOTES: The type was obtained from the Aubé collection in IRSB. The holotype is pinned and carries the following labels: 0/7913/ Amer. Bor. Coll. [. . . unreadable information . . .] Det. Regimb 82 [handwritten]/Type (red label)/Gyrinus picipes Aubé type pp. 694 Amer. Sep Oc Sitka [handwritten] (green label).

SEXUAL DIMOSPHIRM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Label information indicates that 68.5 percent of the collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 14. Records are from southern California to Alaska, east to southern Ontario.

Gyrinus dubius Wallis

Figures 62, 63, 106, 107; Map 14

Gyrinus dubius Wallis, 1926: 93, 94. Fall, 1931: 154. Robert, 1963: 14, 22, 32.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) abdominal segments 4–7 uniformly black, (2) elytron with uniform, barely noticeable microreticulation and dense micropunctation, (3) 11th stria close to outer margin of elytron in apical third, (4) legs darker at base, (5) aedeagus in figures 106, 107, (6) body measurements: male length 4.9–5.7 mm, width 2.7–3.0 mm; female length 5.5–5.7 mm, width 2.9–3.2 mm.

Specimens of this species are very similar to those of *G. picipes* and *G. sayi,* but separable from them by darker thoracic sterna and bicolored legs. Table 7 provides other reliable nongenitalic characters to separate these species.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Moderately sexually dimorphic. Females have uniformly distinct polygonal microreticulation; males have less noticeable microreticulation which is slightly to moderately transverse.

HABITAT INFORMATION: Morrissette (1979) indicated that *G. dubius* prefers running water habitats.

DISTRIBUTION: Map 14. Records are from Newfoundland, Quebec, Manitoba, and Saskatchewan.

Gyrinus sayi Aubé

Figures 60, 61, 92, 93, 153; Map 14

Gyrinus sayi Aubé, 1838: 698–700. Régimbart, 1883: 170, 171; 1902–03: 8. Ahlwarth, 1910: 24. Brinck, 1960: 79.

Gyrinus lugens LeConte, 1868: 369, 372. Régimbart, 1883: 176, 177; 1902–03: 3. Fall, 1922: 299, 300. Ochs, 1930: 136, 137. Hatch, 1953: 241, 242. Sanderson, 1982: 10, 36. Ferkinhoff and Gundersen, 1983: 25, 42.

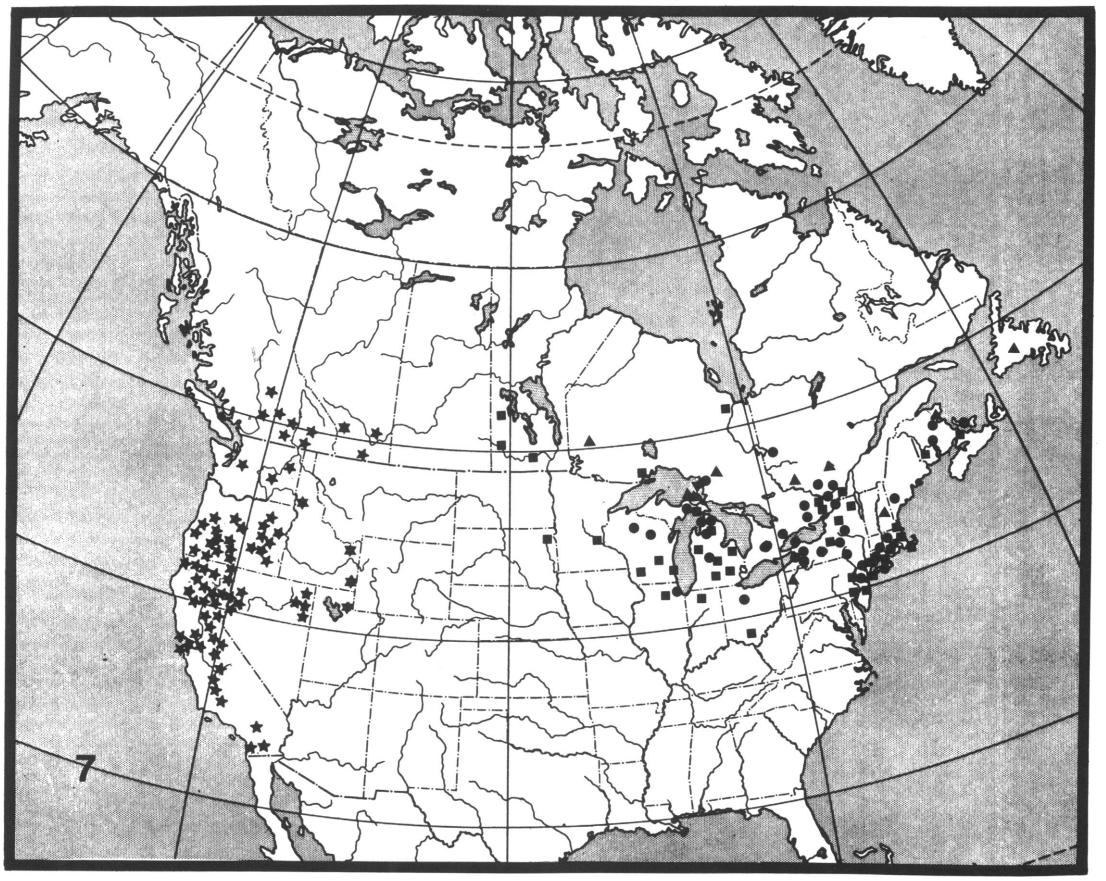
Gyrinus falli: Notman, 1919: 131, 132.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body long and broad, body measurements: male length 5.5–6.4 mm, width 2.8–3.2 mm; female length 5.8–6.6 mm, width 3.2–3.6 mm, (2) elytron with uniform and distinct microreticulation (fig. 61), (3) 11th stria close to outer margin of elytra in apical third, (4) abdominal segments 4–7 uniformly black (fig. 153), (5) aedeagus in figures 92, 93.

This species is confused primarily with *G. picipes* and *G. dubius* and aedeagal examination usually is necessary for conclusive identification. However, some reliable nongenitalic characters which distinguish specimens of these species are provided in table 7.

TYPE INFORMATION AND TAXONOMIC NOTES: Fall (1922) synonymized *G. falli* Notman with *G. lugens* LeConte. Subsequently, Brinck (1960) synonymized *G. lugens* with *G. sayi* Aubé. The type specimen of *G. sayi* Aubé is in the Gory collection at BMNH. The lectotype was designated by Brinck (1960). That specimen, which is a female, is pinned on a yellow card and carries the following labels: Lectotype [purple-circular label]/ G. sayi Aubé/ Coll. Gory, N. America [handwritten]/ Gyrinus sayi, Amer Bor Gory/ 6756/ LECTOTYPUS P. Brinck designativ 1955/ Gyrinus lugens auct. P. Brinck det. 1956 [handwritten]/.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Moderately sexually dimorphic. Microreticulation of females is evidently impressed and moderately transverse. Microreticulation in males is less impressed and transverse sculpticells are more elongate than in females.



Map 7. Distribution in North America of *G. aquiris* (■), *G. consobrinus* (★), *G. gehringi* (▲), and *G. lecontei* (●) based on species examined.

HABITAT INFORMATION: Robert (1955) and Morrissette (1979) indicated that *G. sayi* is found on all water surfaces. In New Jersey, we collected *G. sayi* at the edges of slow-moving streams. Frost found individuals of *G. sayi* in both lakes and rivers, but the number of individuals was higher in rivers (Fall, 1922). Label information indicates that 65.3 percent of collections of specimens were from lentic habitats (table 2).

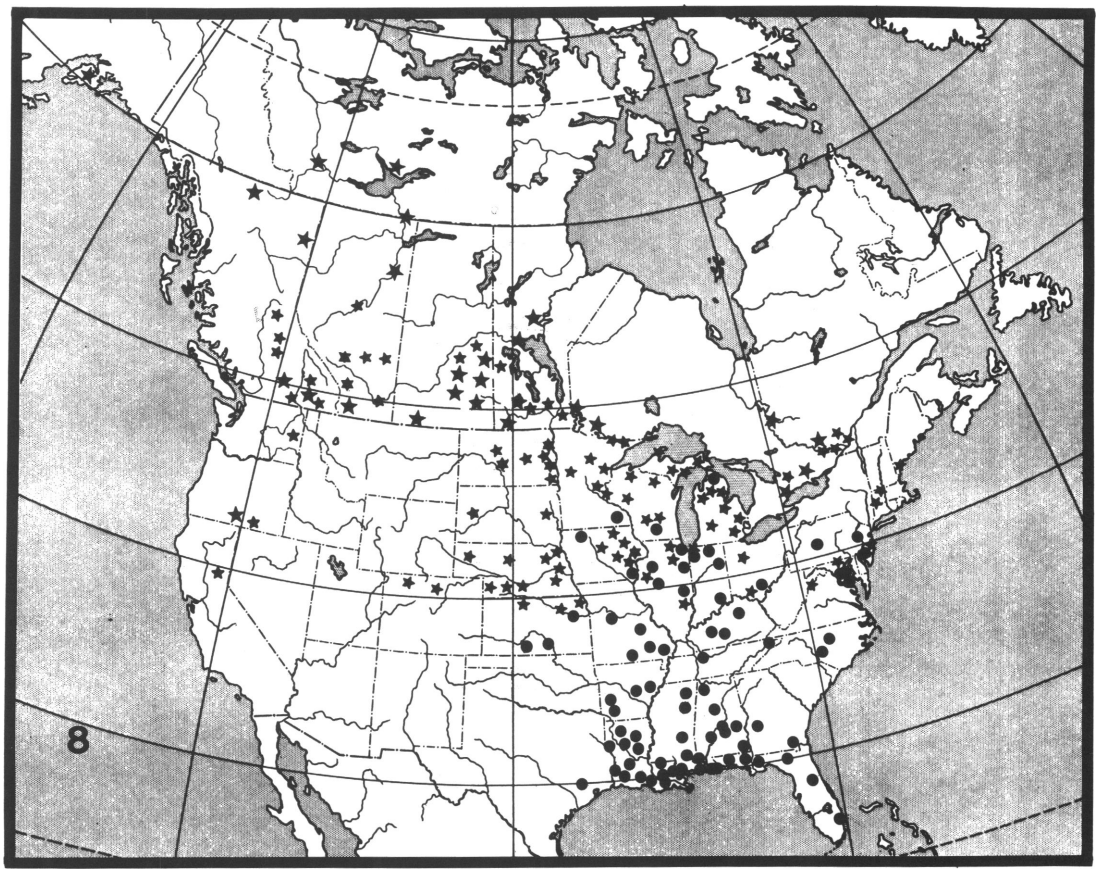
DISTRIBUTION: Map 14. Records are from Newfoundland west to the Northwest Territories, and south to New Jersey.

Gyrinus gehringi Chamberlain
Figures 48, 96–98; Map 7

Gyrinus gehringi Chamberlain, 1929: 247–249. Fall, 1931: 154. Robert, 1963: 10, 23, 33. Ferkinhoff and Gundersen, 1983: 23, 36.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) 11th stria close to outer margin of elytron in apical third, (2) ventral surfaces uniformly reddish, (3) elytral microreticulation barely noticeable at 50×, (4) aedeagus in figures 96–98, (5) body measurements: male length 5.8–6.2 mm, width 3.1–3.5 mm; female length 6.1–6.6 mm, width 3.5–3.8 mm.

G. gehringi is extremely similar to *G. lecontei* and genitalic examination is essential for conclusive identification. The aedeagus is more gradually tapering and more slender in males of *G. lecontei.* The color of the aedeagus is also different. It is uniformly reddish in males of *G. gehringi,* while in males of *G. lecontei* the aedeagus and parameres are medially darker. *G. gehringi* also resembles *G. aquiris* and *G. consobrinus.* The characters



Map 8. Distribution in North America of *G. maculiventris* (★), and *G. analis* (●) based on species examined.

presented in table 6 and locality information are most helpful in recognizing these species.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Slightly sexually dimorphic. Females have uniform, distinctly transverse microreticulate sculpture, which is slightly less distinct in males.

HABITAT INFORMATION: Robert (1955) indicated that *G. gehringi* was more likely to be found in eutrophic, rather than dystrophic, habitats. Morrissette (1979) collected *G. gehringi* from glacial lakes.

DISTRIBUTION: Map 7. Records are from New Hampshire, Pennsylvania, Michigan, Quebec, Ontario, and Newfoundland.

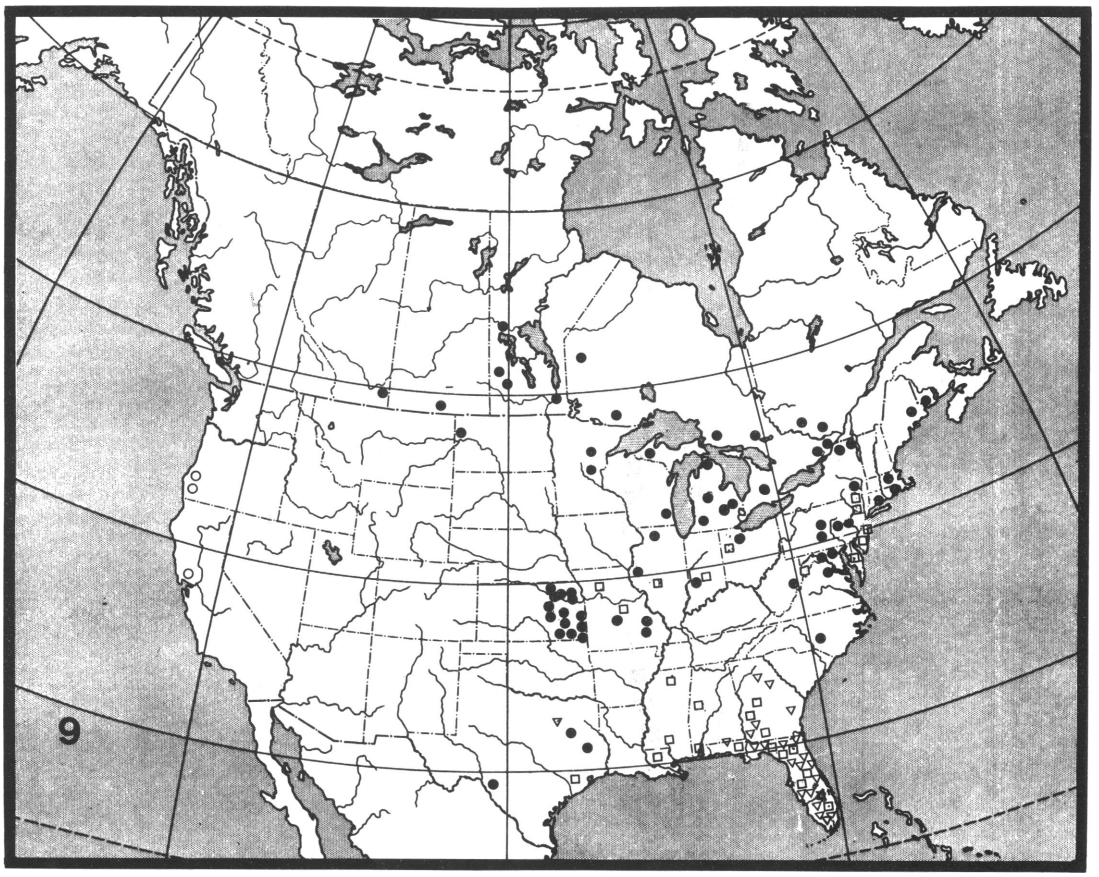
Gyrinus lecontei Fall

Figures 50, 67, 94, 95, 154; Map 7

Gyrinus lecontei Fall, 1922: 291. Criddle 1929: 115. Robert, 1963: 12, 25, 34. Gordon and Post, 1965: 28. Ferkinhoff and Gundersen, 1983: 23, 34.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) body long and broad, body measurements: male length 5.1–5.7, width 2.8–3.2 mm; female length 5.5–6.2, width 3.0–3.6 mm, (2) 11th stria close to outer margin of elytron in apical third, (3) ventral surface medially brownish with lateral areas orange or reddish (fig. 154), (4) elytron with microreticulation barely noticeable, and sparse micropunctation, (5) aedeagus in figures 94, 95.

G. lecontei, G. gehringi, G. aquiris, and *G. consobrinus* are very similar based on external characters and aedeagal examination usually is necessary for conclusive identification. However, the most reliable nongenitalic characters are provided in table 6.



Map 9. Distribution in North America of *G. elevatus* (▽), *G. aeneolus* (●), *G. woodruffi* (□), and *G. rugosus* (○) based on specimens examined.

TYPE INFORMATION AND TAXONOMIC NOTES: The holotype is a male specimen in the Fall collection at MCZ. It is pinned and carries the following labels: C. A. Frost, Sherborn, Mass, XI.18.17/ aquiris or L. [handwritten]/ N.B. 10.10.58 [handwritten]/ type lecontei [handwritten]/ MCZ Type 23984 [red label]/. Aedeagus and parameres are glued on a small card just beneath the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: Slightly sexually dimorphic. In females, microreticulation is lightly impressed, moderately transverse, and uniformly evident. In males, it is visible only posteriorly as extremely fine oblique transverse lines.

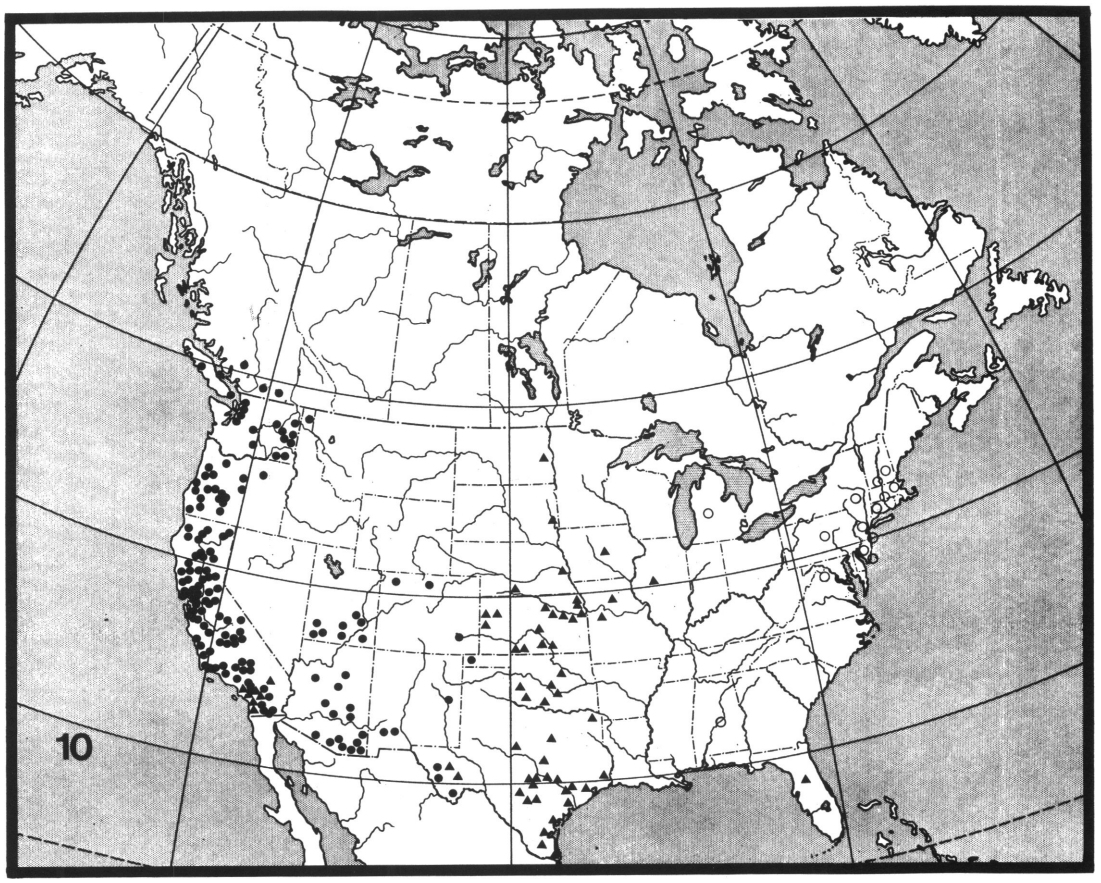
HABITAT INFORMATION: Robert (1955) and Morrissette (1979) indicated that *G. lecontei* was collected from small, deep ponds and less frequently from lakes in Quebec. Label information indicates that 60 percent of collections of specimens are from lentic habitats (table 2).

DISTRIBUTION: Map 7. Records are from New Brunswick west to Ontario and south to New Jersey.

Gyrinus aquiris LeConte
Figures 115–117; Map 7

Gyrinus aquiris LeConte, 1868: 368, 371. Régimbart, 1883: 152; 1902–03: 7. Ahlwarth, 1910: 15. Blatchley, 1910: 238, 239. Fall, 1922: 277, 290, 291. Criddle, 1929: 115. Robert, 1963: 12, 20, 31. Sanderson, 1982: 36. Ferkinhoff and Gundersen, 1983: 23, 35.

DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron



Map 10. Distribution in North America of *G. marginellus* (○), *G. plicifer* (●), and *G. parcus* (▲) based on specimens examined.

without noticeable microreticulation, (2) 11th stria close to outer margin of elytron in apical third, (3) abdominal segments 4–7 reddish brown with sides reddish or orange, (4) aedeagus in figures 115–117, (5) body measurements: male length 4.9–5.6 mm, width 2.8–2.9 mm; female length 5.2–5.9 mm, width 2.9–3.1 mm.

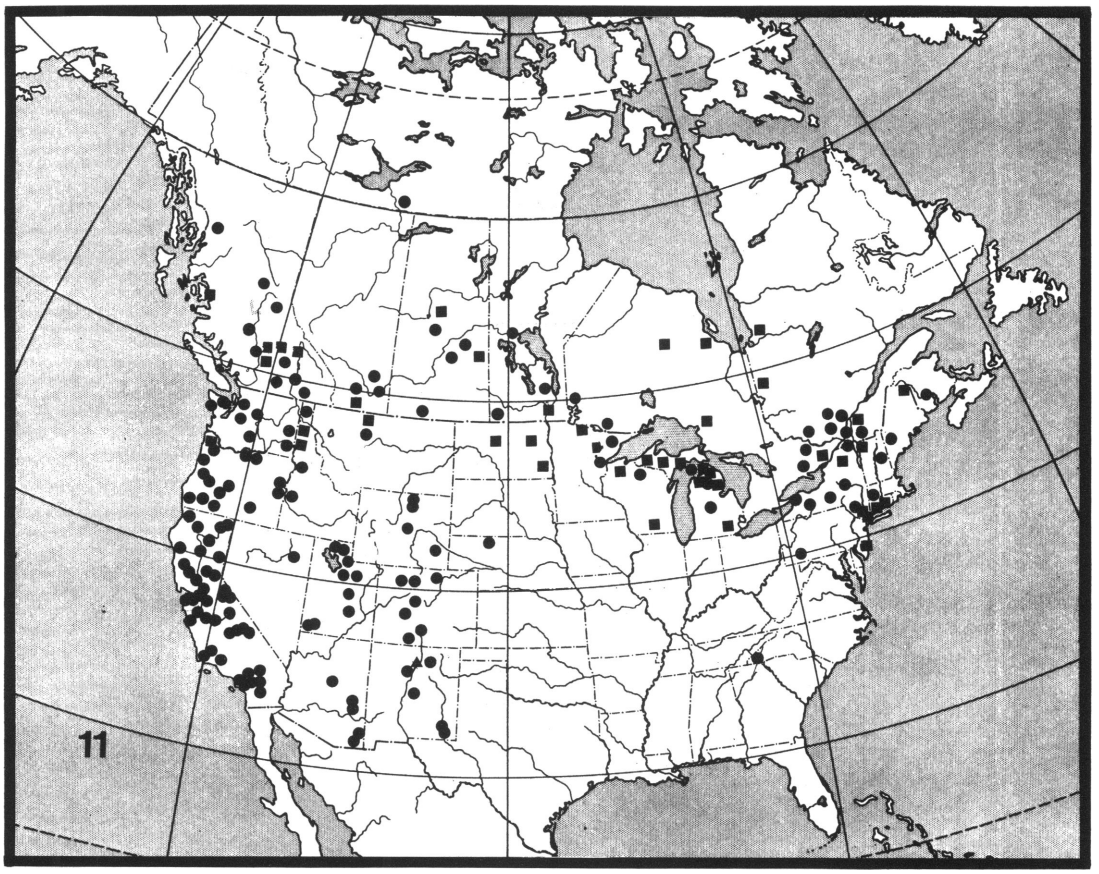
G. aquiris is most similar to *G. consobrinus,* and also can be confused with *G. lecontei* and *G. gehringi* based on external characters. The most reliable nongenitalic characters to separate members of these species are presented in table 6.

TYPE INFORMATION AND TAXONOMIC NOTES: The type series consists of four specimens, and is in the LeConte collection at MCZ. Two of the specimens in the type series are *G. bifarius.* Fall (1922) indicated that the type bore a round, pink locality label. However, there are two female specimens, each with such a pink label, in the collection. Fall did not indicate which one of these was the lectotype. Therefore, we designated the female that carries the following labels as lectotype: pink circular tag/ MCZ Type 6102 [red label]/ G. aquiris Lec. [handwritten].

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Blatchley (1910) found individuals of this species in low meadow ponds in Indiana. Morrissette (1979) found specimens in ponds and lakes invaded by aquatic plants. Label information, though scarce, indicates that 80 percent of the collections of specimens were from lentic habitats (table 2).

DISTRIBUTION: Map 7. Records are from



Map 11. Distribution in North America of *G. bifarius* (●), *G. conifinis* (■), and *G. obtusus* (▲) based on specimens examined.

Nova Scotia west to Manitoba and south to Ohio.

Gyrinus consobrinus LeConte
Figures 113, 114; Map 7

Gyrinus consobrinus LeConte, 1852: 209; 1868: 268, 371. Régimbart, 1883: 153, 154; 1902–03: 7. Ahlwarth, 1910: 17. Fall, 1922: 277, 289, 290. Criddle, 1929: 115, 116. Ochs, 1930: 136. Hatch, 1953: 241.

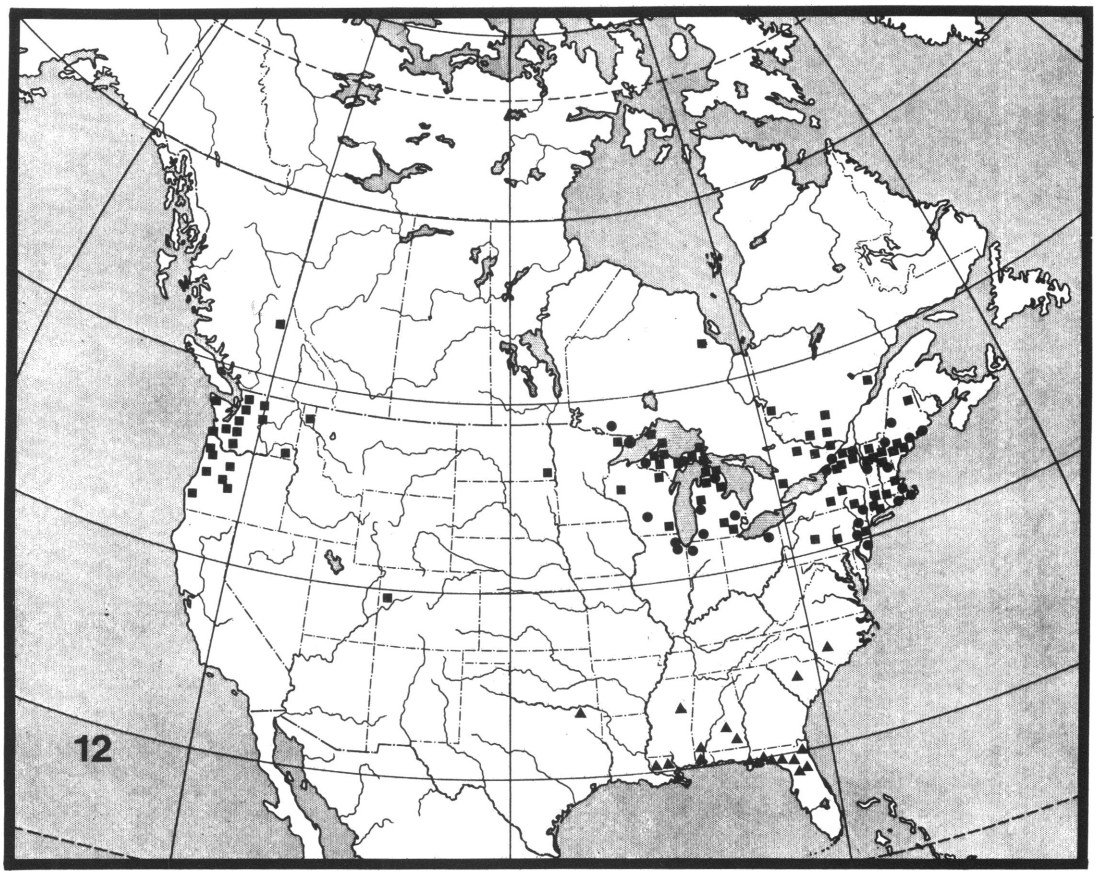
DIAGNOSIS: This species is separated from all other North American species by the following combination of characters: (1) elytron without microreticulation, (2) abdominal segments 4–7 black or dark brown with red areas on sides, (3) 11th stria close to outer margin of elytron in apical third, (4) aedeagus in figures 113, 114, (5) body measurements: male length 4.9–5.5 mm, width 2.5–2.7 mm; female length 5.6–5.9 mm, width 2.8–3.3 mm.

G. consobrinus is extremely similar to *G. aquiris*. Table 6 presents the most reliable nongenitalic characters to separate them.

TYPE INFORMATION AND TAXONOMIC NOTES: The type series consists of nine specimens and is in the LeConte collection at MCZ. One male carries a label (S.Fr.). That specimen was indicated by Fall, which constituted a lectotype designation. It is mounted on a point and carries the following labels: [a circular red tag]/ MCZ Type 6100 [red label]/ G. consobrinus S.Fr [handwritten]. Aedeagus and parameres are glued on a card beneath the specimen.

SEXUAL DIMORPHISM OF ELYTRAL MICROSCULPTURE: None.

HABITAT INFORMATION: Label information



Map 12. Distribution in North America of *G. dichrous* (●), *G. latilimbus* (■), and *G. pachysomus* (▲) based on specimens examined.

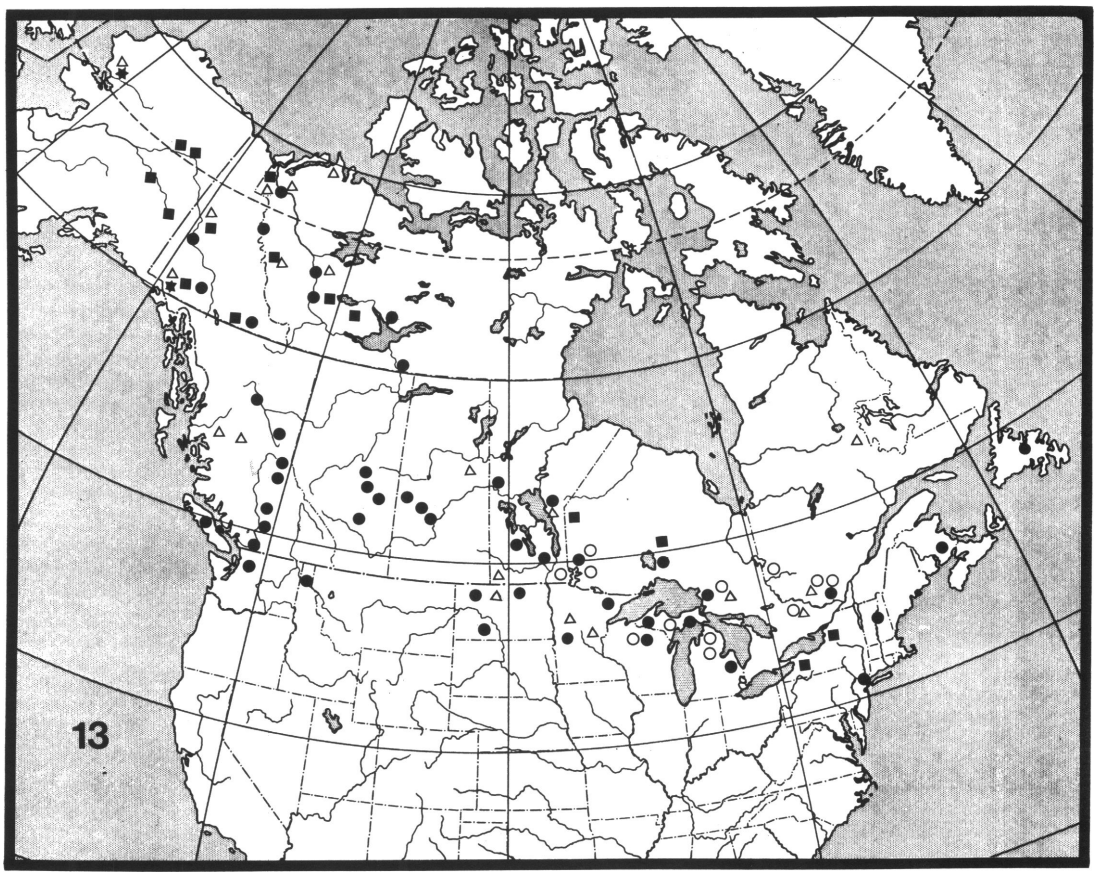
indicates that 65.6 percent of collections of specimens were from lotic habitats (table 2).

DISTRIBUTION: Map 7. Records are from Utah to California, north to British Columbia.

PHYLOGENY

GENERIC-LEVEL PHYLOGENY: There have been several substantial studies on gyrinid relationships based on structure (Hatch, 1925; Ochs, 1926–27; Balfour-Browne, 1950; Brinck, 1955; Larsén, 1966). The purpose of the generic-level analysis herein is to evaluate data from past studies in order to more completely understand the phylogenetic position of *Gyrinus* within Gyrinidae. To achieve this, each genus is analyzed by using the characters discussed in Hatch, and then the characters of Hatch combined with those of Balfour-Browne (1950), Brinck (1955), and Larsén (1966).

The phylogeny of gyrinids presented here differs from previous studies in two main aspects: (1) this study utilized computer-assisted cladistic analysis that allows determination and evaluation of the number of equally parsimonious trees, and (2) whenever possible, character states of the recently discovered primitive genus *Spanglerogyrus* (Folkerts, 1979) are included here. Members of *Spanglerogyrus* have remarkable plesio-



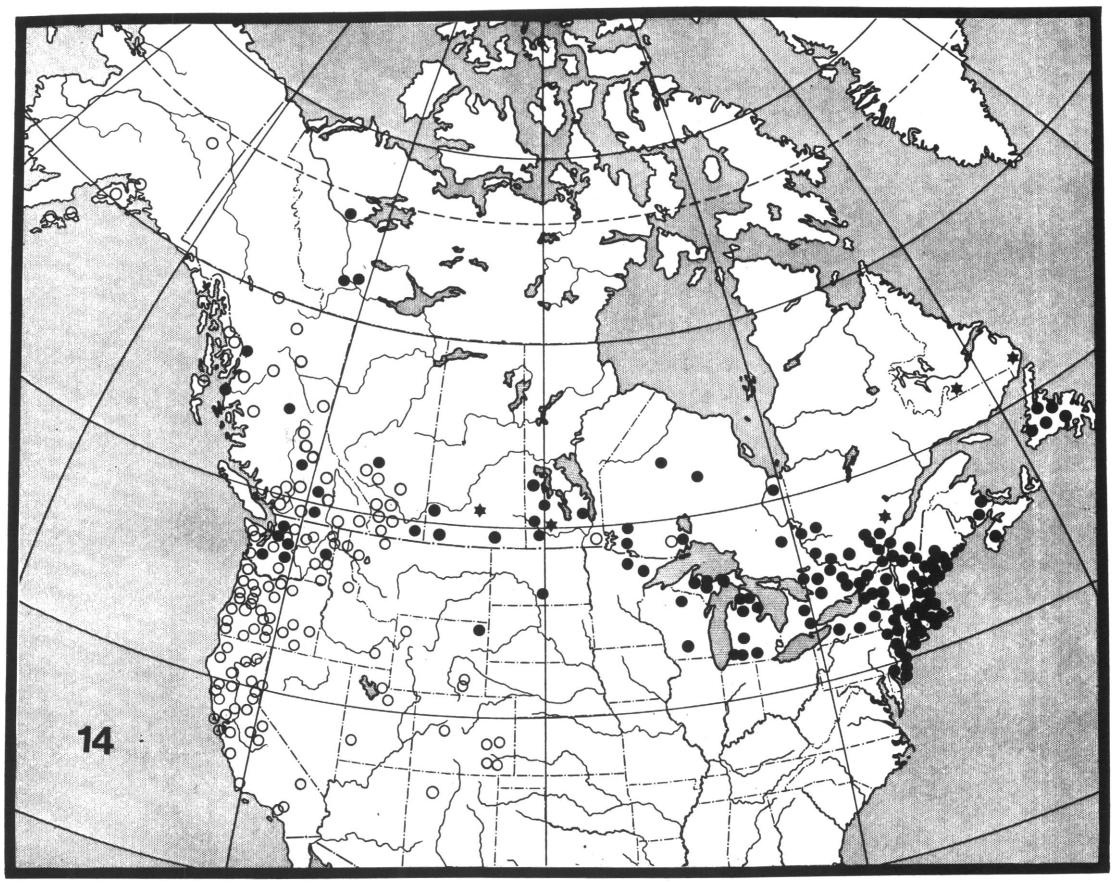
Map 13. Distribution in North America of *G. impressicollis* (○), *G. pectoralis* (●), *G. aeratus* (■), *G. wallisi* (△), and *G. marinus* (★) based on specimens examined.

morphic features and probably represent the sister lineage to all other gyrinids. The most obvious plesiomorphic characters are (1) narrowly divided eyes, (2) meso and metatibia and tarsi that are not nearly as modified for swimming, (3) small size, and (4) divided apical (8th) sternum. Because of its primitive features, *Spanglerogyrus* is used as a natural outgroup (Watrous and Wheeler, 1981) in the generic analysis herein.

Hatch (1925), Ochs (1926–27), Omer-Cooper (1934), Balfour-Browne (1950), and Brinck (1955) recognized at least three major groups within Gyrinidae: (1) Orectochilini (*Orectochilus, Orectogyrus, Gyretes*), (2) Enhydrini (*Dineutus, Macrogyrus, Enhydrus, Andogyrus, Porrorhynchus*), and (3) Gyrinini (*Aulonogyrus, Gyrinus*). These authors generally agreed on the "derived" nature of orectochilines. However, Hatch and Omer-Cooper believed that Gyrinini were more derived than Enhydrini while Ochs (1926–27) suggested that Gyrinini was the least derived tribe of the family. Studies by Balfour-Browne (1950) and Larsén (1966) supported Ochs' view.

Hatch (1925) examined 33 external and internal characters of the head, thorax, and abdomen for representatives of 10 of the 11 currently recognized gyrinid genera (*Spanglerogyrus* was not known at the time). He stated that orectochilines were more closely related to the relatively "primitive" enhydrines than to gyrinines. Despite the fact that gyrinines were more highly "evolved" than orectochilines, Hatch recognized that the latter lineage had many derived features (presumably because it adpated to fast-moving water).

Ochs (1926–27) examined body size, form,



Map 14. Distribution in North America of *G. sayi* (●), *G. picipes* (○), and *G. dubius* (★) based on specimens examined.

elytral microreticulation, sexual dimorphism, and habitat in about 90 members of Dineutini, and proposed a phylogeny for the tribes of gyrinids. He agreed with Hatch that although orectochilines had many derived features, they were not as evolved as enhydrines. However, in contrast to Hatch, Ochs believed that Orectochilini and Enhydrini were not more closely related to each other than either was to Gyrinini.

Compared to those of Hatch (1925) and Ochs (1926–27), the study by Omer-Cooper (1934) was rather superficial. He only discussed characters that were previously analyzed by Ochs. Omer-Cooper's conclusions were similar to those of Hatch. He believed that both orectochilines and gyrinines were very derived and that *Gyrinus* was the most highly "evolved" gyrinid of all.

Balfour-Browne (1950) studied seven characters involving mainly wing venation, but also including genital, thoracic, and abdom-

TABLE 6
Diagnostic Character States for Specimens of *Gyrinus lecontei, G. gehringi, G. aquiris, G. consobrinus*

	lecontei	*gehringi*	*aquiris*	*consobrinus*
Width	2.8–3.2 mm	3.1–3.5 mm	2.8–2.9 mm	2.5–2.7 mm
Elytral margin	wider than interval 11	wider than interval 11	equal to interval 11	equal to interval 11
Ventral coloration	brown and red	uniformly red	brown and red	brown and red
Distribution	eastern	eastern	eastern	western

TABLE 7
Diagnostic Character States for Specimens of *Gyrinus dubius, G. picipes, G. sayi*

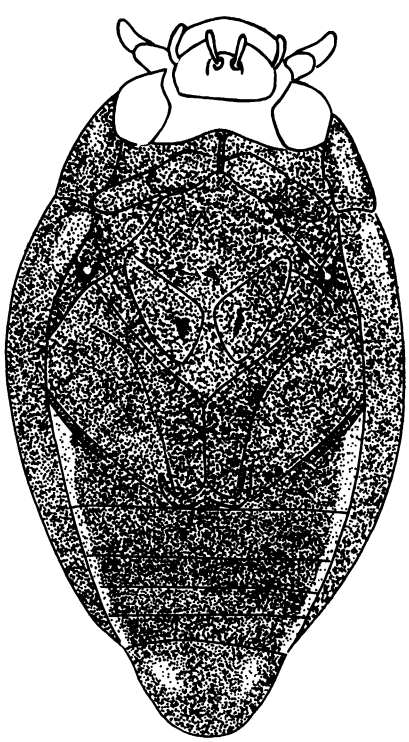
	dubius	*picipes*	*sayi*
Elytral micropunctation	dense	sparse	sparse
Elytral microreticulation	present uniform	absent or not uniform	present uniform
Leg color	darker at base	uniformly red	uniformly red
Locality	western	western	eastern and western
Elytral microreticulation, ♀	more distinct	same as male	more distinct

inal structure. He concluded that orectochilines were more "advanced" than either enhydrines or gyrinines.

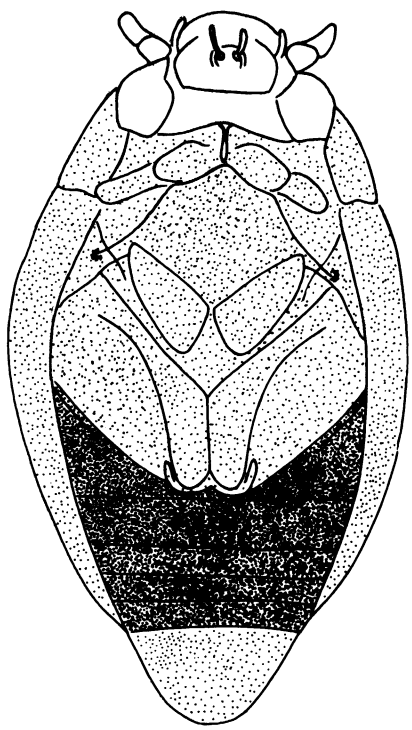
Brinck (1955) compared the female and male reproductive systems (18 characters) of Ethiopian and Swedish species of four genera: *Dineutus* (Enhydrini), *Aulonogyrus* and *Gyrinus* (Gyrinini), and *Orectogyrus* (Orectochilini). Based on analysis of representatives of these genera, he thought that members of Gyrinini were more "generalized" than members of Enhydrini. He also proposed that, in spite of superficial differences, enhydrines were most closely related to orectochilines.

Larsén (1966) analyzed 35 internal and external characters involving thoracic musculature and associated sclerites. His results suggested that *Dineutus* (Enhydrini) and Orectochilini were more closely related to each other than either was to Gyrinini and that *Gyrinus* and *Aulonogyrus* together formed a sister group to all other gyrinids.

Beutel (1989) studied external and internal structures of the head of *Spanglerogyrus al-*



156



157

Figs. 156, 157. **156,** *G. pugionis*; **157,** *G. dichrous.*

TABLE 8

Characters Used for the Phylogeny of Genera of Gyrinidae Characters 1-29 from Hatch, 30-55 from Brinck and Balfour-Browne, and 56-80 from Larsén

	Plesiomorphic	Apomorphic
Head		
1) corpotentorium	absent	present
2) dorsal eyes	anterior to ventral eyes	not anterior to ventral eyes
3) exoculata	not evident	1) evident close to antecava 2) evident distant from antecava
4) antecava	attains frontal ridge	not attaining frontal ridge
5) pseudofrontal ridge	absent	present
6) antennal flagellum	9 segments	1) 8 segments 2) 7 segments 3) 6 segments
7) mandible	proxomedial tooth not evident	1) evident, reduced 2) evident, medially pointed 3) evident, pointed
8) galea	present	absent
34) labrum	transverse/rectangular	elongate/conical
35) larval clypeus	?	1) 2–4-toothed 2) 1-toothed 3) none
Pronotum		
9) pronotum	with transverse impression or color mark	without transverse impression or color mark
10) prosternum	anteromedially not elevated	anteromedially elevated
53) prosternal process	contacting mesosternum	not contacting mesosternum
31) pronotal bristles	absent	present
49) scutellum	exposed	not exposed
11) scutellum	broadly triangular	1) narrowly triangular 2) bilobed
65) anterior longitudinal muscle of prothorax	absent	present
66) pleural remotor of coxa of prothorax	present	absent
67) sternal remotor of coxa of prothorax	present	absent
68) intersegmental muscles	simple	divided
80) tergosternal muscle	not divided	divided
Mesonotum		
18) mesonotum anteriorly	not compressed	compressed
16) mesoprephragma	bilobed	1) bifurcate 2) simple
17) mesoscutum	divided	not divided
55) tergal depressor of trochanter/episternal and sternal depressor	same length	smaller
56) episternal and epimeral branches of pleural muscles	same size	small or absent
Metanotum		
13) metafurca	bilobed	fused
77) episternum	large, broadly triangular	1) parallel, narrow 2) parallel, narrower
26) posterior medial projection of metascutum	absent	present

TABLE 8—(*Continued*)

	Plesiomorphic	Apomorphic
58) tergal pleural muscle	not reduced	reduced
59) metathoracic axillary muscle	present	reduced or absent
60) basalar disk	not reduced	reduced
61) coxabasalar and tergabasalar	present	1) reduced 2) absent
62) epimerosubalar muscle	reduced or absent	developed
63) sternoepisternal muscle	absent	present
64) tergocoxal muscle	present	absent
Protarsi		
33) male protarsomere	not broad	broad
Mesocoxa		
12) mesocoxae	close	1) distant moderately 2) distant widely
69) mesocoxae	movable	fused
70) meso and meta tibia	without rows of cuticular columnae	with rows of cuticular columnae
71) tibial airsacs of meso and meta legs	without accessory airsacs	with accessory airsacs
72) 4th mesotarsal seg.	narrow parallel	wide semilunar
57) tergal remotor of coxa	smaller than coxasubalar	larger than coxasubalar
Metacoxa		
75) metacoxal walls of coxa	anteriorly fused	completely fused
14) metacoxae anteriorly	not oblique	1) less oblique 2) more oblique
15) 5th tarsomere of mid and hind legs	not evident	evident
73) basicostal elements of metalegs	without internal disk	with an internal disk
74) basicosta of metalegs	lower at lateral coxal margin	higher at lateral coxal margin
Elytra		
19) dorsal pubescence	present	absent
25) elytral apex	not evenly rounded	evenly rounded
37) suture of elytra	margined	not margined
50) elytral striae or groove	absent	1) present, less distinct 2) present, more distinct
Abdomen		
20) pleural seg.	chitinized	1) less membranous 2) more membraneous
21) basal tergal seg.	chitinized	1) membranous
22) last abdominal seg.	circular	conical
23) sternasuture	entirely present	1) reduced 2) absent
24) apodemes of 4th sternite	absent	present
30) longitudinal hairs of last sternite	absent	present
32) metacoxal edge/4th abdominal seg.	very close or touching	less distant more distant
Wing		
27) tip of cubital vein	absent	present
28) wedge cell	absent	present
29) vein $3A_2$	absent	present

TABLE 8—(*Continued*)

	Plesiomorphic	Apomorphic
51) horizontal oblangum cell/from R-C4	close to base	distant from base
54) average radiocubital angle	57°	44–44.50°
Male genitalia		
38) aedeagal apex	not notched	notched
39) parameres	flattened, with apical fringe of setae	triangular, with apical and lateral fringe of setae
40) aedeagus	distinctly sclerotized	weakly sclerotized
41) aedeagus/parameres articulation	?	1) M + 2Ant1 + 2Post1 2) 1M + 2Ant1 3) Ant1
42) aedeagus/ductus	attached	not attached
78) testis shape	simple sausage	thick spiral
Female genitalia		
36) ovipositor projection	not evident	1) evident, short 2) evident, long
43) vagina	sac shaped	elongate
44) bursa copulatrix	bending upwards	not bending upwards
45) accessory gland shape	elongate	oval or rounded
46) accessory glands opening in	bursa copulatris	vagina
47) receptaculum seminis	separate	not separate
48) receptaculum seminis	threadlike	saclike
52) ovipositor/valvifers	equal in length	valvifer longer
79) vas deferens consist of	one part	two parts

biventris. His phylogenetic analysis points toward a sister-group relationship between Orectochilini and Gyrinini.

Our first analysis was conducted using only characters from Hatch (1925). The second analysis was based on information in Hatch, Balfour-Browne, Brinck, and Larsén, collectively (see tables 8 and 10). Unfortunately, a number of character states discussed by these four taxonomists (especially Larsén) could not be determined for several genera, particularly *Spanglerogyrus*. Therefore, missing characters are more of a problem in the second analysis.

Reanalysis of Hatch's characters with *Spanglerogyrus* as an outgroup produced six trees. A strict consensus tree of these six genera is shown in figure 158. The consensus tree reveals three major monophyletic groups (1) Orectochilini (*Orectogyrus, Gyretes,* and *Orectochilus*), (2) Enhydrini (*Dineutus, Andogyrus, Macrogyrus, Porrorhynchus,* and *Enhydrus*), and (3) Gyrinini (*Gyrinus, Aulonogyrus*). This corresponds to previous classifications; however, each of the above three clades has been variously recognized at tribal or subfamily level (Régimbart, 1883; Ahlwarth, 1910; Ochs, 1924; Hatch, 1925; Blackwelder, 1944; Brinck, 1955). Within Orectochilini, *Orectochilus* is the sister group to *Orectogyrus* and *Gyretes*. Enhydrini is polychotomous; however, *Dineutus* and *Enhydrus* form a sister group within this polychotomy.

This reanalysis can be evaluated based on the number of synapomorphies, which is the simplest and probably the most objective measure of a hypothesis of monophyly; i.e., the more the better. However this approach should be tempered with other considerations. For example, character gains are regarded as more important than character losses. Also useful is the consistency index (CI) of each character. The CI is a measure of homoplasy and is calculated by dividing the range of a character by the actual length (in terms of character state changes) and varies from 0 to 1 (perfectly consistent, i.e., no homoplasy). A hypothesis of monophyly is considered more conclusive if associated syn-

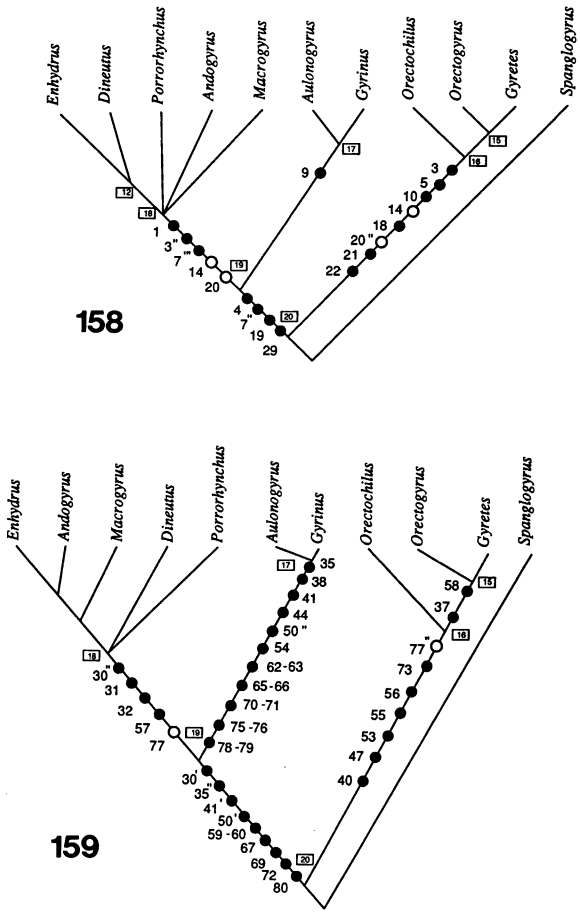
apomorphies have a high CI value (equal to one). For example, the common ancestor to Orectochilini (between nodes 16 and 20) has eight synapomorphies (fig. 158); six of these have CI = 1. Other clades are less conclusive; for example, the common ancestor to Gyrinini (nodes 17–19) has five synapomorphies, but only one synapomorphy has a CI = 1. A few branches have no synapomorphies with CI = 1, e.g., the common ancestor to *Orectogyrus* and *Gyretes,* the common ancestor to *Enhydrus* and *Dineutus.*

In the first analysis, 63 percent of the synapomorphies have a CI = 0.667 to 1, 17 percent a CI = 0.5, and 20 percent a CI = 0.375. Twenty-one percent of the homoplasious characters evolved twice, 24 percent three times, and 14 percent four or five times. The weakest branches of this analysis are the common ancestor to *Enhydrus–Dineutus,* and to *Orectogyrus–Gyretes* because all characters evolved three or more times. Reduction and/or losses occurred in nine of the 29 characters analyzed. Character losses are fewest (20%) in the common ancestor to Enhydrini and Gyrinini (nodes 19–20). Character losses are most common (60%) in the common ancestor to Gyrinini.

When Hatch's characters were combined with those of Balfour-Browne (1950), Brinck (1955), and Larsén (1966), two equally parsimonious trees were found. The strict consensus tree of this analysis (fig. 159) agrees with the former (fig. 158). However, one additional subgroup was recognized which was not resolved in the former analyses: *Macrogyrus* as the sister group to *Enhydrus* and *Andogyrus.*

This second analysis further substantiates the tree based only on Hatch's data. For example, in the former tree (fig. 158), the common ancestor to Gyrinini (nodes 17–19) had only one synapomorphy with CI = 1. In the latter tree (fig. 159) the same branch is justified with 19 synapomorphies of which 16 have a CI = 1. Furthermore, the common ancestor to *Orectochilus* and *Gyretes* (nodes 15–16) is suggested by two synapomorphies each with CI = 1 in the second analysis.

The two consensus trees (from the first and second analyses) uniformly indicate several features: (1) Within Gyrininae, Orectochilini is the sister to Gyrinini and Enhydrini. This



Figs. 158, 159. **158.** Consensus tree 1 for the phylogeny of the genera of Gyrinidae based on characters in Hatch (1925). (●), character with consistency index (CI) = 1, (○), character with CI from 0.667 to 0.999. Nodes without indicated synapomorphies are justified by synapomorphies with CI < 0.5. Numbers inside squares are node numbers. **159.** Concensus tree 2 for the phylogeny of the genera of Gyrinidae based on characters in Hatch (1925), Balfour-Browne (1950), Brinck (1955), and Larsén (1966), see fig. 158 for characters of Hatch (1925). (●), character with consistency index (CI) = 1, (○), character with CI from 0.667 to 0.999. Nodes without indicated synapomorphies are justified by synapomorphies with CI < 0.05. Numbers inside squares are node numbers.

phylogenetic resolution is different from any of the hypotheses suggested before. (2) Within Orectochilini, *Orectochilus* is the sister to *Orectogyrus* and *Gyretes.* (3) Within Gyrinini, *Gyrinus* and *Aulonogyrus* are sisters, but

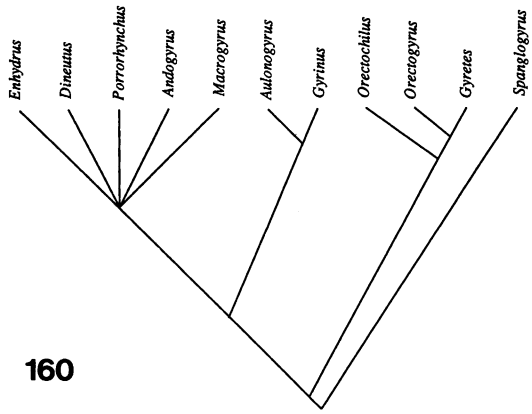


Fig. 160. Final consensus tree for the phylogeny of the genera of Gyrinidae. See trees 158 and 159 for synapomorphies.

Aulonogyrus is more derived (has more synapomorphies). (4) Enhydrini is polychotomous.

In summary, this phylogenetic analysis suggests three distinct monophyletic groups (fig. 160) which correspond to the three tribes Gyrinini (*Gyrinus* and *Aulonogyrus*), Enhydrini (*Dineutus, Macrogyrus, Andogyrus, Enhydrus, Porrorhynchus*), and Orectochilini (*Orectochilus, Orectogyrus, Gyretes*). These tribes were designated by Régimbart as early as 1883. Ahlwarth (1910) raised each of these three groups to subfamily level and this subfamilial status has been favored by Ochs (1924), Blackwelder (1944), and Brinck (1955). However, Hatch (1925) accepted only two subfamilies: Gyrininae (Gyrinini) and Orectochilinae (Orectochilini and Enhydrini). Folkerts (1979) proposed a different classification scheme than any of the above. He recognized three tribes—Gyrinini, Orectochilini, and Enhydrini—under the subfamily Gyrininae, and the monobasic *Spanglerogyrus* within Spanglerogyrininae. We favor Folkerts' classification.

Because all the major lineages of Gyrininae are so highly derived, the utility of any of them as an outgroup for the phylogeny of the species of *Gyrinus* is questionable. *Spanglerogyrus* therefore is chosen as the outgroup for the phylogenetic analysis of species of *Gyrinus*. Studies by Steiner and Anderson (1981), and Beutel and Roughley (1988) also strongly support the importance of *Spanglerogyrus* for phylogenetic analysis of Adephaga. The plesiotypic nature of *Spanglerogyrus* plus the fact that it is still only two nodes away from *Gyrinus* makes it a particularly suitable outgroup for the species-level analysis.

SPECIES-LEVEL PHYLOGENY: The extreme similarity of members of *Gyrinus* has been noted by many authors (LeConte, 1868; Sharp, 1868; Fall, 1922; Ochs, 1926–27; Brinck, 1955; Ferkinhoff and Gundersen, 1983). Most of the similarity is probably the result of convergence induced by constraints of the surface-water habitat. This convergence seriously complicated the phylogenetic interpretation below. Some characters, e.g., male genitalia and coloration, probably are less affected by constraints of aquatic existence; this may explain why they were the most reliable characters in our analysis.

The characters used in this study are shown in tables 9 and 11. Characters 1–4, 6, 8, 10, 12, 15–17, 20–22 were discrete and binary and their polarity was determined rather easily by outgroup comparison. For more complex characters, transformation series were constructed. For some of these characters (e.g., 5, 7, 9, 11), we hypothesized rather simple, linear transformation series. For others we proposed more complex bidirectional transformation (characters 13, 14, 18, 19). For example, we hypothesized that the shape of the aedeagus (characters 18–19) in dorsal view evolved in two different directions from its ancestral evenly tapered aedeagal shape. One morphocline (character 18) included an increasingly constricted genitalic apex (figs. 75–84), and the other one (character 19) an increasingly expanded apex (figs. 136–142). Color of abdominal segments 4–7 was also coded as a rather complex transformation series. The first change in this series was from light (the ancestral state) to a medially infuscate condition. There were two evolutionary lines hypothesized from the medially infuscate state; one led to a distinctly bicolored condition (black and orange, see fig. 155) and the second through a progression of progressively more uniformly darker states (fig. 153).

Interpretation of multistate characters was further complicated by the fact that the character states were more continuous and tended to grade from one condition to the next. Because of these complications, we scaled all

TABLE 9
Characters Used for the Phylogeny of the Species of *Gyrinus*

	Plesiomorphic	Apomorphic
1) scutellum	not carinate	carinate
2) pronotal transverse line	parallel	curved
3) mesosternum	not emarginate anteriorly	emarginate anteriorly
4) mesosternum	not grooved medially	grooved medially
5) metepisternal ostiole	absent	1) small/medium 2) large
6) elytral margin	narrow	wide
7) 11th stria	partially or entirely marginal	entirely remote
8) lateral striae	not impressed or only slightly impressed	distinctly impressed
9) microreticulation	scalelike/polygon	1) moderately transverse 2) distinctly transverse 3) not evident
10) transverse striolate lines	absent	present
11) micropunctation	sparse	1) moderately dense 2) distinctly dense
12) elytral plica	absent	present
13) abdominal coloration 1	yellowish, sometimes yellowish brown medially	1) medially dark brown/black, sides with reddish areas 2) medially metallic black, sides with bright orange areas
14) abdominal coloration 2	yellowish, sometimes yellowish brown medially	1) medially dark brown/black, sides with reddish areas 2) medially black, sides very narrowly defined brownish-reddish areas 3) entirely black
15) leg coloration	not bicolored	bicolored
16) tarsal claw color	yellowish	blackish
17) aedeagal base	not broadened	broadened
18) aedeagal shape 1	evenly tapered narrowly rounded at tip	1) tapered, pointed at tip 2) narrowly constricted, pointed at tip 3) extremely distinctly contricted
19) aedeagal shape 2	evenly tapered	1) moderately constricted, rounded at tip 2) broadly constricted, or expanded
20) aedeagus dorsally	not membranous	membranous
21) aedeagus apically	convex	concave
22) aedeagal apex	not notched	notched

multistate characters to equalize the influence of multistate and binary characters. For example, elytral microreticulation (character 9) consists of four character states. With scaling, these states were coded as 0, 0.333, 0.666, and 1 instead of 0, 1, 2, and 3. Scaling is especially useful in cases involving more continuous characters which can be divided arbitrarily into any number of states (see Swofford, 1985).

Finally, we eliminated identical taxa. For example, *Gyrinus fraternus* and *G. ventralis*; *G. minutus* and *G. rockinghamensis*; *G. pernitidus* and *G. piceolus*; *G. aquiris* and *G. consobrinus*; and *G. wallisi, G. aeratus,* and *G. marinus* are identical pairs or triads of species and only one member of each pair or group was included in the analysis.

The first computer analysis, using all nonidentical taxa, indicated a minimum of 95 equally parsimonious trees. The only recourse to reduce the number of equally par-

simonious trees to a more manageable number was to eliminate some nearly identical taxa, in addition to identical taxa. Nearly identical taxa were defined as those taxa that differed in only one or two states of a continuous character. For example, two sister species, *G. aeneolus* and *G. woodruffi*, differ only in the size of the metepisternal ostiole. Other species pairs in this category are: *G. borealis* and *G. pugionis* (differ in abdominal coloration), *G. opacus* and *G. hoppingi* (differ in microreticulation), and *G. lecontei* and *G. gehringi* (differ in abdominal coloration and microreticulation). After eliminating these nearly identical taxa and using the 29 remaining species, three equally parsimonious trees were found.

MODIFICATIONS TO TREE: We used every means to make this analysis the most conservative phylogenetic hypothesis possible.

First, we used only branches with a minimum branch length greater than zero. This is not always obvious because when there are multiple equally parsimonious trees, some branches may vary in length from tree to tree. Even when minimum branch lengths are "0", the contree program (for calculating consensus trees) draws consensus trees that are fully dichotomously resolved. Therefore, the BL-RANGE option (an algorithm for determining the minimum and maximum possible lengths of each branch that may be obtained under the parsimony criterion) was used to inspect the range of lengths for each branch of each tree used to compute the consensus tree. If maximum branch length is zero, then there is no dichotomous resolution supported by the data. If only the minimum branch length is zero, at least some resolutions do, in fact, support a dichotomous resolution. However, we agree with Swofford (1985) that resolutions are less conslusive if a polychotomy is just as parsimonious as a dichotomy. By using the BL-RANGE option, we eliminated even potentially zero branch lengths. The major change induced by this approach occurred near the base of the tree between the nodes 38–56. Because the branch length for the common ancestor to *G. pachysomus*, and *G. elevatus* and *G. plicifer* varied from 0 to 1 in above nodes of the trees, a dichotomous resolution was not accepted for these species. Most other zero-length branches oc-

TABLE 10
Character Matrix of the Genera of Gyrinidae (see characters 1-80 in table 8)
(Zero equals most plesiomorphic state, progressively higher numbers indicate progressively more apomorphic conditions.)

Character	11111111112222222222333333333344444444445555555555666666666677777777778 12345678901234567890123456789012345678901234567890123456789012345678901234567890
Spanglerogyrus	00900000000000000000000000000000900000900990000009009009999999999990999900990999
Enhydrus	10210331000200121010000021111212109210001199999901199999999999999999999999999991
Dineutus	10210331001100101010001011011211002110001199999911110109000001191191011001110111
Porrorhynchus	10210131002200100010001001011212019110001119909911199199999999999999999999999991
Andogyrus	10210031000200101010001021001210109910001101119901109999999999999999999999999191
Macrogyrus	10210131000200101010001001001212109210001199999909199199999999999999999999999991
Orectochilus	00001011010102101102112101100000013910112199999900111111011211011111111111112912
Orectogyrus	00001311011002121102112001100000013000112111011100191911911121111111111111112112
Gyretes	01001011011102121102112101100000119990112199999910199911911121119911111111112912
Aulonogyrus	00110220101111011011000100101100001001000000100102000009100010090000000000001000
Gyrinus	01110220101101111011001100001100001001000000000002000000100000090000000000001000

TABLE 11

Character Matrix of Nearctic Species of *Gyrinus* (see Characters 1-22 in table 9)

(Zero equals most plesiomorphic state, progressively higher numbers indicate progressively more apomorphic conditions.)

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
spanglerogyrus	0	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
aeneolus	0	0	0	0	1	0	1	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0
aeratus	0	1	0	0	1	1	0	0	3	0	2	0	1	3	0	1	0	0	2	0	0	0
affinis	0	1	0	0	1	1	0	0	1	1	0	0	1	3	0	0	0	0	3	0	0	0
analis	0	0	0	0	1	1	0	0	3	0	1	0	1	3	0	0	0	0	2	0	0	0
aquiris	0	1	0	0	1	1	0	0	3	0	1	0	1	1	0	0	0	1	0	0	0	0
bifarius	0	1	0	0	1	1	1	0	1	0	2	0	0	0	0	0	0	0	2	0	0	0
borealis	0	1	0	0	2	1	0	1	1	0	1	0	1	3	0	0	1	0	3	1	0	0
confinis	0	1	0	0	1	1	1	0	1	0	2	0	0	0	0	0	0	2	0	0	1	0
consobrinus	0	1	0	0	1	1	0	0	3	0	1	0	1	1	0	0	0	1	0	0	0	0
dichrous	0	1	0	0	1	1	0	0	3	0	0	0	1	3	0	0	0	0	2	0	0	0
dubius	0	1	0	0	1	1	0	0	1	0	2	0	1	3	1	0	0	1	0	0	0	0
elevatus	0	1	0	0	2	0	0	1	3	0	0	0	0	0	0	0	0	0	3	0	0	0
fraternus	0	1	0	0	1	1	1	0	3	0	1	0	0	0	0	0	0	2	0	0	0	0
gehringi	0	1	0	0	1	1	0	0	2	0	1	0	0	0	0	0	0	0	1	0	0	0
gibber	0	1	0	0	0	1	0	0	1	0	1	0	1	3	0	0	0	2	0	0	1	0
hoppingi	0	1	0	0	1	1	0	0	2	0	1	0	1	3	1	0	0	2	0	0	0	0
impressicollis	0	1	0	0	1	1	0	0	3	0	2	0	1	3	0	1	0	0	1	0	0	0
latilimbus	0	1	0	0	1	1	0	0	3	0	0	0	0	0	0	0	0	2	0	0	0	0
lecontei	0	1	0	0	1	1	0	0	3	0	1	0	1	1	0	0	0	0	1	0	0	0
maculiventris	0	1	0	0	1	1	0	0	3	0	0	0	2	1	0	0	0	0	1	0	0	0
marginellus	0	0	0	0	2	0	1	0	3	0	0	0	0	0	0	0	0	2	0	0	0	0
marinus	0	1	0	0	1	1	0	0	3	0	2	0	1	3	0	1	0	0	2	0	0	0
minutus	1	0	0	1	1	1	0	0	0	0	1	0	1	3	0	0	0	2	0	0	0	1
opacus	0	1	0	0	1	1	0	0	0	0	1	0	1	3	1	0	0	2	0	0	0	0
obtusus	0	1	0	0	1	1	1	0	3	0	0	0	0	0	0	0	0	0	2	0	0	0
pachysomus	0	1	0	0	2	0	1	1	3	0	0	0	0	0	0	0	0	1	0	0	0	0
parcus	0	1	0	0	1	1	0	1	3	0	1	0	1	3	0	0	0	1	0	0	0	0
pectoralis	0	1	1	0	1	0	1	0	3	0	2	0	1	3	0	1	0	1	0	0	0	0
pernitidus	0	1	0	0	1	1	0	0	3	0	0	0	1	3	0	0	0	2	0	0	0	0
piceolus	0	1	0	0	1	1	0	0	3	0	0	0	1	3	0	0	0	2	0	0	0	0
picipes	0	1	0	0	1	1	0	0	3	0	1	0	1	3	0	0	0	1	0	0	0	0
pleuralis	0	1	0	0	1	1	1	0	3	0	2	0	1	3	0	0	0	0	0	0	0	0
plicifer	0	1	0	0	2	0	0	0	3	0	0	1	0	0	0	0	0	0	3	0	0	0
pugionis	0	1	0	0	2	1	0	0	1	0	1	0	1	2	0	0	1	0	3	1	0	0
rockinghamensis	1	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	1
rugosus	0	1	0	0	0	0	1	0	1	0	1	0	1	3	0	0	0	2	0	0	0	0
sayi	0	1	0	0	1	1	0	0	1	0	1	0	1	3	0	0	0	0	1	0	0	0
ventralis	0	1	0	0	1	1	1	0	3	0	1	0	0	0	0	0	0	2	0	0	0	0
wallisi	0	1	0	0	1	1	0	0	3	0	2	0	1	3	0	1	0	0	2	0	0	0
woodruffi	0	0	0	0	2	0	1	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0

curred closer to the terminal portions of the tree. Elimination of these branches resulted in some notable changes in the tree topology.

Second, characters with CI values less than 0.5 were eliminated (compare figs. 161 and 162). For example, 11th stria (character 7) was gained three times, but lost five times; therefore the CI of this character is very low (CI = 0.250), and the branch based on only this character obviously is not reliable. Relationships based on synapomorphies with a CI value of at least 0.5 are used in the tree; however they are considered only as suggestive of monophyly: e.g., abdominal color-

TABLE 12
Distribution of Characters Among Nearctic Species of *Gyrinus*

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*leconteі*	*maculiventris*	*marginellus*	*marinus*	*minutus*	*obtusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*pernitidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
1 Body																																							
1.1 Length																																							
1.1.1 long	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0
1.1.2 medium	0	1	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	0	0	1	0	1	1	0	1	1	1	1	1	0	1	1	0	1	0	1	0
1.1.3 short	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
1.2 Width																																							
1.2.1 wide	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0
1.2.2 moderately wide	0	1	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	1	0	1	0	0	1	0	1	0
1.2.3 narrow	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	1
1.3 Convexity																																							
1.3.1 distinctly convex	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0
1.3.2. moderately convex	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	0	1	1	0	0	1	1	1	1	1	1
2.Prothorax																																							
2.1 Scutellum																																							
2.1.1 present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2.1.2 absent	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
2.2 Pronotal impressed line																																							
2.2.1 close/parallel	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
2.2.2 remote/moderately curved	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	1	0	1	1	0	1	0	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	0
2.2.3 remote/strongly curved	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
2.3 Hypomera, color																																							
2.3.1 black	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
2.3.2 black and red	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0
2.3.3 brown	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0
2.3.4 reddish brown	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0
2.3.5 light brownish red	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0
2.3.6 orange or yellow	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	0	0	0	1	1	1	1	1	0	1	1	0	1	0	1

TABLE 12—(*Continued*)

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*leconteii*	*maculiventris*	*marginellus*	*marinus*	*minutus*	*obtusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*pernitidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
3 Mesothorax																																							
3.1 Metasternum emarginate																																							
3.1.1 yes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
3.1.2 no	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
3.2 Mesosternal color																																							
3.2.1 black	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	1	0
3.2.2 black and red	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
3.2.3 brown	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0
3.2.4 reddish brown	1	1	1	1	1	0	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1
3.2.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0
3.2.6 orange or yellow	1	0	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0
3.3 Mesepisternal color																																							
3.3.1 black	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	1	0	1	0
3.3.2 black and red	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
3.3.3 brown	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	0	1	0
3.3.4 reddish brown	1	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	0	1	0	0	0	1
3.3.5 light brownish red	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
3.3.6 orange or yellow	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1
4 Metathorax																																							
4.1 Metepisternal ostea																																							
4.1.1 not visible	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
4.1.2 small	0	0	1	0	0	1	0	1	1	1	0	0	1	0	0	0	1	0	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0
4.1.3 medium	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0
4.1.4 large, deep	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1
4.2 Metasternal color																																							
																																						1	0
4.2.1 black	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0
4.2.2 black and red	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0			
4.2.3 brown	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	1	0
4.2.4 reddish brown	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	1	0	0	1	

TABLE 12—(*Continued*)

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*lecontei*	*maculiventris*	*marginellus*	*marimus*	*minutus*	*obiusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*permitidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
4.2.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
4.2.6 orange or yellow	1	0	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0
4.3 Metepisternal color																																								
4.3.1 black	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	1	0	0	0	0	1	1	0	1	0
4.3.2 black and red	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
4.3.3 brown	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0
4.3.4 reddish brown	1	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	0	0	1
4.3.5 light brownish red	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
4.3.6 orange or yellow	1	0	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0
5 Elytra																																								
5.1 Micropunctation																																								
5.1.1 dense	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0
5.1.2 moderate	0	0	0	1	1	0	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0
5.1.3 sparse	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	0	0	1
5.2 Microreticulation																																								
5.2.1 scalelike	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
5.2.2 transverse cells																																								
5.2.2.1 uniformly distinct	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
5.2.2.2 uniformly effaced	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.2.2.3 partially effaced	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0
5.2.3 oblique striolate lines	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.2.4 none	1	1	0	1	1	0	0	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	0	1	0	1	1	1
5.3 Lateral striae, puncture width																																								
5.3.1 distinctly larger	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5.3.2 slightly larger	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	0	1	1	1
5.4 Lateral striae, impressed																																								
5.4.1 yes	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
5.4.2 no	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1

TABLE 12—(*Continued*)

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*lecontei*	*maculiventris*	*marginellus*	*marinus*	*minutus*	*obtusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*pernitidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
5.5 11th stria, posteriorly																																							
5.5.1 close to elytral margin	0	1	1	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0
5.5.2 remote from elytral margin	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1
5.6 Elytral margin, width																																							
5.6.1 wide	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	1	0	0
5.6.2 intermediate	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	1
5.6.3 narrow	1	0	0	1	0	1	0	1	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0	0	1
5.7 Posterior elytral convexity																																							
5.7.1 present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
5.7.2 absent	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1
5.8 Epipleura, color																																							
5.8.1 black	0	1	1	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	1	1	1	1	0	1	1	0	0	0	0	1	0	1	0
5.8.2 black and red	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
5.8.3 brown	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
5.8.4 reddish brown	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1
5.8.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0
5.8.6 orange or yellow	1	0	0	0	0	1	0	1	0	1	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	0
6 Abdomen, color																																							
6.1 4th segment																																							
6.1.1 black	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	1	1	1	1	1	0	1	0	0	1	0	1	0
6.1.2 black and red	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.1.3 brown	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
6.1.4 reddish brown	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	1	1	0	1	0	0	0	1
6.1.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0
6.1.6 orange or yellow	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1
6.2 5th segment																																							
6.2.1 black	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	0	0	1	0	1	1	1	1	1	1	0	1	0	0	1	0	1	0
6.2.2 black and red	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 12—(*Continued*)

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*lecontei*	*maculiventris*	*marginellus*	*marinus*	*minutus*	*obtusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*pernitidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
6.2.3 brown	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
6.2.4 reddish brown	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1
6.2.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0
6.2.6 orange or yellow	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0
6.3 6th segment																																							
6.3.1 black	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	1	1	1	1	1	1	0	1	0	0	1	0	1	0
6.3.2 black and red	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.3.3 brown	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
6.3.4 reddish brown	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0	0	1	1	0	1	0	0	1
6.3.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0
6.3.6 orange or yellow	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0
6.4 7th segment																																							
6.4.1 black	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	0	1	1	1	1	1	1	0	1	0	0	1	0	1	0
6.4.2 black and red	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.4.3 brown	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
6.4.4 reddish brown	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	1	0	1	0	0	0	1
6.4.5 light brownish red	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0
6.4.6 orange or yellow	1	0	0	0	1	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1
6.5 8th segment																																							
6.5.1 black	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6.5.2 black and red	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0
6.5.3 brown	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0
6.5.4 reddish brown	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	1	1	0	0	0	1
6.5.5 light brownish red	1	0	0	1	1	1	0	1	0	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0
6.5.6 orange or yellow	1	0	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	1
7 Legs																																							
7.1 Tarsal claws, length																																							
7.1.1 shorter than pretarsus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7.1.2 equal or longer	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TABLE 12—(*Continued*)

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*leconteі*	*maculiventris*	*marginellus*	*marinus*	*minutus*	*obtusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*permitidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
7.2 Tarsal claws, color																																							
7.2.1 black/reddish black	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
7.2.2 yellow to reddish	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1
7.3 Whole leg, color																																							
7.3.1 uniformly light	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7.3.2 reddish w/dark areas	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0
8 Aedeagus, median lobe																																							
8.1 Dorsal outline, apical third																																							
8.1.1 spinelike/slender	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
8.1.2 gradually, accuminate	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
8.1.3 parallel/subparallel	1	1	0	1	1	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	1
8.1.4 gradually widens																																							
8.1.4.1 narrow at tip	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
8.1.4.2 not narrow at tip	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
8.2 Apically notched																																							
8.2.1 yes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
8.2.2 no	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
8.3 Basally broad																																							
8.3.1 yes	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
8.3.2 no	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
8.4 Dorsal surface, apical third																																							
8.4.1 linear	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
8.4.2 angulate	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0
8.4.3 convex	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	1
8.4.4 flat	0	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	1	0	0	1	1	0
8.4.5 concave	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 12—(*Continued*)

	aeneolus	*aeratus*	*affinis*	*analis*	*aquiris*	*bifarius*	*borealis*	*confinis*	*consobrinus*	*dichrous*	*dubius*	*elevatus*	*fraternus*	*gehringi*	*gibber*	*hoppingi*	*impressicollis*	*latilimbus*	*lecontei*	*maculiventris*	*marginellus*	*marinus*	*minutus*	*obtusus*	*opacus*	*pachysomus*	*parcus*	*pectoralis*	*perniidus*	*piceolus*	*picipes*	*pleuralis*	*plicifer*	*pugionis*	*rockinghamensis*	*rugosus*	*sayi*	*ventralis*	*wallisi*	*woodruffi*
8.5 Lateral view, apical third																																							
8.5.1 compressed	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
8.5.2 weakly compressed	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1
8.5.3 not compressed	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	1	1
8.6 Shape at tip																																								
8.6.1 acute	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
8.6.2 subacute	1	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1
8.6.2.1 notched at mid-tip	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
8.6.3 angulate	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8.6.4 broadly round	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0
8.7 Width at tip																																								
8.7.1 narrower than lateral lobe	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	0	1	0	1	1	1	1	1	0	0	1	1	1	1	0	1	1	1	1	1
8.7.2 wider than lateral lobe	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1
8.8 Carination																																								
8.8.1 angularly carinated	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	1	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
8.8.2 flatly carinated	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	0
8.8.3 not carinated	1	1	1	1	0	1	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	1	1	1	0	0	0	1	1
8.9 Color																																								
8.9.1 uniformly light	1	0	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	0	0	1	0	1	1	0	1	0	0	0	1	0	0	0	1	1	1	0	1	0	1
8.9.2 reddish w/dark areas	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1	0	1	0	0	1	0	1	1	1	0	1	1	1	0	0	0	1	0	1	0

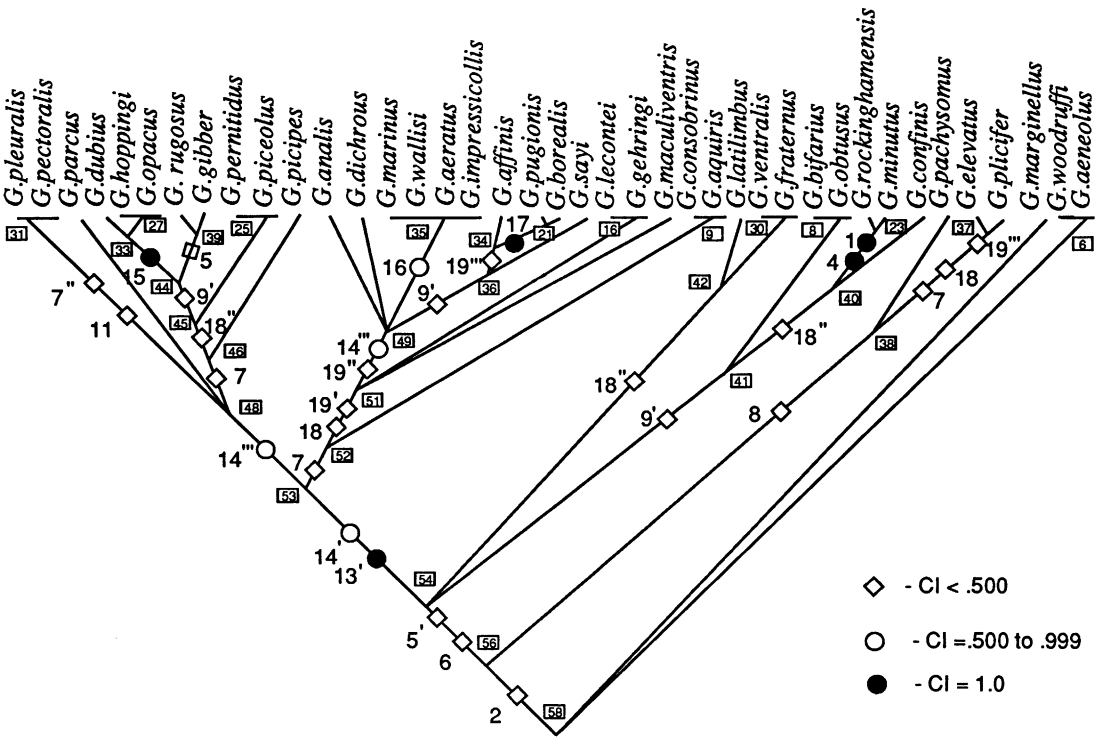


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Fig. 161. Consensus tree for the species of *Gyrinus,* common ancestors not justified by any synapomorphies are suggested only by extreme phenetic similarity; see text. Numbers inside squares refer to node numbers. (●), character with consistency index (CI) = 1, (○), character with CI = 0.5 to 0.999, (□) character with CI < 0.5.

ation 2 which has a CI = 0.5 was gained independently three times, between the nodes 53–54, 48–53, and 49–51.

As a result of modifications based on the above rationale regarding the BL-RANGE and CI index, no branch in the final tree (fig. 162) is supported by more than two synapomorphies. The branch between nodes 1–2 is based on two synapomorphies; one of these, abdominal coloration 1, has a CI = 1, the other, abdominal coloration 2, has a CI = 0.5. The branch between the node 2–3 is based on only one synapomorphy (abdominal color 2) and therefore, the monophyly of this group is regarded as not conclusive (but worth suggesting).

FINAL EVALUATION OF TREE: Monophyly of *Gyrinus* is supported by the following characters: short and flat mid and hind tarsi and tibia, completely divided dorsal and ventral eyes, small size, and undivided apical (8th) sternum.

Our interpretation of the relationships among the species of *Gyrinus* is summarized in figure 162. Despite the above conservative approach, three major clades are recognized. The most basal clade is a large polychotomy consisting of 14 species. Within this clade one species pair is recognized: *Gyrinus rockinghamensis* and *G. minutus.*

The second group is also a polychotomy with five species and is supported by abdominal coloration 1 and 2.

The third group is suggested by abdominal coloration 2 (CI = 0.5). Four species of this clade form a monophyletic subgroup linked

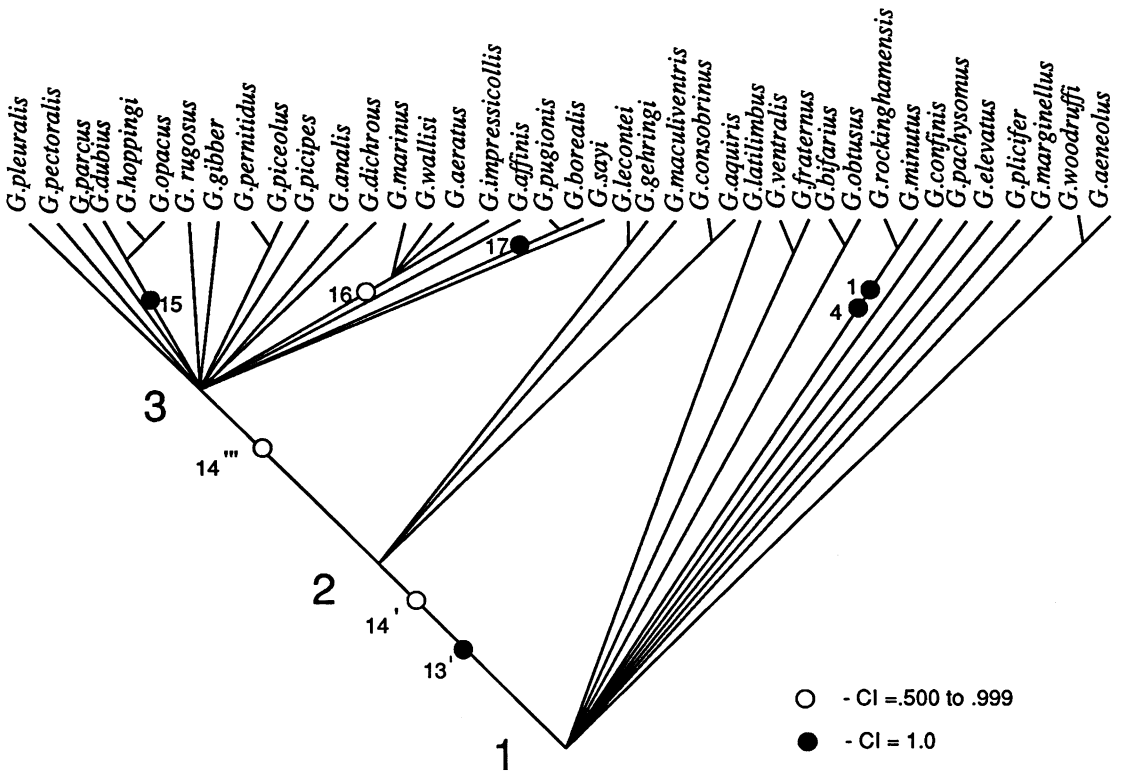

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Fig. 162. Final consensus tree for the species of *Gyrinus*, common ancestors not justified by any synapomorphies are suggested only by extreme phenetic similarity, see text. (●), character with consistency index (CI) = 1, (O) character with CI = 0.5 to 0.999.

by occurrence of dark tarsal claws (CI = 1): *Gyrinus marinus, G. wallisi, G. aeratus,* and *G. impressicollis. Gyrinus opacus* and *G. hoppingi* are the sister species to *G. dubius* within this clade. The only other sister pair in this clade is *G. opacus* and G. hoppingi.

It is interesting that abdominal coloration and aedeagal structure were the most important and reliable characters in this analysis. As predicted above, this may be because these characters were less affected by hydrodynamic constraints of water-surface existence.

Seventy-one percent of the species with a large metepisternal ostiole, 71 percent of species with a convex body, 75 percent of the species with a smooth shiny elytral surface, and 80 percent of the species living in lotic habitats occurred in the basal clade of the tree.

The reconstructed phylogeny of the species of *Gyrinus* needs more investigation than presented here. The study of immatures, and gas–liquid chromatography or electrophoretic analyses, could be fruitful in further resolving the phylogeny of *Gyrinus.*

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