A REVISION OF THE GENUS SYMPHEROBIUS BANKS (NEUROPTERA: HEMEROBIIDAE) OF AMERICA NORTH OF MEXICO WITH A SYNONYMICAL LIST OF THE WORLD SPECIES

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Abstract.—The species of the genus Sympherobius of America North of Mexico are revised. Two species groups containing seventeen species are recognized. Two species, S. constrictus, from California, and S. quadricuspis, from Arizona, are described as new. The previously unknown male of S. pictus is also described. Four new specific synonyms are proposed (junior synonym(s) first): S. brunneus Nakahara and S. stangei Nakahara = S. angustus (Banks), S. gracilis Carpenter = S. umbratus (Banks) and S. texanus Nakahara = S. killingtoni Carpenter. A lectotype is designated for S. perparvus (McLachlan). Annotated synonymical listings summarize the existing literature on each species. Species ranges are summarized and mapped, including known records from regions extralimital to the continental United States and Canada. The relative relationships among the treated species are inferred from a cladistic analysis. An integrated key using forewing and male genitalic characters is presented. The following new terms are proposed for male genital structures or their subdivisions: gonopons, hemigonarcus, extragonarcus, intragonarcus, intrahemigonarcus, extrahemigonarcus, gonopleuron, gonoplax, paragonarcal membrane, pseudomediuncus, basispseudomediuncus and distospseudomediuncus. The monobasic Neotropical genus Sympheromima Kimmins is proposed as a new synonym of Sympherobius. A synonymical listing of the world species of Sympherobius is appended. In this list two new combinations, Sympherobius marginata (Kimmins) [from Sympheromima] and Sympherobius exiguis (Navás) [from Micromus] are proposed.

The hemerobiid genus Sympherobius Banks contains 54 currently recognized species distributed throughout the Nearctic (17 species), Neotropical (17), Palearctic (19) and Ethiopian (1) faunal regions. A comprehensive synonymical listing of these species is given in Appendix 1. Although Sympherobius has never been revised on a worldwide basis, relatively recent taxonomic treatments of the genus are available for the following regions: Amazon Basin (Penny and Monserrat, [1985] 1983), Cuba (Alayo, 1968), Europe (Aspöck et al., 1980), U.S.S.R. (Makarkin, 1986), Japan (Kuwayama, 1962) and southern Africa (Tjeder, 1961).

In this paper the Sympherobius species found in America north of Mexico are revised. Seventeen species are recognized from this region. Distributional and biological data are summarized for each species and an identification key is provided. The phylogenetic relationships among the seventeen species are inferred from a cladistic analysis. The clades indicated by this analysis serve as the basis for a preliminary classification of the Nearctic species.

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TAXONOMIC HISTORY OF NEARCTIC SYMPHEROBIUS

Shortly after establishing the genus in 1904, Banks (1905b) included seven North American species in *Sympherobius* and provided the first description of the genus. Fifteen species have subsequently been described from the Nearctic region by Banks (1911), Navás (1912, 1914a), Carpenter (1940), Gurney (1948) and Nakahara (1960, 1965a). The Nearctic species of *Sympherobius* were last revised by Carpenter (1940) who recognized 15 valid species from the region.

MATERIALS, METHODS AND GEOGRAPHICAL COVERAGE

*Materials.* More than 2,100 specimens of Nearctic *Sympherobius* from the 37 institutional collections listed below have been examined for this revision:

AMNH—American Museum of Natural History, New York; ASUT—Arizona State University, Tempe; BMNH—British Museum (Natural History), London; CAS—California Academy of Sciences, San Francisco; CMP—Carnegie Museum, Pittsburgh; CSU—Colorado State University, Fort Collins; CU—Cornell University, Ithaca; FEM—Frost Entomological Museum (Pennsylvania State University), University Park; INHS—Illinois Natural History Survey, Champaign; ISU—Iowa State University, Ames; LACM—Los Angeles County Museum, Los Angeles; LSU—Louisiana State University, Baton Rouge; MCZ—Museum of Comparative Zoology (Harvard University), Cambridge; MSU—Mississippi State University, Mississippi State; NCSR—North Carolina State University, Raleigh; OKS—Oklahoma State University, Stillwater; OSU—Ohio State University, Columbus; OSUC—Oregon State University, Corvallis; PMY—Peabody Museum (Yale University), New Haven; SMEK—Snow Museum of Entomology (University of Kansas), Lawrence; TAMU—Texas A & M University, College Station; UAF—University of Arkansas, Fayetteville; UAT—University of Arizona, Tucson; UCB—University of California, Berkeley; UCD—University of California, Davis; UCR—University of California, Riverside; UGA—University of Georgia, Athens; UIM—University of Idaho, Moscow; UMAA—University of Michigan, Ann Arbor; UMC—University of Missouri, Columbia; UMSP—University of Minnesota, St. Paul; UNH—University of New Hampshire, Durham; USNM—National Museum of Natural History, Washington, D.C.; UWL—University of Wyoming, Laramie; UWM—University of Wisconsin, Madison; VPI—Virginia Polytechnic Institute and State University, Blacksburg; WSU—Washington State University, Pullman.

*Methods.* Recent characterizations of *Sympherobius* species have relied heavily on male genital sclerites for specific diagnoses. Species treatments in this work include descriptions of diagnostic venational and genitalic features. These are supplemented by forewing photographs and figures of the male ectoproct, gonarcus and parameres. Geographic range maps are also provided for each species.

Male genitalia were prepared for dissection by clearing for 5 to 10 minutes in a sub-boiling solution of 10 percent NaOH. Cleared material was neutralized in dilute acetic acid, rinsed in water, dried on a paper blotter and transferred to glycerin for examination. A compound microscope was used to examine fine structural details of genital sclerites temporarily mounted in glycerin on depression slides.

To better illustrate important details of the parameres, gonarcus and ectoprocts,
these structures have been figured individually. Dorsal and/or lateral illustrations of the parameres (e.g., Figs. 10–11) and 'ninth tergite + ectoproct' (e.g., Fig. 8) of each species are shown in standard orientations with anterior to the left. Lateral views of the gonarcus (e.g., Fig. 9) have been rotated approximately 90 degrees clockwise to facilitate plate composition. In the species treatments relative positional descriptors of gonarcus regions (e.g., dorsal, anterolateral) refer to the gonarcus as figured, not as oriented in situ. The relative in situ positions of the male gonarcus and parameres are illustrated in Figure 2.

When interpreting illustrations of the gonarcus it should be remembered that the pseudomediuncus complex (Fig. 2, pm) articulates freely both with the apex of the gonopons (gpo) and at a second region of flexion located between the basipseudomediuncus (bpm) and distopsseudomediuncus (dpm); the absolute positions of these structures will vary from specimen to specimen. Similarly, each ectoproct (Fig. 1, ect) articulates freely with the adjacent posterolateral margin of the ninth tergite (9t); the shape of the outline of the ectoproct, and its various processes, in lateral view will vary depending upon the absolute positions of these sclerites.

Forewing photographs were produced using Kodak Panatomic-X film from wings slide mounted in Hoyer's solution. Forewing lengths were measured from the anterior margin of the tegula to the wing apex. All drawings and measurements were made using a calibrated ocular grid reticle.

Detailed collection data and repository information are recorded only for the eight species for which fewer than 25 specimens have been examined. The corresponding data for the nine remaining species are summarized by recording for each: (1) geographic distribution by country and state, (2) extremes of temporal occurrence taken from collection labels and (3) a list of institutional collections containing the species. More detailed collection data for these species have been compiled from collection labels and are available from the author upon request. Information recorded for each species under the heading Distributions and Associations has been compiled from data contained on specimen labels and from published sources.

Since female genital structures are inadequate for species diagnosis, and the forewing markings of some species exhibit overlapping ranges of variation, confident identification of females is sometimes not possible.

Geographical coverage. The primary geographic area addressed in this revision is North America north of Mexico (considered here for practicality to be synonymous with the Nearctic faunal region); however, all known extralimital records of Nearctic species are also noted. The species list in Appendix 1 and the listing of generic synonyms given at the beginning of the generic treatment are worldwide in scope.

TERMINOLOGY

Terms used for male and female genital structures are primarily those of Tjeder (1954, 1961, 1970). For descriptions and discussions of the several new terms proposed in this work for male genitalic structures see below under the heading Terminology of Male Genital Sclerites. The venational terminology used is primarily that of Carpenter (1940).

ABBREVIATIONS AND ANNOTATIONS

Abbreviations used for institutional collections are recorded above under the heading Materials. The following abbreviations and symbols have been used to annotate
papers cited in the synonomical listings given at the beginning of each species treatment: A, adult description or characterization; Bic, biocontrol; Bio, biology; C, cocoon; Dst, distribution; E, egg; F, female description or characterization; Key, key or keyed; L#, larva, # indicates instar number; Lst, list or listed; Mg, male genitalia; Mor, morphology (other than taxonomic characters); OD, original description; P, pupa; Par, parasites; PP, prepupa; RD, redescription; Tax, taxonomy (including synonymy, homonymy, type data, etc.); W, wing. An asterisk (*) following any of the preceding abbreviations indicates a figure of the item it follows, e.g., FW* = forewing figure.

**SYMFEROBIUS BANKS**

**Sympherobius** Banks, 1904b:209 (Type species: *Hemerobius amiculus* Fitch, [1855] 1854:799, by monotypy): Banks, 1905b (OD, Key); Banks, 1907b (Lst, Tax); Nakahara, 1915 (RD, Lst, Tax); Comstock, 1918 (Mor); Krüger, 1922 (Tax); Killington, 1936 (Bio, Mor); Killington, 1937 (RD, Key, Tax); Balduf, 1939 (Bio); Carpenter, 1940 (RD, Key, Tax); Kozhantshikov, 1956 (Key, Tax); Nakahara, 1960 (RD, Lst, Tax); Tjeder, 1961 (RD, Key, Tax); Kuwayama, 1962 (Key, Tax); Stange, 1967 (Lst, Tax); Penny, [1978] 1977 (Lst, Tax); Aspöck et al., 1980 (RD, Key, Tax).

**Spadobius** Needham, 1905:16 (Type species: *Hemerobius occidentalis* Fitch, [1855] 1854:799, by original designation, but see Nomenclatural Note below): Banks, 1907b (Tax); Krüger, 1922 (Tax).


**Niremberge** Navás, 1909:377 (Type species: *Niremberge limpida* Navás, 1909 [a junior subjective synonym of *Hemerobius fuscescens* Wallengren, 1863:22], by monotypy): Killington, 1937 (Tax); Aspöck et al., 1980 (Tax).


**Nefasitus** Navás, 1915c:131 (Type species: *Sympherobius amicus* Navás in Silvestri, 1915:332 [a junior subjective synonym of *Sympherobius fallax* Navás, 1908b:408], by original designation): Nakahara, 1960 (Tax); Aspöck et al., 1980 (Tax).


**Sympheromima** Kimmins, 1928:363 (Type species: *Sympheromima marginata* Kimmins, 1928:363, by original designation): New Synonym (see Synonymical Note below).

**Diagnosis.** *Sympherobius* may be distinguished from all other Nearctic hemerobiid genera by the following combination of forewing characters (Fig. 4): (1) forewing radius with only 2 oblique branches ("radial sectors"), (2) recurrent humeral vein present, and (3) forewing outer gradate series composed of only 4 (very rarely 3 or 5) crossveins.

**Description.** The following description is based primarily on Nearctic species, many of the extralimital species have not been examined.

Head: Maxillary palp five segmented, ultimate segment subsegmented; labial palp
three segmented, ultimate segment subsegmented, palpimacula present, consisting of several small, parallel, recumbent setae lying in a shallow depression.

Forewing: length 3–7 mm; humeral crossvein (Fig. 4, h) recurrent and usually pectinately branched but in species with a very narrow costal area (e.g., S. beameri) indistinctly so or nearly simple; radius normally with two oblique branches, R4+5+MA and R2+3 (very rarely one, Fig. 104, or three, Figs. 105–106); four crossveins (Fig. 4, og) in the outer gradate series (rarely three or five); proximal radial crossvein (Fig. 4, prc) present or absent; distal radial crossvein (Fig. 4, drc) present or absent; some setae of the longitudinal veins may be set within individual ‘setal spots’ (spots of darkly tanned cuticle encircling the bases of the setae).

Male terminalia: Tergite nine (Fig. 1, 9t): antecosta prominent; ventral surface along dorsal midline with a prominent costa; lateroventral margins produced posterovertrally as narrow processes which subdend the ectoprocts; anterodorsal margin frequently emarginate in dorsal view. Ectoprocts (Fig. 1, ect): bearing one (e.g., Fig. 8), two (e.g., Fig. 48) or three (e.g., Fig. 1) digitiform process(es) (Fig. 1, dlp, vlp, vmp) of varying length and curvature, each digitiform process bears at or near its apex one (e.g., Fig. 7) or two (e.g., Fig. 68) peg-like or spinose modified macrotrichia; ‘dorsomedial prominence’ (e.g., Figs. 56–57) present or absent; trichobothria of calli cercorum (Fig. 1, cc) with internally rosettiform alveoli. Gonarcus (Fig. 2): composed of a pair of lateral hemigonarcus (hg) oriented symmetrically about the gonopons (gpo); hemigonarcus with well-developed longitudinally oriented gonopleura (glp); gonoplakes (e.g., Fig. 89, gpx) variously but only weakly developed; pseudomediancunc (Fig. 2, pm) present, bipartite; mediuncus-arcessus absent; hemigonarcal (hgr) ribs present or absent. Parameres (Fig. 2): apophysis proxima (ap) elongate, compressed; apophysis proxima cavity (apc) present; one or more pairs of terminal lobes (mlp, ilp) present. Hypandrium internum: a small wedge shaped sclerite with truncate or emarginate apex and revolute lateral margins.

Female terminalia (Fig. 3): Tergite eight (8t): lateral ends widely separated, adjacent or fused ventrally. Tergite nine (9t): expanded ventrally, prominent antecosta and middorsal costa of males absent. Gonapophyses laterales (gl): reniform, styli present. Gonapophyses posteriores: absent. Subgenitale a small oval or subrectangular plate, posterior margin sometimes emarginate. Seminal receptacle a darkly tanned sac or tube, ducts variously convoluted, seminal duct long and well sclerotized.

Terminology of male genital sclerites. Most of the terms coined by Tjeder (1954, 1970) for the male and female genital structures of neuropterous insects have been widely accepted and adopted by later neuropterists. Many of Tjeder’s terms are applicable to Sympherobius. However, for the sake of clarity and precision, a number of new terms are proposed. These are given below, together with descriptions and justifications for each.

Ectoprocts: The digitiform processes of the ectoprocts have been designated as follows (Fig. 1): (1) ventromedial (vmp), (2) ventrolateral (vlp) and (3) dorsolateral (dlp), in reference to the relative positions of their points of insertion on the ectoproct. In like manner, a fourth process, shorter than the digitiform processes and not terminated by a modified macrotrichia (Figs. 56–57), has been designated the dorsomedial prominence. For additional discussion of the processes of the male ectoproct see Character 7 under the heading PHYLOGENETIC RELATIONSHIPS below.

Gonarcus: For descriptive purposes the neuropterous gonarcus is usually divided
Figs. 1–6. *Sympherobius amicus*. 1. Apex of male abdomen, lateral view. 2. *in situ* arrangement of male gonarcus, parameres and adjoining membranes, lateral view with overlying sclerites removed. 3. Apex of female abdomen, lateral view. *S. angustus*. 4. Forewing, the usual position of distal radial crossvein (drc), which is absent in *S. angustus*, is shown as a dashed line. *S. pictus*. 5. Male protibia. *S. killingtoni*. 6. Male protibia. Abbreviations: ap, apophysis proxima; apc, apophysis proxima cavity; bpm, basipseudomediuncus; cc, callus cercus; cu1–cu2, cubital crossvein; dlp, dorsolateral ectoproct process; dpm, distopseudomediuncus; drc, distal radial crossvein; ect, ectoproct; ehg, extrahemigonarcus; gl, gonapophysis lateralis; gls, gonapophysis lateralis stylus; gpl, gonopleuron; gpo, gonopons; gsm, gonosaccal membrane; hc, humeral crossvein; hg, hemigonarcus; hgr, hemigonarcal rib; llp, lateral lobe of parameres; MA, media anterior; mlp, median lobe of parameres; MP, media posterior; ogc, outer gradate crossveins; pgm, paragonarcal membranae; pm, pseudomediuncus; prc, proximal radial crossvein; R#, radial veins; #s, sternites; #t, tergites; vlp, ventrolateral ectoproct process; vmp, ventromedial ectoproct process.
into a pair of laterally oriented, usually bilaterally symmetrical, gonarcus "wings," which are almost universally joined by a transverse dorsal bar or plate termed the gonarcus "bridge." For the "wing" and "bridge" of the gonarcus I propose, respectively, the terms hemigonarcus (Fig. 2, hg; name from the Greek "hemisys," half, and gonarcus; nominative plural = hemigonarcus) and gonopons (Fig. 2, gpo; name formed by elision and compounding of "gonarcus" and the Latin "pons," bridge; nominative plural = gonopontes). Relative to the terms gonarcus "wings" and gonarcus "bridge," the new terms hemigonarcus and gonopons, while remaining adequately descriptive, have the advantages of conciseness, euphony and classical derivation. These terms should be widely applicable to neuropterous gonarcus. In some species of Sympherobius the hemigonarcus possess darkened, obliquely or transversely oriented elongate tumosities near the gonopons. I term these structures the hemigonarcal ribs (Figs. 2, 89, hgr).

I also distinguish between the externally exposed region of the gonarcus, the extragonarcus (name from the Latin "exterus," out, and gonarcus; nominative plural = extragonarcus), and its adjacent internally projecting margin (apodeme), the intragonarcus (name from the Latin "intra-," within, and gonarcus; nominative plural = intragonarcus). These regions are delimited by the line of attachment to the hemigonarcus of the paragonarcal membrane (Fig. 2, pgm; name from the Greek "para-," near or by, and gonarcus; nominative plural = paragonarcal membranes), the anterior membrane attaching around the outside of the gonarcus, the posterior membrane attaching to the gonarcus being the gonosaccal membrane (gsm). The terms intrahemigonarcus (Fig. 89, ihg) and extrahemigonarcus (Figs. 2, 89, ehg) may be used to refer to the internal and external divisions, respectively, of a single hemigonarcus. In Sympherobius much of the extragonarcus is only lightly sclerotized and lightly tanned. Because of this, the boundary between the extragonarcus and adjacent gonosaccal membrane is not always distinct, and the shapes of the extrahemigonarcus may be somewhat variable.

Since hemerobiid genera vary greatly in their relative development of the intra- and extragonarcus, differentiation and identification of these regions should prove useful in discussions of hemerobiid genital morphology. As membranous attachments to the gonarcus have seldom been figured in prior works on the Hemerobiidae, this variation may not be readily apparent from an examination of those works.

In Sympherobius, Nomerobius, Neosympherobius and some other hemerobiid genera each intrahemigonarcus is composed of two more or less distinct regions which I term the gonopleuron (Fig. 89, gpl; name formed by elision and compounding of "gonarcus" and the Greek "pleuron," rib; nominative plural = gonopleura) and the gonoplax (Fig. 89, gpx; name formed by elision and compounding of "gonarcus" and the Greek "plax," anything flat and wide; nominative plural = gonoplakes). The gonopleura (Fig. 2) are elongate thickened regions of the hemigonarcus which lie adjacent, internally, to the line of attachment of the paragonarcal membrane. The gonopleura apparently function as supportive mechanical struts for the hemigonarcus and probably also as sites for muscular attachments. The gonoplakes are thin, sclerotized processes of the gonopleura. These spiniform, cariniform or lamellate structures project into the body cavity from the internal margins of the gonopleura and exhibit considerable intra- and interspecific variation in shape. These structures almost certainly serve as sites for muscle attachments.
Pseudomediuncus: The sclerotized posteromedian process of the gonarcus in Sympherobius has been termed the aedeagus (Killington, 1937:112; Carpenter, 1940:229; Nakahara, 1960:15) the arcessus + mediuncus (Tjeder, 1939:27) or simply the arcessus (Tjeder, 1961:342). Detailed examination of this organ has revealed that it is not a homologue of the structure usually given the term mediuncus or arcessus in other Neuroptera by Tjeder and subsequent authors. Rather, it is a separate sclerotized region lying along the dorsal midline of the paragonarcal membrane immediately adjacent to and continuous with the gonopons. I name this organ the pseudomediuncus (Fig. 2, pm; from the Greek "pseudos," fallacy or lie, and mediuncus; nominative plural = pseudomediunci).

The pseudomediuncus is confluent with the gonarcus at the posterior margin of the gonopons. This arrangement might be expected of either a sclerite developed in the adjacent paragonarcal membrane or a homologue of the normally medially situated mediuncus-arcessus of other Neuroptera. However, two lines of evidence strongly suggest that the pseudomediuncus is not a homologue of the mediuncus-arcessus: (1) the membranes contiguous with the lateral margins of the pseudomediuncus are confluent with the paragonarcal membrane, not the gonosaccal membrane as would be expected for the mediuncus-arcessus homologue (in Sympherobius the gonosaccal membrane is continuous with the posterior margin of the extragonarcus and terminates on the ventral surface of the gonopons near the base of the pseudomediuncus, Fig. 2) and (2) species of the South American genus Nomerobius possess not only a pseudomediuncus but also a structure which is apparently a homologue of the mediuncus of other Neuroptera. This structure is composed of a pair of narrow, laterally adjacent, lobes which insert on the venter of the gonopons. The membranes attaching to the bases of these lobes are confluent with the gonosaccal membrane. This membranous attachment, together with the position of the lobes, suggests that these structures may be mediuncus homologues. A third genus known to possess a pseudomediuncus, Neosympherobius, lacks recognizable mediuncus homologues.

The pseudomediuncus of Nomerobius and Neosympherobius consist of narrow, undivided, weakly sclerotized and weakly tanned strips of cuticle lying longitudinally along the midline of the paragonarcal membrane. In Sympherobius the pseudomediuncus is composed of a pair of sclerites, a proximal basipseudomediuncus (Fig. 2, bpm) and a distal distopseudomediuncus (dpm). These sclerites are joined at a narrowed joint or region of articulation which may be membranous or weakly sclerotized. The lateral margins of the basipseudomediuncus are splayed and recurved forming a shallow basin into which, by articulation at the intervening joint, the distopseudomediuncus may loosely seat. In Sympherobius the pseudomediuncus complex articulates with the posterior apex of the gonopons and frequently hangs down between or slightly posterior to the hemigonarcus. When thus situated it occupies a position filled by the mediuncus in most Neuroptera and thereby adds to the illusion of homology between itself and the true mediuncus-arcessus.

Parameres (Fig. 2): In Sympherobius the parameres are composed of a spatulate apodeme called the apophysis proxima (ap), and one, two or three pairs of terminal lobes (the median [mlp], lateral [llp] and anterior lobes [Fig. 26, alp]) which are arranged in bilateral symmetry about the plane of the apophysis proxima (Fig. 87). At its base, the apophysis proxima encloses a compressed cavity here called the apophysis proxima cavity (Fig. 2, apc). The apophysis proxima itself is a prominent
apodeme which projects for a considerable distance into the body cavity. Diverse configurations of the terminal lobes of the parameres result from differential patterns of sclerotization of the arthrodial membrane located primarily ventral and posterior to the external opening of the apophysis proxima cavity. The margins of the terminal lobes are sometimes not sharply delimited at their boundaries with adjacent unsclerotized membrane.

The innermost pair of terminal lobes, the median lobes ["distal lobes" of Nakahara (1965a)], are present in all species. The inner margins of the median lobes (Fig. 87) are adjoined basally along a line continuous with the longitudinal midline of the apophysis proxima. Distally the median lobes are separated by an emargination of variable shape and depth. The lateral lobes (Fig. 87) ["lateral flaps" of Nakahara (1965a)], when present, arise from the anterolateral margins of the median lobes. The ventral surfaces of the median and lateral lobes are minutely spinulate. The margins of these lobes may be finely or coarsely toothed. The anterior lobes (Fig. 26) ["oblique process" of Carpenter (1940), "middle arm" of Gurney (1948) and others], when present, arise from the anterior margin of the median lobes. The anterior lobes project dorsally and may have simple or expanded apices.

Immature stages. The preadult stages and biology of Sympherobius species are poorly known. Some immature stages of S. amiculus, S. barberi and S. californicus [as S. angustus] have been described by Smith (1923), Smith (1934) and Essig (1910) respectively. Additional descriptions and/or figures of some immature stages of one or more non-Nearctic species are found in the following works: Killington (1931, 1937), New (1967a, b), Withycombe (1923) and Yang (1980). Known larvae and adults are predaceous on small invertebrates. As inferred from published prey records, preferred prey are apparently various sternorrhyncho Homoptera, particularly pseudococcids.

Distribution. The genus Sympherobius is widely distributed throughout the temperate and tropical regions of North and South America and Europe, and the nontropical regions of Africa and Asia. Species have not been reported from tropical Africa, the Oriental or the Australasian faunal regions. The approximate distribution of each world species is given in Appendix 1.

In America north of Mexico, Sympherobius ranges north only to extreme southern Canada with its highest diversity found in the arid regions of the southwestern United States. The ranges of many Nearctic species extend south through Mexico. One species, S. barberi, has been recorded as far south as Peru. No species are Holarctic in distribution.

Etymology. Banks did not give the etymology of the name Sympherobius; however, it is almost certainly derived from the Greek "sympheron," useful, probably in reference to the beneficial predatory habits of the larvae and adults. Gender: masculine.

Synonymical note. Kimmins (1928:363) based his description of Sympheromima marginata, and the monobasic genus Sympheromima, on a single specimen lacking an abdomen collected at Cerro Zunil, Guatemala. None of the characters cited in the generic description, except possibly the slightly falcate posterodistal margin of the forewing, are adequate to distinguish Sympheromima from Sympherobius. The cited two oblique branches of the forewing radius, few crossveins of the forewing outer gradate series, and other venational characters are identical, or nearly so, with states found in Sympherobius.
Recently, a single specimen strongly agreeing with Kimmins' original description of the coloration and venation of the forewing of *Sympheromima marginata* was found in the collection of the National Museum of Natural History (Data—Mexico: Veracruz: near Huatusco; 25/26-VII-1965; Flint and Ortiz). This specimen is apparently the first known male of *Sympheromima marginata*. The ectoprocts of this specimen each bear three digitiform processes, each terminating in a peg-like seta as in many *Sympherobius*. Furthermore, *Sympheromima marginata* possesses the two synapomorphies of *Sympherobius*: (1) a bipartite pseudomediuncus and (2) a laterally expanded basipsseudomediuncus. Based on the presence of the ventromedial, ventrolateral and dorsolateral ectoproct processes, *Sympheromima marginata* would join the cladogram for Nearctic *Sympherobius* (Fig. 114) at some point distal to the position of Character 7 (absence-presence of the dorsolateral ectoproct process), a point well removed from the base of the *Sympherobius* clade.

The above characters, together with the fact that continued recognition of *Sympheromima* would render *Sympherobius* paraphyletic, justify the placement of *Sympheromima* as a junior subjective synonym of *Sympherobius*.

Nomenclatural note. The generic name *Spadobius* appears to have been based on a specimen of *Sympherobius amiculus* misidentified as *Sympherobius occidentalis* (see Carpenter, 1940:227). This is a case of misidentified type species which should be referred to the International Commission on Zoological Nomenclature for type selection under Article 70 of the International Code of Zoological Nomenclature (1985). However, since *S. amiculus* and *S. occidentalis* have been considered congeneric by all authors subsequent to the proposal of the generic name *Spadobius* in 1905 (except Krüger, 1922), nomenclatorial stability is not presently threatened by this misidentification; and submission of this case to the Commission is unnecessary at the present time.

Classification. The following suggested classification of the Nearctic species of *Sympherobius* is based on clades derived from the cladistic analysis presented below. Subsequent inclusion of extralimital species may require revision of the preliminary groupings proposed here.

### CLASSIFICATION OF NEARCTIC SYMPHEROBIUS

*S. perparvus* species group
- *S. perparvus* (McLachlan, 1869)
- *S. beameri* Gurney, 1948
- *S. arizonicus* Banks, 1911
- *S. killingtoni* Carpenter, 1940

*S. pictus* species group
- *S. pictus* (Banks, 1904)
- *S. similis* Carpenter, 1940
- *S. occidentalis* (Fitch, [1855] 1854)
- *S. limbus* Carpenter, 1940
- *S. distinctus* Carpenter, 1940

*S. angustus* complex
- *S. angustus* (Banks, 1904)
- *S. quadricuspis* n. sp.
S. bifasciatus Banks, 1911
S. californicus Banks, 1911
S. constrictus n. sp.
S. barberi complex
  S. barberi (Banks, 1903)
  S. umbratus (Banks, 1903)
  S. amiculus (Fitch, [1855] 1854)

Comment on the classification of European Sympherobius. Aspöck et al. (1980) advocated recognition of the subgeneric name Sympherobius (Niremberge) for the four European species S. fuscescens, S. klapaleki, S. pellucidus and S. riudori; the three other European species of Sympherobius, S. pygmaeus, S. elegans and S. fallax were retained in the nominate subgenus Sympherobius (Sympherobius). Two putative derived characters seem to support the hypothesis that the first four species form a group distinct from the other European species: (1) the forewing usually possesses three (not two) oblique radial branches and (2) the ventrolateral digitiform process of the male ectoproct bears two (not one) modified peg-like apical setae. These four species also lack lateral lobes on the parameres, and have only two digitiform processes on the male ectoproct. Given this distribution of characters, a lineage comprised of these species would join the cladogram in Figure 114 at a point between S. pictus and S. limbus (i.e., above character 3 [presence of the ventrolateral ectoproct process] but below character 7 [presence of the dorsolateral ectoproct process]). It is clear that classification of these species in a subgenus Niremberge would render paraphyletic the nominate subgenus containing all North American and the remaining European species. For this reason, I do not accept the retention of Niremberge as a subgenus.

If differentiation of the four species placed by Aspöck et al. (1980) in the subgenus Niremberge is desirable as an initial estimation of intrageneric relationships within the European Sympherobius fauna, I suggest that use of an informal designation such as the “fuscescens species group” be employed. Deferment of formal nomenclatural designation of such a group is desirable until, through increased documentation of intrageneric relationships worldwide, this genus can be comprehensively divided into monophyletic subunits.

KEY TO ADULT SYMPHEROBIUS OF AMERICA NORTH OF MEXICO

Couplets 2 through 16 of the following key primarily utilize forewing characteristics, couplets 17 through 32 utilize characters of the male genitalia. While color and maculation patterns of the forewing are valuable identification aids and, with some practice, are adequate to identify most species, these characters are subject to considerable intraspecific variation which cannot be efficiently represented in a dichotomous key. For this reason, use of the genitalial portion of the key, and its associated figures, is recommended for maximum accuracy in making identifications. Though positive identification of females is sometimes problematic, females of most species can be identified with reasonable confidence using forewing characters or by association with known males. Five species cannot be confidently keyed using forewing characters. In the forewing section of the following key, couplets leading to these
species are referred directly to the appropriate couplet of the genitalic portion of the key.

1. Key based on forewing characters .................................................. 2
1'. Key based on characters of the male genitalia .................................. 16
2(1). Proximal or distal radial crossvein present (see Fig. 4) ..................... 3
2'. Proximal and distal radial crossveins absent .................................... 10
3(2). Proximal radial crossvein present ............................................. 5
3'. Distal radial crossvein present .................................................... 4
4(3'). Longitudinal veins with distinct setal spotting (at least proximally), membrane hyaline with irregular brown maculations .......................... S. amicus (Figs. 101–102)
4'. Longitudinal veins uniformly dark brown, setal spotting absent, membrane almost uniformly dark brown ................................. S. umbratus (Fig. 64)
5(3). Dorsal surface of pterothorax with an anteriorly opening, yellow or pale chevron; forewing membrane brown with paler stripes adjacent to veins and within cells of discal area ....................... S. occidentalis (Fig. 63)
5'. Pterothorax without a pale dorsal chevron; coloration of forewing membrane various ................................................................. 6
6(5'). Basal third of 1A hyaline or at most with several small dark spots ........ S. bifasciatus (Fig. 79)
6'. Basal third of 1A uniformly brown and frequently narrowly margined with brown (e.g., Figs. 66, 76, 78, 80) ............................ 7
7(6'). Longitudinal radial veins nearly concolorous brown but not with wide fuscous margins (as seen in Fig. 76) ......................... S. similis (Fig. 66)
7'. Longitudinal radial veins with irregularly alternating brown and hyaline segments present at least distally (e.g., Figs. 76, 78, 80), wide fuscous margins may or may not be present adjacent to these veins ......................... 8
8(7'). An irregular, elongate, brown maculation present encompassing cu1-cu2 crossvein, Cu1 anterior to crossvein and adjacent membrane (Figs. 76, 78, 81), maculation may extend beyond this region in some species ............ S. angustus (part), S. constrictus, S. quadricuspis ...................... 17
8'. An elongate maculation absent in the preceding location, at most with several smaller, frequently partly confluent spots, in this region (Figs. 77, 80) .... 9
9(8'). Membrane uniformly light brown ............................................. S. angustus (part, Fig. 77)
9'. Membrane mottled with brownish and hyaline regions .................. S. californicus (Fig. 80)
10(2'). Wing narrow (e.g., Fig. 65), longitudinal veins hyaline ................... 15
10'. Wing broader (e.g., Figs. 17, 21, 61), longitudinal veins hyaline or brown 13
11(10'). Discal area with 3 or 4 transverse brown bands, male foretibia inflated (Fig. 5) ................................................................. S. pictus (Fig. 22)
11'. Discal area variously mottled but not with 3 or 4 prominent bands, male foretibia not inflated (Fig. 6) ............................... 12
12(11'). Wing narrow (e.g., Fig. 65), longitudinal veins hyaline ........................ 15
12'. Wing broader (e.g., Figs. 17, 21, 61), longitudinal veins hyaline or brown 13
13(12'). Longitudinal radial veins uniformly dark brown, forewing length > 5.5 mm ................................................................. S. distinctus (Fig. 61)
13'. Longitudinal radial veins not uniformly dark brown, forewing length < 5.5 mm ..........................
14(13'). Maculations of diffuse yellowish brown, margins of maculations poorly defined, setal spotting of longitudinal veins weak .......... S. limbus (Fig. 21)
14'. Maculations light or dark brown with irregular though usually relatively distinct margins, setal spotting of longitudinal veins usually prominent (Figs. 17–20) .......... S. arizonicus, S. killingtoni .......... 31
15(12). Membrane hyaline with scattered brownish maculations, especially around the inner gradate crossveins and forks of the radial veins .......... S. perparvus (Fig. 65)
15'. Membrane hyaline, immaculate .......... S. beameri
16(1'). Ectoprocts: 1 (e.g., Fig. 8) or 2 (e.g., Fig. 48) digitiform process(es) present; each process with only a single modified terminal seta; dorsomedial prominence absent .......... 21
16'. Ectoprocts: 3 digitiform processes present (e.g., Fig. 1); ventrolateral process with one (e.g., Figs. 92, 97) or two (Figs. 68, 108) modified terminal setae; dorsomedial prominence present (Figs. 57, 72) or absent .......... 17
17(8,16'). Ectoprocts: dorsomedial prominence absent .......... 18
17'. Ectoprocts: dorsomedial prominence present .......... 24
18(17). Ectoprocts: ventrolateral process with two modified terminal setae (Figs. 68, 108) .......... 25
18'. Ectoprocts: ventrolateral process with one modified terminal seta (e.g., Figs. 92, 97) .......... 19
19(18'). Parameres: lateral lobes present (e.g., Figs. 58, 87) .......... 20
19'. Parameres: lateral lobes absent (e.g., Figs. 37, 41) .......... 26
20(19). Parameres: emargination separating median from lateral lobes deep and narrow in dorsal view (Figs. 87, 93) .......... 27
20'. Parameres: emargination dividing median and lateral lobes absent or broad in dorsal view (Figs. 83, 98) .......... 28
21(16). Ectoprocts: 1 digitiform process present .......... 22
21'. Ectoprocts: 2 digitiform processes present .......... 29
22(21). Parameres: anterior lobes present (e.g., Figs. 10, 26); Ectoproct: ventromedial process less than twice as long as its modified terminal setae; calyx of setal socket produced into an elongate tubular sheath (e.g., Figs. 7, 23) .......... 23
22'. Parameres: anterior lobes absent (Fig. 37); Ectoproct: ventromedial process much more than twice as long as its modified terminal seta (Fig. 36), calyx of setal socket not produced into an elongate tubular sheath .......... S. pictus
23(22). Parameres: apices of anterior lobes expanded (Figs. 10, 15); Ectoproct: ventromedial surface of modified seta not impressed (Figs. 7, 12) .......... 30
23'. Parameres: apices of anterior lobes not expanded (Figs. 26, 31); Ectoproct: ventromedial surface of modified seta impressed (Figs. 23, 28) .......... 31
24(17'). Parameres: apices of median and lateral lobes acute, margins with large teeth, emargination dividing median lobes deep and U-shaped (Fig. 73) .......... S. quadricuspis
24'. Parameres: apices of lateral lobes broadly rounded, margins without large teeth, emargination dividing median lobes shallow and V-shaped (Fig. 73) .......... S. angustus
25(18). Parameres: margins of median lobes with large teeth (Fig. 69); Ectoprocts: ventrolateral process short and deeply divided (Fig. 68) .......... S. bifasciatus
25'. Parameres: margins of median lobes without large teeth (Fig. 110); Ectoprocts: ventrolateral process long and only shallowly divided (Fig. 108) .......... S. umbratus
26(19'). Parameres: posterior margin of median lobes with distinct teeth (Fig. 45); Gonarcus: anterior portion of gonopleuron deflexed (Fig. 47) .......... S. limbus
26'. Parameres: posterior margin of median lobes without distinct teeth (Fig. 53); Gonarcus: anterior portion of gonopleuron not deflexed (Fig. 55) ........................................... S. distinctus

27(20). Parameres: lateral lobes subtriangular, posterior margins toothed, longitudinal ridge present (Fig. 87) .................................................. S. californicus

27'. Parameres: lateral lobes elongate-oval, apices reflexed, margins without teeth, ridge absent (Fig. 93) ..................................................... S. barberi

28(20'). Parameres: lateral lobes supported by a thickened rod, margins toothed (Fig. 83) .............................................................. S. constrictus

28'. Parameres: lateral lobes not supported by a thickened rod, margins not toothed (Fig. 98) .......................................................... S. amiculus

29(21'). Parameres: anterior lobes present, apical margins of median lobes toothed (Fig. 49) ............................................................. S. occidentalis

29'. Parameres: anterior lobes absent, apical margins of median lobes not toothed (Fig. 41) .............................................................. S. similis

30(23). Ectoproct: ventromedial process, excluding calyx sheath, distinctly free of ectoproct, process curved ventromedially (Fig. 8), calyx sheath tightly constricting modified seta (Fig. 7) ........................................... S. perparvus

30'. Ectoproct: ventromedial process, excluding calyx sheath, short and indistinct, process directed posterodorsally (Fig. 13), calyx sheath loosely encircling modified seta (Fig. 12) .................................................. S. beameri

31(14',23'). Ectoproct: modified seta terminating a short recumbent process, base of process produced internally as a short apodeme (Fig. 29), calyx sheath tightly constricting modified seta (Fig. 28); Gonarcus: gonopleuron produced well beyond anterior margin of extrahemigonarcus (Fig. 30) .............. S. arizonicus

31'. Ectoproct: modified seta terminating a short, free-standing process, base of process not produced internally (Fig. 24), calyx sheath loosely encircling modified seta (Fig. 23); Gonarcus: gonopleuron ending nearly even with anterior margin of extrahemigonarcus (Fig. 25) ...................... S. killingtoni

SYMPHEROBIUS PERPARVUS SPECIES GROUP

Sympherobius perparvus (McLachlan)
Figs. 7–11, 65, 112

_Hemerobius perparvus_ McLachlan, 1869:22 (OD, A). Lectotype male. UNITED STATES: Texas: Bosque Co. (BMNH, by present designation, see _Type material examined_ below): Banks, 1892 (Lst); Banks, 1903 (MG*, Dst); Banks, 1904a (Dst); McClendon, 1906 (Dst).

_Sympherobius perparvus_ (McLachlan): Banks, 1905b (RD, A, MG*, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Smith, 1925 (Dst); Smith, 1934 (Dst, Key); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key, Tax); Gurney, 1948 (MG*, Key); Nakahara, 1960 (Dst, Tax); Nakahara, 1965a (Dst).

_Sympherobius sparsus_ Banks, 1911:346 (OD, A, Key). Holotype female. UNITED STATES: Kansas: [Douglas Co.?] (MCZ type #11,489): Smith, 1925 (Dst); Smith, 1934 (Dst, Key); Carpenter, 1940 (Tax).

_Eurobius perparvus_ (McLachlan): Krüger, 1922 (Tax).

_Description_. Antennae: Ochraceous to brown, usually darker distally. Forewing (Fig. 65): Length 3.20–4.63 mm (x = 3.77, N = 25). Longitudinal veins hyaline to ochraceous, concolorous; setal spotting weak or absent; gradate crossveins light brown,

Margined with light brown; membrane hyaline with scattered light brown spotting, particularly in distal forks of longitudinal veins; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 7, 8): One elongate unisetose process present; calyx of setal socket produced into a tubular sheath constricting base of seta; process and terminal modified seta curved ventromedially; seta slightly longer than process excluding sheath; ventromedial surface of seta not impressed. Hemigonarcus (Fig. 9): Gonopleuron linear; gonoplax a small, triangular, anterodorsal plate; extrahemigonarcus lobate anteriorly, narrowed posteriorly; hemigonarcal rib absent. Parameres
(Figs. 9, 10): Apices of median lobes reflexed; lateral lobes absent; anterior lobes large, curved dorsally, apices expanded; apophysis proxima broad.

Remarks. For a discussion of similar species see Remarks under S. killingtoni.

Distributions and associations. Geographic distribution (Fig. 112): Central and western United States and northern Mexico. Temporal distribution: 21 March through 15 October. Altitudinal distribution: 270’–6,400’ (82 m–1,951 m). Plant associations: Pine-Oak zone (southern Arizona).

Type material examined. Hemerobius perparvus McLachlan. Lectotype male by present designation. Verbatim label data: “type,” “20/9,” “type,” “Bosque Co. / Texas / Belfrage,” “McLachlan Coll. / B.M. 1938-674,” “Hemerobius / perparvus / McL.,” “Lectotype / Hemerobius / perparvus / McLachlan, 1869 / Oswald, 1985.” Condition: excellent, complete. Right wings pinned below specimen between two cover slips. One male paralectotype, same data as lectotype (BMNH). Only two specimens of the type series of S. perparvus are presently in the British Museum of Natural History (P. C. Barnard, pers. comm.). Three specimens were mentioned by McLachlan (1869) in the original description of S. perparvus. The third specimen is presumed lost. The two syntypes which I have examined are both males. Carpenter (1940) indicates incorrectly that the type series contains two females and one male. Each of the two specimens examined has been labeled “type” and/or “paratype” sometime in the past, but no primary type designation has been published for S. perparvus. I have selected and clearly labeled the better of the two specimens as the lectotype.


Other material examined. 139 specimens. MEXICO: Baja California Sur, Chihuahua, Coahuila; UNITED STATES: Arizona, California, Colorado, Iowa, Kansas, Minnesota, Montana, Nebraska, New Mexico, Nevada, Oklahoma, Oregon, South Dakota, Texas, Utah, Wyoming. Institutions: ASUT, BMNH, CAS, CU, ISU, MCZ, MSU, OKS, OSUC, SMEK, TAMU, UAT, UCB, UCD, UCR, UIM, UMSP, USNM, UWL. Also recorded from UNITED STATES: New York (Nakahara, 1960). This questionable record has not been confirmed.

Sympherobius beameri Gurney
Figs. 12–16, 33


Description. Flagellum light to medium brown, apices usually darker. Forewing: Length 3.64–4.39 mm ($\bar{x} = 3.96$, N = 7). Longitudinal veins and crossveins hyaline, not margined with brown; setal spotting absent; membrane hyaline, immaculate or nearly so; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 12, 13): One short, unisetose process present; calyx produced into a tubular sheath loosely encircling base of seta; seta short and arcuate, directed posterodorsally, ventromedial surface not impressed. Hemigonarcus

(Fig. 14): Gonopleuron linear; gonoplax a triangular anterodorsal plate; extrahemigonarcus broad anteriorly, narrowed posteriorly; hemigonarcal rib absent. Parameres (Figs. 15, 16): Apices of median lobes reflexed; lateral lobes absent; anterior lobes present, curved dorsally, apices expanded; apophysis proxima broad.

Remarks. The forewing of *S. beameri* is similar to that of *S. perparvus* (Fig. 65), but immaculate. The male genitalia are also similar to *S. perparvus* but may be distinguished by the short ectoproct process.

Distributions and associations. Geographic distribution (Fig. 33): Southwestern United States. Temporal distribution: 28 May through 10 September. Altitudinal distribution: 3,050′–7,500′ (930 m–2,286 m). Plant associations: no records.


*Sympherobius arizonicus* Banks
Figs. 17, 28–32, 33


*Description.* Antennae: Dark Brown. Forewing (Fig. 17): Length 2.94–5.10 mm (\(\bar{x} = 4.03, N = 25\)). Longitudinal veins hyaline with prominent setal spotting; gradate crossveins brown and margined with brown; membrane densely covered with brown maculations broken by hyaline regions or spots; maculations particularly dense along
distal and posterodistal border of wing; margin in these regions broken only by short hyaline areas; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 28, 29): One short unisetose process present; process recumbent; calyx of setal socket produced into a tubular sheath which constricts base of modified seta; seta linear or slightly curved proximally, ventromedial surface shallowly impressed; base of process produced internally forming a short apodeme. Hemigonarcus (Fig. 30): Gonopleuron produced anteriorly beyond anterior margin of extrahemigonarcus; gonoplax absent; extrahemigonarcus an angular lobe anteriorly, narrowing posteriorly; hemigonarcal rib absent. Parameres (Figs. 31, 32): Apices of median lobes reflexed; lateral lobes absent; anterior lobes present, apices unexpanded; apophysis proxima narrow.

Remarks. Specimens of Sympherobius arizonicus cannot be confidently separated from dark specimens of S. killingtoni on the basis of forewing coloration. Sympherobius arizonicus and S. killingtoni are also the most difficult pair of species to separate on the basis of the male genitalia. In addition to the characters given in key couplet 31, the gonopleuron of S. killingtoni usually bears a small dark anterodorsal tooth (Fig. 25) which is absent in S. arizonicus.

I have examined specimens of S. arizonicus and/or S. killingtoni from northern Mexico which exhibit states of the ventromedial ectoproct process which are intermediate between the conditions normally found in these species.

Distributions and associations. Geographic distribution (Fig. 33): Arizona and California south to southern Mexico. Temporal distribution: January through December. Altitudinal distribution: 160'-5,350' (49 m-1,631 m). Plant associations: no records.


Other material examined. 139 specimens. MEXICO: Baja California Norte, Baja California Sur, Oaxaca, Puebla and Sonora; UNITED STATES: Arizona, California. Institutions: ASUT, CAS, CU, LACM, MCZ, OSU, OSUC, PMY, TAMU, UAT, UCB, UCD, UCR, UMAA, UMSP, USNM.

Sympherobius killingtoni Carpenter

Figs. 6, 18-20, 23-27, 35


Description. Antennae: Light to medium brown, usually darker basally and distally. Forewing (Figs. 18–20): Length 3.41–4.89 mm ($\bar{x} = 4.07$, N = 25). Longitudinal veins hyaline to brown with distinct setal spotting; gradate crossveins brown and margined with brown; membrane pigmentation varies from mostly hyaline with scattered faint brown maculations to largely covered with brownish maculations divided by hyaline regions or spots; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Figs. 23, 24): One short unisetose process present; calyx
of setal socket produced into a tubular sheath loosely encircling base of modified seta; seta bent proximally, ventromedial surface impressed. Hemigonarcus (Fig. 25): Gonopleuron linear; anterior end nearly even with anterior margin of extrahemigonarcus; gonoplax absent or present as a small anterodorsal tooth; extrahemigonarcus a rounded lobe anteriorly, narrowed posteriorly; hemigonarcal rib absent. Parameres (Figs. 26, 27): Lateral lobes absent; anterior lobes present, apices unexpanded; apophysis proxima wide.

Remarks. Sympherobius texanus is a small specimen of S. killingtoni. Though the male genitalic structures of the holotype are slide mounted and therefore somewhat distorted, they are clearly identical to those of S. killingtoni.

The color and density of forewing maculations in S. killingtoni are quite variable. Darker specimens of S. killingtoni may be mistaken for S. arizonicus. Specimens with light or moderately dark maculations may resemble S. perparvus or S. pictus respectively. In S. perparvus, however, the forewing is narrower (Fig. 65), setal spotting is usually weak or absent and the forewing maculations usually consist of a number of relatively discrete spots or blotches set against a hyaline membrane. In S. killingtoni the wing is wider (Fig. 19), setal spotting is prominent and the membrane is usually lightly mottled with diffuse brown maculations. Sympherobius pictus also has prominent setal spotting but the discal maculations of the forewing are grouped into three or four irregular transverse bands (Fig. 22). See also Remarks under S. arizonicus.

Distributions and associations. Geographic distribution (Fig. 35): Western and south central United States and northern Mexico. Temporal distribution: January through December. Altitudinal distribution: 160'-10,150' (49 m–3,094 m). Plant associations: cypress.


Sympherobius texanus Nakahara. Holotype male. Verbatim label data: “Kerrville Tex / VI 1954 / L.J. Bottimer,” “Holotype,” “Sympherobius / texanus n. sp. / [Holotype] / W. Nakahara.” Condition: Right forewing on one slide. Male genitalia on another slide. One leg, left forewing and right hindwing on point, remainder of body missing.

Other material examined. 324 specimens. MEXICO: Baja California Norte, Chihuahua, Coahuila, Zacatecas; UNITED STATES: Arizona, California, Colorado, Idaho, New Mexico, Nevada, Oregon, Texas, Utah, Washington. Institutions: AMNH, ASUT, CAS, CMP, CU, LACM, MCZ, OSU, OSUC, SMEK, TAMU, UAT, UCB, UCD, UCR, UMSP, USNM, WSU.

SYMPHEROBIUS PICTUS SPECIES GROUP

Sympherobius pictus (Banks)
Figs. 5, 22, 34, 36–39

Hemerobius pictus Banks, 1904c:62 (OD, A). Lectotype female. UNITED STATES: Colorado: “S.W.,” precise locality unknown (MCZ type #11,488, designated by Carpenter, 1940, but see Primary type material examined below).

*Sympherobius pictus* (Banks): Banks, 1905a (Tax); Banks, 1905b (RD, A, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Carpenter, 1940 (RD, F, W*, Dst, Key).

*Description.* Antennae brown, concolorous. Legs: Male foretibia inflated (Fig. 5). Forewing (Fig. 22): Length 3.87–4.52 mm ($\bar{x} = 4.22$, $N = 6$). Longitudinal veins largely hyaline; setal spotting prominent; most crossveins, including both gradate series, brown and widely margined with brown; tips of marginal veinlets dark brown; discal area dominated by three or four transverse brown bands; bands broad and irregular; apical and posterior wing margin also marked with a broad, irregular brown band broken at regular intervals by lighter colored regions; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Fig. 36): One very long unisetose process present; process directed ventrally with its greatest diameter near midlength, terminal seta very short; a broad setose tubercle present above base of ectoproct process. Hemigonarcus (Fig. 39): Gonopleuron linear or slightly sinuate, anterior end decurved; gonopla a small triangular anterodorsal plate with a spiniform process; extrahemigonarcus moderately broad; hemigonarcal rib absent. Parameres (Figs. 37, 38): Anterolateral angle of median lobes forming an acute cusp in dorsal view; anterior and lateral lobes absent; apophysis proxima narrow.

*Remarks.* Males of *S. pictus* are unique in possessing an inflated foretibia (Fig. 5) and a single extremely long, unisetose ectoproct process (Fig. 36). Males and females may be distinguished from other species by the maculations of the discal area of the
forewing which are concentrated into three or four transverse bands (Fig. 22). See also Remarks under S. killingtoni.

**Distributions and associations.** Geographic distribution (Fig. 34): Southwestern United States and northern Mexico. Temporal distribution: 10 May through 15 August. Altitudinal distribution: 5,500′–7,200′ (1,676 m–2,188 m). Plant associations: no records.

**Primary type material examined.** *Sympherobius pictus* Banks. Lectotype female. Verbatim label data: “S.W. Colo. / Oslar,” “Collection / N. Banks,” “TYPE / 11488,” “Hemerobius / pictus / type Bks,” “Lectotype / Sympherobius pictus / designated Carpenter / 1940 lectotype label / reapplied by Oswald 1985.” Condition: left hindleg and right forewing missing, otherwise complete. One female paralectotype also seen, same data as lectotype (MCZ).

Carpenter (1940) examined the two female syntypes of *S. pictus* and stated “one of these has been now labelled the lectotype.” Carpenter (1940:235, pl. 2, Fig. 13) figured the right forewing of the lectotype. I have reexamined the types and neither specimen now bears Carpenter’s lectotype label. One syntype possesses both forewings, but the right forewing does not agree with Carpenter’s figure. The second type is missing the right forewing (having been removed by Carpenter for figuring and now misplaced), but the left forewing agrees well with Carpenter’s figure. This specimen is Carpenter’s lectotype. To clarify the identity of this primary type I have applied the following label to the pin of this specimen: “Lectotype / Sympherobius pictus / designated Carpenter / 1940 lectotype label / reapplied by Oswald 1985.”


*Sympherobius similis* Carpenter

Figs. 40–43, 66, 90


**Description.** Forewing (Fig. 66): Length 3.80 mm (N = 1). Longitudinal veins brownish, anal veins hyaline; setal spotting absent; membrane hyaline with irregular light brown maculations; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 40): Two unisetose processes present; processes adjacent and strongly incurved; each ectoproct of the only available male of this species contains a small oval hole in the ectoproct near the calus cercus, these openings are located in approximately the position a dorsolateral process would originate and may be remnants of a third broken ectoproct process. Hemigonarcus (Fig. 47): An-
terior end of gonopleuron decurved; gonoplax absent or narrow and elongate; extrahemigonarcus moderately broad; hemigonarcal rib present, forked. Parameres (Figs. 45, 46): Median lobes weakly tanned, their margins indistinctly delimited; anterior and lateral lobes absent; apophysis proxima moderately broad.

**Remarks.** The forewing maculations of *S. similis* are similar to those of *S. biformisatus, S. constrictus* and *S. quadricuspis* but with the longitudinal veins nearly evenly brown, not with distinct alternating dark and hyaline segments. The shape of the parameres and forked hemigonarcal ribs of the extrahemigonarcus will also distinguish this species.

**Distributions and associations.** Geographic distribution (Fig. 90): Known only from the Santa Rita Mountains of southern Arizona. Temporal distribution: 20 June and 17 July. Altitudinal distribution: no records. Plant associations: no records.

**Primary type material examined.** *Sympherobius similis* Carpenter. Holotype male. Verbatim label data: “Santa Rita Mts / Ar. 7-17-32 / R. H. Beamer,” “Type,” “Sympherobius / similis Carp. / Holotype.” Condition: good, right mesotibia and tarsus, pedicle and flagellum of left antenna and distal portion of right antenna missing, otherwise complete. Left forewing slide mounted in Hoyer’s solution. Genitalia in glycerin in microvial pinned below specimen. Ninth sternite missing.

**Other material examined.** 1 specimen. UNITED STATES: Arizona: Santa Cruz or Pima Co.: Santa Rita Mts., 20.vi.[year unrecorded] (USNM).

*Sympherobius occidentalis* (Fitch)

**Figs. 35, 48–51, 63**

*Hemerobius occidentalis* Fitch, [1855] 1854:799 (OD, A). Syntype(s?), sex(s) unknown. UNITED STATES: Illinois: Henderson River, precise locality unknown. Type material apparently lost, see under *Types* below.: Banks, 1892 (Lst).

*Sympherobius occidentalis* (Fitch): Banks, 1905b (RD, A, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Smith, 1934 (Dst, Key); Brimley, 1938 (Dst); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key, Tax); Froeschner, 1947 (Dst); Throne, 1971 (Dst); Agnew et al., 1981 (A*, Dst, Key).

*Spadobius occidentalis* (Fitch): not Needham, 1905 (see *S. amiculus*); Krüger, 1922 (Tax).

**Description.** Antennae: Anterior face of scape and pedicel yellow, posterior face brownish; proximal segments of flagellum dark brown, distal segments yellow to yellow-brown. Mesonotum: Brown with an anteriorly opening yellow "V" formed by yellow markings on the prescutum, scutum and scutellum; prescutum also bisected by a longitudinal yellow stripe. Forewing (Fig. 63): Length 3.80–5.23 mm (\(\bar{x} = 4.32, N = 25\)). Longitudinal veins and crossveins monochromatic dark brown, except yellowish base of radius; veins narrowly margined with brown, particularly crossveins and veins of cubital and anal regions; cells with brownish centers surrounded by hyaline membrane; brownish centers of cells in discal area with light brown to hyaline median stripes, proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 48): Two unisetose processes present; processes short, heavily tanned and decurved. Hemigonarcus (Fig. 51): Gonopleuron linear or slightly decurved anteriorly; gonoplax absent; extrahemigonarcus moderately broad; hemigonarcal rib absent. Parameres (Figs. 49, 50): Apices of medial lobes angulate,
margins armed with large teeth; lateral lobes absent; anterior lobes present, apices unexpanded; apophysis proxima narrow.

Remarks. The largely brown to fuscous forewing cells of *S. occidentalis* are similar to those of *S. umbratus* but the male genitalia of *S. occidentalis* possess only two ectoproct processes and the lateral lobes of the parameres are absent. *Sympherobius occidentalis* is also unique in possessing a prominent yellow or pale V-shaped mark on the mesonotum.

Distributions and associations. Geographic distribution (Fig. 35): Eastern United States. Temporal distribution: 20 April through 25 October. Altitudinal distribution: no records. Plant associations: *Pinus* sp.

Types. Carpenter (1940:231) stated that Fitch's type material of *S. occidentalis* was not in the MCZ or USNM, and was apparently lost. Lacking specimens of the species he treated as *S. occidentalis* from the type locality (Illinois) of *S. occidentalis* Fitch, Carpenter refrained from designating a neotype for this species.

Of the 17 Nearctic species of *Sympherobius* two, *S. umbratus* (= Carpenter's *S. gracilis + S. umbratus*) and *S. occidentalis*, possess the lack of mottling and “two faint parallel lines of a more dusky tinge” mentioned by Fitch ([1855] 1854:799) as characteristic of the discal cells of the forewing of *S. occidentalis*. However, *S. occidentalis* is distinguishable from *S. umbratus* on the basis of Fitch's original description of the forewing venation of *S. occidentalis*: “outer fork of the first discoidal vein [=R4+5] anastamosing [i.e., joined by a crossvein] with the rib-vein [=radial stem] near its base instead of with the second discoidal [=R2+3] as in the preceding species [i.e., *S. amiculus*].” In *S. occidentalis* the proximal radial crossvein joins the R4+5 [“outer fork of first discoidal”] to the R1+2+3 [“rib-vein”], as described by Fitch; in *S. amiculus* and *S. umbratus* the distal radial crossvein joins the R4+5 [“outer fork of first discoidal”] to the R2+3 [“second discoidal”]. Since the identity of *S. occidentalis* is not in question, designation of a neotype is unwarranted (ICZN, 1985: Article 75). The species treated here as *S. occidentalis* is the same as that treated by Carpenter under the same name.

Material examined. 43 specimens. UNITED STATES: Alabama, Arkansas, Georgia, Louisiana, Missouri, North Carolina, New York, Ohio, Pennsylvania, Texas, Virginia. Institutions: AMNH, CMP, CU, FEM, INHS, LSU, NCSR, OSU, SMEK, TAMU, UCB, UGA, UMC, USNM. Also recorded from UNITED STATES: District of Columbia, Kansas, Wisconsin (Carpenter, 1940—District of Columbia; Banks, 1905b—Kansas; Throne, 1971—Wisconsin).

*Sympherobius limbus* Carpenter

Figs. 21, 33, 44-47

*Sympherobius limbus* Carpenter, 1940:236 (OD, A, MG*, Key). Holotype male.

UNITED STATES: Texas: Brewster Co., Alpine (SMEK).

Description. Antennae: Flagellum brown, concolorous. Forewing (Fig. 21): Length 3.80–4.24 mm ($\bar{x} = 4.04, N = 3$). Longitudinal veins brownish yellow, concolorous or with alternating lighter brown segments; setal spotting weak; membrane hyaline or mottled with diffuse light brown maculations; vein setae pale; crossveins diffusely margined with light brown; proximal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Fig. 44): Three unisetose processes present; ventral
processes incurved; ventrolateral process very stout, lateral surface with several normal setae in addition to terminal modified seta; dorsolateral process short. Hemi-
gonarcus (Fig. 47): Anterior end of gonopleuron angled ventrally; gonoplax a prominent curved plate; ventral margin of extrahemigonarcus broadly emarginate; hemigonarcal rib present, unforked. Parameres (Figs. 45, 46): Posterior margins toothed; anterior and lateral lobes absent; apophysis proxima broad.

Remarks. Sympherobius limbus may be distinguished from other species without proximal or distal radial crossveins by its faint setal spotting and diffuse yellowish brown membrane. Its male genitalia resemble S. similis in lacking both anterior and lateral lobes of the parameres and in possessing the hemigonarcal rib of the extra-
hemigonarcus, but in S. similis the median lobes of the parameres are without teeth and the hemigonarcal ribs are forked.

Distributions and associations. Geographic distribution (Fig. 33): Southwestern United States. Temporal distribution: June through 4 October. Altitudinal distri-
bution: 5,400’-7,600’ (1,646 m–2,316 m). Plant associations: no records.

Primary type material examined. Sympherobius limbus Carpenter. Holotype male. Verbatim label data: “Alpine, Texas / 7-11-28 / R. H. Beamer,” “Type,” “Sym-
pherobius / limbus Carp. / Holotype.” Condition: good, tips of antennae and several small pieces of wings missing, otherwise complete. Genitalia in glycerin in microvial pinned below specimen.


Sympherobius distinctus Carpenter
Figs. 33, 52–55, 61


Description. Antennae dark brown, concolorous. Forewing (Fig. 61): Length 6.76 mm (N = 1). Longitudinal veins evenly brown, not interrupted by hyaline segments; setal spotting absent; gradate crossveins brown; membrane light brown with irregular hyaline spots or blotches; posterior costal margin with several hyaline regions; prox-
imal and distal radial crossveins absent.

Male genitalia: Ectoprocts (Fig. 52): Three unisetose processes present; dorsolateral process straight; ventral processes incurved. Hemigonarcus (Fig. 55): Gonopleuron linear; gonoplax a broad rounded lobe; extrahemigonarcus moderately broad; hemigonarcal rib present, produced posteroventrally into a narrow elongate process. Par-
ameres (Figs. 53, 54): Median lobes not toothed; lateral and anterior lobes absent; apophysis proxima moderately broad.

Remarks. Sympherobius distinctus is the largest Nearctic Sympherobius species. The brownish longitudinal radial veins and membrane of the forewing are similar to those of S. umbratus, but the membrane of S. distinctus is marked with irregular hyaline regions. The proximal and distal radial crossveins are also absent in S. distinctus. The male parameres are similar to those of S. pictus, S. limbus and S.

*Sympherobius sirnilis* in lacking both the anterior and lateral lobes, but *S. distinctus* is distinguished by the elongate hemigonarcal rib.

**Distributions and associations.** Geographic distribution (Fig. 33): Known only from Arizona and Colorado at high elevation. Temporal distribution: 18 and 19 August. Altitudinal distributions: 9,050' (2,758 m). Plant associations: no records.

**Primary type material examined.** *Sympherobius distinctus* Banks. Holotype male. Verbatim label data: “Pingree Park Colo / Aug 18 1926,” “RCSmith / Collector,” “M.C.Z. / Type / 23677,” “Sympherobius / distincta Carp. / det. F.M. Carpenter.” Condition: fair, right foreleg distal to femur and antennae distal to scapes absent.
Tip of right forewing also missing, otherwise complete. Left forewing slide mountec in Hoyer's solution. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 1 specimen. UNITED STATES: Arizona: Graham Co.: Graham Mts., Hospital Flat, 19.viii.1952 (USNM).

**SYMPHEROBIUS ANGUSTUS SPECIES COMPLEX**

*Sympherobius angustus* (Banks)

Figs. 4, 56–60, 76–78, 90


*Sympherobius angustus* (Banks): Banks, 1905a (Dst); Banks, 1905b (RD, A, MG*, Dst, Key, Lst); Banks, 1907b (Lst); not Essig, 1910 (see *S. californicus*); Banks, 1911 (Key); Cole, 1933 (Bic, Bio, Par); Carpenter, 1940 (RD, F, W*, Dst, Key); Spencer, 1942 (Dst); Nakahara, 1965a (Dst); Nakahara, 1965b (Dst).


*Nefasitus tristis* (Navás): Navás, 1915c (Tax).

*Sympherobius stangei* Nakahara, 1960:16 (OD, A, W*). Holotype, sex unknown. UNITED STATES: California: San Bernardino Co., Barton Flats (not examined, repository unknown, probably in Nakahara Collection, Japan [Lionel Stange, pers. comm.]): Nakahara, 1965a (Dst). New Synonym.


Description. Antennae: flagellum brown, monochromatic. Forewing (Figs. 77–79): Length 4.78–6.36 mm ($\bar{x} = 5.50$, N = 25). Pigmentation pattern of longitudinal veins variable, typically with alternating brown or fuscous and hyaline segments, in some specimens (*stangei* color form) proximal regions of longitudinal veins entirely fuscous with hyaline segments present only distally on some radial veins; veins unmargined to widely margined with fuscous; setal spotting absent; membrane largely hyaline (*stangei* color form), diffusely mottled (typical color form) or evenly tinged with light brown (*brunneus* color form); Cu1 distal to Cu1–Cu2 fork frequently broadly margined with fuscous; gradate crossveins brown to fuscous usually margined with fuscous; proximal radial crossvein present (rarely absent or double), distal radial crossvein absent.

Male Genitalia: Ectoprocts (Figs. 56, 57): Three unisetose processes and dorso-medial prominence present; ventral and dorsolateral processes incurved, ventrolateral process most strongly curved. Hemigonarcus (Fig. 60): Gonopleuron linear; gonoplax variable, large and triangular (as figured) or low and broadly rounded dorsally; extrahemigonarcus broad; hemigonarcal rib present, unforked. Parameres (Figs. 58, 59): Lateral lobes broad (rarely narrowed), posterior margin curved dorsally; anterior lobes absent; apophysis proxima narrow.

Remarks. Nakahara described *S. brunneus* on the basis of the immaculate light
brown tinting of the forewing membrane and S. stangei primarily on the basis of the broad fuscous margining of the longitudinal veins of the forewing. Although these forms are distinct phenotypes based on forewing coloration, the male genitalia of both forms are indistinguishable from those of S. angustus and I consider them junior synonyms.

Sympherobius brunneus appears to be a color form of S. angustus endemic to the Sierra Nevada and Siskiyou mountains of northern California. I have seen specimens of this color form only from four counties in northern California: Mariposa (1 specimen), Placer (1), Siskiyou (7) and Tuolumne (1). The brunneus color form (Fig. 77) is sympatric with the typical angustus color form (Fig. 78) in the Sierra Nevada mountains (typical color form seen from El Dorado, Nevada, Placer and Tuolumne counties). I have not seen the typical angustus color form from the Siskiyou mountains.

The type of S. stangei was described from material sent to the late Dr. Waro Nakahara in Japan by Dr. Lionel Stange. The type of this species has not been examined. However, since the abdomen of the type is missing, its usefulness in verifying the presently proposed synonymy of S. stangei and S. angustus would be limited. Several male specimens (from California: El Dorado Co., San Diego Co.; Colorado: Chimney Gulch; and Oregon: Harney Co.) with the same extensive fuscous margining of the forewing veins (Fig. 76) shown by Nakahara's figure of the forewing

of the holotype of *S. stangei* (Nakahara, 1960, Fig. 13) have been examined. On the basis of male genitalic characters, these specimens are indistinguishable from *S. angustus*.

As indicated above *S. angustus* is extremely variable in forewing pigmentation. Typical *angustus* color forms are easily confused with *S. californicus, S. constrictus, S. bifasciatus* and *S. quadricuspis*. In each of these five species the proximal radial crossvein is present, the distal radial crossvein is absent and the longitudinal veins
are normally marked with alternating brown and hyaline segments. Sympherobius californicus may usually be distinguished by the absence of the elongate dark maculation along the Cu1, and the light brown to yellowish central region of the antennal flagellum. Sympherobius bifasciatus may be distinguished by the hyaline or only spotted basal third of the 1A. Specimens exhibiting extensive fuscous margining of the longitudinal R, M and Cu veins (Fig. 76) may be confidently referred to S. angustus.

Because of limited material, the full range of variation in the forewing maculation patterns of S. constrictus and S. quadricuspis is unknown, with the known variation overlapping that of S. angustus. Consequently, confident identification of these species cannot be obtained without examination of the male genitalia.

Although S. angustus, S. californicus, S. constrictus, S. bifasciatus and S. quadricuspis are difficult to separate with forewing characters, the male genitalia, particularly the shape of the median and lateral lobes of the parameres, are very distinctive for each species.

Distributions and associations. Geographic distribution (Fig. 90): Sympherobius angustus is a montane species restricted to middle and high elevations of southwestern Canada, the western United States and Mexico. Temporal distribution: 25 May through 8 October. Altitudinal distribution: 3,600’–9,600’ (1,097 m–2,926 m). Plant associations: Picea sp. Prey records: Pseudococcus citri (see Cole, 1933).


Sympherobius brunneus Nakahara. Holotype male. Verbatim label data: “Miami Ranger Sta / Mariposa Co. Cal.,” “H.P. Chandler / No. 21 Expo. / 7/5/45 NE / Elv. 5,000 SW,” “H. Chandler / Collection,” “Sympherobius / brunneus n. sp. / [Holotype] / W. Nakahara,” “Holotype.” Condition: poor, left forewing on one slide, male genitalia on another slide, parts of right forewing, right eye and one leg on point, remainder of specimen missing.

Other material examined. 88 specimens. CANADA: British Columbia; MEXICO: Durango, Mexico, Nuevo Leon, Oaxaca; UNITED STATES: Arizona, California, Colorado, Idaho, New Mexico, Nevada, Oregon, South Dakota, Utah. Institutions: CAS, CSU, CU, LACM, MCZ, OSU, OSUC, SMEK, TAMU, UAT, UCB, UCD, UCR, UNH, USNM. Also recorded from MEXICO: Morelos (Nakahara, 1965b). Nakahara’s 1965b records from Mexico: Veracruz and Jalapa are not S. angustus.

Sympherobius quadricuspis, new species
Figs. 62, 72–75, 113

Description. Antennae: Light brown. Forewing (Fig. 62): Length 4.32 mm (N = 1). Longitudinal veins light brown interrupted by hyaline segments; membrane hyaline or very faintly mottled; gradate crossveins brown and margined with brown; central region of Cu1, basal portion of 1A and 3A and posterior fork of 2A margined with brown; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 72): Three unisetose processes and dorsomedial prominence present; ventral processes incurved. Hemigonarcus (Fig. 75): Gonopleu-

ron linear; gonoplax narrow and elongate; extrahemigonarcs moderately broad, produced anteriorly beyond end of gonopleuron; hemigonarcal rib absent. Parameres (Figs. 73, 74): Apices of median and lateral lobes acutely angled, armed with very large teeth; median lobes divided by a deep U-shaped emargination; lateral lobes narrow; anterior lobes present; apophysis proxima narrow.

**Etymology.** From the Greek “quadri-,” four, and “cuspis,” point, in reference to the acute apices of the median and lateral lobes of the parameres.

**Remarks.** For a discussion of similar species see Remarks under *S. angustus*.

**Distributions and associations.** Geographic distribution (Fig. 113): Known only from the Chiricahua Mountains of southeastern Arizona. Temporal distribution: 30 April and 25 July. Altitudinal distribution: 5,400'-7,600' (1,646 m–2,316 m). Plant associations: no records.


**Other material examined.** One male paratype. UNITED STATES: Arizona: Cochise Co.: Chiricahua Mts., Onion Saddle, 25.vii.1966 (CU).
Sympherobius bifasciatus Banks

Figs. 34, 67–71, 79


Description. Scape and pedicle dark brown. Flagellum yellow-brown proximally and distally, yellow medially. Forewing (Fig. 79): Length 4.06–4.94 mm (x = 4.48, N = 3). Longitudinal veins brown with irregularly spaced hyaline segments; hyaline segments without setal spotting; membrane hyaline or faintly mottled with light brown; most crossveins and distal forks of longitudinal veins margined with brown; membrane adjacent to central region of Cu1 forming a brown macula; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Figs. 67, 68): Three processes present; dorsolateral and ventromedial processes unisetose; ventrolateral process bisetose; ventrolateral process deeply forked, base wide. Hemigonarcus (Fig. 71): Gonopleuron with anterior end directed ventrally; gonoplax absent or narrow and elongate; extrahemigonarcus broad; hemigonarcal rib absent. Parameres (Figs. 69, 70): Apical margin of median lobes squarish, armed with very large teeth; lateral lobes curved dorsally; anterior lobes absent; apophysis proxima narrow.

Remarks. For a discussion of similar species see Remarks under S. angustus.

Distributions and associations. Geographic distribution (Fig. 34): Southwestern United States and northern Mexico. Temporal distribution: 12 June through 20 October. Altitudinal distribution: 5,400’–8,400’ (1,646 m–2,560 m). Plant associations: Pine-Oak zone (southern Arizona).


Other material examined. 46 specimens. MEXICO: Durango; UNITED STATES: Arizona, California, Colorado, Utah. Institutions: CU, MCZ, OSU, UAT, UCB, UCR, UMSP, USNM. Also recorded from CANADA: Alberta (Carpenter, 1940).

Sympherobius californicus Banks

Figs. 34, 80, 86–89


UNITED STATES: California: Los Angeles Co., Pasadena (MCZ type #11,487, designated by Carpenter, 1940): Cole, 1933 (Bic, Bio, Par); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key); Nakahara, 1960 (Dst, Tax); Nakahara, 1965a (Dst).

Nefasitus californicus (Banks): Navás, 1915c (Tax).

Description. Antennae: Flagellum usually brownish proximally and distally, separated by a lighter yellowish or light brown region. Forewing (Fig. 80): Length 4.41–
6.47 mm (\(\bar{x} = 5.62, N = 25\)). Longitudinal veins with brown and hyaline segments of irregular length; setal spotting absent; membrane mottled with irregular brown maculations; crossveins dark brown and margined with brown; proximal radial crossvein present (rarely absent), distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 86): Three unisetose processes present; ventral processes incurved, ventrolateral process strongly curved; dorsolateral process straight. Hemigonarcus (Fig. 89): Gonopleuron broad, angled ventrally near midlength; gonoplax narrow and elongate; extrahemigonarcus broad; hemigonarcal rib present, unforked. Parameres (Figs. 87, 88): Apices of median lobes angulate, margins armed with large teeth; lateral lobes subtriangular, attached narrowly to anterolateral corner of median lobes, apical margins with large teeth; lateral lobes with an erect longitudinal keel on the dorsal surface; anterior lobes absent; apophysis proxima broad.

Remarks. The name Hemerobius californicus Banks was published without description or indication and is thus a nomen nudum. Based on the facts that the specimens listed as H. californicus were collected near Stanford University (Palo Alto, California), a locality well within the range of S. californicus, and that no other hemerobiid shares the specific name ‘californicus,’ it seems probable that the material listed under this name was specimens of S. californicus.

Essig’s (1910) figure of “Sympherobius angustus” and his statement that adults were still emerging in January clearly indicate that the species he studied was S. californicus, not S. angustus. Temporal records from pinned specimens indicate that S. californicus adults are commonly present throughout the winter months in California while adults of S. angustus, a montane species, are not.

For a discussion of similar species see Remarks under S. angustus.

Distributions and associations. Geographic distribution (Fig. 34): Sympherobius californicus is a lowland species common to extreme northwestern Mexico and western California. One male from Seattle, Washington, has also been examined. This species is absent from the montane regions of northern and eastern California and the Mohave Desert of southeastern California. Temporal distribution: January through December. Altitudinal distribution: 250’–840’ (76 m–256 m). Plant associations: Orange.

Primary type material examined. Sympherobius californicus Banks. Lectotype male. Verbatim label data: “type,” “Mark [?] F. Grinnell, Jr / Los Angeles County / Pasadena Calif.,” “Collection / N. Banks,” “Type / 11487,” “Sympherobius / californicus / type Bks.” Condition: good, right hindleg, left metatarsus and distal segments of antennae missing, otherwise complete. Genitalia in glycerin in microvial pinned below specimen.

Other material examined. 446 specimens. MEXICO: Baja California Norte; UNITED STATES: California, Washington. Institutions: ASUT, CAS, CU, LACM, MCZ, OSUC, SMEK, UCB, UCD, UCR, USNM.

Sympherobius constrictus, new species

Figs. 81–85, 90

Description. Flagellum brownish, central region lighter brown. Forewing (Fig. 81): Length 4.84–6.43 mm (\(\bar{x} = 5.63, N = 6\)). Longitudinal veins light brown interrupted by short hyaline segments; setal spotting absent; vein setae pale and inconspicuous
against membrane; Cu1 distal to Cu1-Cu2 fork with an elongate brown maculation; crossveins brown and margined with brown; membrane hyaline, except for brown margining of some veins; proximal radial crossvein present, distal radial crossvein absent.

Male genitalia: Ectoprocts (Fig. 82): Three unisetose processes present; ventromedial and ventrolateral processes curved ventromedially; dorsolateral process straight, constricted at base. Hemigonarcus (Fig. 85): Gonopleuron widened anteriorly; gonoplax narrow and elongate; extrahemigonarcus broad; hemigonarcal rib present, unforked. Parameres (Figs. 83, 84): Median lobes rounded apically, margins with large teeth; lateral lobes small subtriangular plates supported by narrow sclerotized rods arising from anterolateral region of median lobes, margins with large teeth; anterolateral corners of median lobes elongate; apophysis proxima narrow.

*Etymology.* From the Latin “constrictus,” drawn together or contracted, in reference to the constricted base of the dorsolateral ectoproct spine.

*Remarks.* Sympherobius constrictus is closely related to *S. californicus*. The forewing maculations of these species are very similar, but the lateral lobes of the parameres are distinctive in each (see also Remarks under *S. angustus*).
Distributions and associations. Geographic distribution (Fig. 90): Known only from the San Francisco Bay region of California, where it is sympatric with S. californicus. Additional collections are necessary to confirm the limits of the range of S. constrictus. Temporal distribution: 16 February to 25 October. Altitudinal distribution: no records. Plant associations: Cupressus macrocarpa, Rhus diversiloba.


Sympherobius barberi Species Complex

Sympherobius barberi (Banks)  
Figs. 91–95, 103–106, 113


Sympherobius barberi (Banks): Banks, 1905b (RD, A, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Smith, 1925 (Dst); Cole, 1933 (Bic, Bio, Par); Smith, 1934 (L3, L1, E, Bio, Dst, Key); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key); Zimmerman, 1940 (Dst); Froeschner, 1947 (Dst); Parfin, 1952 (Dst); Zimmerman, 1957 (A*, MG*, W*, Bic, Bio, Dst); Nakahara, 1960 (Dst, Tax); Nakahara, 1965a (Dst); Nakahara, 1965b (Dst); Throne, 1971 (Dst); Agnew et al., 1981 (A*, Dst, Key); Klimaszewski et al., [1988] 1987 (Dst, Bio).

Description. Flagellum bicolored, brown proximally, yellow distally. Forewing (Figs. 103–106): Length 3.56–5.69 mm (x = 4.61, N = 25). Longitudinal veins pale yellow with brown setal spotting; membrane mottled with irregular light yellowish brown maculations; membrane in area of 2A and 3A with dark maculations; crossveins with or without light brown margining; proximal (very rarely present) and distal radial crossveins absent; darker specimens with membrane maculations darker brown and with most crossveins brown and margined with brown; longitudinal veins with darker setal spotting; membrane hyaline.

Male genitalia: Ectoprocts (Figs. 91, 92): Three unisetose processes present; ventrolateral and ventromedial processes incurved, ventrolateral process abruptly curved; apex of ventrolateral process usually appearing "twisted" (Carpenter, 1940) under low magnification due to its curiously angled setae and odd insertion (Fig. 92), specimens with normal conical, ventrolateral seta have also been examined. Hemigonarcus (Fig. 95): Gonopleuron sinuate, anterior end directed dorsally; gonoplax absent or limited to a small anterodorsal process; extrahemigonarcus wide; hemigonarcal rib absent. Parameres (Figs. 93, 94): Median lobes narrow and elongate,

lateral margins prominently toothed; lateral lobes oval in dorsal view, separated from median lobes by a deep incision, apices reflexed; anterior lobes absent; apophysis proxima moderately broad.

Remarks. *Sympherobius barberi* may be distinguished from *S. amiculus*, which also has bicolored antennae and frequently similar forewing maculations, by the
absence of the distal radial crossvein and the shape of the lateral lobes of the male parameres.

The similarity of forewing maculations in *S. barberi* and many southern *S. amiculus* (compare Figs. 102 and 104) and the occasional presence of specimens with abnormal combinations of male genitalic components suggests the presence of at least occasional hybridization between these species where they are broadly sympatric in the southeastern United States.

**Distributions and associations.** Geographic distribution (Fig. 113): *Sympherobius barberi* is widely distributed in the New World from approximately 43°N south to Peru, and on several remote Pacific island groups: Galápagos Islands, Revillagigedo Islands and Hawaiian Islands. Temporal distribution: January through December. Altitudinal distribution: 1,300'-6,500' (396 m-1,981 m). Plant associations: *Eupatorium adenophorum* (see Klimaszewski et al., [1988] 1987), *Gillarida*, *Juniperus virginiana* (see Throne, 1971), *Lantana camara*, *Platyopuntia sp.*, *Pseudotsuga menziesii* (log), *Quercus chrysolepis, Q. lobata*, oaks (Smith, 1925, 1934), potatoes (Zimmerman, 1940), asparagus fern (Zimmerman, 1957). Prey records: *Aphis medicaqinis* (Aphididae); *Dactylopius sp.*, *Dactylopius tomentosus* (Dactylopiidae); *Aonidiella aurantii* (Diaspididae); *Pseudococcus sp.*, *Pseudococcus citri* (see Cole, 1933), *Pseudococcus longispinus* (see Zimmerman, 1940), *Pseudococcus adonidum* (see Zimmerman, 1957) (Pseudococcidae); mealybugs (Klimaszewski et al., [1988] 1987).

**Primary type material examined.** *Sympherobius barberi* Banks. Holotype female. Verbatim label data: “Williams / 21.7 Ar,” “HSBarber / Collector,” “Type / No 6798 / U.S.N.M.,” “Hemerobius / barberi / type Bks.” Condition: good, tips of antennae missing, otherwise complete, wings spread.

**Other material examined.** 443 specimens. MEXICO: Baja California Norte, Baja California Sur, Chiapas, Coahuila, Oaxaca, Puebla, Revillagigedo Islands [Socorro and Clarion Is.], Sonora, Tamaulipas; PERU; UNITED STATES: Alabama, Arkansas, Arizona, California, Colorado, Florida, Iowa, Illinois, Kansas, Louisiana, Maryland, Mississippi, North Carolina, New Jersey, Oklahoma, Oregon, Pennsylvania, South Carolina, Texas, Utah, Virginia. Institutions: AMNH, ASUT, CAS, CSU, CU, INHS, ISU, LACM, MCZ, MSU, OKS, OSU, OSUC, PMY, SMEK, TAMU, UAT, UCB, UCD, UCR, UMSP, USNM. Also recorded from ECUADOR: Galápagos Islands; MEXICO: Morelos, Nuevo Leon and UNITED STATES: Hawaii, Minnesota, Missouri, New Mexico, Ohio, Wisconsin (Nakahara, 1965b—Morelos, Nuevo Leon; Zimmerman, 1957—Hawaii (introduced); Parfin, 1952—Minnesota; Froeschner, 1947—Missouri; Carpenter, 1940—New Mexico, Ohio; Throne, 1971—Wisconsin; Klimaszewski et al., [1988] 1987—Galápagos Islands).

*Sympherobius umbratus* (Banks)

Figs. 64, 107-112

**Hemerobius umbratus** Banks, 1903:242 (OD, A, MG*). Holotype male. UNITED STATES: Arizona: Coconino Co., Williams (USNM type #6799): Banks, 1904a (Dst).

*Sympherobius umbratus* (Banks): Banks, 1905b (RD, A, MG*, Dst, Key, Lst); Banks, 1907b (Lst); Banks, 1911 (Key); Carpenter, 1940 (RD, A, MG*, Dst, Key, Tax); Froeschner, 1947 (Dst).


**Description.** Antennae: Scape and pedicle brownish yellow; flagellum brownish yellow proximally, brownish distally. Forewings (Fig. 64): Length 4.19–5.20 mm (\( \bar{x} = 4.59, N = 7 \)). Veins monochromatic dark brown; veins narrowly margined with brown; membrane within cells brown bordered by a narrow band of hyaline or lighter brown; central region of membrane in cells of discal area lighter brown than surrounding membrane; proximal radial crossvein absent, distal radial crossvein present (occasionally absent or joining R1+2+3 to R4+5).

Male genitalia: Ectoprocts (Figs. 107, 108): Three processes present; dorsolateral and ventromedial processes unisetose; ventrolateral process bisetose; Carpenter (1940) indicates incorrectly that the ventromedial process is also “furcate”; ventromedial process incurved. Hemigonarcus (Fig. 111): Gonopleuron sinuate, anterior end directed dorsally; gonoplax absent; extrahemigonarcus an angular lobe anteriorly, narrowed posteriorly; anteroventral margin of extrahemigonarcus curved toward gonarcus midline; hemigonarcal rib absent. Parameres (Figs. 109, 110): Lateral lobes
prominent, curving dorsally and medially, anterior margin flared laterally; anterior lobes absent; apophysis proxima broad.

Remarks. Carpenter (1940:230, Figs. 30A, 30B) incorrectly figured the dorsolateral process of the ectoproct as "furcate." The ventrolateral process is actually "furcate" (i.e., bisetose). For a discussion of similar species see Remarks under S. amiculus.

Distributions and associations. Geographic distribution (Fig. 112): Eastern United States; one outlier from Arizona has also been examined. Temporal distribution: 16 March through 5 September. Altitudinal distribution: no records. Plant associations: no records.

Primary type material examined. Sympherobius umbratus Banks. Holotype male. Verbatim label data: “Williams / 10-6 Ar,” “HSBarber / Collector,” “Type / No 6799 / U.S.N.M.,” “Hemerobius / umbratus Bks type.” Condition: excellent, complete, wings spread, abdomen and dissected genitalia in glycerin in microvial pinned below specimen.


Sympherobius amiculus (Fitch) Figs. 1–3, 90, 96–102

Hemerobius amiculus Fitch, [1855] 1854:799 (OD, A). Holotype female. UNITED STATES, precise locality unknown, probably New York or Illinois (see Carpenter, 1940) (MCZ type #10,449): Hagen, 1861 (RD, A, Dst); Banks, 1892 (Lst); Krüger, 1922 (Tax).

Sympherobius amiculus (Fitch) Banks, 1904b (Dst); Banks, 1905b (RD, A, MG*, Dst, Key, Lst); Banks, 1907a (Dst); Banks, 1907b (Lst); Banks, 1911 (Key); Comstock, 1918 (W*); Smith, 1923 (C*, P*, PP*, L3*, L2*, L1, E*, Bio); Smith, 1925 (Dst); Smith, 1934 (Dst, Key); Brimley, 1938 (Dst); Carpenter, 1940 (RD, A, MG*, W*, Dst, Key, Tax); Froeschner, 1947 (Dst); Parfin, 1952 (Dst); Nakahara, 1960 (Dst, Tax); Mann, 1969 (Bio); Throne, 1971 (Dst); Agnew et al., 1981 (A*, W*, Dst, Key).

Palmobius amiculus (Fitch): Needham, 1905 (W*, Tax).

[Spadobius occidentalis (Fitch): Needham, 1905 (Tax). Misidentification.]

Description. Antennae: Flagellum bicolored, dark brown proximally, yellowish brown distally. Forewing (Figs. 101, 102): Length 3.43–5.64 mm ($\bar{x} = 4.44$, N = 25). Proximal radial crossvein absent; distal radial crossvein present (rarely absent). Sympherobius amiculus exhibits considerable interspecific variation in forewing coloration. At least part of this variation appears correlated with a latitudinal morphocline of darker northern forms and lighter southern forms. Specimens from southern latitudes tend to display the following characteristics (Fig. 102): (1) longitudinal veins yellowish with prominent brown setal spotting, (2) membrane largely yellowish hyaline with scattered light brown maculations and (3) inner gradate crossveins broadly margined with dark brown. Forewing frequently with a dark band extending across the inner gradate series from the radius to the posterior margin of the wing; most other crossveins unmargined. Northern specimens tend to display the following corresponding characters (Fig. 101): (1) longitudinal veins predominantly light brown, setal spotting present but not prominent, (2) membrane largely brownish with hyaline maculations and (3) inner gradate series margined or unmargined but forewing without a prominent dark band.
Male genitalia: Ectoprocts (Figs. 96, 97): Three incurved unisetose processes present. Hemigonarcus (Fig. 100): Gonopleuron sinuate, anterior end directed dorsally; gonoplax absent; extrahemigonarcus broadly lobate anteriorly, narrowed posteriorly; hemigonarcal rib present, unforked. Parameres (Figs. 98, 99): Lateral lobes dorsally revolute, anterior margin flared laterally; anterior lobes absent; apophysis proxima moderately broad.

Remarks. The forewing maculations and bicolored antennae of *S. amiculus* are similar to those of *S. barberi*, but in *S. amiculus* the distal radial crossvein is present, in *S. barberi* this crossvein is absent. *Sympherobius umbraetus*, the only other species in which the distal radial crossvein is present, may be distinguished from *S. amiculus* by its dark forewing membrane and bisetose ventrolateral ectoproct process. See also Remarks under *S. barberi*.

Distributions and associations. Geographic distribution (Fig. 90): *Sympherobius amiculus* is the most frequently collected species throughout southeastern Canada and the eastern United States. Its primary distribution extends west to about the 100th meridian. I have also seen single male specimens from Arizona (Maricopa Co.) and Colorado (Larimer Co.). Temporal distribution: 15 January through 11 November. Altitudinal distribution: no records. Plant associations: *Pinus banksiana*, *P. taeda*, *P. virginiana* and "Jap. Holly." Also recorded from apple and oak (Smith, 1923; 1925), *Pinus virginiana* (see Froeschner, 1947), conifers, oaks and vineyards (Agnew et al., 1981). Prey records: Mann (1969:12, 142) reported 'S. amiculus' [=barberi ?] as an important predator of cactus infesting *Dactylopius* sp. (Dactylopiidae) in Texas.


Other material examined. 365 specimens. CANADA: Quebec; UNITED STATES: Alabama, Arizona, Arkansas, Colorado, Connecticut, District of Columbia, Florida, Georgia, Illinois, Iowa, Kansas, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Jersey, New York, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin. Institutions: AMNH, ASUT, CAS, CMP, CSU, CU, FEM, INHS, ISU, LACM, LSU, MCZ, MSU, NCSR, OSU, OUSC, SMEK, TAMU, UAF, UAT, UCB, UCD, UGA, UMAA, UMC, UMSP, UNH, USNM, UWM, VPI, WSU. Also recorded from CANADA: Nova Scotia, Ontario and UNITED STATES: New Hampshire, Oklahoma (Carpenter, 1940).

PHYLOGENETIC RELATIONSHIPS

The relative phylogenetic relationships among the 17 *Sympherobius* species of America north of Mexico are inferred below based on a cladistic analysis. Cladistic analyses utilize hypotheses of synapomorphic (shared derived) character states in conjunction with a parsimony criterion to infer the relative recency of common ancestry among a set of taxa under scrutiny (Hennig, 1966; Wiley, 1981).

In this analysis, the method of outgroup comparison (Watrous and Wheeler, 1981) has been used, in most cases, to determine polarities of character states. Identification of appropriate outgroups proved difficult due to the lack of a well-substantiated prior
Figs. 112, 113. Geographic distributions of Nearctic *Sympherobius*. Only verified records plotted.
hypothesis of hemerobiid intergeneric relationships. Selections for outgroup taxa are justified below.

The hemerobiid family group taxa proposed by Comstock (1918), Krüger (1922), Navás (1933) and Nakahara (1960), having been based on either plastic venational characters or a single character of the male genitalia, were considered insufficiently justified by Tjeder (1961). Following Tjeder, most subsequent authors have recognized no suprageneric taxa within the family. Consequently, intergeneric relationships within the Hemerobiidae are almost entirely unresolved; and the phylogenetic affinities of Sympherobius remain unclear.

Earlier authors suggested that the phylogenetic affinities of Sympherobius may lie near the genus Nomerobius (see Penny and Monserrat, [1985] 1983:894), or Psectra or Notiobiella (see Comstock, 1918:179). These hypotheses were based primarily on the shared presence in these genera of only two oblique branches of the forewing radius, a character also found in several other hemerobiid genera (e.g., Anapsectra, Carobius, Kimminsiella, Neosympherobius and Zachobiella) and probably plesiomorphic within the family.

An examination of representative species (or illustrations) of these and most other hemerobiid genera has revealed the presence of a pseudmediuncus only in the genera Neosympherobius, Nomerobius and Sympherobius. Based on the presence of a pseudomedianuncus and also the shared, and apparently derived, presence of a digitiform process located near the ventromedial margin of the male ectoproct, these three genera appear to form a monophyletic group (Fig. 114), informally named here the Nomerobius genus group. A pair of synapomorphies (losses of the distal radial cross-vein and mediuncus) support the monophyly of ‘Neosympherobius + Sympherobius.’ A further pair of purported synapomorphies (pseudomedianuncus bipartite and basipseudomedianuncus dished and with flared lateral margins) support the monophyly of Sympherobius itself.

As the putative sister groups, respectively, of Sympherobius and ‘Neosympherobius + Sympherobius,’ Neosympherobius and Nomerobius have been used as outgroup taxa in the present analysis. In the succeeding paragraphs I present the 23 binary characters used in the cladistic analysis. Where not based on outgroup comparison to Nomerobius and Neosympherobius (see Table 1), the rationale for assigning character state polarities (0 = plesiomorphic, 1 = apomorphic) is given.

Characters

Venation

1. Proximal radial crossvein (joining R1+2+3 to R4+5): (0) absent, (1) present. See discussion under character 2.
2. Distal radial crossvein (joining R2+3 to R4+5): (0) present, (1) absent. The distal radial crossvein is present in Nomerobius and two species of Sympherobius, absent in Neosympherobius and other Sympherobius. I assume presence of the distal radial crossvein to be plesiomorphic. This state is more widely distributed among hemerobiid genera possessing two oblique radial branches of the forewing (e.g., Nomerobius, Psectra, Anapsectra, Notiobiella, Zachobiella and Kimminsiella) than is the alternate state of absence (Neosympherobius, Carobius).
Carpenter (1940) demonstrated the taxonomic utility of the “radial crossvein” in diagnosing Nearctic Sympherobius. Presented as a single homologous cross-vein of variable location, Carpenter identified three positional states for the “radial crossvein”: (1) joining R1+2+3 to R4+5, (2) absent, or (3) joining R2+3 to R4+5. In a fourth condition recently found in some species of the Oriental-Australian genus Zachobiella and in several undescribed species related to the Australian genus Carobius (T. R. New, pers. comm.) crossveins are present joining both the R1+2+3 to R4+5 [state (1) above] and the R2+3 to R4+5 [state (3) above]. This additional condition strongly suggests that Carpenter’s “radial crossvein” may consist of two separate non-homologous cross-veins. Though this fourth condition is not presently known to occur in species of the Nomerobius genus group, its possibility cannot be ruled out as a transitional state. For this reason, contrary to Carpenter’s (1940) presentation, cross-veins in the positional states (1) and (3) above are interpreted in this work as two independent characters: the proximal (Fig. 4, prc) and distal radial cross-veins (drc) respectively.

Females

3. Tergite 8, lateral ends: (0) widely separated ventrally, (1) adjacent or fused ventrally. The state of this character in Neosympherobius is unknown.

Males

4. Tergite 9, anterodorsal emargination: (0) absent or shallow, (1) deep.
5. Ectoproct, ventromedial process: (0) absent, (1) present. See discussion under character 7.
6. Ectoproct, ventrolateral process: (0) absent, (1) present. See discussion under character 7.
7. Ectoproct, dorsolateral process: (0) absent, (1) present.

Within Sympherobius when a single male ectoproct process is present it always arises from near the ventromedial margin of the ectoproct. When a pair of processes are present they are laterally adjacent and located ventrally on the ectoproct; the inner process occupying a position near the ventromedial margin of the ectoproct. When a third process is present it arises near the middle of the ectoproct dorsal to the ventrals, which retain the relative positions described under the two process condition. The constancy of the relative positions of these processes in all species strongly supports the hypothesis that processes with the same relative positions are homologous.

Independent confirmation of the homology of individual ectoproct processes found in Sympherobius with similar processes found on the ectoprocts of Neosympherobius and Nomerobius is lacking. Applying the relative positional hypothesis used to determine process homology within Sympherobius, I have assumed that the single process of Nomerobius and Neosympherobius ectoprocts is the homologue of the ventromedial process of Sympherobius. In Nomerobius this process is in fact located in a ventromedial position, but in Neosympherobius the lone process arises somewhat more laterally. The ectoproct of Nomerobius also possesses an additional short process located dorsal and laterad to the ventromedial process. This process consists of a thick-
ened, elongate seta borne on a short, narrow chalaza and is not considered to be a homologue of the digitiform processes of the *Nomerobius* genus group which terminate in a spinate or peg-like modified seta.

8. Ectoproct, dorsomedial prominence: (0) absent, (1) present. The dorsomedial prominence is absent in *Nomerobius*, *Neosympherobius* and most *Sympherobius*. The dorsomedial prominence differs from other *Sympherobius* ectoproct processes by lacking a terminal modified seta (though it may bear normal seta laterally, compare Figs. 56 and 97). The lack of a terminal modified seta and the dorsomedial position of the dorsomedial prominence support the hypothesis that it is not a homologue of the non-digitiform chalaza found on the ectoprocts of male *Nomerobius*.

9. Ectoproct, ventromedial process, terminal calyx rim: (0) not sheath-like, (1) sheath-like.

10. Ectoproct, ventromedial process, shape of terminal seta: (0) peg-like, (1) spinose.

11. Ectoproct, ventromedial process, shape of terminal seta: (0) not grooved, (1) grooved.

12. Ectoproct, ventrolateral process, number of modified setae: (0) one, (1) two. *Nomerobius* and *Neosympherobius* lack a ventrolateral process. A single modified seta is assumed to be the plesiomorphic state. This interpretation is supported by observing that the ventromedial process and, when present, the dorsolateral process always terminates in a single modified seta. This is also the most common state for the ventrolateral process.

13. Parameres, anterior lobes: (0) absent, (1) present.

14. Parameres, apices of anterior lobes: (0) narrow, (1) broad. *Nomerobius* and *Neosympherobius* lack anterior paramere lobes. The polarity of this character was determined by congruence with other polarized characters.

15. Parameres, lateral lobes: (0) absent, (1) present.

16. Parameres, lateral lobe curvature: (0) distal margins curved dorsally, (1) distal margins dorsally revolute. *Nomerobius* and *Neosympherobius* lack lateral paramere lobes. The polarity of this character was determined by congruence with other polarized characters.

17. Parameres, lateral lobes, longitudinal rib or ridge: (0) absent, (1) present. *Nomerobius* and *Neosympherobius* lack lateral paramere lobes. The polarity of this character was determined by congruence with other polarized characters.

18. Gonarcus, gonopleuron shape: (0) approximately linear, (1) turned up anteriorly.

19. Gonarcus, gonopleuron shape: (0) approximately linear, (1) turned down anteriorly.

20. Pseudomediuncus: (0) absent, (1) present. *Nomerobius*, *Neosympherobius* and *Sympherobius* are jointly characterized by the presence of a pseudomediuncus. I am unaware of any other hemerobiid genera possessing a comparable sclerotized structure lying along the dorsal midline of the paragonarcal membrane.

21. Pseudomediuncus, form: (0) entire, (1) bipartite. In *Nomerobius* and *Neosympherobius* the pseudomediuncus is a continuous strip of weakly sclerotized cuticle. In *Sympherobius* the pseudomediuncus is clearly divided into a pair
Table 1. Character state matrix for Nearctic *Sympherobius* and outgroups used to generate cladogram shown in Figure 114. Character numbers refer to characters discussed in text. Matrix symbols: 0, plesiomorphic state; 1, apomorphic state; *, state unknown; —, character inapplicable.

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of sclerites which articulate at a membranous or weakly sclerotized region between them.

22. Basipseudomediuncus (or base of undivided pseudomediuncus), form: (0) flat and narrow, strap-like, (1) lateral margins splayed and recurved forming a shallow basin. In *Nomerobius* and *Neosympherobius* the base of the pseudomediuncus is a narrow strap-like sclerite. In *Sympherobius* the lateral margins of the basipseudomediuncus are produced and arched to form a shallow concave basin into which the distopseudomediuncus may seat.

23. Mediuncus: (0) present, (1) absent. A mediuncus is present in *Nomerobius*, but absent in *Neosympherobius* and *Sympherobius*. Based on the presence of a mediuncus in most other Neuroptera, I consider the former state plesiomorphic.

**Analysis and Results**

The character state distributions of the outgroup and ingroup taxa are summarized in Table 1. Unknown characters and characters inapplicable to some species (i.e., characters involving subsequent modifications to structures themselves not present in that species) were coded as missing data. A single most parsimonious tree topology (Length = 28 steps, CI = .75) was derived from these data by employing the Mulpars and Global Branch Swapping options of the Phylogenetic Analysis Using Parsimony (PAUP) computer program (Swofford, 1985). This tree and its supporting characters are illustrated in Figure 114.

**Discussion**

Figure 114 depicts the hypothesized phylogenetic relationships among the 17 Nearctic species of *Sympherobius*. In the discussion below four major lineages within *Sympherobius* displayed on this cladogram are identified, informally named and briefly discussed. Numbers enclosed in square brackets in the following discussion refer to the preceding character listing.

The basal dichotomy within *Sympherobius* separates the *S. perparvus* and *S. pictus* species groups. Gurney (1948) proposed the *S. perparvus* species group for the species *S. beameri*, *S. killingtoni* and *S. perparvus* based on the single digitiform process of the male ectoprocts shared by these species. Gurney further suggested that *S. arizonicus* and *S. pictus*, the males of which were unknown at that time, might also belong to this group. The male of *S. arizonicus* was subsequently described by MacLeod (1963) and confirmed as a member of the *perparvus* group. The male of *Sympherobius pictus*, described here for the first time, possesses a single ectoproct process but, though closely related to, is clearly not a member of the *S. perparvus* species group clade. Since the male ectoprocts of *S. pictus* and the four species of the *S. perparvus* group each bear a single digitiform process, the single character proposed by Gurney is no longer tenable as a synapomorphy of the *S. perparvus* group. My analysis suggests the following three characters as synapomorphies of this group: (1) the rim of the calyx into which the terminal seta of the ventromedial ectoproct process inserts is elongate and sheath-like [9], (2) the terminal seta of the ventromedial process is spinose, not peg-like [10] and (3) the presence of anterior paramere lobes [13]. The last character is independently derived in *S. occidentalis*. With mean forewing lengths
Fig. 114. Cladogram of the Nearctic species of Sympherobius. Numbers refer to characters discussed in the text. Autapomorphies of individual species are omitted except where they are part of a homoplasious complex (e.g., characters 12, 13). Symbols: +, convergent character; −, character reversal.

of 3.77–4.07 mm, most of the smallest Nearctic Sympherobius species are members of the S. perparvus group.

The S. perparvus group appears to occupy an isolated position within Sympherobius. None of the approximately 20 Palearctic and South and southern Central Amer-
ican species examined to date possess the synapomorphies of the *S. perparvus* group. However, some Mexican forms not treated in this revision may belong to this group.

All four species of the *S. perparvus* group occur in arid regions of the southwestern United States. *Sympherobius perparvus*, *S. killingtoni* and *S. arizonicus* have also been recorded from adjacent northern Mexico. Each of the four species of this group further exhibit northerly range extensions into one or more of the following regions: (1) the Central Valley of California, (2) the Great Basin of the western United States and/or (3) the Great Plains of the central United States.

*Sympherobius pictus* and the remaining Nearctic species are placed in a new species group, the *S. pictus* group. This group is characterized by the lateral ends of female tergite 8 being adjacent or fused on the venter of the abdomen [3]. The *S. angustus* (5 species) and *S. barberi* (3 species) complexes are united by the shared presence of lateral lobes of the parameres [15]. The five species of the *S. angustus* complex, *S. angustus*, *S. quadricuspis*, *S. bifasciatus*, *S. californicus* and *S. constrictus*, are generally larger species (mean forewing lengths: 4.32–5.63 mm) characterized by the presence of a proximal radial crossvein [1]. The three species of the *S. barberi* complex, *S. barberi*, *S. umbratus* and *S. amiculus*, are intermediate in size (mean forewing lengths: 4.44–4.61 mm) and are characterized by the distally upturned gonopleuron [18].

The *S. pictus* group is diverse with respect to male ectoproct spination, parameral lobation and radial crossvenation. It seems likely that the phylogenetic affinities of most extralimital species will later be found to be with this group.

The male ectoprocts of most extralimital species examined from the Palearctic region and the Americas south of the United States possess two or three digitiform processes (i.e., the apomorphic states of characters [5] and [6] or [5], [6] and [7]), and lack lateral lobes on the parameres (i.e., the plesiomorphic state of character [15]); the phylogenetic affinities of such species will most likely be with Nearctic species found in the pectinate basal stem of the *S. pictus* group. Some South American species possess three digitiform ectoproct processes (i.e., the apomorphic states of characters [5], [6] and [7]), and lateral lobes on the parameres (i.e., the apomorphic state of character [15]); the affinities of these species may be with the *S. angustus* and/or *S. barberi* complex(es). Since species apparently belonging to the *S. pictus* group are well represented outside the Nearctic region, any analysis of biogeographic patterns within this group at this time would be premature.

**ACKNOWLEDGMENTS**

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Finally, my wife Diane deserves considerable praise for her cheerful forbearance throughout the preparation of this paper.

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Fitch, A. [1855] 1854. Report [upon the noxious and other insects of the State of New York]. Trans. N.Y. State Agric. Soc. 14:705–880. [Dated from the title page of volume 14 containing the transactions for the year 1854 but issued in 1855. The text of this paper was reissued in 1856 as pages 1–176 of Fitch’s work “First and second report on the noxious, beneficial and other insects, of the state of New-York.”]


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APPENDIX 1

Synonymical List of World Sympherobius species

The following list contains all species-group names (valid, junior synonyms, nomina nuda and nomina dubia) which are currently associated with the generic name Sympherobius. 54 valid species-group names (in bold italics in the alphabetical sequence below) and 45 invalid or unavailable species-group names (in non-bold italics) are listed. Complete bibliographic citations for each name can be found in the Literature Cited. Each species-group name is given in its original combination. No attempt has been made to catalogue the subsequent combinations of each species-group name. An indication of the known geographic distribution of each valid species is also given. For additional information on non-Nearctic species see the works cited at the beginning of this paper. Sympherobius exiguus (Navás) and S. marginata (Kimmins) are new combinations. “Sympherobius thaumasta Navás (1915),” cited by Penny ([1978] 1977: 33), is a lapsus calami for Symphrasis thaumasta Navás, 1915e:197 (Mantispidae).

Synonymical List

amiculus (Fitch, [1855] 1854): Southeastern Canada, eastern, central and southwestern United States.
   Sympherobius amiculus Navás, 1912:198.
angustus (Banks, 1904): Southwestern Canada, western United States south to southern Mexico.
   Hemerobius angustus Banks, 1904a:102.
   Sympherobius tristis Navás, 1914a:15.
   Sympherobius stangei Nakahara, 1960:16.
   Sympherobius brunneus Nakahara, 1965a:207.
arizonicus Banks, 1911: Arizona and southern California south to southern Mexico.
   Sympherobius arizonicus Banks, 1911:346.
barleri (Banks, 1903): Southern and eastern United States south to Peru, Galápagos Islands, Hawaiian Islands (introduced), Revillagigedo Islands.
   Hemerobius barleri Banks, 1903:241.
beameri Gurney, 1948: Southwestern United States.
   Sympherobius beameri Gurney, 1948:220.
bellus Navás, 1911. See pygmaeus (Rambur, 1842).
bifasciatus Banks, 1911: Southwestern United States, northern Mexico.
   Sympherobius bifasciatus Banks, 1911:347.
bisignatus (Krüger, 1922): Unknown.
   Spadobius bisignatus Krüger, 1922:171 Nomen Nudum.
blanchardi (Navás, 1930): Chile.
   Coloma blanchardi Navás, 1930b:19.
brunneus Nakahara, 1965. See angustus (Banks, 1904).
buenoi Navás, 1912. See amicus (Fitch, [1855] 1854).
californicus (Banks, 1905). See californicus Banks, 1911.
californicus Banks, 1911: California and northwestern Mexico.

Hemerobius californicus Banks, 1905a:90 Nomen Nudum.
Sympherobius californicus Banks, 1911:346.
carpathicus Kis, 1965. See pellucidus (Walker, 1853).
catalaunicus (Navás, 1930). See elegans (Stephens, 1836).
catalaunicus (Navás, 1930). See elegans (Stephens, 1836).
coccochagus (Göszy, 1852): Sardinia.
Hemerobius coccophagus Göszy, 1852:346 Nomen Dubium (=Sympherobius pygmaeus?).
conspersus Navás, 1908. See pygmaeus (Rambur, 1842).
constrictus Oswald n. sp.: California.
Sympherobius constrictus Oswald, 1908.
dilutus Nakahara, 1960: Japan.
Sympherobius dilutus Nakahara, 1960:19.
distinctus Carpenter, 1940: Arizona and Colorado.
Sympherobius distinctus Carpenter, 1940:238.
domesticus Nakahara, 1954: Japan.
Sympherobius domesticus Nakahara, 1954:43.
elegans (Stephens, 1836): Europe, USSR.
Hemerobius marshami Stephens, 1836:114.
Hemerobius paucinervis Zetterstedt, 1840:1050.
Hemerobius striatellus Klapálek, 1905:725.
Sympherobius venustus Navás, 1908a:27.
Hemerobius vicentei Navás, 1914b:34.
Nefasitus catalaunicus Navás, 1930a:161.
Nefasitus catalaunicos [sic] Navás, 1930a:162 (name unavailable, an incorrect original spelling of N. catalaunicus Navás).
exiguus (Navás, 1908): Canary Islands.
Micromus exiguus Navás, 1908b:407 New Combination.
fallax Navás, 1908: Southern Europe, Middle East and northern Africa.
Sympherobius fallax Navás, 1908b:408.
Sympherobius schmitzi Navás, 1908b:409.
Sympherobius tenellus Navás, 1908a:25.
Nefasitus amicus Navás in Silvestri, 1915:332.
Sympherobius sanctus Tjeder, 1939:43.
fortini Lacroix, 1924. See pygmaeus (Rambur, 1842).
fuscescens (Wallengren, 1863): Europe, Asia and Japan.
Hemerobius inconspicuus McLachlan, 1868:177.
fuscinervis Kozhantshikov, 1956: Turkestan.
Sympherobius fuscinervis Kozhantshikov, 1956:700, 705.
gai Navás, 1910: Chile.
Sympherobius gayi Navás, 1910b:237.
gracilis Carpenter, 1940. See umbratus (Banks, 1903).
gratiosus Navás, 1908. See pygmaeus (Rambur, 1842).
humilis Navás, 1914: Paraguay.
Sympherobius humilis Navás, 1914c:226.
inconspicuus (McLachlan, 1868). See fuscescens (Wallengren, 1863).

Sympherobius insulanus Banks, 1938: Cuba.
Sympherobius insulanus Banks, 1938:292.


Sympherobius italicus (Navás, 1932). See pygmaeus (Rambur, 1842).

Sympherobius killingtoni Carpenter, 1940: Western and south central United States and northern Mexico.
Sympherobius killingtoni Carpenter, 1940:238.

Sympherobius texanus Nakahara, 1965a:209.
Sympherobius klapaleki Zelený, 1963: Europe.


Sympherobius laetus Steinmann, 1967. See pygmaeus (Rambur, 1842).
Sympherobius lambereti Navás, 1910. See pygmaeus (Rambur, 1842).

Sympherobius limbus Carpenter, 1940: Southwestern United States.
Sympherobius limbus Carpenter, 1940:236.


Sympherobius luojiaensis Yang, 1980: China.

Sympherobius luojiaensis Yang, 1980:90, 92.

Sympherobius maculipennis Kimmins, 1929: Southern South America.
Sympherobius maculipennis Kimmins, 1929:189.

Sympherobius manchuricus Nakahara, 1960: Manchuria.

Sympherobius marginatus (Kimmins, 1928): Guatemala, Mexico.

Sympherobius marmoratipennis (Blanchard in Gay, 1851): Southern South America.
Megalomus marmoratipennis Blanchard in Gay, 1851:127.

Sympherobius marshami (Stephens, 1836). See elegans (Stephens, 1836).

Sympherobius matsucocciphagus Yang, 1980: China.
Sympherobius matsucocciphagus Yang, 1980:88, 92.

Sympherobius melanogaster Navás, 1915: Spain.
Sympherobius melanogaster Navás, 1915b:250 Nomen Dubium.
Sympherobius menendezi Navás, 1913. See pygmaeus (Rambur, 1842).

Sympherobius miranda (Navás, 1920): Argentina.


Sympherobius notatus Kimmins, 1932: West Indies (St. Vincent Island).
Sympherobius notatus Kimmins, 1932:160.

Sympherobius occidentalis (Fitch, [1855] 1854): Eastern United States.


Sympherobius parvus (Rambur, 1842): Canary Islands.

Mucropalpus parvus Rambur, 1842:422 Nomen Dubium (=Sympherobius pygmaeus ?).
Sympherobius parvus (Krüger, 1922): Unknown.

Spadobius parvus Krüger, 1922:171 Nomen Nudum.

Sympherobius paucinervis (Zetterstedt, 1840). See elegans (Stephens, 1836).
pellucidus (Walker, 1853): Europe.
   Hemerobius pellucidus Walker, 1853:284.
   Sympherobius carpathicus Kis, 1965:103.
perparvus (McLachlan, 1869): Central and western United States and northern Mexico.
   Hemerobius perparvus McLachlan, 1869:22.
   Sympherobius sparsus Banks, 1911:346.
pictus (Banks, 1904): Southwestern United States and northern Mexico.
   Hemerobius pictus Banks, 1904c:62.
<add other entries as necessary>
texanus Nakahara, 1965. See killingtoni Carpenter, 1940.
tristis Navás, 1914. See angustus (Banks, 1904).

umbratus (Banks, 1903): Eastern United States and Arizona.

Hemerobius umbratus Banks, 1903:242.

Sympherobius gracilis Carpenter, 1940:231.

venosus Navás, 1908. See pygmaeus (Rambur, 1842).

venustus Navás, 1908. See elegans (Stephens, 1836).
vicentei (Navás, 1914). See elegans (Stephens, 1836).

weisong Yang, 1980: China.

Sympherobius weisong Yang, 1980:89, 92.
wuyianus Yang, 1981: China.


yunpinus Yang, 1986: China.


zelenyi Alayo, 1968: Cuba.


Note Added in Proof: In a recent biography of the 19th century American entomologist Asa Fitch, J. K. Barnes (1988, Asa Fitch and the emergence of American Entomology, New York State Museum Bulletin No. 461: viii + 1–120) has provided a comprehensive list of the 451 species described by Fitch during the mid-1800's. Remarkably, from Fitch's detailed personal collection registers, Barnes was able to compile for each species a list of specimens which were present in Fitch's collection no later than the year in which the original description of each was published. Since Fitch did not designate holotypes (Barnes, 1988:86), these lists represent for many species, including two North American species of Sympherobius, the closest available approximation of their syntypical series.

Barnes' (1988:105) data on the syntypes of Sympherobius amiculus (Fitch) and S. occidentalis (Fitch) are given verbatim below with added notes. These data supplement and/or modify the interpretations given in the main text of the primary types of these species. In the quotations below, Barnes' "Extant Specimens" listings include only those specimens known to reside in the collections of the New York State Museum, National Museum of Natural History, Museum of Comparative Zoology (Harvard University) and the Museum National d'Histoire Naturelle, Paris. Other specimens may be present in collections not investigated by Barnes.

"Sympherobius amiculus (Fitch).

Original Specimens: *2131, Salem, NY, 20.viii.1852, on basswood bush, Esq. Martin's meadow; **3964, Salem, NY, 30.v.1854, about the house; 9085, IL, 7.x.1854, beat from peach trees, Burnett's.

Extant Specimens: **3964/Type 10449/Hemerobius amiculus (MCZ); 9085/Fitch Collection/Hem. amic. var. a (UNSM)."

Notes: Since Fitch did not designate types, and since the type series of S. amiculus is now known to have been composed of more than one specimen, Fitch's specimen number "3964" (MCZ type #10,449) cannot now be considered a holotype, as assumed by Carpenter (1940:229) and as stated in the main text above. This specimen must now be interpreted as a lectotype designated by Carpenter's holotype assumption (ICZN, 1985: Article 74b). Barnes' data also allows the type locality of S. amiculus to be stated more precisely: UNITED STATES: New York: Washington Co.: Salem.

"Sympherobius occidentalis (Fitch).

Original Specimens: 8392, IL, 2.x.1854, on ash leaves, beside Henderson River."

Note: The repository of the holotype of S. occidentalis remains unknown. If this specimen is still extant, the additional data provided by Barnes should facilitate its recognition.
Bibliography of the Neuropterida

Bibliography of the Neuropterida Reference number (r#):
5028

Reference Citation:

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Notes:

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