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SEPEDON MCPHERSONI, N. SP., KEY TO NORTH AMERICAN *SEPEDON*, GROUPS IN *SEPEDON S.S.*, AND INTRA- AND INTERGENERIC COMPARISON (DIPTERA: SCIOMYZIDAE)

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Abstract.—***Sepedon mcphersoni*, new species**, from southern Illinois, U.S.A., is described and illustrated, and a key to the 20 North American species of *Sepedon* is presented. The classification of the genus *Sepedon* and six related genera is discussed. All known species of *Sepedon* are classified in nine groups including the subgenus *Parasepedon* Verbeke 1950 as the *Trichrooscelis* group, the subgenus *Mesosepedon* Verbeke 1950 as the *Dispersa* group, and the genus *Sepedomyia* Verbeke 1950 as the Nasuta group. A character matrix of the groups of *Sepedon* and related genera is included. Publications on the life cycles and/or immature stages of *Sepedon* and related genera are summarized.

Key Words: snail-killing flies, taxonomy, classification, biocontrol agents

The classification of snail-killing flies of the genus *Sepedon* Latreille in the Western Hemisphere was last revised by Steyskal (1951), who included 12 North American species and one subspecies. Since then, nine North American species have been described or their status has been changed (Steyskal 1960, 1965b; Fisher and Orth 1969, 1972, 1974; Orth 1986; Manguin 1990). Herein we describe a new species of *Sepedon* from Illinois, present a revised key to the species of North America, propose taxonomic groups for the species of *Sepedon* worldwide, compare these groups with six related genera, and present a list of publications on the life cycles and/or immature stages.

The cosmopolitan genus *Sepedon* and related genera are of special interest to evolutionary and behavioral studies of Sciomyzidae because certain species represent some of the most derived lineages within the family and because some are prime candidates as biological control agents of disease-carrying snails. Study of these genera is beginning to afford an opportunity to understand the evolution of diverse modes of feeding behavior—from obligate parasitoids to predators—by correlating feeding behavior with phylogenetic position established on the basis of morphological character systems. As discussed below, indications of the degree of relatedness and generic and supra-generic characterizations have been provided in a few earlier studies of "*Sepedon*." A cladistic analysis of the family by Marinoni and Mathis (2000) confirms or rejects some of those proposals and provides a more comprehensive basis for comparisons.

Sepedon mcphersoni Knutson and Orth, new species

(Figs. 1–4)

Male.—Gross aspect tawny brown. Head with broadly excavated frons with moderate para-orbital and median ridges. Medifacies with a few, scattered, fine black setae. Orbito-antennal spot and fronto-orbital spot rounded, black, velvety pruinose, separated from eye margin by whitish pruinosity. One (posterior) fronto-orbital bristle. Ocellar bristles absent. Postocellar bristle well developed. Angle of face with oral margin in profile about 90°, rostrum not extended. Palpus present. Scape about ⅓ as long as wide. Pedicel about 2¼ times as long as wide. Arista densely furnished with short, white hairs.

Thorax tomentose dorsally with 4 longitudinal brown stripes, median pair coalescing before mesonotal suture. Mesonotum not angulate anteriorly, transverse mesonotal suture incomplete. Prosternum with a few scattered setae in lower ½. Pleura with sparsely scattered setae, denser on anepisternum. Anterior and posterior notopleural bristles present. Presutural bristle absent. Katatergite (= metapleural) callus dark brown tomentose, with cluster of black setae. Scutellum with pair of apical bristles.

Fore coxa light brown, whitish tomentose; middle and hind coxae slightly darker. Sternal-coxal bridge absent. Legs mostly yellowish; fore femur with brownish area midway on external surface. No strong, erect dorsal bristle on fore femur. Hind femur simple, without midventral notch. Fore and middle tibae brownish at distal ends; hind femur brownish in distal ⅓, hind tibia with straw-colored area in distal ⅓, contrasting with brown before and after; fourth and fifth tarsal segments brownish.

Wing length 4.7 mm. Membrane brownish, hyaline; costal margin and wing veins brownish. Crossveins clouded. Halter, calypter, and calyptral fringe brown.

Abdominal segments brownish. Terminalia as in Figs. 1 and 4. Cochleate vesicle absent, posterior surstylus and epandrium not fused, cerci not fused together, epandrium not closed below cerci, aedeagal filaments present.

Female.—Similar to holotype male except for terminalia. Wing length 5.1 mm.

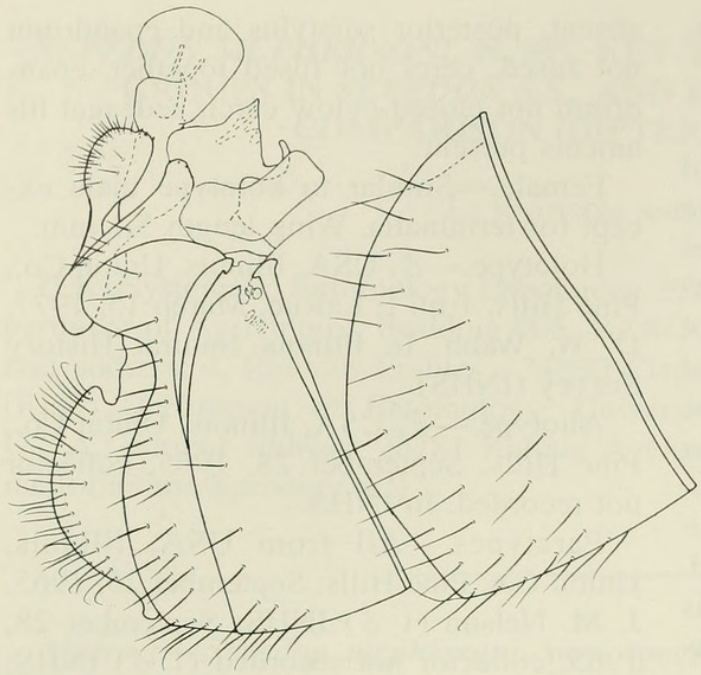
Holotype.—♂, USA, Illinois, Union Co., Pine Hills, 1 mi E LaRue, March 15, 1977, D. W. Webb. In Illinois Natural History Survey (INHS).

Allotype.—♀, USA, Illinois, Union Co., Pine Hills, September 28, 1965, collector not recorded. In INHS.

Paratypes.—All from USA, Illinois, Union Co., Pine Hills: September 25, 1965, J. M. Nelson (1 ♂) INHS; September 28, 1965, collector not recorded (1 ♂) INHS; September 29, 1972, R. W. Vangeison (1 ♀) SIU (Southern Illinois University); March 2, 1973, J. E. McPherson (1 ♂) SIU. Winters Pond, 9 km N Wolf Lake: September 24, 1996, D. W. Webb (2 ♂, 1 ♀) INHS.

Diagnosis.—*Sepedon mcphersoni* is a member of the *S. sphegea* group, which includes 7 Nearctic, 2 Palearctic, and 1 Palearctic-Oriental species. It may be placed in the *S. pusilla* subgroup, which includes *S. borealis* Steyskal, *S. lignator* Steyskal, *S. neili* Steyskal, and *S. pusilla* Loew. All five are North American, north temperate to boreal species and have been found only north of 37°N latitude. Members of this subgroup are identified by their (1) simple, not notched, hind femur (2), evenly arcuate hind tibia (3), small size (wing length less than 5.2 mm), and (4) frequently almost black abdomen with bluish reflections.

Externally, *S. mcphersoni* is distinct from other members of the *S. pusilla* subgroup. The hind femur and tibia are more or less uniformly brown in all species of the subgroup, except *S. mcphersoni*. The hind femur of *S. mcphersoni* is straw colored proximally and brown distally. The hind tibia has a straw colored area in the distal ⅓, contrasting with brown before and after, thus giving the appearance of a yellowish band. The color pattern of the hind leg of *S. mcphersoni* closely resembles that of *S.*



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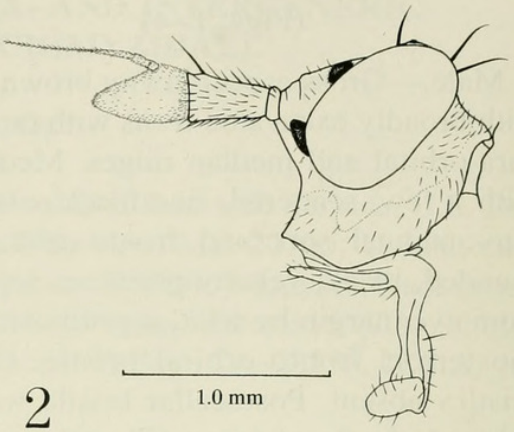

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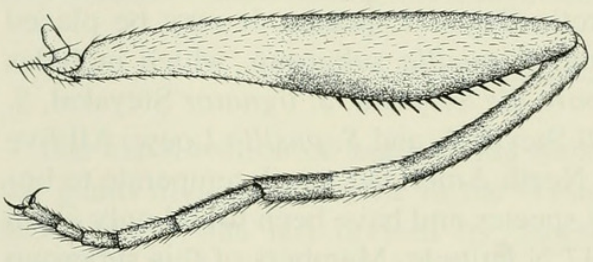

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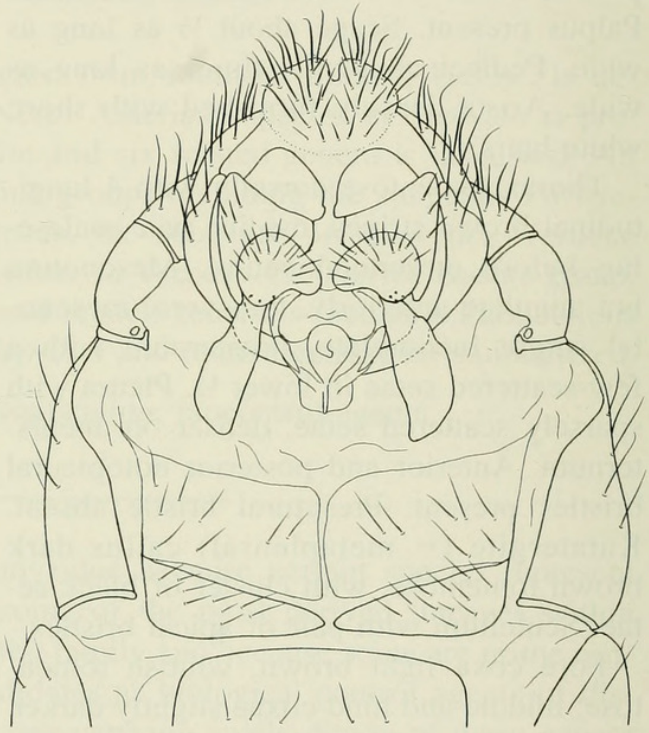

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Figs. 1–4. *Sepedon mcphersoni*. 1, Paratype male, postabdomen (sinistral view, inverted). 2, Holotype male, head. 3, Paratype male, sinistral hind leg. 4, Paratype male, postabdomen (ventral view).

floridensis Steyskal, a much larger Nearctic species in the *S. fuscipennis* group (see Orth 1986). The abdominal segments of *S. mcphersoni* are not as dark as other members of the subgroup, with the exception of *S. pusilla*. The terminalia of the male of *S. mcphersoni* (Figs. 1, 4) show no close similarity to other members of the subgroup.

Distribution and habitat.—*Sepedon mcphersoni* is known only from the LaRue-Pine Hills Ecological Area, Shawnee National Forest, Union County, southernmost Illinois. The two specific localities according to the specimen labels, 1 mi. E LaRue and Winters Pond, are about 3.6 km apart, near the southern edge and at the northern edge, respectively, of the Area. D. W. Webb, (in litt.) noted that "all of the *Se-*

pedon were collected along the edges of swamps." The Area, comprising 1,996 acres, has been described by Evers and Page (1977). It is bordered on the west, in part, by the Big Muddy River, a tributary of the Mississippi River, and on the east, in part, by the up to 33 m high, cherty limestone bluffs of the Pine Hills. The swamps are in an old channel of the Big Muddy River below the mostly west facing bluffs. Evers and Page (1977) noted: "The swamps are of interest botanically for the occurrence of several species that are rare in Illinois. Several species of duckweeds, including *Wolffiella floridana,* live in the water of this swamp, as do frog-bit and swamp loosestrife, the last a species more common much farther north. Here can also be found the rare grass, *Glyceria pallida.*— Especially unusual invertebrates at LaRue-Pine Hills are an endemic scud, *Gammarus minus pinicollis* (Cole 1970); the dwarf crayfish, *Cambarellus shufeldtii*; the scorpionflies, *Boreus brumalis, Merope tuber,* and *Bittacus punctiger*; the stonefly, *Hastaperla brevis*; the thrips, *Heterothrips azaleae* and *Oxythrips divisus*; the grasshoppers, *Schistocera obscura* and *Neotettix femoratus*; and the butterflies, *Amblyscirtes carolina, Autochton cellus,* and *Atlides halesus.*"

Other species of Sciomyzidae that we have identified from the Area are *Atrichomelina pubera* Loew, *Pherbellia nana* Fallén, *Sepedon floridensis* Steyskal, *S. f. fuscipennis* Loew, *S. tenuicornis* Cresson, *Dictya stricta* Steyskal, *Trypetoptera canadensis* Macquart, and *Limnia septentrionalis* Melander.

Biology and immature stages.—Unknown.

Etymology.—This species is named after Dr. Jay E. McPherson, Department of Zoology, Southern Illinois University, Carbondale, Illinois, in recognition of his studies of the LaRue-Pine Hills Area and of his efforts to maintain and preserve this important habitat.

Annotated Key to Species of *Sepedon* of North America

1. Katatergite callus with black setae 2
– Katatergite callus without black setae, completely bare (*S. fuscipennis* group of Orth 1986) 17
2. Medifacies with or without fine black setae; if without, katatergite callus densely setose 3
– Medifacies without fine black setae; katatergite callus sparsely setose. Male genitalia with apical process of aedeagus a large, recurved crest; as figured in Steyskal 1951: 294 (Alaska, widespread in Canada, Washington south to northern California, east to Maine south to Ohio) . . . . . *S. spinipes americana* Steyskal
3. Large species; wing length 5.8–8.9 mm; hind femur of male without midventral notch . . . 4
– Smaller species; wing length 3.6–5.5 mm; hind femur of male with or without midventral notch 5
4. Face yellowish to amber, with or without scattered fine black setae on medifacies; wing length: male 5.8–7.2 mm, female 6.3–7.3 mm; hind femur usually less than 4 mm long. Male genitalia with apical plate of aedeagus truncate in anterior view; as figured in Fisher and Orth 1972: 9 (Nebraska, Kansas, Colorado, Utah, Arizona, New Mexico, Mexico (highlands to Oaxaca)) . . . . . *S. praemiosa* Giglio-Tos
– Face amber to brownish, medifacies with fine black setae scattered to moderately dense; wing length; male 7.2–8.9 mm, female 7.0–8.0 mm; hind femur usually greater than 4 mm long. Male genitalia with apical plate of aedeagus bilobed in anterior view; as figured in Fisher and Orth 1972: 10 (British Columbia east to Saskatchewan, USA west of Mississipi River, Baja California Norte) . . . . . *S. pacifica* Cresson
5. Male hind femur emarginate ventrally; female hind femur simple; hind tibia distinctly more curved in distal third; abdomen brown with little more than a trace of bluish reflection; oral margin usually raised, forming a right angle in profile (Canada, USA, Mexico) (*S. armipes* group of Steyskal 1951) 6
– Hind femur of both sexes simple; hind tibia more or less evenly arcuate; abdomen frequently almost black with bluish reflections; oral margin usually low, angle with face frequently forming a somewhat acute angle in profile (north of 37°N. latitude) (S. *pusilla* subgroup of Steyskal 1951) 13
6. Frons with no more than a trace of black fronto-orbital spots 7

– Frons with distinct, velvety black fronto-orbital spots 8

7. Vein M slightly turned anteriad at apex; hind tibia with median dark brown band. Male genitalia with processes of hypandrium strongly curved mesad, sharply pointed, with bimucronate anterior branch and 2 small subsidiary teeth; as figured in Steyskal 1960: 41 as *S. haplobasis* (Mexico, D.F., Hidalgo, Michoacán) . . . . . *S. relicta* Wulp

– Vein M not turned anteriad at apex; hind tibia without median band. Male genitalia with expanded and irregularly toothed surstylus; as figured in Steyskal 1951: 281 (California, Baja California Norte) . . . . . *S. bifida* Steyskal

8. Fronto-orbital black spots very large, extending nearly to vertex. Male genitalia with quadrangular cercus with apical tooth; as figured in Steyskal 1951: 281 (Washington (Snoqualmie Pass)) . . . . . *S. melanderi* Steyskal

– Fronto-orbital black spots smaller, extending ⅔ or less of distance to vertex 9

9. Fronto-orbital spots extending approximately ⅔ of distance to vertex, intense dull black, oval; central area of anterior dorsum with pinkish-orange hue. Male genitalia with knob-like process ventrally near base of aedeagus; as figured in Fisher and Orth 1974: 293 (Oregon) . . . . . *S. cascadensis* Fisher and Orth

– Fronto-orbital spots extending halfway or less to vertex. Male genitalia with fanlike crest on ventral surface or flat 10

10. Ventral surface of aedeagus with fanlike crest; as figured in Steyskal 1956: 86 (Alaska, south to Utah, east to Minnesota, north to Manitoba) . . . . . *S. anchista* Steyskal

– Ventral surface of aedeagus flat 11

11. Apex of aedeagus not at right angle to base; as figured in Fisher and Orth 1969: 155, 156 (western USA) . . . . *S. capellei* Fisher and Orth

– Apex of aedeagus at right angle to base . . 12

12. Distance between gonopore and basal anterior process of aedeagus short; as figured in Fisher and Orth 1969: 155, 156 (widespread in Canada, USA, south to northern Sonora, Mexico, not far western USA) . . . . . *S. armipes* Loew

– Distance between gonopore and basal anterior process of aedeagus twice as long as in *S. armipes;* as figured in Fisher and Orth 1969: 155, 156 (British Columbia and northwestern USA) . . . . . *S. pseudarmipes* Fisher and Orth

13. Median stripe of pruinosity on face extending in a point to oral margin 14

– Median stripe not extending to oral margin, blunt at apex 15

14. Oral margin usually low, in profile angle with face acute. Male genitalia with strongly lobate cercus; as figured in Steyskal 1951: 284 (Idaho east to Manitoba and Quebec, south to Georgia, west to Utah) . . . . . *S. neili* Steyskal

– Oral margin raised, in profile angle with face approximately right angle. Male genitalia with cerci small, placoid; as figured in Steyskal 1951: 284 (widespread in southern Canada and northern USA) . . . *S. lignator* Steyskal

15. Hind tibia with straw colored area in distal ⅓, contrasting with light brown basad and dark brown apicad. Genitalia with aedeagus keel-like but not extended as in *S. spinipes;* as figured in text, Figs. 1, 4 (known only from southern Illinois) . . . . . *S. mcphersoni,* n. sp.

– Hind tibia more or less uniform in color . . 16

16. Darker-colored species; fronto-orbital black spots large, intensely pigmented. Male genitalia with surstylus much longer than cercus, simple and tapering to a point but somewhat twisted, ultimate sternites without protuberances; as figured in Steyskal 1951: 284 (widespread in North America north of 37°N. latitude) . . . . . *S. borealis* Steyskal

– Lighter-colored species; fronto-orbital black spots of moderate size, not intensely pigmented. Male genitalia with surstylus shorter than cercus, narrow, with rectangular pre-apical prong; ultimate sternite with 2 pairs of protuberances; as figured in Steyskal 1951: 284 (Indiana east to District of Columbia, south to Georgia, west to Mississippi) . . . . . *S. pusilla* Loew

17. Pedicel approximately 2½ times as long as wide in lateral view 18

– Pedicel 4 or more times as long as wide in lateral view 20

18. Hind tibia with straw colored area in distal ½, contrasting with dark brown before and after; male hind tibia with short setae on dorsal surface. Male genitalia with basal process of aedeagus narrowed apically, directed anteriorly; as figured in Orth 1986: 67, 68 (Illinois and Maryland south to Louisiana and Florida) . . . . . *S. floridensis* Steyskal

– Hind tibia without contrasting area, more or less uniform brown; male hind tibia with setae on dorsal surface as long as width of tibia 19

19. Frons with distinct, velvety black, fronto-orbital spot. Male genitalia with 2 long, subequal, parallel processes; as figured in Orth 1986: 67, 68 (Illinois east to New Jersey, south to Florida, west to Texas) . . . . . *S. fuscipennis fuscipennis* Loew

– Frons usually with no more than a trace of black fronto-orbital spot in specimens from Canada and western USA, eastern specimens with darker spot. Male genitalia with apical process of aedeagus shorter and narrower than

basal process; as figured in Orth 1986: 67, 68 (Alaska, Canada, USA generally north of 40°N. latitude; also New Mexico) . . . . . *S. fuscipennis nobilis* Orth (Electrophoretic studies by Manguin (1990) suggest that *S. fuscipennis* is a single species.)

20. Pedicel approximately 4 times longer than wide. Male genitalia with apical process of distiphallus long, narrowly tapered; basal process tapered (lateral view); as figured in Orth 1986: 67, 68 (Minnesota east to southern Ontario and Quebec: Maine south to Pennsylvania and west to Iowa) . . *S. gracilicornis* Orth
- Pedicel approximately 5 times longer than wide. Male genitalia with apical process of distiphallus shorter, broadly tapered; basal process strongly lobate, reflexed (lateral view); as figured in Orth 1986: 67, 68 (New York and Massachusetts southwest to Texas and Oklahoma) . . . . . *S. tenuicornis* Cresson

Character Analysis and Classification of *Sepedon* and Related Genera

The modern suprageneric classification of the family Sciomyzidae has been discussed by Verbeke (1950, 1961), Hennig (1965), Steyskal (1965), Griffiths (1972), Berg and Knutson (1978), Barnes (1979a, b, 1981), Vala (1984, 1989), McAlpine (1989), and a preliminary, computer-based cladistic analysis of 50 of the 58 genera has recently been completed (Marinoni and Mathis, 2000). *Sepedon,* with 74 species is the second largest genus, after *Pherbellia* Robineau-Desvoidy, in the family, and it and at least 6 related genera include some of the most derived forms in the family. Extensive life cycle information gained over the past years on *Sepedon* and some of the related genera has generated renewed interest in their phylogenetic placement.

Although almost all authors since Enderlein (1939) have placed *Sepedon* and related genera in Tetanocerini *sensu* Steyskal (1965) (= Tetanocerinae of authors), seven, especially the earlier authors, placed at least *Sepedon* in a separate tribe or subfamily. Interestingly, this historically represents the most concerted agreement on the status of a suprageneric category in Sciomyzidae, other than the more recent widely held recognition of Phaeomyiidae, Salticellinae, and Sciomyzinae, with 2 tribes. It is over 100 years since Acloque (1897) designated the tribe Sepedonini. Cresson (1920) used the tribe Sepedontini for 5 North American species of *Sepedon* s.s. (plus *Thecomyia* and "probably" *Dichetophora*) along with 2 other tribes in his subfamily Euthycerinae (= modern Tetanocerini). Hendel (1923) used the tribe Sepedonina for *Sepedon* and *Dichetophora.* Malloch (1928) included *Sepedon, Thecomyia,* and *Dichetophora* in his Sepedonini. Crampton (1944) in a simple list grouping families of Acalyptrata based on the male terminalia listed "Tetanoceratidae, or Sciomyzidae" and "Sepedonidae (possibly merely a subfamily of the Tetanoceratidae)." Verbeke (1950) created the subfamily Sepedoninae for *Sepedon* and his new Afrotropical genera *Sepedomyia, Sepedoninus,* and *Sepedonella.* In describing the Neotropical genera *Sepedomerus* and *Sepedonea,* Steyskal (1973) did not recognize that subfamily, considering it not sufficiently distinct from more typical Tetanocerini, especially from such genera as *Hedria* and *Dichetophora,* and preferred to call it the *Sepedon* group. He recognized *Sepedoninus* as a genus and under *Sepedon* he included Verbeke's subgenera *Mesosepedon* and *Parasepedon* and genus *Sepedomyia,* noting the latter is very doubtfully more than subgenerically distinct on the basis of the elongate scape. Notably, Hennig (1965) analyzed the subfamily and tribe classifications of Steyskal (1965) and Verbeke (1950) in detail and recognized Sepedoninae Verbeke as a subfamily and monophyletic group. Marinoni and Mathis (2000) placed *Sepedon* and related genera in the Tetanocerini, subfamily Sciomyzinae.

Until now, there has been no overall proposal of subgeneric categories for the genus *Sepedon* on a world basis. Groups have been designated for 17 of the 20 North American species (*Armipes* and *Pusilla* groups, [Steyskal 1951] and *Fuscipennis* group, [Orth 1986]); the 3 known Central-South American species (*Macropus* group, Steyskal, 1951), placed in the new genus

Table 1. Matrix of characters of adults in groups of *Sepedon sensu strictu* and related genera.

Taxa	1 medifacial setae	2 katatergite setae	3 fronto-orbital bristles (1)	4 postocellar bristles	5 ant. notopleural bristle	6 presutural bristle	7 scutellar bristles	8 dors. bristle fore femur	9 palpi
Groups in *Sepedon s.s.*									
1. *Sphegea* — P, O, Na	±	+	1	+	+	−	+	−	+
2. *Neanias* — P, O	+	+	1	+	+	−	+	−	+
3. *Spinipes* — P, Na	−	+	1	+	+	+	+	−	+
4. *Fuscipennis* — Na	±	−	1	+	+	−	+	−	+
5. *Armipes* — Na	+	+	1	+	+	−	+	−	+
6. *Trichrooscelis* — Af, O, AO	−	−	1	+	−	±	+	+	+
7. *Dispersa* — Af	−	−	1	+	−	±	+	+	+
8. *Lobifera* — O	−	−	0	+	−	−	−	−	+
9. *Nasuta* — Af	−	−	1	+	−	+	+	+	+
Related Genera									
1. *Sepedomerus* — Na, Nt	−	+	1	−	+	−	+	−	+
2. *Sepedonea* — Nt	−	−	1,2	+	+	+	+	+	+
3. *Thecomyia* — Nt	−	−	0,1	−	−	−	+	−	−
4. *Sepedonella* — Af	−	−	1	−	−	−	+	−	+
5. *Sepedoninus* — Af	−	−	0,2	+	−	±	+	−	+
6. *Sepedonites* — F	−	−	2	+	+	+	+	?	+

(1) Usual number present given first.
(2) Distinct and continuous across middle of mesonotum.
(3) Rudimentary.
(+) present, (−) absent.
Abbreviations: P = Palearctic; Na = Nearctic; Nt = Neotropical; Af = Afrotropical; O = Oriental; AO = Australian-Oceanian; F = Fossil.

Sepedomerus by Steyskal 1973; and the subgenera *Parasepedon* with 7 species groups (24 species) and *Mesosepedon* (2 species) for the Afrotropical species known at the time (Verbeke 1950). Steyskal and Knutson (1975), in their study of the highly apomorphic cochleate vesicle (sperm pump), listed 28 Afrotropical, Oriental, and Australian species as to presence or absence of this structure, which is not present in any Nearctic, Palearctic, or Neotropical species of *Sepedon* or in any of the related genera.

Steyskal in Steyskal and Verbeke (1956) noted a few species do not fit well in any group, and preferred not to use groups. Verbeke (1961) provided a key to and new arrangement of eight groups of *Parasepedon.* Groups of Afrotropical *Sepedon* were not recognized subsequently. *Sepedomyia* with *S. nasuta* and *S. alaotra* Verbeke, 1962, *Mesosepedon* with 5 species, and *Parasepedon* with 33 species, were presented as subgenera of *Sepedon* in the catalog of Afrotropical Diptera (Knutson 1980). Barraclough (1985) noted that Verbeke's (1950) subgenera *Mesosepedon* and *Parasepedon* were established primarily on genitalic differences (*Mesosepedon* with sixth and seventh abdominal terga poorly developed, aedeagus without spiral filament, and presutural seta usually strong; *Parasepedon* with genital segments well developed, aedeagus with spiral filament, and strong presutural bristle present in some species, absent in others). *Mesosepedon,* unlike *Parasepedon,* lack a cochleate vesicle. Barraclough (1985: 484) stated "Subgeneric status appears to be valid, because *Sepedomyia* species are clearly distinguished from other *Sepedon* species by the longer first antennal segment, the presence of a humeral seta, and a distinct hypopygial structure. . . . It thus appears that only aedeagal characters can separate *Mesosepedon* from *Parasepe-*

Table 1. Extended.

10 fronto-orbital spot	11 orbito-antennal spot	12 scape elongate	13 rostrum extended	14 hind femur modified	15 sternal-coxal bridge	16 complete mesonotal sut. (2)	17 mesonotum angulate anter.	18 cerci fused	19 epand. closed below cerci	20 post. surst. & epand. fused	21 cochleate vesicle	22 aedeagal filaments	23 aqua. predaceous larvae	24 terrest. parasitoid larvae
−	+	−	−	−	−	−	−	±	−	−	−	+	+	−
+	+	−	−	−	−	−	−	+	+	+	−	−	+	−
+	+	−	−	−	−	−	−	−	−	−	−	+	+	−
±	+	−	−	−	−	−	−	−	−	−	−	+	+	−
±	+	−	−	+	−	−	−	−	−	−	−	−	+	−
±	−	−	−	−	−	−	−	−	−	−	±	±	+	+
+	−	−	−	−	−	−	−	−	−	±	−	−	?	?
+	−	−	−	−	−	−	−	−	−	−	+	−	?	?
+	−	+	−	−	−	+	+	−	−	+	−	+	?	?
−	+	−	−	−	−	−	−	−	−	−	−	−	+	−
−	−	−	−	−	−	−	−	−	+	−	−	−	+	−
+	−	−	+	−	+	−	−	−	−	+	−	−	+	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
+	−	−	−	−	−	+	+	−	−	+	+(3)	−	?	?
?	?	?	?	−	?	?	?	?	?	?	?	?	?	?

Table 2. Explanation of Characters. The presumed plesiomorphic (P) condition within the tribe Tetanocerini is indicated for each character below by a + (present) or − (absent) sign or the number 2 for number of fronto-orbital bristles. The genus *Tetanocera* was used as the outgroup for comparison.

1. medifacial setae (P = +)
2. katatergite callus setae (P = +)
3. number of fronto-orbital bristles (P = 2)
4. postocellar bristles (P = +)
5. anterior notopleural bristle (P = +)
6. presutural bristle (P = +)
7. scutellar bristles (P = +)
8. dorsal bristle on fore femur (P = +)
9. palpi (P = +)
10. fronto-orbital spot (P = +)
11. orbito-antennal spot (P = +)
12. scape elongate (P = −)
13. rostrum extended ventrally (P = −)
14. hind femur modified (P = −)
15. sternal-coxal bridge (P = −)
16. complete mesonotal suture (P = −)
17. mesonotum angulate anteriorly (P = −)
18. cerci fused (P = −)
19. epandrium closed below cerci (P = −)
20. posterior surstyli and epandrium fused (P = −)
21. cochleate vesicle (P = −)
22. aedeagal filaments (P = −)
23. aquatic predacious larvae (P = +)
24. terrestrial parasitoid larvae (P = −)

don, and that these two subgenera should at best be considered species groups."

Miller (1995) noted that the "subgeneric categories will have to be modified or may fall away, because several species do not possess both the cochleate vesicle and aedeagal spiral filament (Steyskal and Knutson 1975), yet appear to fall into *S.* (*Parasepedon*)."

Herein we do not recognize subgenera of *Sepedon.* We recognize the *Armipes* group as proposed by Steyskal, but place his *Pusilla* group as a subgroup with the *Sphegea* subgroup in the *Sphegea* group (stem group). We propose the *Dispersa* group for the subgenus *Mesosepedon* and the *Trichrooscelis* group for the subgenus *Parasepedon* plus 11 Oriental and Australian species having a cochleate vesicle. We propose the *Nasuta* group for the genus *Sepedomyia* and 3 other new groups: *Spinipes* - 1 Holarctic species; *Neanias* - 1 Palearctic and Oriental species; and *Lobifera* - 1 Oriental species. Characters of the groups are shown in Table 1. Members of groups are listed in Table 3.

Genera that seem to be related to *Sepe-*

Table 3. Groups of *Sepedon sensu stricto*, with characters apomorphic in relation to the *Sphegea* group (compare numbers in parentheses after the characters to Table 1).

1. *Sphegea* group — Nearctic, Palearctic, Oriental Regions.
   Stem group, without apomorphic characters in relation to other groups, except for characters 3, 6, 8, 18 (in *S. noteoi* and *S. oriens*), and 22.
   a. *Sphegea* subgroup
      aenescens Wiedemann 1830 — P, O
      femorata Knutson & Orth 1984 — P
      noteoi Steyskal 1980 — O
      oriens Steyskal 1980 — O
      pacifica Cresson 1914 — Na
      praemiosa Giglio-Tos 1893 — Na (medifacial setae present or absent)
      sphegea Fabricius 1775 — P
   b. *Pusilla* subgroup
      borealis Steyskal 1951 — Na
      lignator Steyskal 1951 — Na
      mcphersoni Knutson & Orth, n. sp. — Na
      neili Steyskal 1951 — Na
      pusilla Loew 1859 — Na
2. *Neanias* group — Palearctic and Oriental Regions
   cerci fused — (18)
   epandrium closed below cerci — (19)
   posterior surstyli and epandrium fused — (20)
      neanias Hendel 1913 — P, O
3. *Spinipes* group — Nearctic and Palearctic Regions
   medifacial setae absent — (1)
      spinipes Scopoli 1763 — H
4. *Fuscipennis* group (Orth 1986) — Nearctic Region
   medificial setae absent — (1)
   katatergite setae absent — (2)
      floridensis Steyskal 1951 — Na
      fuscipennis Loew 1859 — Na
      gracilicornis Orth 1986 — Na
      tenuicornis Cresson 1920 — Na
5. *Armipes* group (Steyskal 1951) — Nearctic Region
   hind femur modified — (10)
      anchista Steyskal 1956 — Na
      armipes Loew 1859 — Na
      bifida Steyskal 1951 — Na
      capellei Fisher & Orth 1969 — Na
      cascadensis Fisher & Orth 1974 — Na
      melanderi Steyskal 1951 — Na
      pseudarmipes Fisher & Orth 1969 — Na
      relicta Wulp 1897 — Na
6. *Trichrooscelis* group — Afrotropical, Oriental, Australian-Oceanian Regions
   medifacial setae absent — (1)
   katatergite setae absent — (2)
   anterior notopleural bristle absent — (5)
   dorsal bristle present on fore femur — (8)
   orbito-antennal spot absent or weak — (11)
   cochleate vesicle usually present — (21)
   aedeagal filaments usually present — (22)
   = subgenus *Parasepedon* Verbeke, 1950 and the following species:
      costalis Walker 1858 — O
      crishna Walker 1849 — O
      ferruginosa Wiedemann 1824 — O
      lata Bezzi 1928 — AO
      plumbella Wiedemann 1830 — O, AO
      senex Wiedemann 1830 — O
      spangleri Beaver 1974 — O

Table 3. Continued.

7. *Dispersa* group — Afrotropical Region
   medifacial setae absent — (1)
   katatergite setae absent — (2)
   anterior notopleural bristle absent — (5)
   dorsal bristle on fore femur present — (8)
   orbito-antennal spot absent — (11)
   posterior surstyli and epandrium usually fused — (20)
   = subgenus *Mesosepedon* Verbeke 1950
      convergens Loew 1862
      dispersa Verbeke 1950
      ethiopica Steyskal 1956
      knutsoni Vala, Gbedjissi, & Dossou 1994
      pleuritica Loew 1862
      schoutedeni Verbeke 1950
      tuckeri Barraclough 1985
8. *Lobifera* group — Oriental Region
   medificial setae absent — (1)
   katatergite setae absent — (2)
   fronto-orbital bristles absent — (3)
   anterior notopleural bristle absent — (5)
   scutellar bristles absent — (7)
   orbito-antennal spot lacking — (12)
   cochleate vesicle present — (21)
      lobifera Hendel 1911
9. *Nasuta* group — Afrotropical Region
   medifacial setae absent — (1)
   katatergite setae absent — (2)
   anterior notopleural bristle absent — (5)
   orbito-antennal spot absent — (11)
   scape elongate — (12)
   complete mesonotal suture — (16)
   = genus *Sepedomyia* Verbeke 1950
      alaotra Verbeke 1962
      nasuta (Verbeke) 1950

don are included in Table 1 for comparison. As Steyskal (1951) noted, other genera such as *Tetanoptera* and *Dichetophora* show a relationship with *Sepedon.* In describing the male of *Tetanoptera,* Knutson and Vala (1999) compared the genus with *Sepedon* and related genera, along with *Elgiva, Hedria, Oligolimnia, Verbekaria, Dichetophora* and *Neosepedon,* in a matrix of characters including characters 2–6, 9, 20, 21 as in Table 1, but also 16 other characters. They concluded that *Tetanoptera* appears to be related to *Dichetophora,* and intermediate in an evolutionary lineage between the primitive *Tetanocera* and the advanced *Thecomyia.*

Because information on the life cycles and immature stages of *Sepedon* is so dispersed we have listed in Table 4 the more important publications for each species, for which information has been presented.

Shortly after this manuscript was completed, we received a copy of Marinoni and Mathis' (2000) cladistic analysis of the family. Their analysis of 50 of the 58 genera was based on study of the type species of each genus, and thus does not speak to the groups within *Sepedon s.s.,* but it is of interest to compare their comprehensive analysis of the generic relationships to our Table 1. The 36 morphological characters they used included only characters 5, 6, and

Table 4. Publications on the life cycles and/or immature stages of *Sepedon* and related genera. The literature prior to 1966 was summarized by Neff and Berg 1966.

	Neotropical Region
Sepedomerus	
caeruleus (Melander)	Neff & Berg 1966; Neff 1964
macropus (Walker)	Neff & Berg 1966; Neff 1964; Chock et al. 1961
Sepedonea	
barbosai Knutson & Bredt	Freidberg et al. 1991; Bredt & Mello 1978
guatemalana Steyskal	Neff & Berg 1966
guianica (Steyskal)	Freidberg et al. 1991
isthmi (Steyskal)	Knutson & Valley 1978
lagoa (Steyskal)	Freidberg et al. 1991
lindneri (Hendel)	Freidberg et al. 1991
telson (Steyskal)	Freidberg et al. 1991
Thecomyia	
limbata (Wiedemann)	Abercrombie & Berg 1975
	Palearctic Region
Sepedon	
hispanica hispanica Loew	Knutson et al. 1967
sphegea Fabricius	Gercke 1876; Neff & Berg 1966; Knutson et al. 1973; Tirgari & Massoud 1981; Ghamizi 1985; Vala & Manguin 1987; (summarized by Knutson & Orth 1984)
spinipes americana Steyskal	Neff & Berg 1966
spinipes spinipes Scopoli	Gercke 1876; Beaver 1972, 1973, 1974a, b; Neff & Berg 1966; Vala & Manguin 1987
	Nearctic Region
Sepedon	
anchista Steyskal	Neff & Berg 1966
armipes Loew	Neff & Berg 1966
bifida Steyskal	Neff & Berg 1966
borealis Steyskal	Neff & Berg 1966
fuscipennis Loew	Neff & Berg 1966; Needham & Betten 1901; Neff 1964; Eckblad & Berg 1972; Peacock 1973; Eckblad 1973; Barnes 1976; McCoy & Joy 1977; Arnold 1978; Juliano 1981, 1982; Berg et al. 1982; Manguin 1990; Manguin & Hung 1991
neili Steyskal	Neff & Berg 1966
praemiosa Giglio-Tos	Neff & Berg 1966
pusilla Loew	Neff & Berg 1966
relicta van der Wulp	Neff & Berg 1966 (as *S. haplobasis*)
spinipes americana Steyskal	Neff & Berg 1966
tenuicornis Cresson	Neff & Berg 1966; Geckler 1971
	Oriental Region
Sepedon	
aenescens Wiedemann	Nagatomi & Kushigemachi 1965; Nagatomi & Tanaka 1967; ChannaBasavanna & Yano 1969; ChannaBasavanna & Prasad 1971; Beaver et al. 1977; Yano 1978; (summarized by Knutson & Orth 1984)
ferruginosa Wiedemann	Beaver et al. 1977
plumbella Wiedemann	Beaver et al. 1977; Bhuangprakone & Areekul 1973
senex Wiedemann	Beaver et al. 1977; Beaver 1989
spangleri Beaver	Beaver et al. 1977; Chandavimol et al. 1975

Table 4. Continued.

	Afrotropical Region
Sepedon	
hispanica ruhengeriensis Verbeke	Knutson 2000
neavi Steyskal	Barraclough 1983
ruficeps Becker	Knutson et al. 1967; Gbedjissi 1997
scapularis Adams	Knutson et al. 1967; Maharaj et al. 1992
testacea Loew	Barraclough 1983
trichrooscelis Speiser	Vala et al. 1995; Knutson 2000
Sepedonella	Vala et al. 2000
Sepedoninus	No published biological data.

7 in our Table 1, but their analysis was for broader purposes and thus included many characters of importance to genera other than *Sepedon* and related genera. Their analysis agreed with Steyskal's (1973) *Sepedon* group of genera (*Sepedon, Sepedonella, Sepedoninus, Sepedomerus,* and *Sepedonea*), but with the addition of *Ethiolimnia* (8 Afrotropical species) and *Teutoniomyia* (2 Neotropical species). The Afrotropical genera *Tetanoptera* and *Verbekaria* were not included in their analysis. They found 5 groups of genera within the Tetanocerini, with the monophyletic *Ethiolimnia* to *Sepedonea* subgroup in the fourth group, along with 7 other genera (*Guatemalia, Elgiva, Dichetophora, Hedria, Coremacera, Dictyacium,* and *Euthycera*). The monophyly of their *Ethiolimnia* to *Sepedonea* subgroup was established by 8 characters ("6-anterior surstylus absent, 9-pedicel approximately twice the length of first flagellomere, 28-prominent eyes, 30-ocellar setae absent, 31-post pronotal setae absent, 32-one pair of scutellar setae, 33-one notopleural seta, and 35-head sutures indistinct"), and they concluded it was the most "corroborated" lineage in their analysis.

We consider it appropriate to utilize somewhat disparate sets of characters when making non-numerical phylogenetic analyses of limited groups of genera, for example the analysis of *Sepedon* and relatives presented here, for *Tetanoptera* and relatives (Knutson and Vala 1999), and for *Verbekaria* (Vala, Greve, and Knutson 2000). But for either a numerical or non-numerical analysis of the family as a whole, obviously a comprehensive set of characters is needed. The analyses of *Sepedon, Tetanoptera, Verbekaria,* and relatives are steps in the preparation of a comparative anatomy comprising all species of the family (Knutson, in prep.). This will indicate for which species, genera, and higher categories the character might be appropriately used, and the historical use of the character by others, but will not include minor characters of use only in distinguishing between closely related species, except as they might be useful in higher level distinctions. Further analysis of the *Ethiolimnia* to *Sepedonea* subgroup, including *Tetanoptera,* will be of interest after the many undescribed species known to us, K. Elberg (in litt.), R. M. Miller (in litt.), C. Kassebeer (in litt.) and possibly others are published. Characters used by Marinoni and Mathis (2000) along with some of the characters in Table 1 should be considered.

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