PAN-PACIFIC ENTOMOLOGIST
January 1981, Vol. 57, No. 1, pp. 149–175

NOTES ON NOMENCLATURE AND CLASSIFICATION OF *HYDROPORUS* SUBGENERA WITH THE DESCRIPTION OF A NEW GENUS OF HYDROPORINI (COLEOPTERA: DYTISCIDAE)[1]

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Nearctic species of *Hydroporus* Clairville were last revised by Fall (1923). He considered *Oreodytes* Seidlitz and *Deronectes* Sharp to be subgenera of *Hydroporus*. His subgenus *Hydroporus* had four species groups: *niger-tenebrosus* (=subgenus *Hydroporus*) (48 nearctic species); *pulcher-undulatus* (50 species); *oblitus* (9 species); and *vilis* (17 species).

Subsequent American workers have treated nearctic species on a regional basis and in various ways. For example, Hatch (1953), dealing with the fauna of northwestern America, referred *Deronectes* species (*sensu* Fall) to the subgenus *Potamonectes* Zimmermann, put *Oreodytes quadrimaculatus* Horn in the subgenus *Deronectes* and put the *vilis, oblitus* and *pulcher-undulatus* group species in the subgenus *Heterosternus* Zimmermann. Young (1954), working on Florida water beetles, referred the *pulcher-undulatus* species to *Sternoporus* (=*Heterosternus,* preoccupied) and the *niger-tenebrosus* species to *Hydroporus* (*s. str.*). Leech and Chandler (1956) and Anderson (1962), working on California and Utah species respectively, accepted *Oreodytes* and *Deronectes* as genera. Larson (1975), dealing with the Alberta fauna, felt that the various species groups of *Hydroporus* probably deserved subgeneric status but treated all species under *Hydroporus* (including *Deronectes* and *Oreodytes*) because the groups were inadequately defined. Zimmerman and Smith (1975) partially revised nearctic *Deronectes* and treated it as a genus, but added that *Hydroporus* was a heterogeneous assemblage of species and that there were significant differences between the species groups within it.

Hydroporus has been a dumping ground for unrelated groups of species and this is especially true of the *pulcher-undulatus* species group (*sensu* Fall) which consists of approximately 50 species. There are three species groups within the *pulcher-undulatus* group that we feel require subgeneric or generic status: *pilatei-triangularis* group (2 species); *pulcher* group (13 species); and *undulatus* group (about 35 species). All three are probably limited to the Nearctic Region.

Use of subgenera seems especially warranted within *Hydroporus*. Opinions vary concerning desirability of using subgeneric names. Misuse (overuse) of them in the past has contributed to a great deal of nomenclatural confusion.

We have elected to use subgeneric names in certain situations for several reasons. (1) *Hydroporus* is a large, diverse genus and there are a number of distinct lineages within it that are more closely related to each other than any single group is to an excluded group. Although subgeneric differences are not of the same magnitude as generic differences, many subgenera are still readily recognized in the field (even by nonspecialists). (2) In speciose genera, such as *Hydroporus,* subgeneric designations allow specialists to conveniently refer to specific parts of a genus. (3) Although informal species group names may sometimes be just as convenient, subgeneric names are already available.

Here we discuss nomenclatural problems of *Hydroporus,* especially as they pertain to the *pulcher-undulatus* group (*sensu* Fall); describe a new genus of Hydroporini, and review species assigned to it.

Nomenclature

There has been considerable confusion over the authorship of the genus *Hydroporus*. Most authors have cited either Clairville or Schellenberg or both. Helvetische Entomologie was published anonomously in 2 volumes (1798 and 1806). The section dealing with aquatic Adephaga appears in volume 2. The volumes are arranged with one page in German and the facing page in French. According to Andrews (1939), Clairville only translated Schellenberg's work. However, according to Méquignon (1940), Clairville wrote both volumes and Schellenberg only did the illustrations. Méquignon's evidence is rather persuasive, especially where it concerns segments of the prefaces of volumes 1 and 2. Furthermore Schellenberg died in 1806. Therefore, based on evidence available to us we believe that Clairville should be recognized as author of *Hydroporus*.

There have been numerous type designations, summarized by Leech (1948), that are invalid for various reasons: *Dytiscus depressus* Fabricus and *Dytiscus duodecimpunctatus* Fabricius (not originally included species); *Dytiscus parvulus* Linnaeus (species inquirendum); and *Dytiscus palustris* (on Clairville's list as *Dytiscus sexpustulatus*; Fabricius, however, the synonym wasn't noted in the type designation).

The type of *Hydroporus* is *Hyphidrus pubescens* Gyllenhal, designated by

Guignot (1946). Zaitzev (1953) designated *Dytiscus erythrocephalus* Linnaeus as the type of *Hydroporus,* but Guignot's designation has priority.

The genus *Hydroporus* has been variously divided into a number of subgenera. Des Gozis (1914) described *Suphrodytes* as a monotypic subgenus to include *Hydroporus dorsalis* Fabricius and this is still accepted by most workers. Zimmermann (1919) described the subgenus *Heterosternus* basing the separation of this group from *Hydroporus* (*s. str.*) on the shape of the medially produced postmetacoxal process, the prosternal process, and the vittate or fasciate color pattern. His group of 37 species, although composed primarily of nearctic *pulcher-undulatus* species (*sensu* Fall), also included species now assigned to the *vilis* and *oblitus* species groups (*sensu* Fall) and the palearctic *Hydroporus picicornis.* Although Zimmermann didn't designate a genotype, the figure of the metacoxal process characteristic of *Heterosternus* was that of *Hydroporus concinnus* LeConte (=*wickhami* Zaitzev).

There have been several type designations for *Heterosternus.* Leech (1950) designated *Hydroporus concinnus* LeConte as the type of *Heterosternus* stating correctly that the designation of Guignot (1945) wasn't valid. However, Guignot (1942) stated (concerning Zimmermann's description of *Heterosternus*), "Il désigne donc ainsi implicitement, mais formellement, l'espéce *concinnus* LeC. comme le type du nouveau sous-genre." This is a valid type designation according to article 69 (a) iii. Finally Guignot definitively designated the type again in 1949.

Falkenström in 1930 described *Sternoporus* as another new subgenus, within *Hydroporus.* Although without formal designation, he used *Hydroporus longicornis* Sharp as a standard of comparison and it seems obvious that this should be considered the type.

Guignot (1931, 1942) incorrectly stated that Falkenström designated *H. longicornis* as the type of *Sternoporus.* This is a valid type designation according to Article 69(a)iii. Guignot (1931) also put *Sternoporus* in synonymy with *Heterosternus* Zimmermann. He then described a new subgenus, *Neoporus,* with *Hydroporus hebes* Fall as the type-species. His major diagnostic character was the medially produced metacoxal process which was straight-edged on each side, not sinuate.

Strand (1935) recognized that *Heterosternus* Zimmermann was a homonym and proposed the name *Heterosternuta.* Falkenström (1938) stated that because *Heterosternuta* Strand was feminine and Strand hadn't redefined the subgenus when he proposed the name that a new name was necessary and he therefore proposed *Heterostethus.* Subgeneric names do not have to agree in gender with their species and name changes do not require a redefinition, so *Heterostethus* was unnecessary.

Guignot (1942) pointed out that *Heterosternuta* also wasn't necessary because the name *Sternoporus* Falkenström (1930) was available. Brinck

(1943), apparently unaware of Guignot's 1942 paper, realized that *Heterostethus* Falkenström was itself a homonym and suggested retaining *Heterosternuta* with *Hydroporus concinnus* LeConte as the type, but this was not necessary at this time because *Sternoporus* Falkenström had priority as Guignot had already synonymized *Sternoporus* and *Heterosternus*.

In 1945, Guignot created the subgenus *Hydroporinus* (type *Hydroporus neglectus* Sturm) and he also synonymized *Neoporus* Guignot with *Sternoporus* Falkenström. He then created the subgenus *Circinoporus* with *Hydroporus cimicoides* Fall as the type. This indicates Guignot didn't understand how closely related *Hydroporus cimicoides* was to *H. hebes* Fall, Guignot's type for *Neoporus*. In fact, Young (1954) indicates that *H. hebes* may intergrade with both *H. cimicoides* and *H. lobatus*. Although Guignot didn't give a formal definition of *Circinoporus,* he did indicate diagnostic characters in a key.

In 1947 Guignot included five more species in *Hydroporinus*. One of these was *H. longicornis,* the type of *Sternoporus*. Although *Sternoporus* had priority over *Hydroporinus,* Guignot continued to use the name *Hydroporinus* for this group (including the type of *Sternoporus*) but he also continued to apply the name *Sternoporus* to some nearctic species.

Later Guignot (1949) acknowledged this mistake. He then took *Heterosternuta* out of synonymy with *Sternoporus*; *Neoporus* out of synonymy with *Sternoporus*; synonymized *Hydroporinus* with *Sternoporus* and described a new subgenus, *Hydroporidius* (type *Melanarius* Sturm). Therefore, he recognized seven subgenera within *Hydroporus*: *Hydroporus* Schellenberg (type *pubescens* Gyllenhal); *Hydroporidius* Guignot (type *melanarius* Sturm); *Sternoporus* Falkenström (type *longicornis* Sharp); *Suphrodytes* Des Gozis (type *dorsalis* Fabricius); *Neoporus* Guignot (type *hebes* Fall); *Circinoporus* Guignot (type *cimicoides* Sharp) and *Heterosternuta* Strand (type *concinnus* LeConte).

Palearctic workers have generally continued to use at least the first four of these subgenera (see, for example, Franciscolo, 1979; Freude et al, 1971; Zaitzev, 1953), and Zaitzev (1953) also used *Hydroporinus* as including *longicornis*. Galewski (1971) however, used none of the subgenera. Nearctic workers have generally ignored these groups although the name *Sternoporus* has been applied to Fall's *pulcher-undulatus* group (see Young, 1954).

The net effect of Guignot (1949) was to isolate the *pulcher-undulatus* species (*sensu* Fall) in the last three subgenera (*Neoporus, Circinoporus* and *Heterosternuta*), because he separated *Sternoporus* and *Heterosternuta*. *Neoporus* contained *H. superiorus, uniformis, hebes* and *consimilis*; *Circinoporus* was monotypic with *cimicoides*; and *Heterosternuta* contained the remaining species.

We are synonymyzing *Circinoporus* and *Neoporus*. These two subgeneric names are obviously synonyms when respective types are considered as we discussed above. Furthermore we are moving all species within *Heterosternuta,* except the 13 *pulcher* group species, to *Neoporus.*

The *pulcher* group species, in this sense, constitute the subgenus *Heterosternuta* (which has been revised, Matta and Wolfe, 1981). These species form a monophyletic unit and deserve subgeneric rank. One other European work has a direct bearing on taxonomy of nearctic groups. Franciscolo (1979) described a new monotypic genus of Hydroporini, *Sanfilippodytes,* from a cave in Mexico. The type-species, *S. sbordonii* Franciscolo, has reduced eyes, is depigmented and the prosternal process does not reach the metasternal process. Genitalia and the metacoxal process structure strongly suggest that *Sanfilippodytes* may be congeneric with other nearctic *vilis* group species currently included in *Hydroporus.* The relationship between *vilis* group species and *Sanfilippodytes* needs to be studied carefully.

The following list summarizes our concept of subgeneric status within *Hydroporus*:

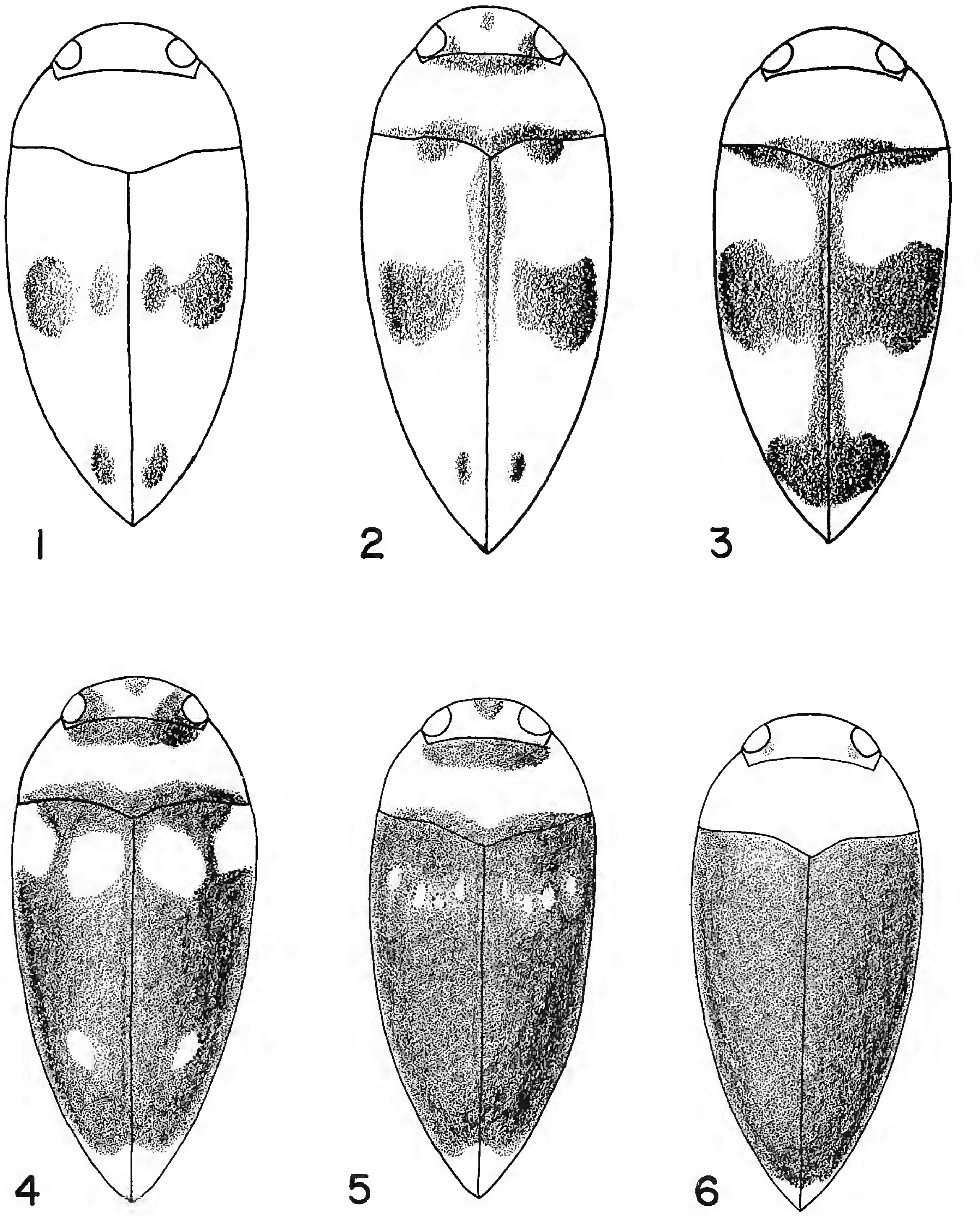
Hydroporus Clairville 1806. Type *Hyphidrus pubescens* Gyllenhal by subsequent designation, Guignot (1942).

- S. G. *Suphrodytes* Des Gozis 1914. Type *H. dorsalis* Fabricius by monotypy.
- S. G. *Heterosternuta* Strand 1935. Type *H. concinnus* LeConte (=*wickhami* Zaitzev) by subsequent designation, Guignot (1942).
  nec Heterosternus Zimmermann (1919),
  nec Heterostethus Falkenström (1938).
- S. G. *Sternoporus* Falkenström 1930. Type *H. longicornis* Sharp by subsequent designation, Guignot (1931).
  Hydroporinus Guignot 1945. Type *H. neglectus* Sturm by original designation.
- S. G. *Neoporus* Guignot 1931. Type *H. hebes* Fall by original designation.
  Circinoporus Guignot 1945. Type *H. cimicoides* Sharp by original designation.
- S. G. *Hydroporidius* Guignot 1949. Type *H. melanarius* Sturm by original designation.

Balfour-Browne (1940) also recognized *Graptodytes* Seidlitz, *Stictonectes* Brinck, and *Scarodytes* Des Gozis as subgenera of *Hydroporus.* However, more recent palearctic workers recognize those three taxa and *Metaporus* Guignot and *Porhydrus* Guignot as distinct genera.

Falloporus, new genus

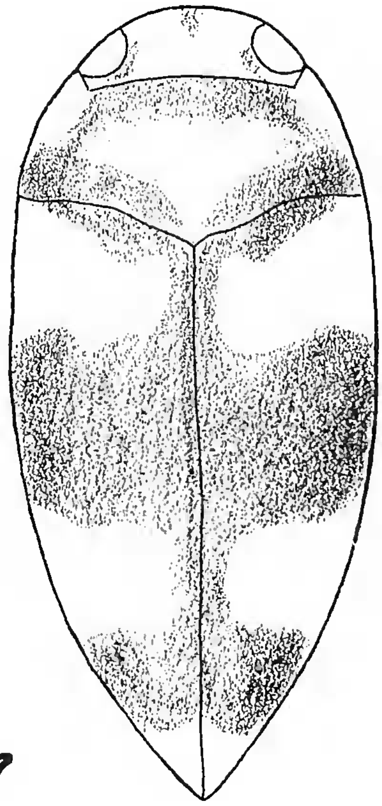
Diagnosis.—Among nearctic hydroporine groups, *Falloporus* is immediately recognizable by its enlarged fourth or fourth and fifth antennal segments (Figs. 14–21), protarsal cupule (Fig. 32), and subapical setae of the



Figs. 1–6. *F. triangularis*: Fig. 1. Scott Co., TN. Fig. 2. Blount Co., TN. Fig. 3. Van Buren Co., TN. Figs. 4–6. Baldwin Co., AL.

parameres (Figs. 11–12). In addition, the metasternal process does not touch the mesosternum (Fig. 27), there are no pronotal stria, and the prosternum is declivitous, but not at all protuberant (Fig. 27).

Description.—Form elongate oval (length twice width); sides subparallel,



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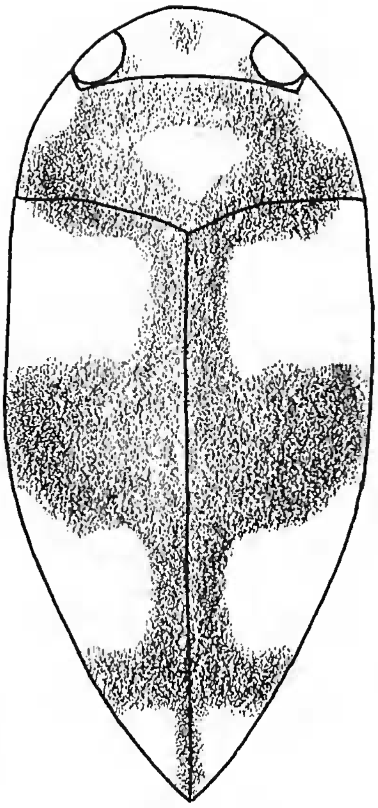

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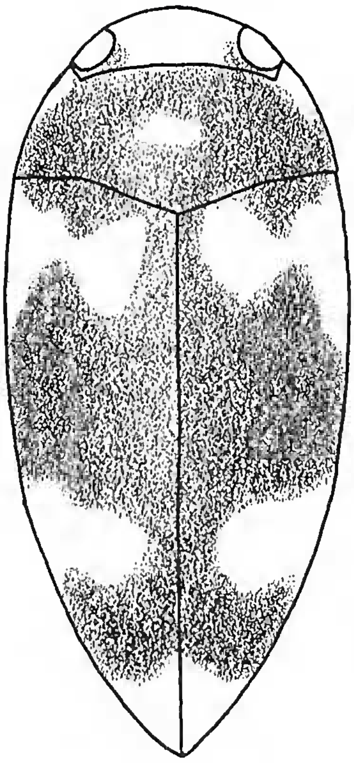

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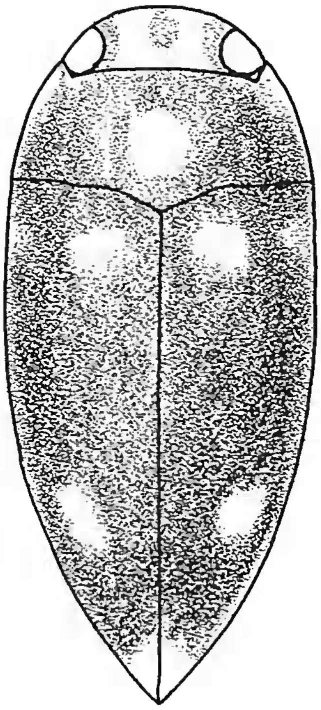

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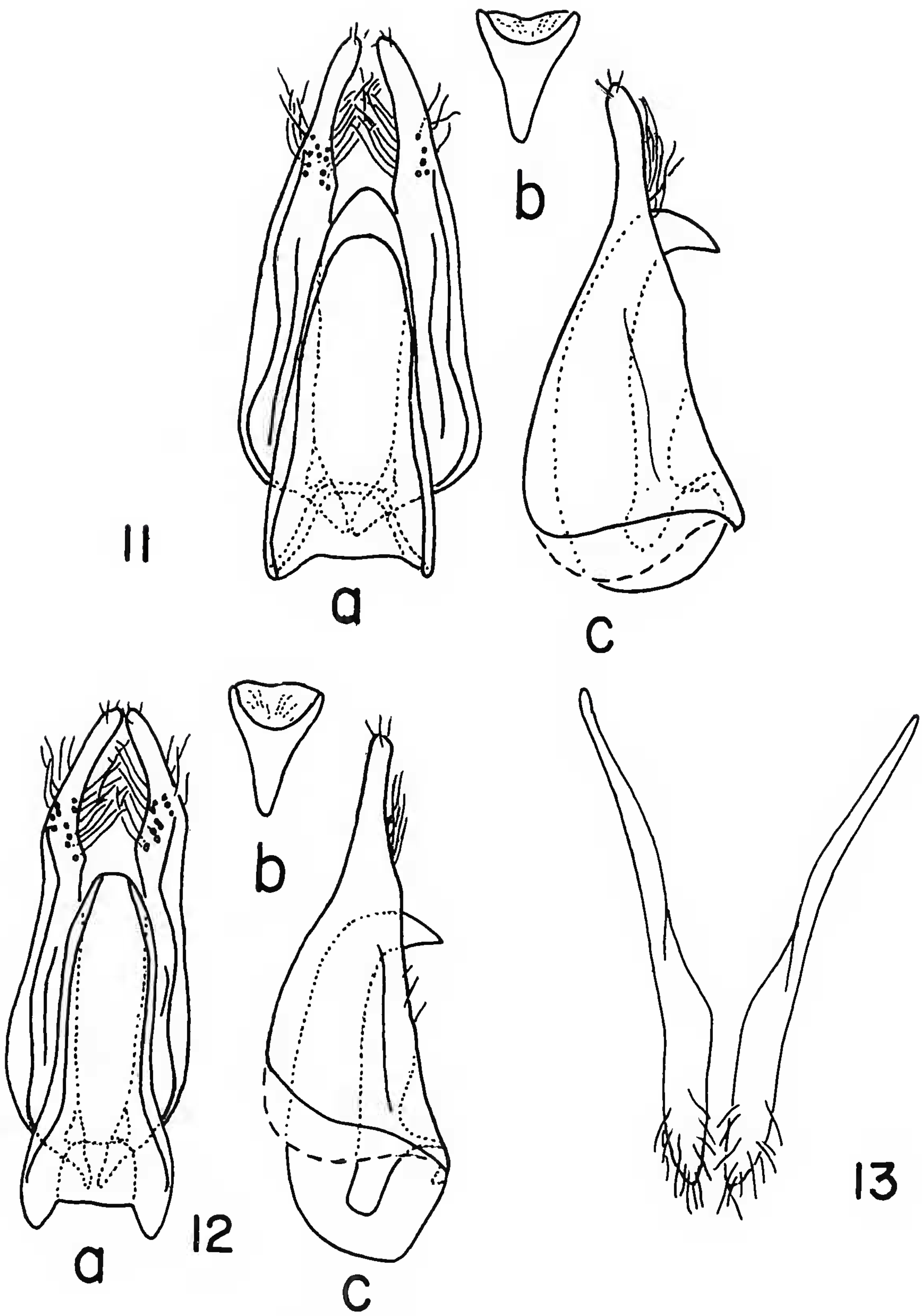
Figs. 7–10. *F. pilatei*: Fig. 7. Gilchrist Co., FL. Figs. 8–9. Lauderdale Co., TN. Fig. 10. Miller Co., GA.

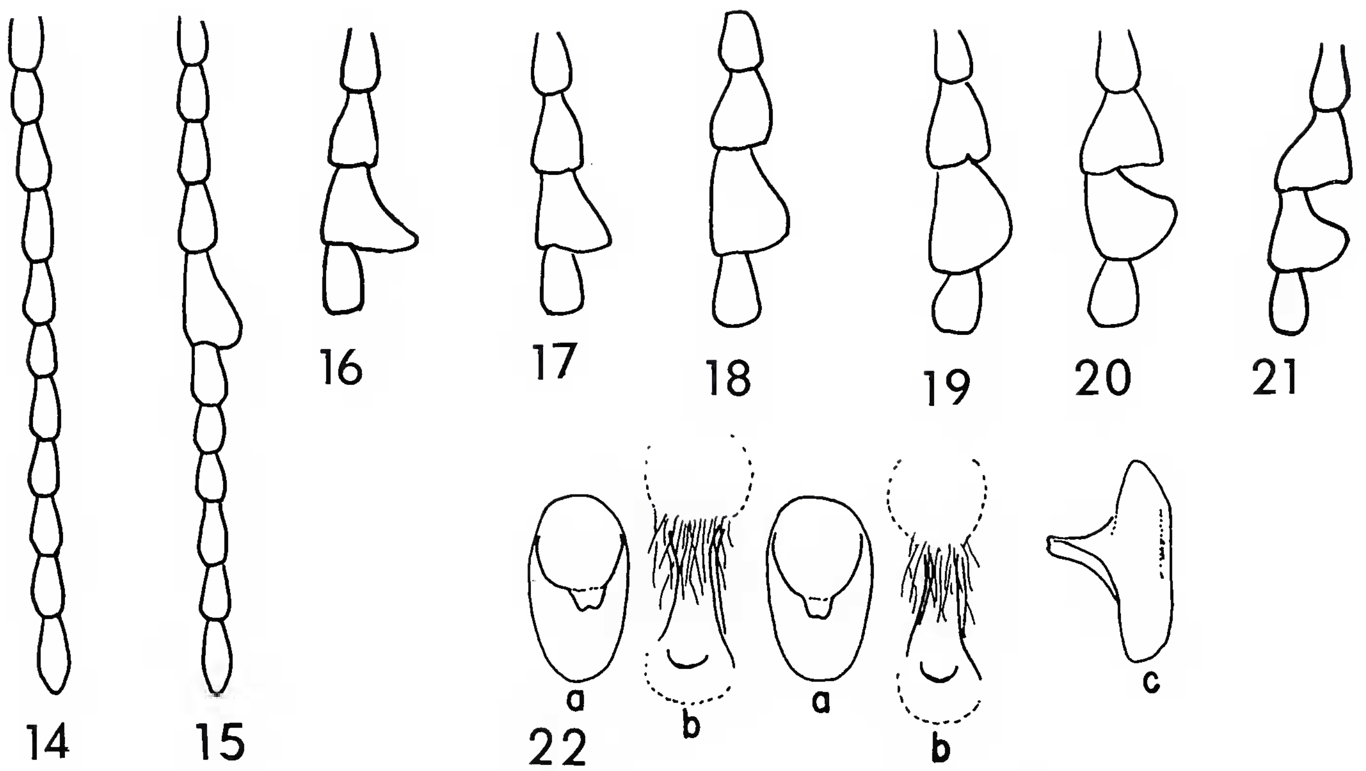
pronotum and elytra continuous; rather depressed. Color variable with dark fascia which vary from small spots to complete coalescence (Figs. 1–10). Surface shining, but with microreticulation; entire dorsal and ventral surface, palps, antennae and metafemora densely covered with "button-like"



Figs. 11–13. Fig. 11. *F. pilatei*. a. dorsal view of aedeagus and parmeres. b. apical (posterior) view of deflected tip of aedeagus. c. lateral view of aedeagus and parameres. Fig. 12. *F. triangularis*. a. dorsal view of aedeagus and parmeres. b. apical (posterior) view of deflected tip of aedeagus. c. lateral view of aedeagus and parameres. Fig. 13. *F. triangularis* ovipositor.

sensilla (Figs. 29–31). Scattered large setigerous punctures separated by three times their width (Figs. 29–30).

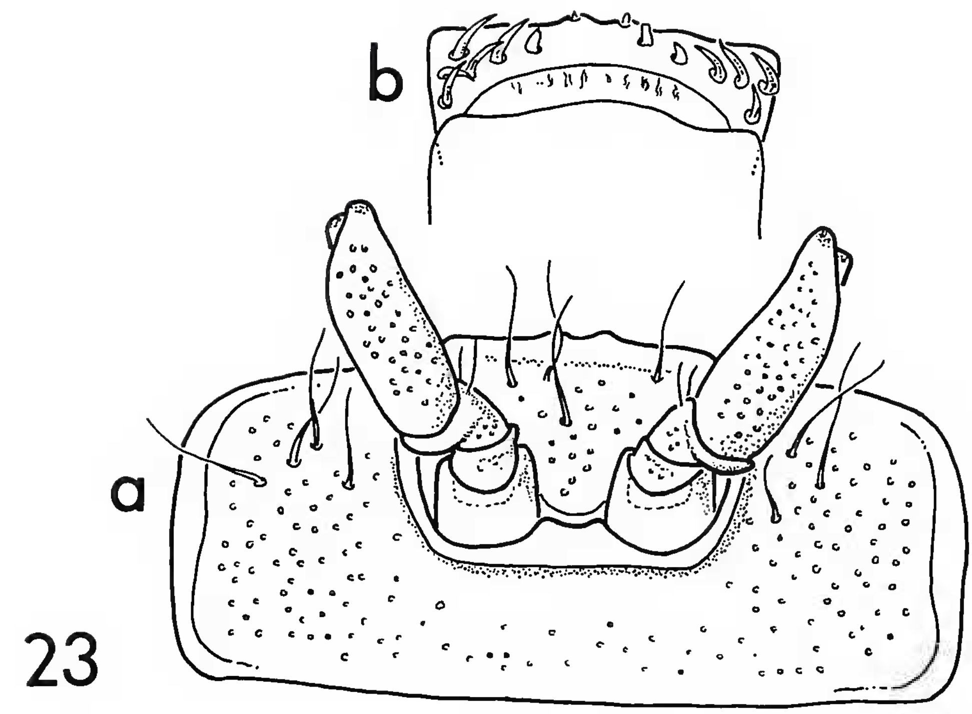
Head broadest at posterior portion of eye; front and back margin of eye shallowly emarginate. A series of coarse punctures at anteromedial corner

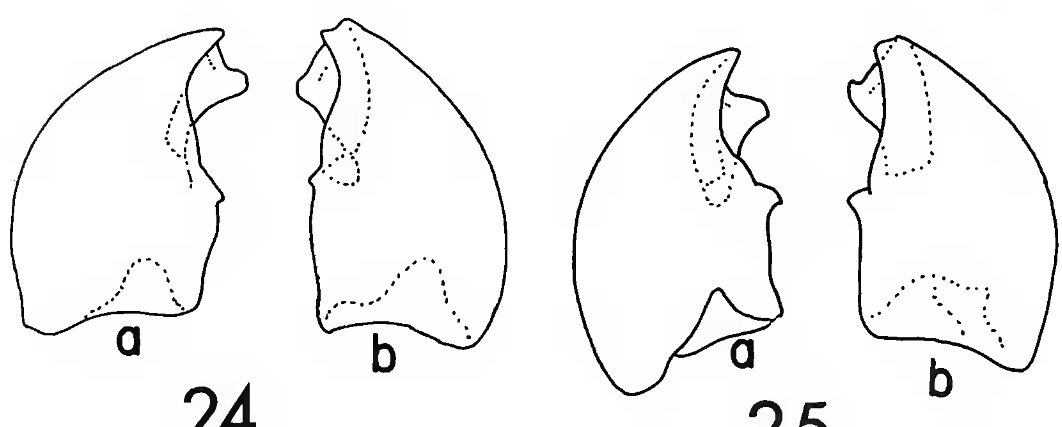


Figs. 14–22. Figs. 14–19. *F. triangularis*. 14. Female antenna. 15. Male antenna, Benton Co., TN. 16–19. Male antenna (segments 3–6). 16. Sauk Co., WI. 17. Lincoln Co., MS. 18. Blount Co., TN. 19. Macon Co., AL. Figs. 20–21. *F. pilatei*, male antenna (segments 3–6). 20. Macon Co., GA. 21. Miller Co., GA. Fig. 22. *F. triangularis*. Inner view of sclerotized lobes of proventriculus. a. oval, toothed outer lobe. b. inner valve-like ciliate lobe. c. side view of outer lobe showing medially projecting tooth.

of eye. Clypeus not thickened, slightly margined laterally; labrum emarginate, with dense golden setae medially. Mandibles with reduced medial teeth, no medial fringe of setae (Figs. 24–25). Maxillary palps four segmented; last segment distinctly emarginate apically, its length approximately equal to the basal three segments combined. Ligula subtriangular in ventral view, micropunctate with a few sparse slender setae (Fig. 23a); a row of stout spines along dorsal anterior edge (Fig. 23b). Mentum strongly lobed anteriorly, lobes rounded, not arcuate; medial portion between labial palps produced (Fig. 23b). Labial palpus four segmented, last segment distinctly notched. Antennae with fourth or fourth and fifth segments variably broadened (Figs. 14–21).

Pronotum slightly more than 2 times broader than long, very narrowly margined, lateral bead about 10–15% width of second antennal segment. Pronotum without posterior lateral stria, anterior lateral angles produced and subacute, posterior lateral angles rather sharp. A small pore-like opening present at each ventral anterolateral corner of pronotum. Prosternum declivitous but not at all protuberant or rugose (Fig. 27). Prosternal process lanceolate, widely margined laterally, distinctly longitudinally convex medially; apex moderately acute; extending between mesocoxae and fitting in





Figs. 23–25. Fig. 23. *F. pilatei*. a. Ligula and mentum, ventral view (250×). b. Apical-dorsal edge of ligula showing arrangement of spines (250×). Figs. 24–25. Ventral view of mandibles (a, right mandible; b, left mandible). 24. *F. triangularis*. 25. *F. pilatei*.

metasternal sulcus. Mesosternum and metasternum distinctly separated (Fig. 27). Metafurca rather well developed (Fig. 26). Proventriculus of hydroporine type: outer lobes oval, with transverse teeth; inner lobes valve-like and ciliate (Fig. 22).

Scutellum concealed. Elytra widest in basal third, edges often parallel in basal third; in side view straight, not ascending at base; epipleura gradually narrowing posteriorly; epipleural width at anterior edge of second abdominal sternite about 40% its basal width; no humeral carina on epipleura; no inner ligula. Metasternum with a deep longitudinal sulcus medially for 50–75% of its length (Fig. 27). Anterior and posterior edges of metacoxal plate subparallel;

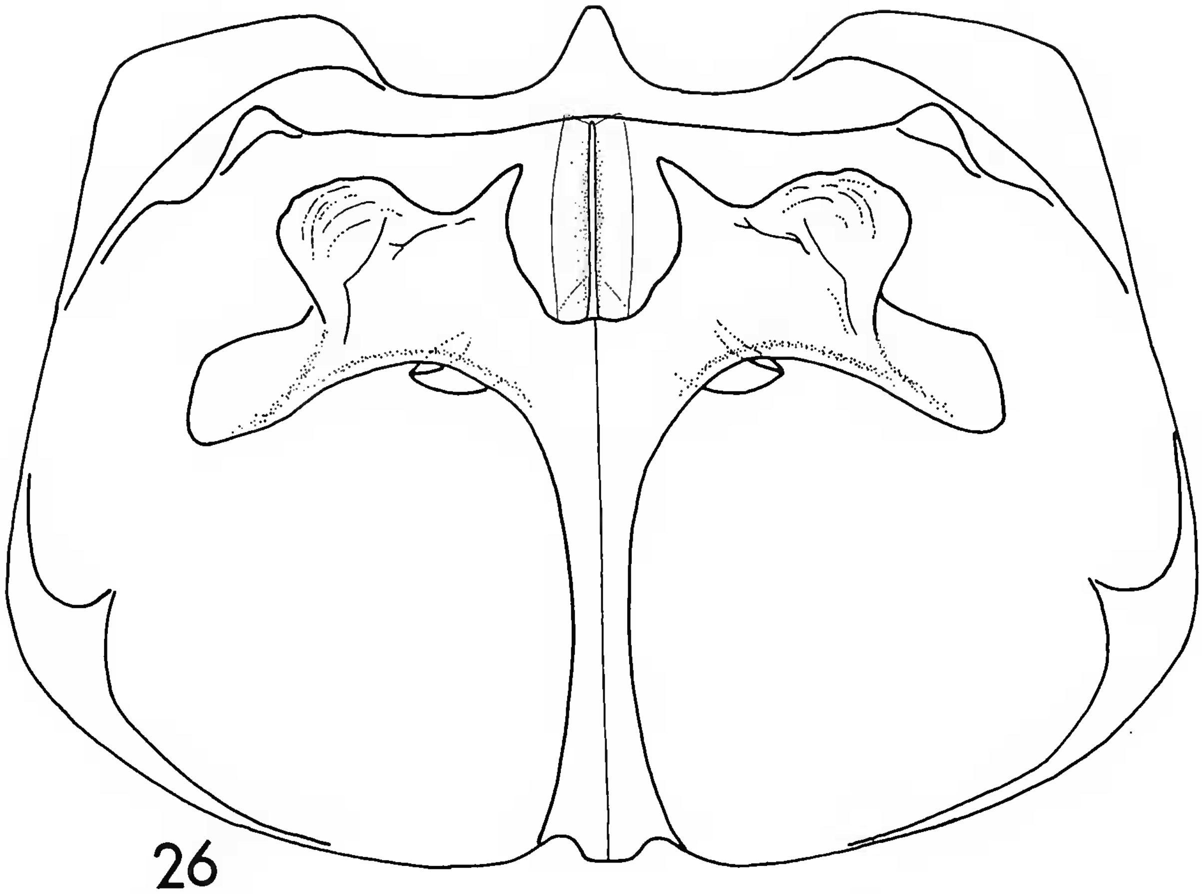


Fig. 26. *F. pilatei,* metafurca.

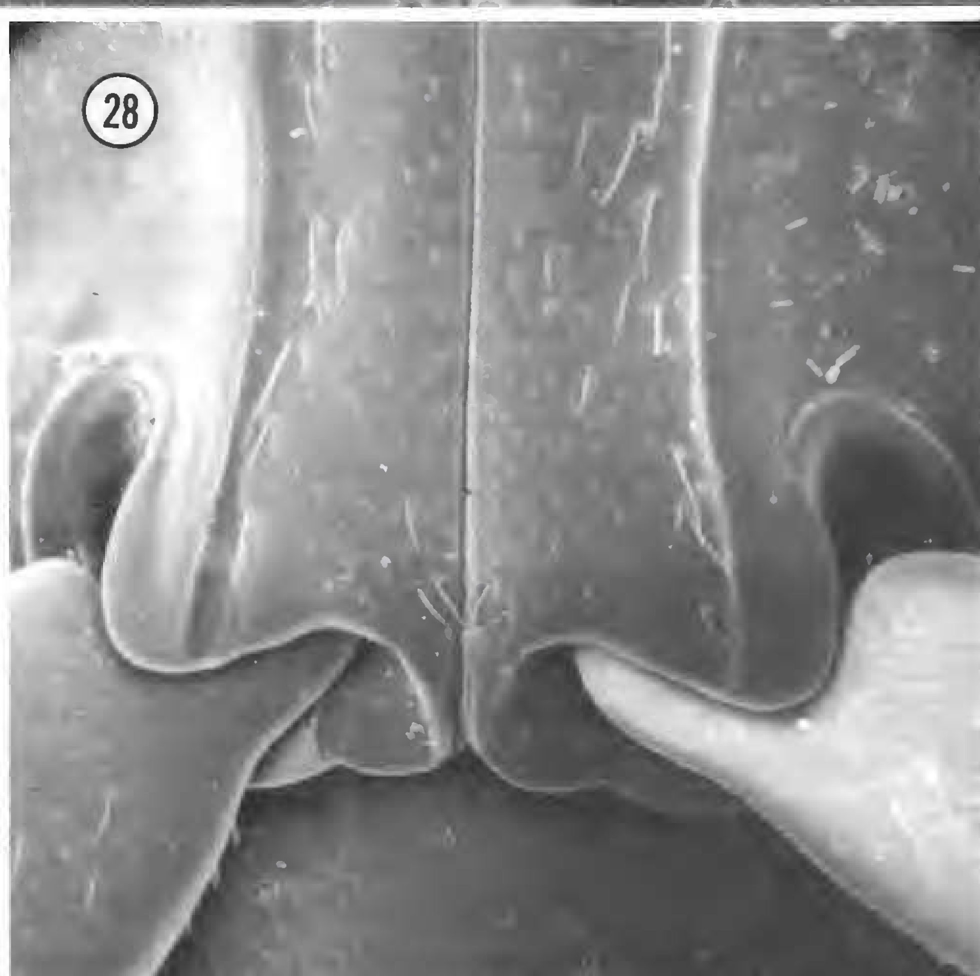
metacoxal lines extending anteriorly to metasternum, almost parallel (not diverging anteriorly). Posterior metacoxal process posterolaterally produced, covering base of hind trochanters, concave on each side of middle; medially produced, metacoxal cavities totally separate (Fig. 28). Metafemoral base not touching metacoxal process. Metafemur appearing somewhat shining but evenly covered with modified sensilla (micropunctate), with barely perceptible sparse median line of setigerous punctures; posterodorsal edge carinate.

Protarsus and mesotarsus pseudotetramerous. Male protarsus slightly broadened with cupule containing many foliate sensillae (Fig. 32). Anterior male protarsal claw not modified; evenly curved and tapered from base to apex. Parameres broadest at base, strongly tapered towards apices with long subapical setae; aedeagus strongly ventrally deflected and subacute apically (Figs. 11–12). Ovipositors (Fig. 13) with anteriorly extended strut, valvifer absent.

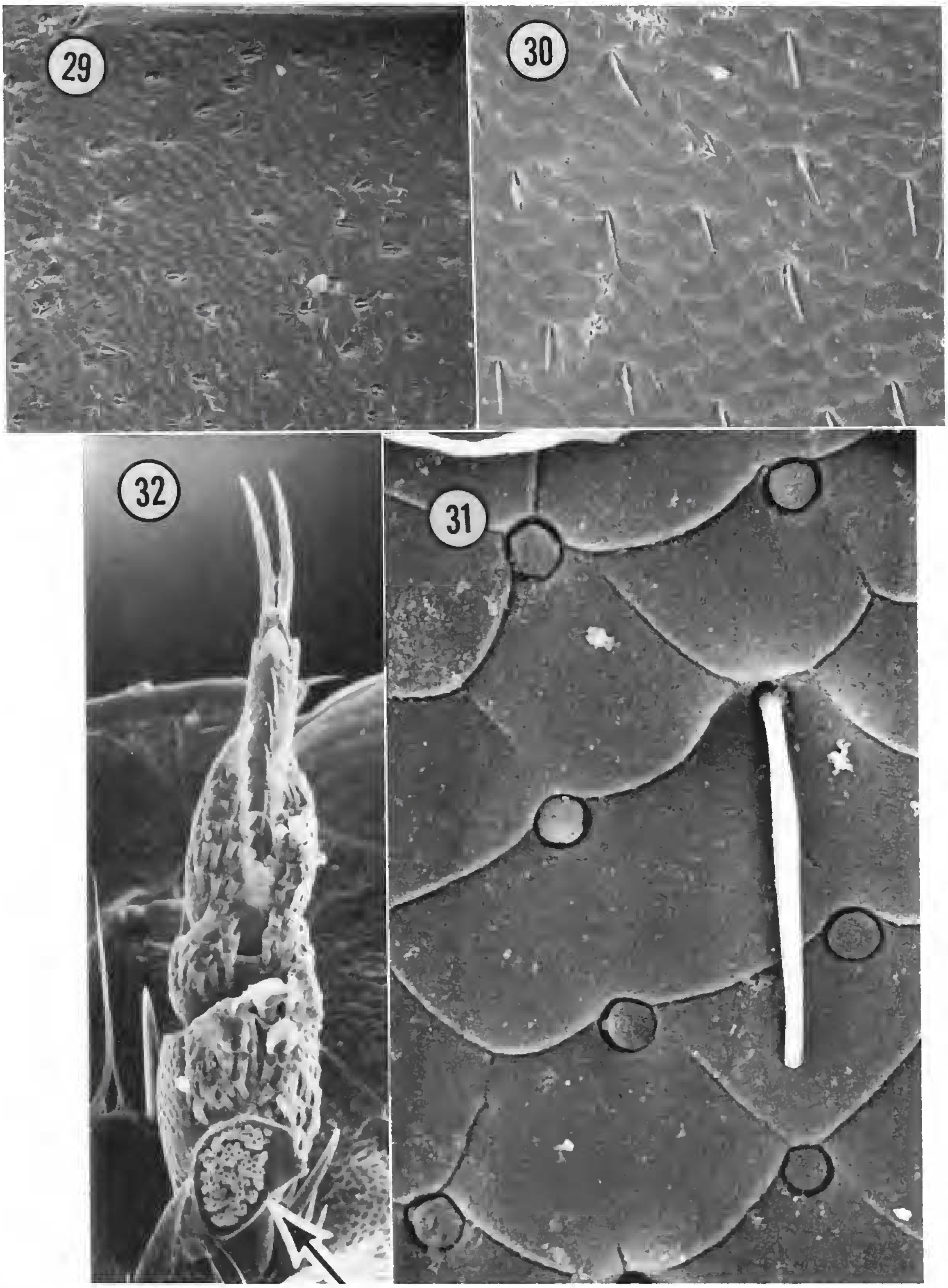
Type-species.—Hydroporus triangularis Fall (1917:170).

Etymology.—This genus is named in honor of Henry C. Fall. He made many significant contributions to knowledge of North American water beetles.

Gender.—Masculine.



Figs. 27–28. Fig. 27. *F. triangularis.* Metasternal process and prosternum, pro- and mesocoxae removed. Note sulcate metasternum; metasternum not attaining mesosternum; and non-protuberant prosternum (100×). Fig. 28. *F. triangularis.* Metacoxal apex (200×).



Figs. 29–32. *F. triangularis*. Fig. 29. Metacoxa (115×). Fig. 30. Elytron (115×). Fig. 31. Elytron (2000×). Fig. 32. Protarsus with basal cupule (arrow) (160×).

Taxonomic Notes

Subgeneric status was first considered for *Falloporus*. This might seem more consistent since *Heterosternuta* and *Neoporus* are kept as subgenera and they are substantially larger groups (13 and 35 species respectively). However, based on mesosternum-metasternum relationships, subgeneric status within *Hydroporus* is untenable because *Falloporus* is more closely

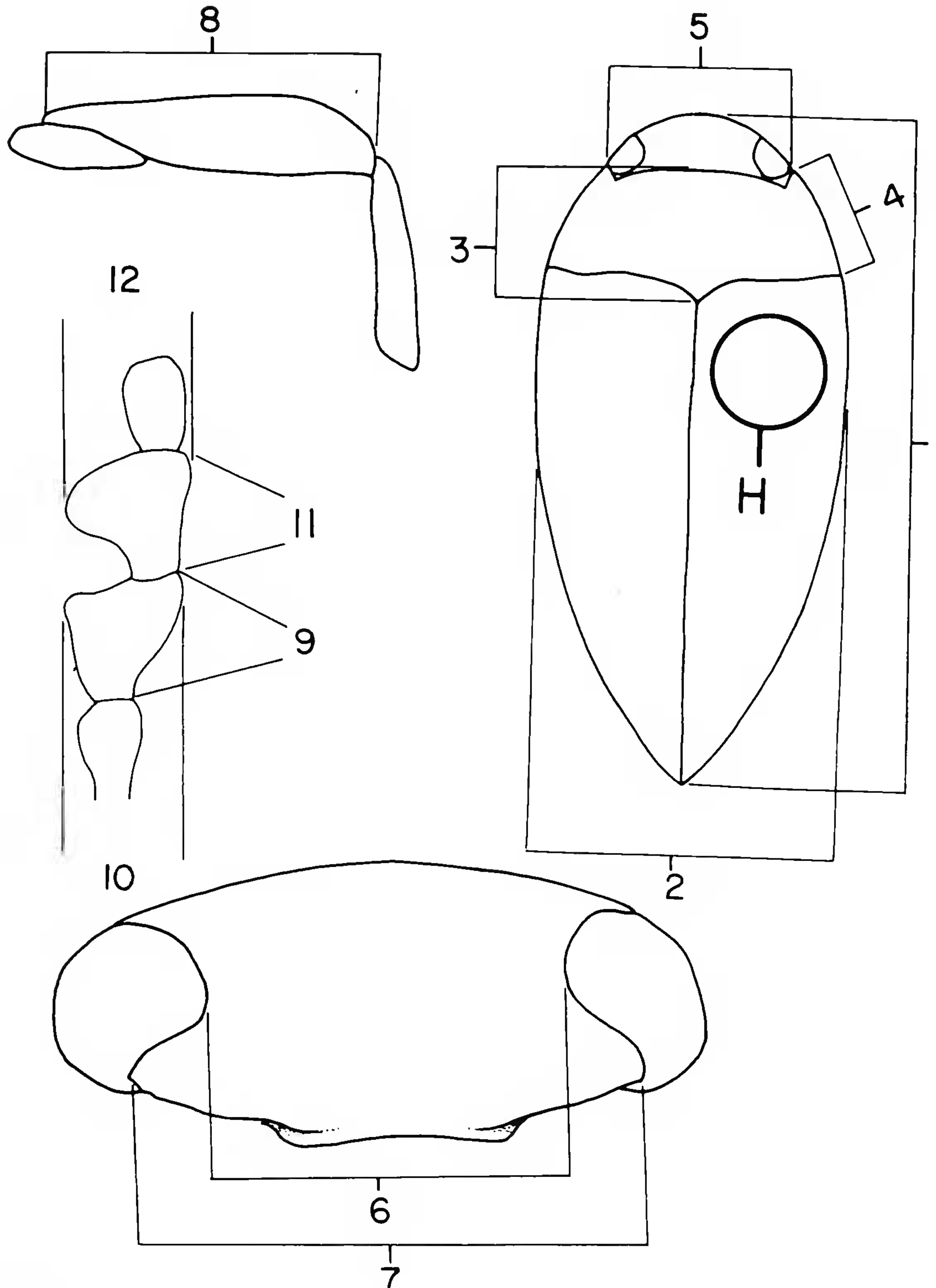


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Fig. 33. 1–12 indicate measurements made for phenetic analysis. Area H encloses area from which SEM photographs were taken (see Figs. 30–31).

related to other genera in Hydroporini. Each of these more closely related groups (excluded from *Hydroporus*) justifiably deserves generic status and *Falloporus* is at least as distinct from each of them as they are from each other.

Among Hydroporini, we have examined all species of *Heterosternuta* and *Neoporus* and the mesosternum and mestasternum always contact each other

Table 1. List of OTUs with locality and identification data.

OTU	Group	Sex	Species	Locality
1	1	M	P	Miller Co., GA
2	1	F	P	Miller Co., GA
3	2	F	P	Lawrence Co., MS
4	3	M	T	Tapallosa Co., AL
5	4	M	P?	Macon Co., AL
6	4	F	P?	Macon Co., AL
7	5	M	P	Baldwin Co., AL
8	5	F	P	Baldwin Co., AL
9	6	F	P	Houston Co., AL
10	7	M	T	Escambia Co., AL
11	8	M	T	Logan Co., KY
12	8	F	T	Logan Co., KY
13	9	M	P	Lauderdale Co., TN
14	9	F	P	Lauderdale Co., TN
15	10	M	P	Dorchester Co., SC
16	10	F	P	Dorchester Co., SC
17	11	F	P	Haywood Co., TN
18	12	M	P	Gilchrist Co., FL
19	12	F	P	Gilchrist Co., FL
20	13	M	P	Montgomery Co., AL
21	13	F	P	Montgomery Co., AL
22	14	F	T	Bay Co., FL
23	15	F	P	Alachua Co., FL
24	16	F	P	Jackson Co., FL
25	17	M	P	Levy Co., FL
26	18	F	P	Bleckely Co., GA
27	19	M	P	Baker Co., GA
28	20	F	P	Caddo Par., LA
29	21	F	P?	Smith Co., TX
30	22	F	P	Nacogdoches Co., TX
31	23	M	P	Arkansas
32	23	F	P	Arkansas
33	24	M	P	Robeson Co., NC
34	25	F	T	Indiana, PA
35	26	M	T	E. Cont., MO
36	27	F	P	Jackson Co., MO
37	28	M	T	Boone Co., MO
38	29	M	T	Scioto Co., OH
39	30	M	T	Scott Co., TN
40	31	M	T	Benton Co., TN
41	32	M	T	White Co., TN
42	33	M	T	Stewart Co., TN
43	33	F	T	Stewart Co., TN
44	34	M	T	Bledsoe Co., TN
45	34	F	T	Bledsoe Co., TN
46	35	M	T	Baldwin Co., AL
47	35	F	T	Baldwin Co., AL

Table 1. Continued.

OTU	Group	Sex	Species	Locality
48	36	M	T	Van Buren Co., TN
49	36	F	T	Van Buren Co., TN
50	37	M	T	Lincoln Co., MS
51	37	F	T	Lincoln Co., MS
52	38	M	T?	Blount Co., TN
53	38	F	T?	Blount Co., TN
54	39	M	T	Sauk Co., WI
55	39	F	T	Sauk Co., WI

ventromedially. Sharp (1882) and Balfour-Browne (1940) have shown that the mesosternum and mestasternum contact in *Hydroporus s. str.*, *Laccornis* Des Gozis, *Oreodytes, Graptodytes, Stictonectes, Scarodytes, Porhydrus,* and *Metaporus*. Fall (1923) and Zimmerman and Smith (1975) have shown that a few nearctic *Deronectes* have contacting segments. Non-contacting segments are known in *Paroster* Sharp, *Antiporus* Sharp, *Nectrosoma* M'Leay, *Megaporus* Brinck, *Hygrotus* Stephens, and most *Deronectes* (Sharp 1882). We also found the non-contacting conditions in *Peschetius* Guignot and *Falloporus*.

A detailed discussion of hydroporine phylogeny is the subject of another paper (in preparation), however, it can briefly be stated that there is strong evidence that non-contact between the mesosternum and metasternum is an apotypic condition. This indicates *Falloporus* does not belong in *Hydroporus*; instead, it shares a more recent common ancestor with other Hydroporini genera. Since *Falloporus* is at least as distinct as other nearctic and palearctic genera, we have elected to raise it to generic status. *Falloporus* is probably most closely related to *Hygrotus* or *Deronectes*.

Phenetics

Extreme variation in color pattern and antennal modification suggested the possibility of one highly variable species rather than two distinct species. Therefore, a cluster cluster, ordination, and discriminant analysis were performed on specimens of both presumed species of *Falloporus*.

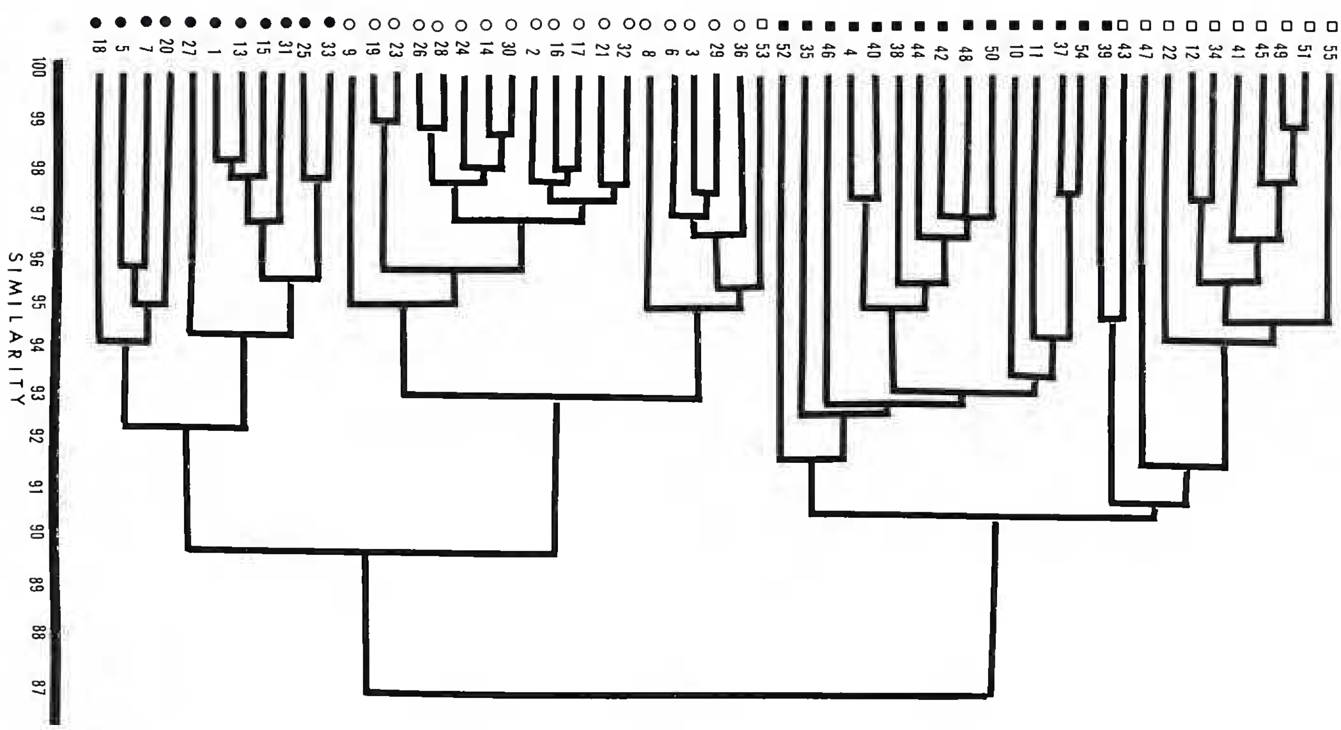
All available specimens of *Falloporus* have been examined and at least a representative sample of specimens from each collection, but usually the entire collection, were measured for 14 characters. Measured characters used are depicted in Fig. 33: 1; total length (TL), 2; total width (TW), 3; median pronotal length (MPL), 4; lateral pronotal length (LPL), 5; head width (HW), 6; interoccular distance (ID), 7; frons width (FW), 8; femur length (FL), 9; width of 4th antennal segment (4W), 10; length of 4th antennal segment (4L), 11; width of 5th antennal segment (5W), 12; length of 5th

Table 2. Average of each OTU for measured variables. N = sample size. See text for other abbreviations.

OTU	TL	TW	MPL	LPL	HW	ID	FW	FL	4W	4L	5W	5L	PC	EC
1	76.80	34.63	31.25	27.90	41.34	24.09	31.38	30.50	5.44	6.74	5.13	5.32	4.75	6.50
2	78.10	36.30	31.46	32.72	43.78	24.94	32.40	31.50	3.00	4.64	3.00	3.80	5.60	6.10
3	78.50	37.10	31.00	27.50	42.00	25.50	32.50	31.50	2.90	5.00	2.85	3.90	1.75	5.25
4	66.00	32.00	30.00	23.50	37.00	24.00	30.20	26.00	3.10	4.00	4.10	5.00	1.00	5.00
5	77.64	33.21	31.26	27.88	42.88	26.81	34.15	29.88	4.57	4.91	5.66	7.27	3.00	5.44
6	78.17	36.33	30.67	27.67	42.33	27.67	34.67	29.83	3.00	4.37	3.10	4.10	2.00	5.17
7	78.17	36.50	31.33	27.67	41.67	25.73	33.33	30.00	4.33	5.80	5.67	6.07	2.00	6.33
8	77.59	36.21	31.09	28.55	42.00	26.20	32.91	29.91	3.01	5.31	3.04	4.43	1.77	10.54
9	81.00	36.00	33.00	29.00	45.00	25.00	32.00	31.20	3.00	4.00	3.00	5.00	3.50	6.00
10	73.00	36.30	31.00	27.00	41.00	26.50	33.00	29.00	4.00	9.00	6.00	6.10	1.00	5.50
11	69.00	39.00	31.00	25.00	40.00	25.00	32.00	27.00	4.00	3.80	6.00	4.90	1.00	5.00
12	68.00	33.75	30.00	28.25	39.00	25.00	31.50	26.25	2.25	5.00	2.15	4.25	1.00	4.25
13	78.00	35.93	31.67	28.33	41.83	24.43	31.33	30.67	6.00	6.00	5.33	5.17	5.50	6.67
14	83.50	38.00	35.00	30.00	44.00	25.00	33.00	33.00	3.00	4.50	3.00	3.80	4.50	5.00
15	78.00	36.00	31.00	29.00	41.00	24.00	31.00	31.00	6.20	6.80	6.00	5.00	5.00	6.00
16	80.67	37.43	32.33	29.33	42.67	25.33	32.67	31.67	3.23	4.60	2.93	3.70	6.17	5.83
17	84.00	38.00	34.00	30.00	44.00	25.00	34.00	32.60	3.00	4.50	3.00	3.50	6.50	5.50
18	80.50	36.50	27.00	29.50	44.50	28.50	35.10	31.25	5.05	4.75	6.45	8.00	1.75	5.50
19	85.00	38.00	33.00	31.00	45.00	26.00	33.80	33.00	3.00	5.00	3.00	4.00	6.00	10.00
20	84.00	40.00	33.00	31.00	44.00	26.00	35.00	33.00	5.80	6.00	5.20	6.00	3.00	5.50
21	82.00	38.00	32.00	29.00	44.00	26.00	35.00	32.00	3.00	4.80	3.00	4.00	6.50	7.00
22	71.50	35.00	30.00	27.00	39.00	25.00	32.00	28.00	2.30	5.00	2.80	3.50	1.00	11.00
23	84.00	40.00	33.00	30.50	46.00	26.00	34.00	33.00	3.00	5.00	3.00	4.50	6.00	9.50
24	85.00	39.00	34.00	30.00	44.50	27.00	34.00	33.00	3.00	5.00	3.00	4.00	5.00	6.00
25	81.50	37.00	34.00	30.00	44.00	26.00	34.00	33.00	6.00	8.00	5.50	5.00	5.50	11.00
26	81.00	38.00	31.00	29.00	43.00	25.00	32.00	31.00	3.00	5.00	3.00	4.00	5.00	5.50
27	75.00	36.00	24.00	26.00	41.00	24.00	32.00	30.00	5.00	6.00	4.80	5.00	4.00	5.50
28	79.00	37.00	32.00	28.00	43.00	25.00	33.00	31.00	3.00	5.00	3.00	4.00	4.00	5.50
29	79.00	37.00	32.00	29.00	43.00	27.00	34.00	30.00	2.50	5.00	3.00	4.00	1.50	5.00

Table 2. Continued.

OTU	TL	TW	MPL	LPL	HW	ID	FW	FL	4W	4L	5W	5L	PC	EC
30	85.00	39.00	33.00	30.00	45.00	25.50	34.00	32.00	3.00	4.50	3.00	4.00	5.00	5.00
31	81.00	37.25	31.50	29.50	43.50	24.50	32.00	31.50	5.75	6.00	5.50	5.75	6.75	6.25
32	80.00	37.00	32.00	28.00	42.00	25.00	33.00	31.00	3.00	5.00	3.00	3.80	7.50	6.00
33	80.00	36.00	33.00	29.00	44.00	26.00	32.80	30.00	5.50	7.00	5.50	5.00	5.00	10.00
34	73.00	36.00	31.00	28.00	41.00	25.00	33.00	29.00	2.00	5.00	2.30	4.00	1.00	4.00
35	75.00	35.00	21.00	28.00	40.00	26.00	31.00	28.00	3.00	6.00	6.50	4.50	1.00	4.00
36	80.00	37.00	32.00	28.00	44.00	27.00	33.00	31.00	2.50	4.00	3.00	4.00	2.00	4.00
37	77.00	36.00	32.00	29.00	41.00	26.00	32.00	28.00	3.50	4.00	8.00	6.00	1.00	5.00
38	69.00	34.00	30.50	27.00	39.50	26.00	31.50	26.00	4.50	5.25	4.30	5.00	1.00	3.50
39	75.00	36.00	32.00	29.00	41.00	26.00	34.00	29.00	3.50	4.80	5.00	6.00	1.00	1.00
40	68.00	32.50	29.00	25.00	37.00	25.00	30.00	26.00	3.00	4.00	4.60	6.00	1.00	4.00
41	76.00	38.00	32.00	29.00	42.00	28.00	35.00	31.00	2.00	4.00	3.00	4.00	1.00	3.00
42	69.80	33.00	30.00	27.00	39.00	25.00	31.00	28.00	3.20	3.80	5.50	6.50	1.00	3.00
43	72.00	35.00	32.00	27.00	41.00	27.00	34.00	29.00	2.80	4.00	2.80	4.00	1.00	1.00
44	71.00	34.00	30.00	26.00	40.00	27.00	33.00	26.50	4.00	4.00	4.50	7.00	1.00	3.00
45	70.00	33.60	29.00	26.00	39.00	25.00	32.00	26.00	2.00	4.00	2.80	4.00	1.00	3.00
46	71.00	33.79	29.43	25.71	39.14	25.07	30.71	27.29	3.91	4.73	5.84	6.31	1.00	11.93
47	71.00	34.25	29.50	27.00	39.50	25.75	32.00	28.00	2.90	4.55	3.00	4.30	1.00	55.50
48	73.71	34.50	29.75	27.44	40.63	26.79	32.63	28.19	3.18	4.23	4.48	5.94	1.00	2.63
49	74.00	35.00	30.50	27.50	41.00	27.50	32.50	27.75	2.55	4.25	3.00	4.15	1.00	3.25
50	72.50	35.00	31.00	28.00	40.50	25.50	31.50	29.00	3.50	4.15	5.10	6.00	1.00	3.50
51	73.38	34.75	30.25	28.00	39.88	25.63	32.00	29.00	2.72	4.13	2.95	4.07	1.00	3.13
52	78.33	38.00	33.33	29.33	44.33	27.83	34.50	30.33	4.03	4.67	5.60	6.83	1.33	2.17
53	81.00	37.50	33.00	29.00	45.00	38.00	35.00	30.50	3.00	5.00	3.50	4.50	2.00	4.00
54	78.00	36.00	31.50	29.00	40.75	25.50	33.00	30.00	3.30	4.00	7.45	6.75	1.00	6.00
55	74.00	36.00	30.00	28.00	41.00	26.00	33.00	30.00	3.00	4.10	3.00	4.00	1.00	6.50

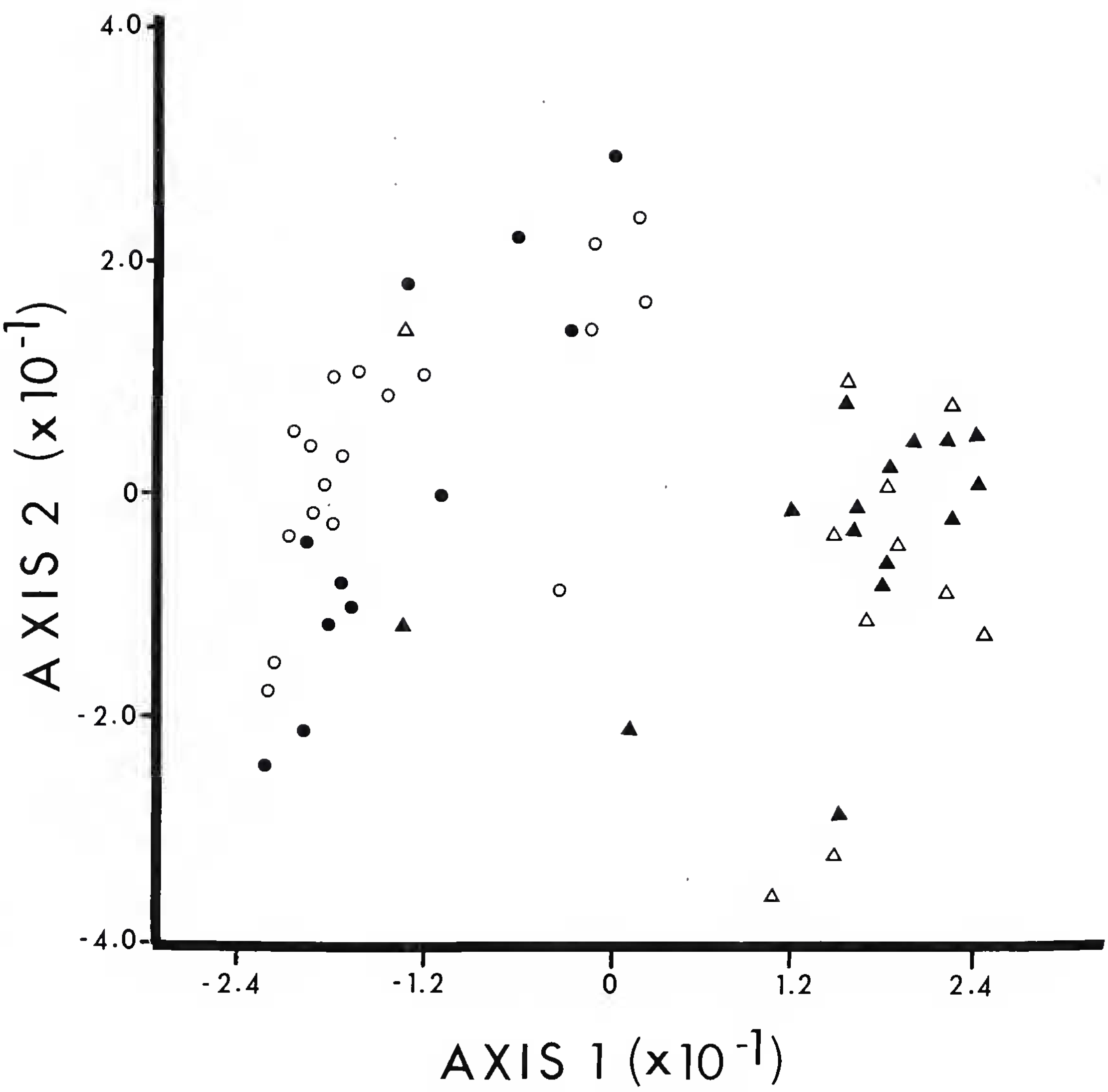


34

Fig. 34. Dendrogram resulting from cluster analysis. Squares are *F. triangularis,* circles are *F. pilatei*; open figures are females, closed figures males.

antennal segment (5L). Degree of pronotal color (PC) and elytral color (EC) were also numerically coded. Male 4th and 5th antennal segment shape was also recorded but since both males and females were used in the analysis these characters were not used. Each collection was divided by sex because of the sexual dimorphism exhibited by members of *Falloporus* and all members of a single sex from one collection made up an OTU. A total of 39 collections produced 55 OTUs and these are listed in Table 1 with their collection localities. Before clustering and ordination were performed, the 39 collections were identified as *pilatei, triangularis,* or 'intermediate.' Our identifications were based primarily on the characters presented by Fall (1923) for distinguishing the two species.

Values for each variable in each OTU were averaged and these data are reported in Table 2. These values were used to calculate a similarity coefficient matrix. The Canberra metric (Lance and Williams, 1967) was chosen because it is not affected by the entire range of characters in the data set, but only reflects those groups being compared (Sneath and Sokal, 1973). This was thought desirable because of the presence of characters exhibiting extreme sexual dimorphism. The similarity matrix was subjected to both cluster analysis (group average) and ordination (PCORD technique) in order to examine the relationships between the OTUs. Neither cluster analysis nor ordination is preferred for the study of population variation and when both are used additional insight is gained into the relationship between the OTUs.



35

Fig. 35. Ordination of 55 OTUs on the first two principal coordinates. Triangles are *F. triangularis*, circles are *F. pilatei*; open figures are females, closed figures males.

The result of the cluster analysis is presented in Fig. 34. The primary grouping (at similarity level 0.874) is of the two putative phena. Within these two major phena, OTUs are grouped into clusters of males and females. A single OTU (53), *triangularis* female from Blount Co., TN, was misclassified by the cluster analysis. Males from the same collection (52) were correctly classified.

This result supports the two species concept. Alternative results (e.g. three major clusters with the 'intermediates' clustering by themselves or severe mixing of the previously designated *pilatei* and *triangularis* OTUs in the same cluster) would have supported the single species concept.

A principal coordinate analysis was performed on the similarity matrix and an ordination of the OTUs on the first two coordinates is shown in Fig. 35. The efficiency of the coordinates decreases rapidly because of the sexual dimorphism exhibited by members of *Falloporus*. The first two coordinates

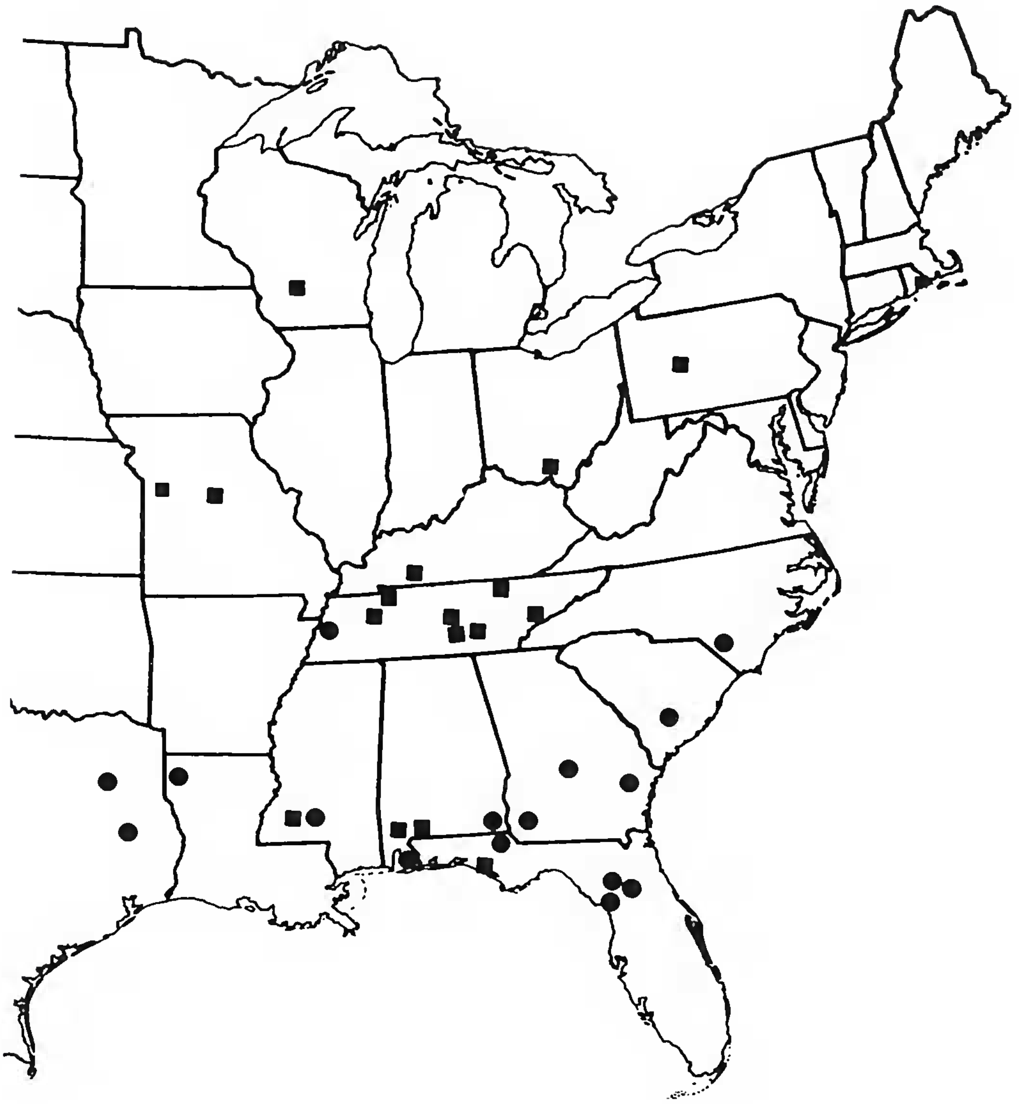

36

Fig. 36. Distribution of *F. triangularis* (squares) and *F. pilatei* (circles).

(28.138 and 19.397) explain 47.5% of the variance in the similarity matrix. The pattern in Fig. 35 indicates that the primary separation of species occurs along the first axis with some minor separation along the second axis.

An examination of the loading matrix indicates that length (TL), width of the 4th antennal segment (4W), and pronotal color (PC) load heavily on the first coordinate while both 4th and 5th antennal segment width (4W and 5W) load heavily on the second coordinate.

The ordination produced an interesting grouping of *pilatei* OTUs (centroid; Axis I = 0.0, Axis II = +2.0). These collections are all from the southern coastal plain, but not all collections from this area are included in the grouping. These collections appear to be specimens of *pilatei* which have unusually reduced pronotal coloration. The collections which we had *a priori* identified as 'intermediate' did not fall in the area between the two phena as would have been expected if they represented true intermediate forms. They were rather uniformly distributed within each major grouping.

Two OTUs (52 and 53) which we identified as *triangularis* fell into the *pilatei* group; one of these (53) was misclassified by cluster analysis. Reexamination revealed that pronotal coloration is about as in members of *triangularis,* but length and width of the fourth and fifth antennal segments are slightly larger than would be expected in *triangularis*. These OTUs (males and females from the same collection) may represent hybrids between the two species or may simply be extreme examples of *Falloporus triangularis*.

Discriminant analysis indicated that the most reliable characters for separating the two species were size, antennal width, and antennal length (although there was some overlap in these characters). Pronotal coloration, which we have found to be a fairly reliable character for separating species of *Falloporus* and which was also important in both clustering and ordination, was not heavily weighted in the discriminant analysis. This was probably due to high interpopulation variation within each species. Although discriminant analysis did not emphasize pronotal coloration, classification by these techniques indicated 2 phena and in this respect was still in close agreement with the results of the cluster and ordination analysis. There were several exceptions. According to discriminant analysis, OTU's 5 and 6 (originally identified as 7 male and 3 female *pilatei*) were a mixture of both species or possibly represented an intermediate population. OTU 52 which was misclassified by ordination analysis and OTU 53 which was misclassified by both cluster and ordination analyses, were both classified correctly by discriminant analysis.

All three analyses indicate that there are two distinct phena and we conclude that the statistical evidence does not support synonomization at this time. Furthermore, the phena appear to prefer different habitats. *Falloporus triangularis* is more common in streams with undercut banks and is usually found in upland situations. *Falloporus pilatei* usually occurs in sluggish swampy rivers or streams or in adjacent pools, and occasionally in dangling roots of shrubs in swamps. It is typically found on the coastal plain.

A Key to *Falloporus* Species

1. Fourth and fifth male antennal segments broadened (Figs. 20–21); pronotum more broadly infuscate (Figs. 7–10) .... *pilatei*
   Only fifth male antennal segment distinctly modified (Figs. 14–19); pronotum less broadly infuscate (Figs. 1–6) .... *triangularis*

Falloporus triangularis (Fall) **NEW COMBINATION**

Hydroporus triangularis Fall, 1917:170.

Diagnosis.—This species is distinguished from *Falloporus pilatei* by the lack of modification of the 4th antennal segment of males (Figs. 14–19) and by the less infuscate head and pronotum (Figs. 1–6). In dorsal view the aedeagal apex of *triangularis* is slightly more truncate than that of *pilatei* (Figs. 11a and 12a).

Description.—Males—Size (N = 51), length = 3.80 (3.39 to 4.26); width = 1.82 (1.64 to 2.05); L/W = 2.09. Form elongate oval, tapered posteriorly, widest at middle or just anterior; pronotum and elytra continuous. Lateral edges of pronotum gradually curved inward toward anterior angles, bead extremely fine, not broadened anteriorly; much narrower than second antennal segment. Prosternum declivitous (Fig. 27), not angularly protuberant. Prosternal process lanceolate, bluntly pointed, clypeus not thickened, metasternum sulcate (Fig. 27). Fifth antennal segment variable but distinctly broadened apically, usually appearing somewhat triangular.

Color pattern variable but almost always maculate (Figs. 1–6). Head usually uniformly yellowish orange, sometimes variably infuscate bordering eyes. Pronotum usually uniformly light yellowish orange, sometimes with narrow infuscation along anterior and posterior edge. Elytral pattern with variable light and dark fascia; sutural stripe usually vague, but sometimes distinct or completely lacking; extending along basal edge to varying degrees to form basal infuscation which is seldom connected to middle dark fascia. Middle and apical dark fascia often extending from suture to lateral margin and usually not connected to each other. The middle fascia is sometimes isolated from the sutural stripe and narrower than usual, sometimes even broken into two isolated spots. Apical fascia also sometimes greatly reduced. Apices of elytra yellowish. Venter yellowish orange.

Microreticulation evident; dorsal and ventral surfaces usually densely micropunctate (Figs. 29–31). Punctation of head extremely fine and dense; coarser punctures in shallow depressions at anteromedial corners of eyes. Pronotal punctation extremely fine and dense, coarser punctures along anterior edge and scattered across disc; coarser punctures in discal area separated by two to three times their width. Elytral punctures approximately as coarse as coarser pronotal discal punctures, separated by two to three times their width (Fig. 30); vague discal longitudinal series of denser punctures evident. Metacoxa and metasternum with scattered punctures, coarsest on metasternum, microreticulation evident (Fig. 29).

Anterior protarsi not appreciably broadened, with distinct circular cupules at basal end of first segment (Fig. 32). Aedeagus with ventral portion deflected apically, much shorter than parameres; parameres with long subapical setae (Fig. 12).

Females—Size (n = 43), length = 3.92 (3.44 to 4.26); width = 1.87 (1.67 to 2.00); L/W = 2.09. Similar to male. Antennae not modified. Ovipositor as in Fig. 13.

Type locality.—Sauk City, Wisconsin.

Type data.—Fall (1917) states that his description of *triangularis* was based on four males and six females from Sauk City, Wisconsin. These were supposed to have been collected for Mr. J. D. Sherman by Mr. W. S. Marshall. There is a series of four specimens of *triangularis* (two males and two females) in the H. C. Fall collection at the Museum of Comparative Zoology, Harvard University. All bear collection labels for Sauk City, Wisconsin. Additionally one has the date represented as VIII—9.

One male, which we have designated as the lectotype, bears labels as follows: (1) Sauk City, Wisconsin; (2) a male symbol; (3) TYPE *triangularis* (*triangularis* is handwritten); (4) M.C.Z. type 23962; (5) H. C. FALL COLLECTION; (6) Handwritten Lectotype label with GWW in the lower left corner. The other three specimens have been designated paralectotypes and handwritten paralectotype labels (with GWW in the lower left corner) have been affixed to the pins.

Range.—This species ranges from Wisconsin to the southern Gulf coastal plain (Fig. 36).

Habitat.—This is a lotic species, preferring undercut banks of clear water streams. Teneral specimens were collected in August. The gut contents of one of the specimens which we dissected contained a ceratopogonid pupa.

Falloporus pilatei (Fall) **NEW COMBINATION**

Hydroporus pilatei Fall, 1917:170.

Diagnosis.—Distinguished from *triangularis* by enlarged 4th antennal segment (Figs. 20–21) and generally darker coloration of the head and pronotum (Figs. 7–10). In dorsal view, the aedeagus of *pilatei* is slightly more apically tapered than that of *triangularis* (Figs. 11a and 12a).

Description.—Males—Size (N = 31); length = 4.02 (3.79 to 4.31); width = 1.81 (1.65 to 2.05); L/W = 2.22. Prosternum, body form and most morphological characters as in *triangularis* except 4th and 5th antennal segments modified, appearing triangular (Figs. 20–21).

Coloration darker than *triangularis* (Figs. 7–10). Head infuscate around eyes. Pronotum broadly infuscate. Discal area appearing lighter. Elytra with light and dark fascia; sutural stripe distinct, extending along basal edge to form basal fascia. Middle dark fascia broad, extending from sutural stripe to the lateral margin, often connected to basal dark fascia, thus breaking the basal yellowish fascia into two isolated spots. Apical dark fascia connected to sutural stripe, sometimes expanded so light fascia between it and middle dark fascia are reduced to restricted lateral spots. Apices of elytra yellowish. Ventral surface orange.

Protarsi not appreciably broadened, with circular cupule at the base of the tarsal segment. Anterior protarsal claw not modified; aedeagus and parameres as in Fig. 11.

Females—Size (N = 38); length = 4.08 (3.67 to 4.36); width = 1.89 (1.69

to 2.05); L/W = 2.15. Similar to males, antennal segments unmodified; ovipositor very similar to that of *trinagularis*.

Type locality.—Winnfield, Louisiana.

Type data.—Fall's 1917 description of *pilatei* was based on a unique male from Winnfield, Louisiana, collected by Mr. G. R. Pilate. The specimen bears the following labels: (1) Winnfield VI-17 La.; (2) TYPE *pilatei* (*pilatei* is handwritten); (3) M.C.Z. Type 23944; (4) H. C. FALL COLLECTION; (5) *Hydroporus pilatei* Fall (handwritten); (6) a handwritten lectotype label with GWW in the lower left corner. The speciment is very teneral.

Range.—Gulf and Atlantic coasts from North Carolina to Texas and north to Tennessee (Fig. 36).

Habitat.—Unlike *triangularis* this species appears to prefer swampier habitats and sluggish streams. Specimens have been collected from dangling roots of marginal shrubs and from submerged vegetation on gently sloping banks. Teneral specimens were collected in June and October.

Summary

Clairville is recognized as the author of *Hydroporus* and the correct type-species is *Hyphidrus pubescens* designated by Guignot (1946). Within Fall's *pulcher-undulatus* group: *Circinoporus* is designated a synonym of *Neoporus*; *Heterosternuta* is recognized as the valid name for *pulcher* group species (type *H. concinnus* = *H. wickhami*); and the name *Neoporus* is applied to all other species except *pilatei* and *triangularis*. A new genus, *Falloporus,* is described for *pilatei* and *triangularis* because these species are phylogenetically out of place in *Hydroporus*. The primary evidence for removal from *Hydroporus* is that the mesosternum and metasternum contact each other in all species groups and subgenera of *Hydroporus,* but do not contact in *Falloporus*. Non-contacting segments is considered apotypic and this indicates *Falloporus* has a more recent common ancestor with other Hydroporini genera than it does with *Hydroporus*.

It was initially suspected that *pilatei* and *triangularis* were actually a single variable species; however, a phenetic analysis (cluster, ordination and discriminant analysis) distinguished two phena. All but one specimen from suspected hybrid zones and all specimens that were *a priori* considered intermediate in appearance were readily classified into two phena by the analysis. Statistical evidence can never prove there are, in fact, two species; however, here it is of sufficient strength that synonymizing *pilatei* and *triangularis* would be unwise.

Falloporus keys to couplet 15 in Leech and Chandler's (1956) Dytiscidae key and may be separated using the following interpolation:

15. Prosternal process not protuberant (Fig. 27); male with fourth or fourth and fifth antennal segments enlarged (Figs. 14–21); male protarsal cupule present (Fig. 32); length greater than 3.3 mm . . . . *Falloporus*

Prosternal process usually protuberant (if not protuberant then length less than 3.3 mm); male with fourth and fifth antennal segments not enlarged and protarsal cupule absent 15a

15a. Hind angles of pronotum rectangular or obtuse. .... (in part) *Hydroporus*

Hind angles of pronotum acute .... (in part) *Deronectes*

Acknowledgments

Hugh Leech's taxonomic and nomenclatural Dytiscidae studies have provided a solid basis for this and other studies. Mr. W. Steiner (Smithsonian Institution) and Drs. F. N. Young (Indiana University), G. Folkerts (Auburn University), W. Hilsenhoff (University of Wisconsin) and P. J. Spangler (Smithsonian Institution) generously loaned specimens. Mr. N. Stone (Museum of Comparative Zoology, Harvard University) arranged for type specimen loans from the H. C. Fall Collection. Technical work involved with specimen preparation for scanning electron microscope use was provided by Ms. Mary Jacque Mann and Mrs. Susan Braden. Dr. Spangler also allowed extensive use of his personal library of Dytiscidae literature. Mr. R. E. Roughley (University of Alberta) and Drs. F. C. Thompson (USDA, Smithsonian Institution) and T. Erwin (Smithsonian Institution) reviewed the manuscript and provided critical, but always helpful and constructive, suggestions.

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Footnote

[1] Portions of this work were completed during graduate study at the University of Tennessee and during a postdoctoral fellowship at the Smithsonian Institution.