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Cladistics, classification and identification of the brachycercine mayflies (Insecta: Ephemeroptera: Caenidae)

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Cladistics, classification and identification of the brachycercine mayflies (Insecta: Ephemeroptera: Caenidae)

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Abstract

The mayfly subfamily Brachycercinae (Pannota: Caenidae) is redefined and shown to be an apotypic, monophyletic group based on numerous synapomorphies, including, for example in the larvae, the presence of ocellar tubercles, an anterior row of long setae on the larval head capsule, a patch of long setae posterior to the base of the glossae, a broad prosternum, and the absence of toothlike claw denticles. Over 100 morphological characters of larvae, adults, and eggs discovered to be useful for phylogenetic analysis and diagnoses are detailed and illustrated. Thirty-eight species are recognized among the genera Brachycercus Curtis, Caenoculis Soldán, Cercobrachys Soldán, Insulibrachys Soldán, Sparbarus, n. gen., Oriobrachys, n. gen., Latineosus, n. gen., Susperatus, n. gen., and Alloretochus, n. gen., by adopting a strictly phylogenetic classification, including a first tribal classification within the subfamily. Brachycercus ojibwe, n. sp., Cercobrachys fox, n. sp., C. lilliei, n. sp., C. pomeiok, n. sp., C. winnebago, n. sp., Latineosus cayo, n. sp., L. cibola, n. sp., Oriobrachys mahakam, n. sp., Sparbarus choctaw, n. sp., S. coushatta, n. sp., S. miccosukee, n. sp., and Susperatus tonkawa, n. sp. are newly described. The Nearctic Brachycercus articus Soldán, n. syn., and B. edmundsi Soldán, n. syn., are shown to be equivalent to B. harrisella Curtis, proving the latter to be a widespread Holarctic species. Sparbarus capnicus (Zhou, Sun and McCafferty), n. comb., S. corniger (Kluge), n. comb., S. europaeus (Kluge), n. comb., S. gilliesi (Soldán and Landa), n. comb., S. japonicus (Gose), n. comb., S. kabyliensis (Soldán), n. comb., S. lacustris (Needham), n. comb., S. maculatus (Berner), n. comb., S. nasutus (Soldán), n. comb., S. tubulatus (Tshernova), n. comb., Susperatus prudens (McDunnough), n. comb., and S. tuberculatus (Soldán), n. comb., are transferred from Brachycercus. Alloretochus peruanicus (Soldán), n. comb., and Latineosus colombianus (Soldán), n. comb., are transferred from Cercobrachys. Caenis dangi (Soldán), n. comb., is transferred from Caenoculis and Brachycercinae to Caeninae, and provisionally placed in Caenis Stephens. Sparbarus flavus (Traver), n. comb., is transferred from Brachycercus and considered to be a nomen dubium. Nomenclatural history, new or revised descriptions as appropriate, diagnoses, illustrations, and keys are provided for known stage of species. Origins and evolutionary relationships of the Brachycercinae are hypothesized based on cladistic results. Brachycercinae is considered to have originated from a Caenis-like ancestor. The genera Caenoculis and Insulibrachys represent more ancestral lineages, whereas the genera Sparbarus, n. gen., Brachycercus, Oriobrachys, n. gen., Latineosus, n. gen., Susperatus, n. gen., Alloretochus, n. gen., and Cercobrachys appear more derived. Cercobrachys pomeiok and other closely related species are most apotypic in terms of numbers of accumulated apomorphies.

Key words: Brachycercinae, Caenidae, Brachycercus, Cercobrachys, Insulibrachys, Caenoculis, Sparbarus, Oriobrachys, Latineosus, Susperatus, Alloretochus, mayflies, Ephemeroptera, systematics, phylogeny

Introduction

The subfamily Brachycercinae of the pannote mayfly family Caenidae and superfamily Caenoidea represents one of the most apotypic groupings of the Pannota and of mayflies in general (McCafferty and Wang, 2000). Although this grouping has generally been known to include those caenids with larvae having pronounced ocellar tubercles on the head, the exact concept has been modified over several decades and has remained somewhat tenuous, particularly in terms of generic boundaries for species involved and the exact genera that should or should not be included within the taxon. Although species of the group have been known since 1834, comparative studies at the species and genus level within the subfamily have been inadequate and have remained somewhat contentious. Edmunds et al. (1976) acknowledged that identification of species was difficult and the taxonomic status of morphologically similar species was confusing. Because of the specialized psammophilous habit and seldom collected sand-bottom riverine habitats of the larvae and the apparently mostly nocturnal adults, adequate collections of this group have been difficult to come by and to compare across their Holarctic, Oriental, and to some degree Neotropical range of distribution. Existing keys to species (Traver, 1935; Berner, 1950; Tshernova, 1952, 1964; Soldán, 1986; Kluge, 1991; Burian et al., 1997) have been either incomplete, inaccurate, or based on misinterpretations of characters. Because considerable diversity and variability has not been adequately documented, especially in North America, mayfly taxonomists, stream ecologists, and conservationists have historically experienced extreme difficulties or impossibility when attempting to identify Brachycercinae.

This research has been oriented towards rectifying all of the above problems, in particular via the study of new characterization, discovery of additional diversity, and cladistic analysis, major goals of the research have been to develop a phylogenetically sound generic and species classificatory revision of the subfamily augmented by fully illustrated descriptions, diagnoses, and keys, and to present comprehensive hypotheses of evolution.

The first species known of Brachycercinae was *Brachycercus harrisella* Curtis. Curtis (1834) originally placed his new genus *Brachycercus* Curtis in the family Ephemeridae, which at the time was equivalent to the present-day order Ephemeroptera. *Brachycercus harrisella* had been based on adults collected from England and informally described, but not named, by Moses Harris in 1776 (see Campion, 1923). This initial species has also been known as the most widespread species of Brachycercinae, subsequently having been reported from many regions of Eurasia (e.g., Bogoescu, 1958; Brittain, 1972; Itämies et al., 1979; Belfiore et al., 1996; Quan et al., 2002).

Brachycercus thus was also the first genus now recognized in the family Caenidae. One year later when Stephens (1835) established the genus *Caenis* Stephens (also originally based on adults), he treated *Brachycercus* as a so-called section under *Caenis* ("B. With filaments scarcely longer than the body, or shorter, stout at the base"). Burmeister (1839) incorporated the concepts of both *Brachycercus* and *Caenis* in his *Oxycypha* Burmeister, which is now a synonym of *Caenis* (Jacob, 1974). Westwood (1840) recognized both *Brachycercus* and *Caenis*. Pictet (1843–45) treated *Brachycercus* as a synonym of *Caenis*, as Stephens had, and this was continued by several early European workers, including Walker (1853), Hagen (1863), Eaton (1883–88), Klapálek (1909), and Lestage (1917). It was Klapálek (1909) who first established the family name Caenidae.

The first larval description attributable to the subfamily Brachycercinae was apparently that given by Eaton (1868) under the name *Caenis halterata* Fabricius. This reference to *C. halterata*, however, was actually a misidentification of *B. harrisella* (see Eaton 1884).

Bengtsson (1917) established the genus *Eurycaenis* Bengtsson evidently not realizing his concept was preoccupied by the name *Brachycercus* (see Campion 1923). Subsequent to this, either *Caenis* continued to be used for *Brachycercus* or the name *Eurycaenis* was commonly used, for example, by Lestage (1919), Ulmer (1920), Schoenemund (1930), and Traver (1932). Campion (1923), whose work was not known by some workers, demonstrated the validity of *Brachycercus*, but mistakenly considered the name *Caenis* invalid and proposed the unnecessary replacement *Ordella* Campion, evidently first rejected by Ulmer (1924). In the meantime, the first known species of Brachycercinae in North America, which had been collected in Michigan in 1907, was originally described as *Caenis lacustris* Needham (1918).

Lestage (1924) established the family Brachycercidae to include both *Brachycercus* and *Ordella*. Such an arrangement was adopted, for example, by Tshernova (1928) and Lestage (1931), and in the latter instance, certain eventual Tricorythidae and Leptohyphidae genera were also included in Brachycercidae. The family Brachycercidae (instead of Caenidae) was also later inappropriately adopted as the official name for the present concept of Caenidae by Demoulin (1955). Caenidae preceded Brachycercidae, and according to the International Code of Zoological Nomenclature, the type genus of the family (*Caenis*) does not have to be the earliest established genus (*Brachycercus*). Since the 1920s and quite generally in the last half century, the name Caenidae (= Caeninae of Baetidae of some authors) has been accepted as the name of the taxon that includes *Caenis*, *Brachycercus*, and other similar genera (e.g., Ulmer, 1920; Spieth, 1933; Traver, 1935).

The 1920s and 1930s in North America were considered the Golden Age of Discovery for Ephemeroptera (McCafferty, 2001a) due principally to the descriptive works of Jay Traver and John McDunnough. This indeed involved additional descriptions of Brachycercinae in North America, i.e., *Eurycaenis prudens* McDunnough (1931) from Saskatchewan, *E. nitidus* Traver (1932) from North Carolina, and the unresolvable *Brachycercus flavus* Traver (1935) from Louisiana (see discussion and disposition of the latter under *Sparbarus*, n. gen., below). From South America during this period, Navás (1932) described *B. tenella* Navás from Argentina; however, this concept was based on an inconsequential description, and because its types are lost, it cannot even be placed to family (Soldán, 1986; Domínguez, per. comm.). It therefore must be considered a nomen dubium, family incertae. Barnard (1932) described *Austrocaenis capensis* Barnard from South Africa and considered it a close relative of *Brachycercus. Austrocaenis* Barnard, however, was shown to be equivalent to *Caenis* by McCafferty and de Moor (1995).

Berner (1946) described *Brachycercus maculatus* Berner from Florida. Tshernova (1952) described *Brachycercus minutus* Tshernova and *B. tubulatus* Tshernova from eastern Russia. Thew (1960) presented a revision of Caenidae wherein he hypothesized the relationships of genera within the family based on phenetic analysis of the morphology of the male genitalia. He recognized six genera (*Brachycercus, Caenodes* Ulmer, *Caenomedea* Thew, *Austrocaenis, Tasmanocaenis* Lestage, and *Caenis*), but no subfamily classification was suggested. Some 20 years later, Gose (1980) was next to make a contribution to our knowledge of Brachycercinae with his description of *B. japonicus* Gose from Japan.

Soldán (1986) made the most significant contribution up to this time to our knowledge of Brachycercinae, based to a large degree on his study of larval materials from around the world that were held at the University of Utah. As part of his study, he described three additional genera that possessed ocellar tubercles as larvae, including *Caenoculis* Soldán, *Cercobrachys* Soldán, and *Insulibrachys* Soldán. Although, Soldán (1986) did not suggest a subfamilial classification, he believed that these genera along with *Brachycercus* s.s. represented a "common phyletic line which evolved from an unspecialized pre-*Caenis* ancestor." *Caenoculis* was thought to be the most ancestral in the group because of its possession of certain characteristics associated with *Caenis*, for example, three-segmented maxillary and labial palpi. *Brachycercus* and *Insulibrachys* was thought to be the

most derived lineage in the group. Soldán's genera and their differentiation have been followed by such workers as Provonsha (1990) and Edmunds and Waltz (1996), although they have been called into question by some workers (see below).

Soldán (1986) also contributed to our knowledge of the diversity of the Brachycercinae with the description of several species, including in *Brachycercus*, two species from the southeastern USA, one from southwestern and midwestern USA, and one from Algeria; in *Cercobrachys*, one species from Colombia, one from Peru, one from Thailand, one from the southeastern USA, and two from the midwestern USA; in *Caenoculis*, one species from Malaysia and two from Vietnam; and in *Insulibrachys*, one from the West Indies. Unfortunately, most of the Soldán species were based on very limited numbers of specimens, and thus he was unable to assess intraspecific variability.

Malzacher (1987) established the genus *Afrocercus* Malzacher for one species of Caenidae known from adults from Uganda. He also proposed the subfamily Brachycercinae to include *Afrocercus* together with genera whose larvae had ocellar tubercles and two-segmented maxillary and labial palpi (*Brachycercus, Cercobrachys,* and *Insulibrachys*). Characters that Malzacher used to distinguish the subfamilies Caeninae and Brachycercinae included ratio of pedicel to scape, shape of the prosternum and metanotum, development of abdominal processes, and structures of the male genitalia and egg chorion.

Kluge (1991) synonymized *Cercobrachys* with *Brachycercus*, assuming there was no clear differentiation between them because certain characters assigned to these genera by Soldán (1986) were inaccurate or inconsistent. For example, "pedicel slightly longer than scape" was supposed to be exclusive to *Cercobrachys*, but was also present in *B. tuberculatus* Soldán, and although *Brachycercus* species were considered to lack long setae at the anterior margin of the mesosternum, *B. harrisella* possesses such setae. Kluge (1991) also described *B. corniger* Kluge and *B. europaeus* Kluge from Russia. Soldán and Landa (1991) added *Cercobrachys gilliesi* Soldán and Landa from Sri Lanka.

Malzacher (1995) described the genus *Madecocercus* Malzacher based on adults from Madagascar. He placed this genus in Brachycercinae because of its similarities to the adults of *Afrocercus*, which had previously been placed in that subfamily. Malzacher (1997) considered certain characteristics as supportive of monophyly for this grouping, i.e., the presence of ocellar tubercles, upturned abdominal processes, two-segmented maxillary and labial palpi, and well-developed forceps muscles and grooved forceps. The inclusion of the Afrotropical genera made such a classification tenuous at best because the first three of the above characteristics could only be presumed for *Afrocercus* and *Madecocercus*, which remained unknown to Malzacher as larvae. In addition, the presence of ocellar tubercles in *Caenoculis* was apparently not deemed significant.

McCafferty and Wang (1995) had described highly unusual pannote mayfly larvae from Madagascar as a new genus, which they named Provonshaka McCafferty and Wang. They tentatively placed Provonshaka in the family Teloganellidae. However, based on knowledge of the association study between larval and adult stages (see Elouard and Sartori 2001), McCafferty and Wang (2000), in their phylogenetic revision of the supergeneric classification of Pannota, indicated that the larvae of Provonshaka actually represented the undescribed larvae of the caenid genus *Madecocercus*, and thus synonymized *Provonshaka* with the latter. Because these larvae of *Madecocercus* held no resemblance to the *Brachycercus*-like genera, e.g., the fact that they lacked ocellar tubercles, Madecocercus and the supposed closely related Afrocercus were placed in a third subfamily, Madecocercinae. Thus, McCafferty and Wang (2000) recognized the concept of Brachycercinae as including Brachycercus, Cercobrachys, and Insulibrachys. They also suggested a sister group relationship between a Brachycercinae + Madecocercinae clade and Caeninae. The genus Caenoculis had not been studied by them and thus by default remained in the Caeninae, following the opinion of Malzacher (1997). This concept of Brachycercinae was followed e.g., by Kluge (2004) and Malzacher and Staniczek (2006), although Kluge (2004) suggested a sister group relationship between Brachycercinae and a Madecocercus + Caeninae clade, and he treated Afrocercus as incertae sedis under Caenidae. Malzacher and Staniczek (2006) described a new genus Tigrocercus Malzacher and three new species of Afrocercus from West Africa (including an assumed larval stage of the genus). These authors considered both the latter genera and *Madecocercus* to belong to Madecocercinae. The proposed phylogeny by Malzacher and Staniczek (2006) for Caenidae sub-families was similar with that of McCafferty and Wang (2000).

In the twenty-first century, three species of Brachycercinae were described prior to this revision. They include a species of *Cercobrachys* from central Canada and north-central USA (Sun et al., 2002), a species of *Caenoculis* from southern China (Zhou et al., 2003a), and a species of *Brachycercus* from southern China (Zhou et al., 2003b). In addition, in South America, the first adults of *Cercobrachys peruanicus* Soldán were recorded and described from Bolivia by Molineri and Goitia (2006). A single larval specimen of Brachycercinae has recently been collected from Brazil by C. R. Lugo-Ortiz (pers. comm.) but has yet to be studied in detail.

Little is known about the biology of Brachycercinae. Most observed larvae have been taken in lotic habitats, living near the edge or in shallows of streams on sand with a very thin overburden of silt or in mixtures of sand and silt in moderate current (McCafferty, unpubl.). Thus they may occur most commonly in waters 3–12 cm in deep, but larvae have also been taken from sandy beds some four or more meters deep (e.g., Burian et al., 1997). They may also occur on wave-beaten, sandy shores of lakes (Edmunds et al., 1976). Leonard and Leonard (1962) stated that *B. lacustris* appeared to prefer sluggish areas in larger streams where the water is subject to local warming.

Larval behavior is poorly known, but typical of pannote mayflies in general, Brachycercinae have been observed to be slow sprawlers and are secretive (McCafferty and Edmunds, 1979; McCafferty and Wang, 2000). Their long claws are typical of most other psammophilous mayflies (McCafferty, 1991). Edmunds (pers. comm.) believed that the short forelegs are used for cleaning the head of substrate. *Cercobrachys cree* Sun et al. has been observed to swim in captivity by awkwardly dog-paddling and also to quickly flex the abdomen to achieve momentum (McCafferty and L. Jacobus, pers. comm.). Larvae demonstrate stealth when removed from water and if threatened often raise and curve the tip of the abdomen forward in the "scorpion behavior" seen in other pannote mayflies (McCafferty, 1981; McCafferty and Wang, 2000). Time required for larval development is unknown, and there are few reports on emergence or alate behavior (Edmunds et al., 1976; Edmunds and McCafferty, 1988; Berner and Pescador, 1988). Alates have been taken in warm months, as late as September in Idaho and Canada and possibly throughout the year in Florida. Known subimagos emerge in early morning in some species and at night in others, molting to adults within minutes, with flights being observed in early and mid morning and after dark. The adult stage may be very brief, lasting only a few hours at most.

Material and Methodology

Material

Over 5,000 specimens were examined during the course of this study, including those secured from a number of institutional and personal collections worldwide. Most specimens examined, however, are held in the Purdue Entomological Research Collection, including a considerable number recently collected in the central plains areas of North America. Acronyms used herein for cited institutional collections are as follows: CNC (Canadian National Collection of Insects, Arachnids and Nematodes), CSU (C. P. Gillette Museum of Arthropod Diversity, Colorado State University), CU (Cornell University), FAMU (Florida A & M University), INHS (Illinois Natural History Survey), IIAS (Institute of Insect and Animal Science, National Institute of Agrobiological Sciences, Japan), KU (Snow Entomological Collection, University of Kansas Natural History Museum), NDNR (North Carolina Department of Natural Resources), NNU (Nanjing Normal University, China), NYEC (New York Department of Environmental Conservation), PERC (Purdue Entomological Research Collection), SWU (Seoul Women's University, Korea), TAMU (Texas A & M University), UI

(Hygienic Laboratory, University of Iowa), UM (University of Michigan), and USK (University of Saskatchewan, Canada).

Material examined citations given herein include an indication of life history stage (larva, subimago, adult), sex of alates, locality, date of collection, collectors, and place of deposition. If stages are associated by rearing, that information is also given. Materials are listed alphabetically by nation, state or province, and county or equivalent subunit. Most specimens are preserved in 70% ethanol, although some adults are pinned and are noted as such. Any parts residing on slides are also indicated. The following abbreviations frequently appear in cited locale information: Br (Bridge), Co (County), Cr (Creek), E (east), fk (fork), Hwy (Highway), jct (junction), km (kilometer), mi (mile), Mt (Mountain), N (north), Nat (National), nr (near), Rd (Road), Prk (Park), Prov (Province), R (River), Rd (Road), S (south), St (State), and W (west). In the Account of Taxa section below, genera are treated in phylogenetic order, and species within genera are treated in alphabetical order.

Methodology

The body size of caenid mayflies is relatively small. Most mature larvae, for example, are under 5.0 mm in length (lengths cited never include caudal filaments). This size made detailed morphological examination tedious and required meticulous preparation and observation because distinguishing traits in Brachycercinae often proved subtle, and there is often considerable variation among populations. Characters involving size related characters, color pattern, shape of ocellar tubercles, and gross structure of the thorax and abdomen were examined under dissecting microscopy. Structures associated with appendages, including antennae, mouthparts, legs, and gills usually required slide mounting and examination under compound microscopy, including phase contrast. In conjunction with light microscope usage, illustrations were prepared using an attached camera-lucida, and photographs were taken using an attached digital camera.

Scanning electron microscopy (SEM) was extensively employed in this study because of the significance of ultrastructure to characterization in Brachycercinae. Such microscopy has been used in more recent studies of Caenidae, notably by Provonsha (1990) and Hwang and Bae (1999). Characterization involving chaetotaxy of microtrichia and other minute armature, as well as cuticular topography would not have been decipherable without the use of SEM. Alcohol-preserved specimens of larvae and alates were fixed in 4% glutaraldehyde (buffered with 0.1M NaH2PO4-Na2HPO4 solution) and then treated with 2% osmium tetroxide. Fixed specimens were then dehydrated via ethanol gradient baths from 70% to 100%, followed by the use of a LADD Critical Point Dryer. Eggs were dehydrated through ethanol gradient baths and then placed directly in acetone. Specimens were mounted and covered with gold-palladium with a Hummer I Sputter Coater. A JEOL JSM-840 Scanning Electron Microscope was used for examination and producing micrographs of ultrastructure.

Strict cladistic methodology (Hennig 1966, Wiley 1981) was employed in this study to hypothesize the phylogenetic relationships within the Brachycercinae. Presumed homologous morphological characters that were found to have comparative value among the Brachycercinae or between this subfamily and outgroups were used for cladistic analysis. Character states were polarized based on comparison with primary, second-ary, and tertiary outgroups (within Caenidae, Caenoidea, and Pannota, respectively), or if structures unique to Brachycercinae were involved, e.g., ocellar tubercles, polarities were deduced from universal evolutionary tendencies of organisms. Polarized character states were numerically encoded, recorded in a character matrix, and then input into MacClade 4.01 (Maddison and Maddison 2000) to generate a Nexus file. This file was further analyzed using PAUP* 4.0b10 (Swofford 2002) based on parsimony criterion. Best trees were obtained by the Heuristic Search method. Support for individual branches was evaluated by the Bootstrap method with full heuristic search and 1,000 replicates. A TRE file containing all best trees was opened in MacClade for character tracing. Resolving Options were set to ACCTRAN and then DELTRAN to examine the evolution of character states. Synapomorphies for genera were determined by tracing character states in the ACCTRAN mode.

Comparative Morphological Characters

Larvae

Size and coloration. Body lengths are given as the dorsal distance from the anterior margin of the vertex to the posterior margin of tergum 10. The length of the middle ocellar tubercle is not included in the body length because it is not necessarily proportional to the body. Caudal filament length is given separately as the length of the median caudal filament.

General body coloration of Brachycercinae is yellow-brown. Mature larvae are relatively darker or paler, depending on the species group. Such differences are usually discernible in the field (Figs. 245, 258). Color patterns may or may not be of taxonomic use. Many species lack a color pattern, although dark brown maculae on the vertex, antennae, legs, operculate gills, and abdominal terga may sometimes distinguish a few species. The presence of one or two transverse dark brown stripes posterior to the compound eyes and certain abdominal markings may be of some use in distinguishing some North American species (Fig. 137, 138, 155), but are subject to some individual variability.

Head capsule. The anterior transverse row of long, fine head setae, which in part defines the Brachycercinae, is positioned generally ventral to the antennal base and compound eye in most species (Fig. 528), but is dorsal to the base of the clypeus in one species (Fig. 199). Certain species also have dense, long setae on the occiput (Fig. 31), whereas others have sparse setae in this region, and some have no long setae there (Fig. 470). In some species, the occiput is nearly parallel with the longitudinal axis of the body, at least with respect to the portion immediately posterior to the compound eye (Fig. 175). This lateral area, when protruding was referred to as the posterolateral lobe by Soldán (1986), but such a development was not always accurately applied as a diagnostic characteristic in Soldán's key.

Compound eyes. In Brachycercinae, the relative anterior position of the eyes varies. In some, the anterior margin of the eyes is at the same position as the anterior margin of the vertex (Fig. 424), and in some others, the anterior margin is distinctly posterior to the anterior margin of the vertex (Fig. 24). The eyes are also variously developed dorsally, with some species having strongly produced eyes (Fig. 314) similar to those of the genus *Machadorythus* Demoulin (Machadorythidae) from the Afrotropics (McCafferty and Wang, 2000).

Ocellar tubercles. Ocellar tubercles are triangulate or cone shaped in most Brachycercinae (Fig. 215). In a number of species, the anterior margin of the lateral tubercles is somewhat concave, and the apex is elongated, forming a nipplelike or fingerlike process (Fig. 117). The length and shape of these lateral tubercles vary among species, populations and individuals and may or may not be stable taxonomic characters. In some species, the apex of the middle tubercle is acutely pointed (Fig. 424), whereas in others, it tends to be blunt (Fig. 451). Ocellar tubercles are hemispherical with a rounded apex in some species (Fig. 400), and are cylindrical, with a nearly truncate apex in one species (Fig. 198). The middle tubercle is either equally or less produced than the lateral tubercles in most species (Fig. 139). Only in a few species is the middle tubercle distinctly longer (Fig. 175). Tubercle length and basal width, which are of some taxonomic use, are measured in the dorsal aspect for the middle tubercle and in the lateral aspect for the lateral tubercles. The middle tubercle does not curve in most species (Fig. 139), slightly curves upward (Fig. 31) in some, and curves ventrally in two (Fig. 328). Long, fine setae are found apically on the tubercles of one species (Fig. 198), shorter setae are found in this region in some other species (Fig. 31), and no such setae are present in most species (Fig. 400). The degree of setal development appears gradational in some species.

Antennae. In many species, the pedicel is highly elongated relative to the scape (Fig. 63), whereas in some others, the pedicel is only slightly longer than the scape (Fig. 337). The actual pedicel-to-scape ratio is of taxonomic use; however, some variability among individuals and populations exists. Moderately dense, long setae are found on the pedicel in certain species (Fig. 208), but in others, there are only a few noticeable setae on the pedicel (Fig. 369).

Labrum. In certain species, the lateral margin of the labrum is strongly produced, giving the lateral por-

tion of the labrum a rounded or somewhat triangulate shape (Fig. 394). In others, the lateral margin is nearly straight, giving the labrum a quadrate or trapezoidal shape (Fig. 302). It can be difficult, however, always to separate the labrum into two such types because of intermediacy in some species. The anterior margin can be straight or slightly emarginated (Fig. 141).

Maxillae. The shape of the galealaciniae can be expressed in part by the ratio of length to width. Length is measured from the base of the galealacinia to the base of the apical spines, and width is measured as the greatest width at about one-third the length from the base. In some species, the galealaciniae appear elongate and sickle shaped, with the ratio of length to width about 3.0 (Fig. 160). Other species have stout, somewhat triangulate galealaciniae, with this ratio less than 2.0 (Fig. 514). Certain species have three-segmented palpi (Fig. 29), and others have two-segmented palpi (Fig. 206). In the latter, segment 2 appears equivalent to segments 2 +3 of the former. Thus, relative combined length of segment 2 and 3 in those species with three-segmented palpi are comparable to the length of the fused segment 2 of those with two-segmented palpi. In some species, segment 2 is more elongate compared to segment 1 (Fig. 380). In some species, including those with threesegmented palpi, the width (measured at midlength) of segment 1 is clearly greater than that of segment 2 (Fig. 99), whereas in others, the width of segment 1 is subequal to, or only slightly greater than, that of segment 2 (Fig. 525). Stout, long setae are present along the inner margins of segments 2 and 3 in those species with three-segmented palpi. In those with a fused segment 2, such setae usually appear at least in part in the apical two-thirds of that segment (Fig. 335). In some, however, stout setae are present within the apical half of segment 2 (Fig. 171). The number of inner marginal setae among species can be categorized either as more than 20 (Fig. 335) or fewer than 15 (Fig. 171). The number of long, fine setae on the outer margin in the apical portion of segment 2 is 10 or less in some species (Fig. 171), and in others, this number exceeds 15 (Fig. 398).

Hypopharynx. The lateral margins of the superlinguae are convex in most species (Fig. 305), whereas in others, the lateral margins are more strongly produced and forming a nearly triangulate shape (Fig. 467).

Labium. Palp segmentation characteristics associated with the labium parallel those of the maxilla to a large degree. Again, in those species with two-segmented palpi, segments 2 appears equivalent to segments 2 and 3 of those with three-segmented palpi (Figs. 30, 336). In many species, a patch of long, fine setae is present on the ventral surface of palp segment 1 (Fig. 469), but in many others, such long setae are absent (Fig. 146).

Pronotum. Shape of the pronotum is largely determined by the width and shape of the lateral edge of the pronotum. In Brachycercinae, the general shape of the pronotum is trapezoidal. Lateral anterior angulate expansions are distinct in certain species (Fig. 215), but not in others (Fig. 117). In those with such expansions, they may be located in the anterior fourth (Fig. 24) or the anterior two-fifths to one-half (Fig. 227), depending on the species. Rarely, the lateral margins are convexly produced throughout (Fig. 198). In some, anterior margin can be straight (Fig. 24) or more commonly with an emargination having various degrees of concavity (Fig. 342). Presence and development of a pair of lateral transverse ridges was used for species identification by Soldán (1986). Such ridges, however, exist in all species of Brachycercinae, extending from the lateral margin to near the midline of the pronotum (Figs. 177, 342). In some species, these ridges are simply stained by black and thus are more apparent (Fig. 79).

Prosternum. The shape of the prosternum is nearly subquadrate in the Brachycercinae, with the forecoxae separated by more than one-half the distance between the midcoxae (Fig. 546). Although *Caenoculis* was described as having nearly contiguous forecoxae by Soldán (1986), the prosternum of this genus has forecoxae as widely separated as in other Brachycercinae. Some species have a medial process on the prosternum that is covered with a tuft of short setae (Fig. 228). In some, this prosternal process is strongly developed, being nearly cylindrical or appearing parallel sided in lateral view, and the tuft is made up of numerous long setae (Fig. 361). One species uniquely has the lateral ends of the median transverse ridge produced ventrally posterior to the forecoxae (Fig. 200).

Meso- and metasterna. Certain species lack apparent setae or have only several short, scattered setae on

the anterior margin of the mesosternum (Fig. 140). Others have a tuft of setae there that can be distinctly short or long, depending on the species (Fig. 343, 546). Although most Brachycercinae do not have ventral processes on the basisternum and sternellum of the meso- and metasterna (Fig. 140), a very few species do. The process on the basisternum of the mesosternum may be strongly developed in combination with a process of the sternellum being slightly and broadly produced, but with no process on the metasternum (Fig. 228). Alternatively, the process on the sternellum of the mesosternum can be as developed as, or more produced than, that on the basisternum, along with having a developed process on the metasternum (Fig. 329).

Legs. The forelegs of Brachycercinae are reduced in size relative to the mid- and hindlegs, and this reduction varies somewhat in degree. Many species have hindlegs more than one and one-half times as long as the forelegs (Figs. 148, 149). The ratio of the length of the foretibiae to foretarsi varies among species. A few species have foretibiae distinctly longer than the foretarsi (Fig. 209), and most species have foretibiae shorter than the foretarsi to a greater or lesser extent (Figs. 478, 535). In some species, there is a platelike process found on the dorsal margin of the hindcoxae (Fig. 34).

Leg setation. Leg setation provides a number of valuable taxonomic characters. Dorsal and ventral margins and anterior and posterior surfaces, as used in this study, are illustrated clearly by accompanying figures (Figs. 19–23). Some species have long, fine setae on the ventral margin of the forefermora that are twice as long as the width of the forefermora (Fig. 506). In some of these species, these setae are arrayed in two rows (Fig. 461), whereas in others of these species, they form a single row (Fig. 518). Other species have fewer and shorter setae on the ventral margin of the forefemora (Fig. 148). Certain species have a row of setae along the ventral margin of the foretibiae that in length measure twice or more the width of the foretibiae (Fig. 390). Such setae are much shorter in others (Fig. 33). Setae on the posterior surface of the foretibiae are short and scattered in some species (Fig. 69). In others, they are as long as one and one-half times or more the width of the foretibiae, but much shorter than the length of the foretibiae and not in the form of a distinct row (Fig. 33). In some species, however, a distinct longitudinal row of long setae is found on the posterior surface of the foretibiae, extending from the ventrobasal corner to the dorsodistal corner (Fig. 518). This row consists of four to seven setae that are as long as or longer than the foretibiae. Long setae may or may not be present on the ventral margin of the foretarsi. When present, the setae vary among species, with some having a setal row made up of long and short setae intermixed (Fig. 412), and others having only long setae three to four times as long as the width of the foretarsi (Fig. 535). Some species have only short, mostly scattered setae on the anterior and posterior surfaces of the foretarsi (Fig. 69). Others may have long setae that are not arrayed in distinct rows (Fig. 209). A few species have row of long setae that grade in length up to four times the width of the foretarsi (Fig. 441). The number and length of rows of long setae along the dorsal margin of the mid- and hindtibiae and mid- and hindtarsi vary among species. Some have no more than 20 such setae present on the hindtibiae (Fig. 34), others have 30–50 (Fig. 442), and a few have more than 70 (Fig. 536). The length of such setae in many species is up to twice the width of the hindtibiae (Fig. 34), but in many others, they are over two and one-half times the width of the hindtibiae (Fig. 536).

Claws. Claws of Brachycercinae are relatively slender and evenly curved or nearly straight (Fig. 34). The longest found has a ratio of hindclaw length to basal width of about 10.0 (Fig. 224). Although there are no tooth-shaped denticles (Fig. 344), some species have a series of minute, rounded nodules on the inner margin of the claws (Fig. 547), and many are without any armature.

Abdominal terga. Some Brachycercinae have a median process at the posterior margin of abdominal tergum 1. In two of these species, the process is well developed and cone shaped (Fig. 35) and in others of these species, it is much reduced and indistinct. The former two species also have a triangulate median process at the posterior margin of tergum 2 (Fig. 24). A short, fingerlike process immediately anterior to the basal insertion of the operculate gills is present in some species (Fig. 217). The process is a non-articulated, fixed outgrowth, although Berner and Pescador (1988) claimed that this process articulated with a socket on the tergum. A row of dense, long setae is present at the posterior margin of abdominal terga 7 and 8 (Fig. 24).

Such setae are few and sparse or absent in some species (Fig. 532). Among these species, a few have a setal row only on tergum 6 (Fig. 473). Although Soldán and Landa (1991) and Tojo (2001) reported a medial projection at the posterior margin of tergum 9 in two species, these species and all others do not have such a structure on tergum 9. The so-called projection is apparently attributable to black maculae at the emarginate anterior margin of tergum 10 (Fig. 116). In most species the anterior margin of the tergum 10 is strongly emarginated medially; whereas in two species it is nearly straight.

Abdominal sterna. The abdominal sterna of the vast majority of Brachycercinae are flat (Fig. 550). The exception involves the presence of a transverse ridge anteriorly on sterna 1–4, appearing as a rounded tubercle in lateral view (Fig. 330). The posterior margin of sternum 9 varies among sexes and species. In male larvae, a small notch is present in the lateral areas of the margin (Fig. 188), but is absent in females (Fig. 212). Otherwise, the margin is rounded in most species (Fig. 392), but somewhat truncate and medially notched in some species (Fig. 443). In one species it is angulated medially (Fig. 53).

Abdominal posterolateral projections. In most species of Brachycercinae, the lateral margin of abdominal segment 2 is indistinct, being slightly produced laterally (Fig. 313), or produced to form a projection shorter than its basal width, and apically forming a blunt or rounded right angle (Fig. 166). This projection can be slightly more developed and gradational in some other species, but rarely as developed as posterolateral projection 3 (Fig. 187). The shapes of the well-developed posterolateral projections 3–6 vary among species. In some, they are slender, with the ratio of length to basal width no less than 3.5 in projection 5 (Fig. 218). This ratio is frequently less than 3.0 in other species (Fig. 415). In many species, projection 6 is directed nearly posteriorly (Fig. 345). In a few species, projection 6 is directed posteromedially and forms an angle of 30 to 45 degree with the posterior margin of the tergum 6, (Figs. 480, 548). In some species, the apex of projection 6 strongly curves medially, becomes transversely oriented, being parallel or nearly so with the posterior margin of the tergum 6 (Fig. 531). Among the latter species, projection 6 may be twisted along its longitudinal axis in such a way that either its outer margin appears posterior to its inner margin in dorsal view (Fig. 531) or the outer margin appears anterior to its inner margin in the dorsal view (Fig. 318). The apex of projection 6 is blunt in some species (Fig. 480), and more acutely pointed in others (Fig. 345). Although the amount that projections 5–7 overlap each other has been used for species differentiation previously (Soldán, 1986), this is an unstable character that varies among individuals within species. Projection 7 is considerably shorter than the projection 6, but more than one-half the length of projection 6 in some (Fig. 24), and less than one-fifth the length of projection 6 or minute in others (Fig. 318). The length of projection 9 is greater than three-fourths the length of tergum 10 in some species (Fig. 24), but shorter than one-half of tergum 10 in all others (Fig. 404).

Operculate gills. The subquadrate operculate gills of Brachycercinae vary somewhat among species with respect to length to width ratio (width taken at midlength). The narrowest operculate gill, for example, has a ratio of about 1.5 (Fig. 340). In most species, the posterolateral corner of the operculate gill is nearly the same shape as the posteromedial corner or slightly less protruding (Figs. 150, 340). In other species, the posterolateral corner is distinctly produced (Fig. 254). Long setae are present in the lateral region on the dorsum in some species (Fig. 340). These setae are sparse or entirely absent in other species (Fig. 405). At least one species has short and relatively flat setae in this region (Fig. 300). Setae on the posterior margin are relatively long in Brachycercinae (Fig. 444), except for a few species whose posterior marginal setae are less than one-sixth the operculate gill length (Fig. 537). The marginal setae at the posteromedial and posterolateral corners are similar in length in some species (Fig. 213). In others, setae on the posteromedial corner are much longer than those on the posterolateral corner, sometimes more than twice the length (Fig. 463). Among species with long marginal setae, few have marginal setae of the posterolateral corner that are distinctly longer than those at posteromedial corner (Fig. 37).

The Y-ridge on the dorsal surface of the operculate gills is well developed in most Brachycercinae (Fig. 37), but in others it is narrow and weakly produced and often indistinct (Fig. 509). Certain North American

species have black markings on the outer branch of the Y-ridge (Fig. 150), and although the shape and size of these markings were used for species identification, e.g., by Burian et al. (1997), size and shape and even the presence of such marks varies considerably within species. A row of setae or at least several long setae are present along the Y-ridge in many species (Fig. 37), but are absent in others (Fig. 509). Besides the Y-ridge, one species uniquely has another longitudinal ridge in the sublateral area of the operculate gill (Figs. 283, 284).

Multiple ventral submarginal rows of microtrichia are associated with the operculate gills of some Brachycercinae. The microtrichia are usually hairlike (Fig. 151) but are palmate in some (Fig. 39). They are usually along the lateral and posterior margins continuously (Fig. 151), but in one species the row is only at the posterior margin (Fig. 291). In most species, the rows of ventral microtrichia are adjacent to the margin (Fig. 151), and only in a few species are they more distant from the margin (Fig. 256). Some species entirely lack these submarginal rows of microtrichia (Fig. 428).

Caudal filaments. The median caudal filament and the cerci are subequal in length in most Brachycercinae, with one exception involving a median caudal filament that is about one and one-fourth times the length of the cerci and another exception involving a median caudal filament that is shorter than the cerci by about one-third (Fig. 271). In many species, fine setae whorled on the segments in the apical third of the filaments are distinctly longer than those on the more basal segments (Fig. 393).

Adults

Size and coloration. Some species of Brachycercinae are significantly larger than others, and thus can be distinguished from some others on the basis of body length. Although body length has been used in keys given, e.g., by Traver (1935) and Soldán (1986), one caveat remains that lengths can vary within some species based on geographic location of populations and possibly cohort developmental time.

Species-specific coloration is very limited in Brachycercinae, and may only be useful when dealing with local populations within limited geographic areas. Color pattern differs among groups of species but is often not reliable for species identification. Maculae and diffuse shading are frequently carried over from the larval stage but tend to be paler. For example, the adults may have abdominal or other color patterns similar to larvae, as discussed previously (Fig. 164). In a few instances, presence of diffuse black shading on the thoracic sterna can serve to help distinguish between species in closely related pairs (Fig. 458).

Antennae. The ratio of pedicel length to that of the scape is carried over from the larval stage (see above, under larvae).

Prosternal process. In species that have a strongly developed process on the prosternum in their larval stage, such a medial prosternal process is also present in the adults, being usually cylindrical in lateral view (Fig. 433).

Vestiges of abdominal posterolateral projections. Short, lateral, peglike vestiges of abdominal projections are present on abdominal segments 3–6 or 3–7 in most Brachycercinae (Figs. 164, 243). In addition, those species whose projection 2 is developed in the larval stage will have a vestige of such in the alates. The vestige of projection 6 is directed posteriorly in most species but curves dorsally or medially in some others (Fig. 436), largely related to the larval orientation.

Male genitalia. A lateral facing longitudinal groove is present on the forceps of most Brachycercinae (Fig. 244). There is evidence from a pharate adult (Zhou et al., 2003b) that such a groove is not always present in the subfamily (Fig. 41). Although generally there are no hairlike or spinelike outgrowths on the venter of forceps of Brachycercinae (Fig. 429), there may be some unsocketed spinelike outgrowths in this area in some species (Fig. 41).

Eggs

Shape. Although the eggs of certain species are generally more slender than others, there is no real con-

sistency among species groups, and egg shape varies dramatically within some species. Previous statements and generalities regarding Brachycercinae egg shapes by Soldán (1986) and McCafferty and Wang (2000) were based on too small a sample size of eggs and species, and therefore do not strictly apply.

Polar caps. All Brachycercinae species for which eggs have been studied or previously described have a single polar cap (Fig. 555). The cap is covered by series of rounded tubercles in certain species (Fig. 563), but these tubercles are entirely absent in others (Fig. 558). When present, the number of such tubercles varies among species.

Chorionic costae. Elongate costae (ridges) are present on the chorionic surface of most Brachycercinae (Fig. 555). The chorion of at least one, and possibly more, species are smooth throughout (Fig. 567). One species has numerous small punctures rather than costae (Fig. 568). The costae, when present, are symmetrical in cross-section in some species and asymmetrical in others. In the symmetrical costae, the costae overlap the adjacent inter-costal grooves in both directions (both sides of the costa) (Fig. 556). Asymmetrical costae overlap the adjacent inter-costal grooves on only one side of the costa (Fig. 559). In some species, this more developed side of the costa can be relatively broad (Fig. 575). The number of costae varies among species. In a lateral half of the egg, some species have more than 15 costae (Fig. 557), some have 20 or more (Fig. 560), and some have as few as three or four (Fig. 574).

Micropyle. Although Koss and Edmunds (1974) stated that there was only one micropyle per egg, at least some species have multiple micropyles (Fig. 568).

Accounts of Taxa

Brachycercinae

Genera Included: Alloretochus, n. gen., Brachycercus Curtis, Caenoculis Soldán, Cercobrachys Soldán, Insulibrachys Soldán, Latineosus, n. gen., Oriobrachys, n. gen., Sparbarus, n. gen., and Susperatus, n. gen.

Mature Larva: Body length 3.3–8.5 mm. Caudal filaments length 1.5–4.7 mm. General coloration ranging from pale yellow-brown to dark red-brown. Body somewhat depressed (Fig. 19), covered with simple, long, fine setae on various parts (Fig. 24). Head: Head capsule ovate (Fig. 475) to subquadrate (Fig. 175) in dorsal view, anteriorly with transverse row of long, fine setae (Fig. 528). Clypeus with row of long setae subequal to, or longer than, one-half width of clypeus (Fig. 528) in most species. Compound eye laterally (Fig. 24) or anterolaterally (Fig. 424) oriented; posterior margin not reaching posterior margin of head capsule, with distance from posterior margin of head about one-half or more diameter of compound eye in female (Fig. 248). Ocelli distinctly produced, forming conical (Fig. 248), cylindrical (Fig. 199), or hemispherical tubercles (Fig. 400). Frons (Fig. 31) not produced anteriorly into distinct projection. Frons and vertex without protruding processes other than ocellar tubercles (Fig. 424). Antenna (Fig. 32) with scape and pedicel stout, distinctly broader than flagellum. Labrum subquadrate (Fig. 25) to ovate (Fig. 510), with stout setae on dorsal surface and along anterior margin. Mandible (Figs. 26, 27) with clusters of long setae on outer margins; outer incisor with three denticles; inner incisor with two or three denticles. Hypopharynx lingua subquadrate; superlingua ovate (Fig. 28) to somewhat triangulate (Fig. 541). Maxilla with galealacinia sickle shaped (Fig. 29) to nearly triangulate (Fig. 542); maxillary palp two or three segmented (Figs. 29, 206); terminal segment with row of long setae along inner margin and at apex (Fig. 234). Labium with tuft of long, fine setae posterior to base of glossa ventrally as long as, or longer than, glossa (Fig. 30). Labial palp two or three segmented (Figs. 30, 207), with long, fine setae along outer margin, and cluster of stout, short bristles at apex of apical segment (Fig. 30). Thorax: Pronotum trapezoidal (Fig. 24); anterior margin straight (Fig. 24) or emarginate (Fig. 533); lateral margin anteriorly either broadly and slightly convex (Fig. 533), convexly produced (Fig. 198), or produced to form blunt to right angle (Fig. 215). Prosternum with distance between forecoxae greater than onehalf distance between midcoxae (when legs fully spread laterally) (Fig. 343), with (Fig. 361) or without (Fig. 216) produced medial process. Meso- and metasternum with (Fig. 361) or without (Fig. 140) protruding processes. Legs ventrolaterally oriented; forecoxa directed vertically (Fig. 200); hindleg with ventral margins directed posteroventrally in natural state (Fig. 19). Foreleg more or less shorter than mid- and hindlegs (Figs. 209, 210). Femur, tibia and tarsus elongated, cylindrical, not flattened, with rows of long, fine setae (Figs. 209, 478). Hindclaw (Figs. 344, 426) slender, evenly and moderately curved to nearly straight; inner margin without tooth-shaped denticles. Abdomen: Terga with or without color patterns. Tergum 1 with row of fine setae on posterior margin (Fig. 35). Terga 6–8 with or without fine setae present on posterior margin (Figs. 24, 473, 474). Tergum 10 with anterior margin nearly straight or emarginate (Fig. 549). Segments 2-9 or 3-9 with developed posterolateral projections (Fig. 24). Posterolateral projections 2–6, 3–6, or 3–7 blade shaped, more developed than others, at least slightly upturned, forming "gill basket" protecting gills 3–6 (Fig. 375); apical half of posterolateral projection 6 curving medially in some (Fig. 403); projection 7 distinctly shorter than projection 6 (Fig. 229). Gills 1-6 present. Gill 1 (Fig. 35) filamentous, dorsolaterally oriented. Gills 2-6 recumbent, dorsally oriented. Gill 2 operculate, subquadrate (Fig. 37) to somewhat ovate (Fig. 417); dorsum with Y-shaped ridge (Fig. 37); posterior marginal setae usually long (Fig. 213); venter with (Fig. 38) or without (Fig. 428) marginal or submarginal rows of microtrichia; when present, microtrichia palmate (Fig. 38) or hairlike (Fig. 256). Caudal filaments (Fig. 393) whorled with fine setae.

Adult: Male body length 3.0–5.8 mm; wing length 2.8–5.8 mm, about twice that of greatest width (Fig. 76); caudal filaments length 10.0–16.0 mm. Female body length 3.5–7.5 mm; wing length 3.0–6.5 mm; caudal filaments length 0.8–5.0 mm. General coloration ranging from pale yellow to dark black-brown. *Head*: Compound eye black, large, laterally oriented; pair widely separated (Fig. 74). Ocelli hemispherical, with basal portion black and apical portion translucent (Fig. 74). Scape and pedicel stout; flagellum slender, not distinctly segmented (Fig. 348). *Thorax*: Pronotum short, subquadrate (Fig. 241). Prosternum with distance between forecoxae greater than one-half distance between midcoxae (Fig. 458). Metanotum with medial triangulate to rounded expansion on posterior margin (Fig. 430). All legs of both sexes functional. Forefemur usually with longitudinal brown stripes (Fig. 434); mid- and hindlegs pale. Male with foreleg shorter than body, but about twice as long as mid- and hindlegs; female with foreleg two-thirds length of mid- and hindlegs. Forewing venation as in figure 240. *Abdomen*: At least segments 3–6 usually with distinct vestiges of larval posterolateral projections (Fig. 74). Male genitalia with forceps one segmented, blade shaped, with longitudinal groove in most species (Fig. 244), usually slightly bowed (Fig. 244) or with angulate bend near base (Fig. 154); penes lobe subquadrate, with lateral margin somewhat convex distally (Fig. 409).

Egg: Shape ovate (Fig. 568) to elongate-ovate (Fig. 570). One polar cap present (Fig. 555). Chorion with longitudinal costae (Fig. 555) in most species. One or more micropyles present (Figs. 560, 568).

Diagnosis: The larvae of Brachycercinae are distinguished from those of other subfamilies of Caenidae by numerous characteristics as follows. The head has an anterior transverse row of long setae (Fig. 528). The clypeus has a row of long setae that are as long as, or longer than, one-half the width of the clypeus (Fig. 528) in most species. Compound eyes are separated from the posterior margin of the head by a distance of about one-half or more of the diameter of the compound eye in the female (Fig. 246). The ocelli are modified into conical (Fig. 246), cylindrical (Fig. 199), or hemispherical (Fig. 400) tubercles. The maxillary palpi are present. The labium has a tuft of long, fine setae ventrally at the base of each glossa (Fig. 30), and these setae are at least as long as the glossa. The forecoxae are separated by more than one-half the distance between the midcoxae (Fig. 343), as measured when the legs are fully spread. The forelegs are distinctly shorter than mid-and hindlegs (Figs. 209, 210) in most species. The forecoxae are oriented vertically (downwards) (Fig. 200). The ventral margin of forefemura has some setae that are at least as long as one-half the width of the forefemur (Fig. 33). The hindlegs have ventral margins directed ventrally or posteroventrally (Fig. 19). The major segments of the legs are not flattened (Fig. 19). The claws are evenly curved or nearly straight and lack tooth-shaped denticles (Fig. 344). The well-developed abdominal posterolateral projections are at least slightly

curved dorsally (Fig. 375), projection 5 is as long as, or longer than, about twice of its basal width, and projection 7 is distinctly shorter than projection 6 (Fig. 229).

Besides Brachycercinae two subfamilies, Caeninae and Madecocercinae are currently recognized in Caenidae (McCafferty and Wang 2000). Larvae of the cosmopolitan subfamily Caeninae do not have long setae associated with the head capsule (Figs. 1, 11) and labium (Fig. 10) as do Brachycercinae; their compound eyes nearly reach the posterior margin of the head (Fig. 11); the forecoxae are separated by less than one-half that of the midcoxae (Fig. 13); the setae on the ventral margin of forefemura are shorter than one-third width of the forefemur (Fig. 2); the hindclaws are strongly curved at least in some species, and have tooth-shaped denticles (Fig. 3); and the posterolateral projections (Fig. 14) are short; projection 5 is as long as, or shorter than, one and one-half times of its basal width. In the larvae of the Afrotropical subfamily Madecocercinae, maxillary palpi are absent; the forefemora are greatly flattened. These two subfamilies can be additionally distinguished from those of Brachycercinae by the presence of ocelli that are not modified into tubercles (but can be slightly produced in some) (Fig. 11), forelegs that are only slightly shorter than hindlegs (Figs. 2, 3), forecoxae that are oriented horizontally (forwards) (Fig. 13), mid- and hindlegs that have ventral margins directed anteroventrally (Fig. 1), abdominal projections that are posterolaterally oriented (Fig. 14), and the projection 7 that is slightly shorter than, or nearly as long as, projection 6 (Fig. 14).

The adults of Brachycercinae are distinguished from those of Caeninae by the distance between the forecoxae being greater than one-half the distance between the midcoxae (Fig. 458), and by the blade-shaped forceps with longitudinal folding in a majority of species (Fig. 244). This assessment does not include consideration of the male genitalia of genera *Caenoculis* and *Insulibrachys*, which remain unknown, and presumes the forecoxae characterization will be carried over from the larvae. The known Brachycercinae adults are distinguished from Madecocercinae by the male forceps that are strap like and are gradually bowed (Fig. 244). Whereas in Madecocercinae, the male forceps are stout and strongly bowed (see figure 35 in McCafferty and Wang 2000).

The eggs of Brachycercinae are distinguished from those of other subfamilies of Caenidae by the presence of a single polar cap (and longitudinal chorion costae in the majority of species) (Fig. 555). This assessment does not include consideration of the eggs of genera *Caenoculis* and *Insulibrachys*, which remain unknown.

Distribution: Palearctic: Algeria, Europe, Asian regions of Russia, Kazakhstan, Mongolia, northern China, Korea, Japan; Oriental: southern China, Thailand, Vietnam, Sri Lanka, Malaysia, Indonesia; Nearctic: Canada, U.S.A.; Neotropical: Cuba, Belize, Colombia, Peru, Bolivia, Brazil.

Caenoculini, New Tribe

Type genus: Caenoculis Soldán

Diagnosis: The larvae of Caenoculini are distinguished from those of all other tribes of Brachycercinae by the presence of three-segmented maxillary and labial palpi (Figs. 29, 30), rather than two-segmented palpi as in all other tribes (Figs. 206, 207).

Caenoculis

Caenoculis Soldán, 1986:347. **Type species:** *Caenoculis bishopi* Soldán.

Species Included: C. acutalis Zhou, Sun and McCafferty, C. bishopi Soldán, and C. nhahoensis Soldán.

Mature Larva: Body length 3.5–7.0 mm. Caudal filaments length 2.1–4.0 mm. General coloration pale brown to dark brown. *Head*: Head capsule anterolaterally with transverse row of long setae between antenna

and base of mandible (Fig. 31). Clypeus and occiput (Fig. 31) with long setae at least in some species. Occiput lateral margin curved inward posterior to compound eve (Fig. 24). Compound eve (Fig. 24) laterally oriented, not strongly produced dorsally; female compound eye with anterior margin not reaching anteriorly as far as base of middle ocellar tubercle, and with distance from posterior margin of head about one-half diameter of eve. Ocellar tubercles of at least some species with dense, short setae no longer than one-half length of ocellar tubercle (Fig. 31). Lateral ocellar tubercles (Fig. 31) triangulate in lateral view; distal portion not curved anteriorly; apex rounded or bluntly pointed. Middle ocellar tubercle (Figs. 24, 31) triangulate or rounded in dorsal view, curved dorsally in lateral view in at least some species; length subequal to, or shorter than, lateral ocellar tubercle. Pedicel (Fig. 32) about 2.0 X length of scape, with more than 10 setae one-half or more length of pedicel at least in some species. Labrum (Fig. 25) trapezoidal. Hypopharynx (Fig. 28) with superlingua ovate, not triangulate laterally. Maxilla (Fig. 29) with galealacinia sickle shaped, with length about 2.8–3.0 X basal width; maxillary palp three segmented; segment 1 wider than segment 2 and 3; segments 2 and 3 together longer than segment 1; segment 3 with row of long, stout setae along inner margin, with long, fine setae at apex and along outer margin, and without dense, long setae on ventral surface. Labial palp (Fig. 30) three segmented; segment 1 ventrally with patch of setae one-half or more length of segment 1. Thorax: Pronotum (Fig. 24) trapezoidal; anterior margin slightly emarginate; lateral margin produced to form angulate expansion in about anterior fourth. Propleuron not visible in dorsal view (Fig. 24). Prosternum (Fig. 31) with median ridge not produced medially or laterally, with some short setae in at least some species. Mesosternum with anterior margin with row of short setae in at least some species (Fig. 31). Meso- and metasternum without processes on basisternum or sternellum. Forefemur (Fig. 33) ventrally with short setae and few setae as long as femur width. Foretibia (Fig. 33) as long as, or slightly shorter than, foretarsus; ventral margin with setae as long as, or shorter than, width of tibia; posterior surface without distinct long setal row. Foretarsus (Fig. 33) ventral margin setae shorter than width of tarsus; anterior and posterior surfaces and dorsal margin with some relatively long setae not arrayed in distinct row. Mid- and hindcoxa (Fig. 34) of at least some species with flat process on dorsal margin. Hindleg (Fig. 34) slightly longer than foreleg. Hindfemur length less than 5.0 X width. Hindtibia and hindtarsus dorsally with row of short or long, fine, setae. Hindclaw (Fig. 34) length less than 6.0 X basal width, slightly to moderately curved, without armature on inner margin. Abdomen: Terga 1 and 2 with median conical process at posterior margin (Fig. 35). Tergum 2 with finger-shaped process on either side immediately anterior to base of operculate gill in some species (Fig. 35). Terga 7 and 8 with row of long, fine setae along posterior margin in at least some species (Fig. 24). Tergum 10 (Fig. 24) anterior margin nearly straight. Posterolateral projections (Fig. 24) developed and slightly upturned on at least segments 4–7. Sterna flat throughout (Fig. 35). Operculate gill (Fig. 37) subquadrate, with posterolateral corner strongly produced and more protruding than posteromedial corner; marginal setae at posterolateral corner distinctly longer than those at posteromedial corner in at least some species; Y-ridge strongly developed; venter with multiple submarginal rows of palmate microtrichia adjacent to lateral and posterior margins (Figs. 38, 39).

Adult: Unknown (see discussion of pharate subimago below).

Egg: Unknown.

Diagnosis: The larvae of *Caenoculis* can be distinguished from those of other genera of Brachycercinae by the presence of three-segmented maxillary and labial palpi (Figs. 29, 30), rather than two-segmented palpi as in all others. *Caenoculis* is also the only Brachycercinae known to have operculate gills with palmate microtrichia ventrally (Fig. 39). Other genera either have hairlike microtrichia in rows (Fig. 151), or in the case of *Oriobrachys*, n. gen., *Susperatus*, n. gen., *Alloretochus*, n. gen., *Cercobrachys*, and most species of *Latineosus*, n. gen., microtrichia are entirely absent (Fig. 428). *Caenoculis* can be additionally distinguished by having ocellar tubercles covered with only very short setae (Fig. 31), a labial palp segment 1 that is covered with a patch of long setae ventrally (Fig. 30), thoracic sterna that are flat throughout, abdominal terga 1 and 2 with a posteromedial cone-shaped process (Fig. 35), a posterolateral projection 6 that is not curved medially (Fig. 24), and operculate gills without a longitudinal ridge in the sublateral area but with a protruding

edge at the posterolateral corner (Fig. 37). In *Insulibrachys*, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In *Sparbarus*, n. gen., long setae are absent on the ventral surface of labial palp segment 1 (Fig. 146). In *Brachycercus*, abdominal tergum 1 has a low and indistinct posteromedial process, and tergum 2 does not have a posteromedial process. In *Oriobrachys*, n. gen., operculate gills have a strongly developed longitudinal ridge in the sublateral area (Fig. 284). In *Susperatus*, n. gen., thoracic sterna have multiple conical processes (Fig. 361). In *Latineosus*, n. gen., *Alloretochus*, n. gen., and *Cercobrachys*, posterolateral projection 6 is distinctly curved medially (Fig. 375).

Discussion: The adult stage of *Caenoculis* remains unknown; however, pharate male subimago genitalia were dissected from a last instar larva of *C. acutalis* and suggested possible adult differences from all other Brachycercinae. The forceps (Figs. 40, 41) are somewhat flattened, without a longitudinal groove or fold, and they are covered with dense, fine spinelike (unsocketed) outgrowths. Adults of other genera have forceps that are blade shaped, with a distinct longitudinal groove (fold), and their surface is smooth. Although these characteristics of the *Caenoculis* pharate subimago are similar to those of male adult *Caenis*, it is not certain if there will be much additional developmental transformation in the adult genitalia of *Caenoculis*. In any case, possible retention of relatively ancestral male genitalia in *Caenoculis* is consistent with its hypothesized phylogenetic position within the Brachycercinae (see below).

When Soldán (1986) established the genus Caenoculis, he described a species, Caenoculis dangi, from Vietnam. Based on his formal descriptions, this species was distinctly different in appearance from other Caenoculis. In this study, we found that the placement of C. dangi to be problematic in term of its characteristics being consistent with *Caenoculis* and Brachycercinae. In the questionable species, the labrum is ovate, with the anterolateral corner rounded, similar to that of Caenis. In Caenoculis, as well as Brachycercus, Insulibrachys, and Sparbarus, the labrum is nearly trapezoidal, with the anterolateral corner somewhat angulate. Although the labrum is nearly ovate in many *Cercobrachys* species, that shape is due mainly to the convexly produced lateral margins, which are essentially different from those of the questionable species. Claws of the questionable species are similar to those of *Caenis*, being stout and strongly hooked, and with tooth-shaped denticles on the inner margin. None of these claw characteristics are associated with Brachycercinae. The forelegs of the questionable species are longer than the midlegs, whereas the forelegs are shorter than the midand hindlegs in all Brachycercinae. An illustration given by Soldán (1986) showed the operculate gills of his species to have a single ventral submarginal row of microtrichia, which is indeed shared by *Caenis* and several closely related Caeninae genera, whereas in Brachycercinae, the ventral submarginal microtrichia of the operculate gills, when present, are always arrayed in multiple rows. In the same illustration, the posterolateral corner of the operculate gill does not have a produced edge that is more protruding than the posteromedial corner, which is present in all other known Caenoculis species. Furthermore, one of the most important apomorphies defining Brachycercinae is the presence of the well-developed ocellar tubercles, which in the questionable species were noted to be poorly developed, and in the case of the middle ocellar tubercle, "hardly distinguishable" (Soldán, 1986). It is quite common in *Caenis* to have lateral ocelli somewhat produced. Considering all of the above and the fact that other defining synapomorphies for Brachycercinae (see below) are not found in the questionable species, the species is here removed from *Caenoculis* and Brachycercinae to the subfamily Caeninae, and provisionally placed in the genus *Caenis*, as *Caenis dangi* (Soldán), n. comb.

Distribution: Oriental: southern China, Vietnam, Malaysia.

Caenoculis acutalis Zhou, Sun and McCafferty

Caenoculis acutalis Zhou, Sun and McCafferty, 2004:185.

Mature Larva: Body (Fig. 69) length 4.5–7.0 mm. Caudal filaments length 2.0–4.0 mm. General coloration

dark yellow-brown. Body dorsal surface without toad-stool shaped setae. Head: Coloration yellow-brown. Frons (Figs. 24, 31) with variously scattered, dense, short and long, fine setae. Occiput stained with irregular black-brown patterns, with variously scattered, dense, short and long, fine setae (Figs. 24, 31). Branches of epicranial suture forming low, transverse ridge (Fig. 31). Ocellar tubercles distally with dense setae shorter than one-half length of ocellar tubercle (Fig. 31). Lateral ocellar tubercle (Fig. 31) triangulate in lateral view, slightly longer than basal width; apex rounded to bluntly pointed. Middle ocellar tubercle (Figs. 24, 31) conical, curved dorsally in lateral view, slightly shorter than lateral ocellar tubercle, and slightly longer than basal width; lateral margin straight; apex bluntly pointed. Antenna (Fig. 32) pale brown; pedicel with black macula apically, 2.0 X length of scape, and whorled with some short, stout setae mixed with about 20 stout setae onehalf or more length of pedicel. Labrum (Fig. 25) distal margin slightly concave medially. Maxilla (Fig. 29) with galealacinia length to width ratio—3.1; maxillary palp segment 1 width 1.5 X width of segment 3; segments 2 and 3 subequal in length, together 1.5 X length of segment 1; segment 2 with about three long, stout setae on inner margin, and about eight long, fine setae on outer margin; segment 3 with about 15 long, stout setae on inner margin, and with numerous long, fine setae at apex and along outer margin. Labial palp (Fig. 30) segment 2 length 2 X length of segment 3. Thorax: Pronotum (Fig. 24) stained with diffuse black, with some long, fine marginal setae; medial line prominent, forming low ridge; subanterior transverse ridge distinct. Propleuron with some marginal setae. Prosternum (Fig. 31) median transverse ridge covered with some setae shorter than one-fourth length of forefemur. Mesonotum (Fig. 24) dark yellow-brown, with small triangulate projection at anterolateral corner directed laterally and bluntly pointed at apex, and with dense, long marginal setae laterally. Mesosternum anterior margin with row of setae shorter than one-fourth length of midfemur (Fig. 31). Legs pale brown throughout, without maculae. Ratios of length of body: foreleg: midleg: hindleg-2.8: 1.0: 1.2: 1.2. Ratios of length of forefemur: tibia: tarsus: claw-3.0: 1.7: 1.5: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.3: 1.9: 1.9: 1.0. Forefemur (Fig. 33) dorsally with row of dense, long and short setae. Foretibia (Fig. 33) ventrally with row of about 10 stout, short setae; posterior surface with some setae measuring in length up to 2.0 X width of tibia. Foretarsus (Fig. 33) ventrally with row of about 10 stout, short setae; anterior and posterior surfaces with some scattered setae longer than width of tarsus. Hindcoxa (Fig. 34) with flat process on dorsal margin triangulate, much longer than that of midcoxa. Hindfemur (Fig. 34) length 4.7 X width; dorsal margin with row of long setae interspersed with some short setae; ventral margin with very short setae. Hindtibia and hindtarsus (Fig. 34) each with row of about 20 long, fine setae along dorsal margin, and row of short, stout setae along ventral margin. Hindclaw (Fig. 34) length 5.7 X basal width, nearly straight. Abdomen: Terga (Fig. 24) yellow-brown, somewhat paler than head and thoracic nota, stained with diffuse black. Terga 1 and 2 with narrow medial cone-shaped process on posterior margin with apex pointed and directed dorsally (Figs. 24, 35). Tergum 2 with stout process immediately anterior to base of operculate gill (Figs. 24, 35). Tergum 7 with row of dense, long setae along posterior margin; terga 8–10 with much fewer setae along posterior margin (Fig. 24). Tergum 10 anterolaterally with small, somewhat triangulate process on either side (Fig. 24). Posterolateral projections on segments 3–9 (Fig. 24), with apices pointed; projections 4, 5 and 6 longest, length about 3.5 X basal width, and longer than projections 3 and 7 by about one-third; projection 8 about one-half length of projection 7; projection 9 slightly shorter than projection 8, longer than three-fourths length of tergum 10. Sterna paler than terga; sternum 9 posterior margin convexly produced (Fig. 36). Operculate gill (Figs. 37, 38, 39) with length 1.1 X width, yellow-brown, nearly concolorous with abdominal terga; lateral region with some long setae; posterolateral corner with row of dense, long setae up to about two-fifths length of operculate gill, and distinctly longer than those of posteromedial corner; Y-ridge with row of long setae. Caudal filaments pale brown; cerci length 0.75–0.80 X that of median caudal filament; segments whorled with setae; setae on apical segments subequal in length to those of basal segments.

Adult: Unknown. Egg: Unknown.

Diagnosis: Larvae of *C. acutalis* are distinguished from *C. bishopi* and *C. nhahoensis* as follows. The mesonotum has a small triangulate process at the anterolateral corners (Fig. 24), tergum 10 has a small triangulate process at the anterolateral corners (Fig. 24), and posterolateral projections are present on abdominal segments 3–9 (Fig. 24). In *C. bishopi* and *C. nhahoensis*, the above mentioned processes on the mesonotum and abdominal terga are absent, and posterolateral projections are present on abdominal segments 4–7 (*C. bishopi*) (Fig. 52) or on segments 4–8 (*C. nhahoensis*).

Distribution: China: Yunnan Province.

Material Examined: Two larva PARATYPES, China, Yunnan Prov, Er-Yuan Co, 26.06 N 99.56, 2262 m Alt, Fu-Tian village, Mei-Yuan R, V-24-1996, JC Morse, L-F Yang, B-X Wang, C-F Zhou (PERC).

Caenoculis bishopi Soldán

Caenoculis bishopi Soldán, 1986:384.

Mature Larva: Body (Fig. 42) length 4.1 mm. Caudal filaments length 2.1 mm. General coloration yellowbrown. Body with dorsal surface evenly covered with dense, toad-stool shaped setae (Figs. 42, 43). Head: Coloration yellow-brown. Frons (Fig. 44) with scattered, short, fine setae. Occiput (Fig. 44) without blackbrown patterns, with scattered, short, fine setae. Branches of epicranial suture slightly prominent (Fig. 44). Ocellar tubercles generally without setae (Fig. 44). Lateral ocellar tubercle (Fig. 44) blunt-triangulate in lateral view, shorter than basal width by one-third; apex rounded. Middle ocellar tubercle (Figs. 42, 44) rounded, not curved dorsally, shorter than lateral ocellar tubercle by one-half, and slightly longer than basal width; lateral margin straight; apex rounded. Antenna pale brown; pedicel without macula, 2.0 X length of scape, and whorled with some short, stout setae. Labrum (Fig. 47) distal margin slightly concave medially. Maxilla (Fig. 48) with galealacinia length to width ratio—2.8; maxillary palp segment 1 width 2.6 X width of segment 3; segments 2 and 3 subequal in length, together 1.7 X length of segment 1; segment 2 with one or two long, stout setae on inner margin, and without long, fine setae on outer margin; segment 3 with about 10 long, stout setae on inner margin, and with some long, fine setae at apex. Labial palp (Fig. 49) segment 2 length about 1.5 X length of segment 3. Thorax: Nota yellow-brown, without maculae. Pronotum with few, short, fine marginal setae; medial line prominent, forming low ridge; subanterior transverse ridge distinct. Propleuron and prosternum generally without setae. Mesonotum (Fig. 42) without triangulate projection at anterolateral corner, and without dense, long, marginal setae. Mesosternum anterior margin without long setae. Legs pale brown throughout, without maculae. Ratios of length of body: foreleg: midleg: hindleg-3.1: 1.0: 1.0: 1.4. Ratios of length of forefemur: tibia: tarsus: claw-3.6: 2.2: 2.0: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.8: 2.5: 2.5: 1.0. Forefemur (Fig. 50) dorsally with row of sparse, short setae. Foretibia (Fig. 50) ventrally with row of about 10 stout, short setae; posterior surface with some stout setae shorter than one-half width of tibia. Foretarsus (Fig. 50) ventrally with row of about 12 stout, short setae; anterior and posterior surfaces with some scattered setae as long as width of tarsus. Hindcoxa (Fig. 51) without noticeable flat process on dorsal margin. Hindfemur (Fig. 51) length 3.0 X width; dorsal and ventral with row of sparse, fine, short setae. Hindtibia and hindtarsus (Fig. 51) each with row of short, fine setae along dorsal and ventral margin. Hindclaw (Fig. 51) length 4.5 X basal width, moderately curved. Abdomen: Terga (Fig. 42) pale yellowbrown, paler than head and thoracic nota. Terga 1 and 2 with narrow medial cone-shaped process on posterior margin with apex pointed and directed dorsally (Fig. 45). Tergum 2 without apparent process anterior to base of operculate gill. Tergum 7 with row of dense, long setae along posterior margin; tergum 8 with few, short setae along posterior margin. Tergum 10 without triangulate process at anterolateral corner. Posterolateral projections on segments 4–7 (Figs. 42, 52), with apices pointed; projections 5, 6 and 7 longest, length about 3.5 X basal width, and about 2.0 X length of projection 4. Sterna paler than terga; sternum 9 posterior margin bluntly angulated medially (Fig. 53). Operculate gill (Figs. 42, 46) with length 1.3 X width, yellow-brown, nearly concolorous with thoracic nota; lateral region with some relatively long setae; posterolateral corner with row of dense, long setae up to about one-third length of operculate gill, and longer than those of posteromedial corner; Y-ridge generally without long setae. Caudal filaments pale brown; cerci and median caudal filament subequal in length; segments whorled with setae; setae on apical segments longer than those of basal segments.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of *Caenoculis bishopi* are distinguished from other *Caenoculis* as follows. The mesonotum does not have a triangulate process at the anterolateral corners, and abdominal tergum 10 does not have a small triangulate process at the anterolateral corners. In *C. acutalis*, such processes are present on the mesonotum and abdominal tergum 10 (Fig. 24). In *C. bishopi*, the posterolateral projections are present on abdominal segments 4–7 (Fig. 52), and in *C. nhahoensis*, the posterolateral projections are present on abdominal segments 4–8.

Distribution: Malaysia.

Material Examined: Larva HOLOTYPE, Malaysia, Trib of Gombak R, 16.5 mi N of Kuala Lumpur on Bentong Rd, XII-12-1968, JE Bishop (FAMU).

Caenoculis nhahoensis Soldán

Caenoculis nhahoensis Soldán, 1986:352.

Larva: Material of *C. nhahoensis* were not available to us for study; however, see formal description by Soldán (1986), figures 55–60, and diagnosis below.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of *Caenoculis nhahoensis* are distinguished from other *Caenoculis* as follows. The mesonotum does not have a small triangulate process at the anterolateral corners, and abdominal tergum 10 does not have a triangulate process at the anterolateral corners. In *C. acutalis*, such processes are present (Fig. 24). In *C. nhahoensis*, the posterolateral projections are present on the abdominal segments 4–8, and in *C. bishopi*, the posterolateral projections are present on the abdominal segments 4–7 (Fig. 52).

Distribution: Vietnam.

Sparbarini, New Tribe

Type genus: Sparbarus, New Genus

Diagnosis: The larvae of Sparbarini are distinguished from those of all other tribes of Brachycercinae by having segment 1 of the labial palpi lacking a patch of long setae on the ventral surface (Fig. 146), and abdominal posterolateral projection 6 being directed posteriorly or only slightly curved medially (Fig. 137). In all other tribes except for *Latineosus*, n. gen. (Latineosini, n. trib.), segment 1 of the labial palpi has a patch of long setae on the ventral surface (Fig. 235). In Latineosini, n. trib., and most Cercobrachini, n. trib., projection 6 is distally strongly curved medially (Fig. 313).

Type Species: Caenis lacustris Needham.

Species Included: *S. capnicus* (Zhou, Sun and McCafferty), n. comb., *S. choctaw*, n. sp., *S. corniger* (Kluge), n. comb., *S. coushatta*, n. sp., *S. europaeus* (Kluge), n. comb., *S. gilliesi* (Soldán and Landa), n. comb., *S. japonicus* (Gose), n. comb., *S. kabyliensis* (Soldán), n. comb., *S. lacustris* (Needham), n. comb., *S. maculatus* (Berner), n. comb., *S. miccosukee*, n. sp., *S. nasutus* (Soldán), n. comb., and *S. tubulatus* (Tshernova), n. comb.

Mature Larva: Body length 4.0–8.1 mm. Caudal filaments length 1.6–4.5 mm. General coloration pale yellow to yellow-brown. Head: Head capsule anterolaterally with transverse row of long setae between antenna and base of mandible (Fig. 176). Clypeus with long setae. Occiput with sparse, fine, short or long setae; lateral margin posterior to compound eye curved inward (Fig. 116) or parallel with long axis of body (Fig. 78). Compound eye laterally (Fig. 116) or anterolaterally (Fig. 78) oriented, strongly produced dorsally (Fig. 139) or not (Fig. 117); female compound eye not extending anteriorly beyond base of middle ocellar tubercle, and with distance from posterior margin of head one-half or more diameter of compound eye (Fig. 137). Ocellar tubercles without apparent setae. Lateral ocellar (Fig. 137) tubercle triangulate in lateral view. Middle ocellar tubercle shorter than (Fig. 156), as long as (Fig. 117), or longer than (Fig. 175), lateral tubercle, short-triangulate (Fig. 155) to elongate-conical (Fig. 175) in dorsal view. Pedicel (Fig. 63) 2.0 X or more length of scape, with more than five setae as long as, or longer than, one-half length of pedicel. Labrum (Fig. 141) subquadrate; lateral margin slightly produced or nearly straight. Hypopharynx (Fig. 144) superlingua ovate; lateral margin moderately and convexly produced. Galealacinia (Fig. 145) sickle shaped; ratio of length to basal width greater than 2.5; maxillary palp (Fig. 145) two segmented; segment 1 width 1.5–2.0 X width of segment 2; segment 2 1.2–1.8 X length of segment 1, with row of 10 or fewer long, stout setae along distal half of inner margin and no more than 15 long, fine setae at apex and distally along outer margin in most species, and without dense, long setae on ventral surface. Labial palp (Fig. 146) two segmented; segment 1 ventrally without patch of long setae as long as, or longer than, one-half length of segment 1. Thorax: Pronotum (Fig. 137) trapezoidal; anterior margin slightly emarginate; lateral margin broadly and slightly produced or nearly straight, without angulate expansion or strongly curved edge (Fig. 68). Median ridge of prosternum not produced ventrally, covered with scattered setae or tuft of setae no longer than one-third length of forefemur (Fig. 140). Mesosternum (Fig. 140) anterior margin without apparent setae or with only sparse, scattered setae one-fourth or less length of midfemur. Meso- and metasternum (Fig. 140) without medial processes. Legs (Figs. 148, 149) without flat process at dorsal margin of coxa. Forefemur (Fig. 148) ventrally with setae shorter than 2.0 X width of femur. Foretibia (Fig. 148) as long as, or slightly shorter than foretarsus; ventral margin with setae as long as, or shorter than width of tibia; posterior surface with only scattered setae shorter than 2.0 X width of tibia. Foretarsus (Fig. 148) ventral marginal setae length subequal to, or shorter than, width of tarsus; dorsal margin and anterior and posterior surfaces with some setae measuring in length up to 2.0 X width of tarsus, not arrayed in distinct rows. Hindleg 1.5–2.0 X length of foreleg. Hindfemur (Fig. 149) length 4.5–7.0 X width, dorsally with some setae measuring in length 1.5–2.0 X width of femur. Hindtibia and hindtarsus (Fig. 149) each with row of less than 30 long setae measuring in length 2.0–3.0 X width of tibia. Hindclaw (Fig. 178) nearly straight or slightly and evenly curved; length 4.0–7.0 X basal width; inner margin without armature. Abdomen: Terga 1 and 2 (Fig. 19) without process at posterior margin. Tergum 2 without process immediately anterior of base of operculate gill. Terga 7 and 8 (Fig. 61) with long, fine setae at posterior margin. Tergum 10 (Fig. 61) anterior margin strongly emarginate medially. Segment 2 lateral margin produced into blunt to acute angle (Figs. 116, 155) or distinct posterolateral projection (Fig. 187). Posterolateral projections 3–7 (Fig. 71) well developed and strongly upturned; projection 5 length 2.0–4.5 X basal width; projection 6 directed posteriorly or slightly curved medially; projection 7 short but longer than one-third length of projection 6; projections 8–9 (Fig. 137) shorter; projection 9 one-half or less length of tergum 10.

Sterna flat throughout. Operculate gill (Fig. 73) nearly subquadrate; length 1.1–1.3 X width; posterolateral corner without produced edge; dorsum with or without long setae; posteromedial corner with long marginal setae distinctly longer than those at posterolateral corner; Y-ridge strongly developed, with or without long setae; ventral submarginal rows of hairlike microtrichia present and adjacent to lateral and posterior margins (Fig. 151).

Adult: Male body length 3.0–5.2 mm; wing length 2.8–5.0 mm; caudal filaments length 10.0–16.0 mm. Female body length 4.0–6.3 mm; wing length 3.8–6.2 mm; caudal filaments length 1.8–3.8 mm. General coloration pale yellow. *Head*: Pedicel (Fig. 163) length 2.0 X or more length of scape. *Thorax*: Pronotum (Fig. 74) trapezoidal; lateral margin not convexly produced. Prosternum not distinctly produced ventrally. Meso-and metasternum flat, without vestiges of medial processes. Male foreleg (Fig. 75) from three-fifths length of body to slightly shorter than body length, 1.5–2.5 X length of mid-and hindlegs; foretibia about 2.0 X length of forefemur. *Abdomen*: Terga with or without distinct brown or black maculae (Figs. 74, 164). Vestiges of posterolateral projections usually present on segments 2–7 or 3–7 (Fig. 152). Male genitalia with penes lobe nearly subquadrate (Fig. 165); forceps blade shaped, slightly bowed (Fig. 165) or angled (Fig. 154) at least in some species, and with longitudinal folding.

Egg: Shape ovate (Fig. 565). Polar cap with or without tubercles (Figs. 562, 563). Chorion with more than five costae in lateral half (Figs. 564, 565). Costa asymmetrical in cross-section, overlapping intercostal groove on one side only (Fig. 559). One micropyle present at least in some species (Fig. 560).

Diagnosis: The larvae of *Sparbarus* are distinguished from all other genera of Brachycercinae, except Latineosus, n. gen., by having segment 1 of the labial palpi lacking a patch of long setae on the ventral surface (Fig. 146). Additionally, they can be distinguished by ocellar tubercles that lack apparent setae (Fig. 175), a middle ocellar tubercle that is straight or with the apical portion curved dorsally in the lateral view (Fig. 176), the maxillary and labial palpi that are two segmented (Fig. 145, 146), thoracic sterna that are flat throughout (Fig. 140), an abdominal tergum 2 without a posteromedial process or processes at the base of the operculate gills (Fig. 19), a posterolateral projection 6 not strongly curved medially (Fig. 137), and operculate gills with ventral submarginal rows of hairlike microtrichia (Fig. 151), but without a longitudinal ridge in the sublateral area nor a protruding edge at the posterolateral corner (Fig. 73). In *Caenoculis*, palpi are three segmented (Figs. 29, 30), and abdominal tergum 2 has one posteromedial cone-shaped process (Fig. 35). In Insulibrachys, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In Brachycercus, abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In Oriobrachys, n. gen., operculate gills have a strongly developed longitudinal ridge in the sublateral area (Fig. 284). In Susperatus, n. gen., the apical portion of the middle ocellar tubercle is curved ventrally in the lateral view (Fig. 360), and the thoracic sterna have multiple conical processes (Fig. 361). In Latineosus, n. gen., Alloretochus, n. gen., and Cercobrachys, posterolateral projection 6 is distinctly curved medially (Fig. 375), and ventral submarginal rows of microtrichia are lacking on operculate gills in most species (Fig. 428).

Adults of *Sparbarus* are distinguished from those of *Insulibrachys*, *Susperatus*, n. gen., and *Cercobrachys* by having an antennal pedicel that is twice or more the length of the scape (Fig. 163), a pronotum that has nearly straight lateral margins (Fig. 74), a prosternal median ridge that is not distinctly produced, and usually distinct vestiges of posterolateral projections on abdominal segments 2–7 or 3–7 (Fig. 152). In *Insulibrachys*, the lateral margins of the pronotum are continuously rounded throughout. In *Susperatus*, n. gen., *Alloretochus*, n. gen., and *Cercobrachys*, the prosternal median ridge is distinctly produced medially (Fig. 349). Additionally, in *Cercobrachys* the pedicel length is one and one-half times that of the scape or shorter (Fig. 489), vestiges of posterolateral projections are usually present on no more than abdominal segments 3–6 (Fig. 430). Adults of *Sparbarus* and those of *Brachycercus* cannot be consistently distinguished at the genus level at present, but all known adults of the two genera are readily identifiable at the species level (see the key below).

The eggs of Sparbarus are distinguished from those of Brachycercus and Susperatus, n. gen., by having

multiple costae that are asymmetrical in cross-section (Figs. 558, 559). Eggs of *Brachycercus* are symmetrical in cross-section (Figs. 555, 556), and those of *Susperatus*, n. gen., lack costae (Figs. 567). Eggs of *Sparbarus*, *Latineosus*, n. gen., and *Cercobrachys* cannot be distinguished clearly; however, in *Latineosus*, n. gen., and *Cercobrachys*, the polar cap lacks tubercles (Fig. 571), and the number of costae in the lateral half is less than 10 in most species (Figs. 566, 569). In many North American *Sparbarus*, tubercles are present on the polar cap (Fig. 563), and in the vast majority of species the number of costae in the lateral half is more than 10 (Fig. 563).

Discussion: The species concept of *Brachycercus flavus* Traver (1935) cannot be resolved. Otherwise, it apparently falls under the concept of Sparbarus. Our examination of the types associated with this name, consisting of a male adult holotype and paratypes from "Louisiana, Sabine R Ferry opp Orange, VI-20-1917" and deposited at Cornell University, revealed the following generic characteristics: The antennal pedicel is longer than twice that of the scape, the pronotum has nearly straight lateral margins, the prosternal median ridge is not distinctly produced, and abdominal terga 7-9 have a medial dark stripe. These characteristics taken together place Traver's species in the genus Sparbarus. Traver (1935) mentioned a transverse black line between the ocelli, which is also commonly found among North American Sparbarus, but is not apparent in the type specimens at this time. At the species level, this species is not distinguishable from either S. lacustris, n. comb., or S. maculatus, n. comb., because we have found that supposed color pattern differences among them are variable and unreliable. Only Traver's (1935) illustration of the male forceps would suggest a difference between her species and S. lacustris. Unfortunately, such cannot be verified because the male genitalia are missing from the type material. This is critical because in some other instances Traver's illustrations of genitalia have proven to be unreliable (e.g., McCafferty 2001b). No larvae have ever been clearly associated with Traver's species, although those that are clearly S. lacustris have mistakenly been referred to Traver's species in the past (see discussion of S. lacustris, below). It is impossible to know what the exact concept of Traver's species is, and thus whether it may be distinct or equivalent to some other species of *Sparbarus*. From all of the above, we must treat it as Sparbarus flavus, n. comb., nomen dubium.

Etymology: The generic nomen is a Latinized compound word in the masculine gender and is an allusion to the labial palp segment 1 that does not have ("spar") long setae or hair ("bar") on the ventral surface.

Distribution: Palearctic: Algeria, European and eastern Asian regions of Russia, northern China, Korea, Japan; Oriental: southern China, Sri Lanka; Nearctic: Canada, U.S.A.

Sparbarus capnicus (Zhou, Sun and McCafferty), New Combination

Brachycercus capnicus Zhou, Sun, and McCafferty, 2003b:312.

Mature Larva: Body (Fig. 61) length 3.4–5.0 mm. Caudal filaments length 1.8–2.3 mm. General coloration pale yellow-brown. *Head*: Coloration pale yellow. Frons stained with diffuse brown. Occiput (Fig. 61) stained with brown medially, without dark brown patches or black bands posterior to lateral ocellar tubercle, covered with several short setae; lateral margin posterior to compound eye curved inward. Compound eye (Fig. 62) not strongly produced dorsally. Lateral ocellar tubercle (Figs. 61, 62) length slightly greater than width at base; anterior margin slightly concave; apex rounded. Middle ocellar tubercle (Figs. 61, 62) triangulate in dorsal view, straight in lateral view; length about two-thirds that of lateral ocellar tubercle, and about 1.3 X basal width; apex rounded to bluntly pointed. Antenna (Fig. 63) pale, without macula; pedicel 2.0 X length of scape, with about 10 setae one-half or more length of pedicel. Labrum as in Figure 64. Hypopharynx as in Figure 65. Maxilla (Fig. 66) with galealacinia length 2.9 X basal width; palp segment 1 width 1.6 X width of segment 2; segment 2 1.8 X length of segment 1, with about 10 long, stout setae on distal one-half of inner margin, and with less than 10, fine setae at apex and on outer margin. Labial palp as in Figure 67. *Thorax*: Nota (Fig. 61)

yellow-brown, without distinct black maculae; sterna pale yellow, with diffuse black staining. Pronotum (Figs. 61, 68) darker medially. Propleuron not visible in dorsal view, with sparse marginal setae. Prosternum median transverse ridge with several scattered setae shorter than one-third length of forefemur. Mesosternum anterior margin with several scattered setae shorter than one-fourth length of midfemur. All legs pale throughout, without basal band or apical macula (Figs. 61, 69, 70). Ratios of length of body: foreleg: midleg: hindleg-3.1: 1.0: 1.5: 1.5. Ratios of length of forefemur: tibia: tarsus: claw-3.3: 1.6: 1.7: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.9: 2.5: 2.7: 1.0. Forefemur (Fig. 69) dorsally with row of very short setae in addition to some relatively long setae, and ventrally with row of short setae and less than 10 setae as long as, or slightly longer than, width of femur. Foretibia (Fig. 69) ventral margin with row of four or five short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus (Fig. 69) ventral margin with row of about 10 short setae; anterior and posterior surfaces with some scattered setae as long as width of tarsus. Hindfemur (Fig. 70) length 4.3 X width; dorsal margin with row of short setae interspersed with some setae as along as 1.5 X width of femur; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 70) each dorsally with row of 15–20 long, fine setae as long as about 2.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw (Fig. 70) moderately curved; length 4.0 X basal width. Abdomen: Terga (Fig. 61) pale yellow, without distinct maculae; terga 1, 2, 7–9 with medial area somewhat darker; tergum 10 darkened anteromedially. Posterolateral projection 2 triangulate and blunt at apex (Fig. 71); projections 3-6 (Figs. 61, 71) with apices bluntly pointed; projections 5 and 6 subequal in length, about 2.0 X basal width; projection 6 slightly curved medially; projections 7 and 8 (Figs. 71) short, about one-half length of projection 6; projection 9 (Fig. 61) small. Sterna pale vellow, with diffuse black staining; sternum 9 (Fig. 72) with posterior margin convexly produced. Operculate gill (Fig. 73) yellow-brown except outer and posterior margins pale; length 1.3 X width; dorsum laterally with a few long setae; posteromedial corner with row of long marginal setae about one-half length of operculate gill; posterolateral corner with marginal setae about one-half length of those at posteromedial corner, intermixed with several very short setae; Y-ridge somewhat darker than adjacent areas, with stem and outer branch evenly stained with diffuse brown and with several long setae. Caudal filaments pale yellow.

Male Adult: Body (Fig. 74) length 3.5-3.7 mm. Wing length 3.5 mm. Caudal filaments length 11.0-12.0 mm. *Head*: Frons pale diffuse brown medially dorsal to middle ocellus. Stem of epicranial suture (Fig. 74) bordered with diffuse pale brown staining. Occiput (Fig. 74) pale yellow, stained with diffuse pale brown. Scape and pedicel (Fig. 74) pale brown; pedicel 2.3 X length of scape; flagellum pale. *Thorax*: Pronotum (Fig. 74) pale yellow, with extensive black shading. Prosternum median transverse ridge blackened. Mesonotum (Fig. 74) yellow-brown. Mesosternum yellow, with diffuse black staining; sternacostal suture not blackened. Metanotum posteromedial projection broadly triangulate; apex bluntly pointed. Legs with coxae and trochanters brown; femora without black dorsodistal macula. Forefemur (Fig. 75) pale brown, with brown stripes; foretibia and foretarsus (Fig. 75) pale. Mid- and hindlegs pale. Ratios of length of body: foreleg: midleg: hindleg—2.5: 2.3: 1.0: 1.1. Ratios of length of forefemur: tibia: tarsus—1.0: 2.9: 1.9. Ratios of length of foretarsus segment I: II: III: IV: V—1.0: 12.7: 5.3: 3.0: 2.0. Forewing (Fig. 76) with ratio of length to greatest width— 1.9; Sc, R₁ and adjacent area pale brown; other veins pale. *Abdomen*: Terga (Fig. 74) generally pale, without macula and diffuse shading; terga 3–6 somewhat paler. Sterna pale. Segments 3–7 with vestiges of posterolateral projection 7 short (Fig. 74). Genitalia (Fig. 77) with penes lobes moderately convex laterally in distal half; forceps evenly curved, not angled. Caudal filaments pale.

Female Adult: Body length 4.0 mm. Caudal filaments length 1.2 mm. Forewing length 4.5 mm, with ratio of length to greatest width—2.0. Ratio of length of body: foreleg: midleg: hindleg—2.2: 1.0: 1.3: 1.4. Coloration and vestiges similar to males.

Egg: Habitus as in figure 576. Length about 160 mm. Shape elongate-ovate. Polar cap about one-third length of entire egg, without tubercles. Chorion with 10–15 broad costae in lateral half.

Diagnosis: Certain eastern Asian Sparbarus species, including S. capnicus, S. japonicus, and S. gilliesi,

are similar in that they have a middle ocellar tubercle that is the same length or shorter than the lateral tubercles (Fig. 62); whereas, in S. tubulatus and S. europaeus, the middle ocellar tubercle is distinctly longer than the lateral ones (Fig. 192). In the three mentioned eastern Asian species, posterolateral projections on abdominal segment 2 are no longer than one-half of the length of those on segment 3 (Fig. 71); however, in S. corniger and S. kabyliensis, projections on segment 2 are as long as, or only slightly shorter than, those on segment 3 (Fig. 90). The three eastern Asian species also lack any black bands on the occiput posterior to the lateral ocellar tubercles (Fig. 61). In North American species of Sparbarus, such black bands are always present (Fig. 155). With respect to diagnosing the three eastern Asian species from each other, in S. capnicus, the lateral ocellar tubercles are not finger shaped apically in lateral view (Fig. 62), the middle ocellar tubercle is shorter than twice its basal width in dorsal view and shorter than the lateral tubercles by about one-third (Figs. 61, 62), and the abdominal sterna are stained with diffuse black shading. In S. japonicus, the apical portion of the lateral ocellar tubercles is fingerlike in lateral view (Fig. 117), the middle ocellar tubercle is about two and one-half times as long as its basal width and about the same length of lateral tubercles (Fig. 117), and the abdominal sterna are not shaded with black. In S. capnicus, the pedicel (Fig. 63) is twice as long as the scape and has about 10 relatively long setae, and the abdominal terga (Fig. 61) lack maculae. According to Soldán and Landa (1991), in S. gilliesi, the pedicels are longer than three times the length of scapes and have more than 20 relatively long setae (Fig. 108), and abdominal terga 1, 2, and 7–9 have a pair of brown bands.

Adults of *S. capnicus* are distinguished from the other known adults of *Sparbarus* as follows. Vestiges of posterolateral projections are absent on abdominal segment 2 (Fig. 74), whereas according to Kluge (1991) they are well developed in *S. corniger*. In *S. capnicus*, vestiges of posterolateral projection 6 are directed posterolaterally (Fig. 74), whereas they are strongly curved dorsally in *S. europaeus* (Kluge, per. comm.). Extensive pale black shading is present on the thoracic sterna in *S. capnicus*, but is absent in *S. japonicus*. Abdominal terga are pale, not stained with brown color patterns in *S. capnicus* (Fig. 74), but such coloration is present in all known adults of North American *Sparbarus* species (Fig. 164).

Among Palearctic and Oriental *Sparbarus* species, eggs of *S. capnicus*, *S. corniger*, and *S. japonicus* are similar in that the polar cap is one-third or more the total length of the egg (Fig. 576). In *S. europaeus*, the polar cap is about one-fourth the length of the egg (Fig. 578). The eggs of *S. capnicus* and *S. corniger* can be distinguished by having about 12 costae in the lateral half (Fig. 576). In *S. japonicus*, eggs have about 16 costae in the lateral half (Fig. 562).

Distribution: China: Yunnan, Guizhou.

Material Examined: Two larva, three male adult PARATYPES, China, Yunnan Prov, Jing-Gu Co, Wei-Yuan R (23.30 N, 100.41 E), Feng-Shan Village, IV-8-2001, CF Zhou (PERC).

Sparbarus choctaw, New Species

Mature Larva: Body (Fig. 78) length 6.0 mm. Caudal filaments length 3.8 mm. General coloration yellowbrown. *Head*: Frons (Figs. 78, 79) with black transverse band dorsal to middle ocellar tubercle. Occiput (Figs. 78, 79) stained with diffuse brown patterns medially, with pair of somewhat oblique transverse dark brown bands posterior to lateral ocellar tubercle extending medially from eye to posterior margin; surface covered with several short, fine setae; lateral margin posterior to compound eye nearly parallel with long axis of body. Compound eye (Fig. 79) distinctly produced dorsally. Lateral ocellar tubercle (Fig. 79) slightly longer than basal width; distal half fingerlike and curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 78, 79) elongate-conical in dorsal view and straight in lateral view; length slightly shorter than that of lateral ocellar tubercle, and about twice that of basal width; apex bluntly pointed. Antenna (Fig. 80) pale; scape with black macula; pedicel 2.0 X length of scape, with about 10 setae one-half or more length of pedicel. Labrum as in Figure 81. Hypopharynx as in Figure 82. Maxilla (Fig. 83) with galealacinia length 3.3 X basal width; palp segment 1 width 2.0 X width of segment 2; palp segment 2 1.4 X length of segment 1, with about eight long, stout setae at distal one-third of inner margin, and less than 10 long, fine setae distally on outer margin. Labial palp as in Figure 84. Thorax: Nota (Figs. 78, 79) without distinct black maculae except for few irregular stripes on mesonotum; sterna somewhat paler, stained with diffuse black shading. Pronotum (Figs. 78, 79) subanterior transverse ridge stained brown. Propleuron narrowly visible in dorsal view, with few marginal setae (Fig. 78). Prosternum median transverse ridge with several fine setae shorter than one-fourth length of forefemur. Mesonotum (Fig. 78) laterally with sparse marginal setae. Mesosternum anterior margin with only several scattered, fine setae shorter than one-fourth length of midfemur. All legs pale (Fig. 78); femora with basal half darker, and with small, black dorsodistal macula (Fig. 78); tibiae with basal one-fourth to one-third somewhat darker. Ratios of length of body: foreleg: midleg: hindleg-3.6: 1.0: 1.6: 1.7. Ratios of length of forefemur: tibia: tarsus: claw—2.5: 1.3: 1.5: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.3: 1.9: 2.1: 1.0. Forefemur dorsal margin with row of very short setae in addition to some relatively long setae; ventral margin with row of short setae and less than 10 setae as long as, or slightly longer than, width of femur. Foretibia ventral margin with row of about five short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus ventral margin with row of about seven short setae; anterior and posterior surfaces with some scattered setae as long as 2.0 X width of tarsus. Hindfemur length 5.7 X width; dorsal margin with row of short setae interspersed with some setae as long as 2.0 X width of femur; ventral margin with short setae. Hindtibia and hindtarsus each dorsally with about five fine setae as long as about 2.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw slightly curved; length 6.0 X basal width. Abdomen: Terga (Fig. 78) with distinct dark brown markings as follows: terga 1 and 2 extensively stained with diffuse shading in medial area; terga 7–9 with anterior margin with pair of transverse bands sublaterally, and broad medial macula nearly connected to lateral bands, and with posterior margin with pair of narrow transverse bands sublaterally except on tergum 9; tergum 10 darkened anteriomedially, with broad longitudinal stripe medially, and broad transverse band at posterior margin. Posterolateral projection 2 (Fig. 78) well developed, with length as long as, or longer than, basal width, and with bluntly pointed apex forming acute angle; projections 3–9 (Fig. 78) apices pointed; projections 4–6 subequal in length, about 3.0 X basal width; projection 6 directed posteriorly; projection 7 about two-thirds length of projection 6; projections 8 and 9 small. Sterna without diffuse black staining; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 78) yellow-brown, with some diffuse black shading medially; length 1.1 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae about one-fifth to one-fourth length of operculate gill; posterolateral corner with marginal setae about two-thirds length of those at posteromedial corner, intermixed with several very short setae; Y-ridge with outer branch and adjacent area stained with pale black, without apparent long setae. Caudal filaments pale yellow.

Adult: Unknown.

Egg: Habitus as in Figure 560. Length about 200 mm. Shape elongate-ovate. Polar cap about one-fourth length of entire egg, without tubercles. Chorion with 23–28 costae in lateral half.

Diagnosis: Among the larvae of Nearctic *Sparbarus* species, *S. choctaw* is most similar to *S. lacustris* and *S. nasutus*. These three species have an elongate-conical middle ocellar tubercle that is as long as twice or more of its basal width (Fig. 79), and posterolateral projections on abdominal segment 2 that are at least as long as their basal width and have an acute apex (Figs. 78, 187). Other North American *Sparbarus* species have a short triangulate middle ocellar tubercle (Fig. 156), and have undeveloped posterolateral projections on abdominal segment 2 (Fig. 155). With respect to diagnosing *S. choctaw*, *S. lacustris*, and *S. nasutus*, in *S. choctaw*, the middle ocellar tubercle is slightly shorter than the lateral tubercles (Fig. 79), whereas in *S. nasutus*, the middle ocellar tubercle is distinctly longer than the lateral ones (Fig. 175). In *S. choctaw*, the frons has a transverse black band dorsal to the middle ocellar tubercle (Fig. 79), posterolateral projections on abdominal segment 7 are about two-thirds of the length of those on segment 6 (Fig. 78), and the sublateral maculae on the anterior margin of terga 7–9 are elongate bands nearly connected by a broad medial macula (Fig. 78). In *S.*

lacustris, the frons does not have a transverse black band, projections on segment 7 are one-half or less of the length of those on segment 6 (Fig. 137), and the sublateral maculae at the anterior margin of abdominal terga 7–9 are short and generally dotlike (Fig. 137).

Eggs of *S. choctaw* and *S. lacustris* do not have any tubercles on the polar cap (Fig. 560), whereas in all other North American *Sparbarus*, including *S. nasutus*, *S. maculatus*, *S. coushatta*, n. sp., and *S. miccosukee*, n. sp., tubercles are present on the polar cap (Fig. 563). Furthermore, the eggs of *S. choctaw* have 23–28 costae in the lateral half (Fig. 560); whereas in *S. lacustris*, eggs have 15–20 costae in the lateral half (Fig. 558).

Etymology: The specific epithet a noun in apposition and is after the native North American people of the Choctaw tribe, inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: Mississippi.

Material Examined: Larva HOLOTYPE, Mississippi, Harrison Co, Cat No 8-2254-1, L Berner (PERC).

Sparbarus corniger (Kluge), New Combination

Brachycercus corniger Kluge, 1991:16.

Larva, Adult, and Egg: Material of *B. corniger* were not available to us for study; however, see formal description by Kluge (1991), figures 85–93, 577, and diagnosis below.

Diagnosis: Larvae of *S. corniger*, together with North African species *S. kabyliensis* and the Nearctic species *S. nasutus*, can be distinguished from all other *Sparbarus* species by the presence of strongly developed posterolateral projections on abdominal segment 2 that are as long as, or only slightly shorter than, those on segment 3 (Fig. 90). In the remainder of the genus, projections on segment 2 are at the most only one-half of the length of those on segment 3 (much less in most species) (Fig. 71). *Sparbarus corniger* has a maxillary palp segment 2 with long, stout setae along the distal one-third to two-fifths of the inner margin (Fig. 89). In *S. kabyliensis*, such setae are present in the distal three-fourths of the inner margin of maxillary palp segment 2 (Fig. 131). In *S. corniger*, the middle ocellar tubercle and lateral ocellar tubercles are subequal in length (Figs. 85, 86), and the occiput does not have black bands posterior to the lateral ocelli. In *S. nasutus*, the middle ocellar tubercle is twice or more as long as the lateral ocellar tubercles (Fig. 175), and the occiput has a pair of black bands posterior to the lateral ocellar tubercles (Fig. 174).

Adults of *S. corniger* and *S. nasutus* are distinguished from all other *Sparbarus* (and Brachycercinae) species known as adults by having distinct vestiges of posterolateral projections on the abdominal segment 2. Adults of *S. corniger* do not have brown bands posterior to the lateral ocelli nor brown medial stripes and lateral maculae on the abdominal terga, whereas such markings are present in *S. nasutus* (Fig. 189).

Among Palearctic and Oriental *Sparbarus* species, eggs of *S. corniger*, *S. capnicus*, and *S. japonicus* are similar in that the polar cap is one-third or more the total length of the egg (Fig. 577). In *S. europaeus*, the polar cap is about one-fourth the length of the egg (Fig. 578). The eggs of *S. capnicus* and *S. corniger* can be distinguished by having about 12 costae in the lateral half (Figs. 576, 577). In *S. japonicus*, eggs have about 16 costae in the lateral half (Fig. 562).

Distribution: Eastern Russia.

Sparbarus coushatta, New Species

Mature Larva: Body (Fig. 94) length 4.8–5.6 mm. Caudal filaments length 2.2–3.0 mm. General coloration pale yellow-brown. *Head*: Occiput (Fig. 94) stained with diffuse brown patterns medially, with pair of somewhat oblique transverse dark brown bands posterior to lateral ocellar tubercle extending medially from eye to posterior margin (absent in some); surface covered with several short, fine setae; lateral margin posterior to

compound eye nearly parallel with long axis of body. Compound eye (Fig. 95) distinctly produced dorsally. Lateral ocellar tubercle (Fig. 95) as long as, or slightly longer than, basal width; distal half slightly curved anteriorly; apex rounded to bluntly pointed. Middle ocellar tubercle (Fig. 95) triangulate in dorsal view, straight in lateral view; length subequal to basal width, and about two-thirds length of lateral tubercle; apex pointed. Antenna (Fig. 96) pale; scape with black macula; pedicel about 2.5 X length of scape, with less than 10 setae one-half or more length of pedicel. Labrum as in Figure 97. Hypopharynx as in Figure 98. Maxilla (Fig. 99) with galealacinia length 3.0 X basal width; palp segment 1 width 1.8 X width of segment 2; palp segment 2 1.3 X length of segment 1, with about 10 long, stout setae in distal half of inner margin, and about 10 long, fine setae distally on outer margin. Labial palp as in Figure 100. Thorax: Nota (Fig. 94) brown, with some irregular black maculae; sterna somewhat paler, stained with diffuse black shading. Propleuron not visible or only narrowly visible in dorsal view, with few marginal setae (Fig. 94). Prosternum median transverse ridge with tuft of fine setae one-fourth to one-third length of forefemur. Mesonotum laterally with sparse marginal setae. Mesosternum anterior margin with only several scattered, fine setae shorter than one-fourth length of midfemur. All legs pale throughout, except femora somewhat darker at basal portion but not with distinct band, and with small, black dorsodistal macula (Fig. 94). Ratios of length of body: foreleg: midleg: hindleg-3.9: 1.0: 1.6: 1.7. Ratios of length of forefemur: tibia: tarsus: claw—2.4: 1.2: 1.3: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.4: 1.9: 2.3: 1.0. Forefemur dorsal margin with row of very short setae in addition to some setae slightly longer than width of femur; ventral margin with row of short setae and less than 10 setae as long as, or slightly longer than, width of femur. Foretibia ventral margin with row of about eight short setae: posterior surface with some scattered setae as long as width of tibia. Foretarsus ventral margin with row of about 12 short setae; anterior and posterior surfaces with some scattered setae as long as 2.0 X width of tarsus. Hindfemur length 5.0 X width; dorsal margin with row of short setae interspersed with some setae slightly longer than width of femur; ventral margin with short setae. Hindtibia and hindtarsus each dorsally with row of 10–15 long, fine setae as long as about 2.5 X width of tibia, and ventrally with row of short, stout setae. Hindclaw evenly curved; length 5.0 X basal width. Abdomen: Terga (Fig. 94) with distinct dark brown markings as follows (absent in some): terga 1 and 2 stained with diffuse black at medial area and on posterior margin; terga 7–9 with pair of short transverse bands sublaterally at anterior margin, and with broad longitudinal stripe medially; tergum 10 with broad band on posterior margin. Posterolateral projection 2 shorter than basal width, with apex forming right angle (Fig. 94); projections 3–9 (Fig. 94) apices pointed; projections 4–6 subequal in length, about 2.2 X basal width; projection 6 directed posteriorly; projection 7 length about twofifths that of projection 6; projections 8 and 9 small. Sterna without diffuse black shading; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 94) pale yellow-brown; length 1.2 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae up to two-fifths length of operculate gill; posterolateral corner with row of marginal setae about one-half length of those of posteromedial corner and intermixed with several very short setae; Y-ridge with adjacent areas extensively stained with diffuse pale black shading, with outer branch stained with black at distal portion. Caudal filaments pale yellow.

Adult: Unknown.

Egg: Habitus as in Figure 561. Length about 200 mm. Shape elongate-ovate. Polar cap about one-fourth length of entire egg, with number of tubercles. Chorion with about 18 costae in lateral half.

Diagnosis: Larvae of the North American *Sparbarus* species *S. coushatta, S. miccosukee*, n. sp., and *S. maculatus* are relatively similar. These three species share an apically pointed middle ocellar tubercle that is triangulate and about as long as its basal width (Fig. 95), and posterolateral projections on abdominal segment 2 that are shorter than their basal width and form a blunt right angle apically (Fig. 94). Larvae of the other three North American species, *S. choctaw, S. lacustris*, and *S. nasutus*, have an elongate-conical middle ocellar tubercle that is as long as twice or more of its basal width (Fig. 139), and posterolateral projections on abdominal segment 2 that are as long as, or longer than, their basal width and have an acute apex (Fig. 137). In *S. coushatta*, the femora have an apical black macula on the dorsal margin (Fig. 94), whereas in *S. maculatus*,

these markings are absent (Fig. 155). In *S. coushatta*, abdominal terga 7–9 have a medial longitudinal stripe (Fig. 94), and the pedicels are about two and one-half times the length of the scape (Fig. 96), whereas in *S. miccosukee*, n. sp., abdominal terga 7–9 have a pair of long and broad submedially triangulate maculae (Fig. 166), and the pedicels are about twice the length of the scape (Fig. 168).

Among egg types that have a number of tubercles on the polar cap, those of *S. coushatta* and *S. nasutus* are most similar and are difficult to distinguish (Figs. 561, 565). However they can be distinguished from other species by having 17–20 costae in the lateral half. Eggs of *S. miccosukee*, n. sp. have only seven to eight costae in the lateral half (Fig. 564), and eggs of *S. maculatus* have 11–15 costae in the lateral half (Fig. 563).

Etymology: The specific epithet a noun in apposition and is after the native North American people of the Coushatta (Alabama Coushatta) tribe.

Distribution: U.S.A.: Texas.

Material Examined: Larva HOLOTYPE, Texas, San Jacinto Co, Site 56-F, Winters Bayou, VI-15-1998, DE Bowles (PERC). One larva PARATYPE, same data as holotype (TAMU). TEXAS, Austin Co: one larva, San Bernard R at I-10 near Sealy, V-20-1997, NA Wiersema (TAMU); San Jacinto Co: three larvae, Site B, E fk San Jacinto R, VIII-11-1998, G Linam, T Jurgensen (TAMU), one larva, Site F, E fk San Jacinto R, VIII-11-1998, G Linam, T Jurgensen (TAMU).

Sparbarus europaeus (Kluge), New Combination

Brachycercus europaeus Kluge, 1991:19.

Larva, Adult, and Egg: Material of *B. europaeus* were not available to us for study; however, see formal description by Kluge (1991), figures 101–105, 578, 579, and diagnosis below.

Diagnosis: The eastern European species *S. europaeus* and the eastern Asian species *S. tubulatus* are similar in the larval stage in that they share a developed middle ocellar tubercle that is distinctly longer than the lateral ocellar tubercles (Figs. 101, 102). In all other Palearctic and Oriental *Sparbarus*, the middle ocellar tubercle is as long as, or shorter than, the lateral tubercles (Fig. 62). In *S. europaeus*, the length of segment 2 of the maxillary palpi is one and one-half times the length of segment 1 (Fig. 103), whereas in *S. tubulatus*, segment 2 is only slightly longer than segment 1 (Fig. 196). The North American species *S. nasutus* also has a middle ocellar tubercle that is distinctly longer than the lateral tubercles (Fig. 175); however, it can be distinguished from *S. europaeus* by the pair of black bands posterior to the lateral ocellar tubercles (Fig. 174) and the strongly developed posterolateral projections on the abdominal segment 2 (Fig. 187) that are as long as those on segment 3.

In adults of *S. europaeus*, abdominal segment 2 does not have vestiges of posterolateral projections, whereas in *S. corniger*, they are well developed and distinct. In *S. europaeus*, vestiges of the posterolateral projections on abdominal segment 6 are strongly curved dorsally (Kluge, per. comm.), whereas in *S. capnicus* and *S. japonicus*, these vestiges are directed posterolaterally (Fig. 74). In *S. europaeus*, the abdominal terga do not have brown medial stripes and sublateral maculae, whereas such markings are present on terga 7–9 in all Nearctic species of *Sparbarus* (Fig. 164).

Among Palearctic and Oriental *Sparbarus* species, eggs of *S. europaeus* can be distinguished by having a polar cap that is about one-fourth the total length of the egg (Fig. 578). In *S. corniger*, *S. capnicus*, and *S. japonicus*, the polar cap is one-third or more the length of the egg (Fig. 562).

Distribution: Western Russia.

Sparbarus gilliesi (Soldán and Landa), New Combination

Brachycercus gilliesi Soldán and Landa, 1991:235.

Larva: Material of *B. gilliesi* were not available to us for study; however, see formal description by Soldán and Landa (1991), figures 108–115, and diagnosis below.

Adult: Unknown.

Egg: Unknown.

Diagnosis: The larvae of *S. gilliesi* are similar to those of two eastern Asian species, *S. capnicus* from China and *S. japonicus* from Japan. These three species share a middle ocellar tubercle that is the same length as, or shorter than, the lateral tubercles, whereas in the Palearctic species *S. tubulatus* and *S. europaeus*, the middle ocellar tubercle is distinctly longer than the lateral ones (Fig. 192). In the three similar Asian species, posterolateral projections on abdominal segment 2 are no longer than one-half of the length of those on segment 3, whereas in the Palearctic species *S. corniger* and *S. kabyliensis*, projections on segment 2 are as long as, or only slightly shorter than, those on segment 3 (Fig. 94). The three similar Asian species also lack any black bands on the occiput posterior to the lateral ocellar tubercles. In North American species of *Sparbarus*, such black bands are always present (Fig. 155). Among the three similar Asian species, *S. gilliesi* is distinguished, according to Soldán and Landa (1991), by the presence of a pedicel that is longer than three times the length of the scape and that has dense (more than 20) relatively long setae (Fig. 108). In *S. capnicus* and *S. japonicus*, the pedicels are twice the length of the scapes and are covered with about 10 or fewer relatively long setae (Fig. 118).

Distribution: Sri Lanka.

Sparbarus japonicus (Gose), New Combination

Brachycercus japonica Gose, 1980:454. *Brachycercus japonicus* Gose, 1980: Bae, 1997:409.

Mature Larva: Body (Fig. 116) length 4.8 mm. Caudal filaments length 3.1 mm. General coloration pale yellow-brown. Head: Coloration pale yellow. Frons (Fig. 117) stained with brown. Occiput (Fig. 116) stained with brown medially, without dark brown bands posterior to lateral ocellar tubercles; surface with several short setae: lateral margin posterior to compound eve curved inward. Compound eve (Fig. 117) not strongly produced dorsally. Lateral ocellar tubercle (Fig. 117) length greater than basal width; distal portion fingerlike, slightly curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 116, 117) elongate-conical in dorsal view, straight in lateral view; length subequal to that of lateral ocellar tubercle, and about 2.5 X basal width; apex rounded to bluntly pointed. Antenna (Fig. 118) pale, without macula; pedicel 2.0 X length of scape, with about 10 setae one-half or more length of pedicel. Labrum as in Figure 119. Hypopharynx as in Figure 120. Maxilla (Fig. 121) with galealacinia length 2.9 X basal width; palp segment 1 width 1.8 X width of segment 2; segment 2 1.5 X length of segment 1, with about 10 long, stout setae in distal half of inner margin, and with less than 10 fine setae at apex and on outer margin. Labial palp as in Figure 122. Thorax: Nota (Fig. 116) yellow-brown, without distinct black macula; sterna pale yellow, without diffuse black stain. Propleuron narrowly visible in dorsal view, with sparse marginal setae. Prosternum median transverse ridge with several scattered setae shorter than one-third length of forefemur. Mesonotum laterally with sparse marginal setae. Mesosternum anterior margin with several scattered setae shorter than one-fourth length of midfemur. All legs pale throughout, without basal band or apical macula (Fig. 116). Ratios of length of body: foreleg: midleg: hindleg-3.0: 1.0: 1.5: 1.6. Ratios of length of forefemur: tibia: tarsus: claw-3.5: 1.8: 1.9: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—4.4: 2.6: 2.6: 1.0. Forefemur dorsal margin with row of very short

setae in addition to some relatively long setae; ventral margin with row of short setae and less than 10 setae as long as, or slightly longer than, width of femur. Foretibia ventral margin with row of about six short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus ventral margin with row of about 10 short setae; anterior and posterior surfaces with some scattered setae as long as width of tarsus. Hindfemur length 5.8 X width; dorsal margin with row of short setae interspersed with some setae as along as 1.5 X width of femur; ventral margin with short setae. Hindtibia and hindtarsus each dorsally with row of about 20 long, fine setae as long as about 3.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw moderately curved; length 5.0 X basal width. Abdomen: Terga (Fig. 116) pale yellow, without distinct maculae; tergum 9 somewhat paler; tergum 10 darkened anteriomedially. Posterolateral projection 2 (Fig. 116) short, somewhat triangulate and blunt at apex; projections 3–7 (Fig. 116) apices bluntly pointed; projections 5 and 6 subequal in length, about 2.0 X basal width; projection 6 directed posteriorly; projection 7 short, about one-half length of projection 6; projections 8 and 9 (Fig. 116) small. Sterna pale yellow, without diffuse black staining; sternum 9 with posterior margin convexly produced. Operculate gill (Fig. 116) yellow-brown except outer and posterior margins pale; length 1.2 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae one-fourth to one-third length of operculate gill; posterolateral corner with row of marginal setae two-thirds length of those at posteromedial corner intermixed with several very short setae; Y-ridge somewhat darker than adjacent area, without black staining, and with several long setae. Caudal filaments pale yellow.

Male Adult: Body (Fig. 123) length 3.2–4.0 mm. Wing (Fig. 125) length 3.1–3.4 mm. Caudal filaments length 11.0–14.0 mm. *Head*: Frons stained with some diffuse brown medially. Occiput (Fig. 123) pale yellow, without distinct macula. Stem of epicranial suture (Fig. 123) bordered with diffuse pale brown. Scape and pedicel (Fig. 123) pale brown; pedicel 2.0 X length of scape; flagellum pale. *Thorax*: Pronotum (Fig. 123) pale yellow, without black shading. Prosternum median transverse ridge blackened. Mesonotum (Fig. 123) yellow-brown. Mesosternum yellow, without diffuse black staining; sternacostal suture not blackened. Metanotum posteromedial projection broadly triangulate; apex bluntly pointed. Legs with coxae and trochanters brown; femora without black dorsodistal macula. Forefemur (Fig. 124) pale brown, with brown stripes; foretibia and foretarsus (Fig. 124) pale. Mid- and hindlegs pale. Ratios of length of body: foreleg: midleg: hindleg—2.4: 1.9: 1.0: 1.1. Ratios of length of forefemur: tibia: tarsus—1.0: 2.5: 1.8. Ratios of length of foretarsus segment I: II: III: IV: V—1.0: 8.0: 3.6: 2.0: 1.2. Forewing (Fig. 125) with ratio of length to greatest width—1.8; Sc, R1 and adjacent area pale brown; other veins pale. *Abdomen*: Terga (Fig. 123) and sterna pale throughout, without macula and diffuse shading. Segments 3–7 with vestiges of posterolateral projection 7 relatively short. Genitalia (Fig. 126) with penes lobes moderately convex distolaterally; forceps evenly curved, not angled. Caudal filaments pale.

Female Adult: Body length 4.4–4.6 mm. Caudal filaments length 2.0–2.3 mm. Forewing length 3.8–4.1 mm, with ratio of length to greatest width—2.1. Ratio of length of body: foreleg: midleg: hindleg—3.6: 1.0: 1.5: 1.6. Coloration and vestiges similar to males.

Egg: Habitus as in Figure 562. Length about 200 mm. Shape elongate-ovate. Polar cap about one-third to one-half length of entire egg, without tubercles. Chorion with about 15 broad costae in lateral half.

Diagnosis: The larvae of *S. japonicus* are similar to those of the other two Asian species, *S. capnicus* and *S. gilliesi*, in that they share a middle ocellar tubercle that is the same length or shorter than the lateral tubercles (Fig. 117). In the Palearctic species *S. tubulatus* and *S. europaeus*, the middle ocellar tubercle is distinctly longer than the lateral ones (Fig. 192). In the three similar Asian species, posterolateral projections on abdominal segment 2 are no longer than one-half of the length of those on segment 3 (Fig. 116). In the Palearctic species *S. corniger* and *S. kabyliensis*, projections on segment 2 are as long as, or only slightly shorter than, those on segment 3 (Fig. 90). The three similar Asian species also lack any black bands on the occiput posterior to the lateral ocellar tubercles (Fig. 116). In North American species of *Sparbarus*, such black bands are always present (Fig. 155). With respect to the diagnosis of the three eastern Asian species from each other, in *S.*

japonicus, the apical portion of the lateral ocellar tubercles is fingerlike in lateral view (Fig. 117), the middle ocellar tubercle is about two and one-half times as long as its basal width and about the same length of the lateral tubercles (Fig. 117), and the abdominal sterna are not stained with black shading (Fig. 116). In *S. capnicus*, the lateral ocellar tubercles are not finger shaped apically in lateral view (Fig. 62), the middle ocellar tubercle is shorter than one and one-half times of its basal width and shorter than the lateral tubercles by about one-third (Fig. 61), and the abdominal sterna are stained with diffuse black shading. In *S. japonicus*, the pedicels are twice as long as the scapes and have about 10 relatively long setae (Fig. 118), and the abdominal terga lack maculae (Fig. 116); whereas according to Soldán and Landa (1991), in *S. gilliesi*, the pedicels are longer than three times the length of the scapes and have more than 20 relatively long setae (Fig. 108), and abdominal terga 1, 2, and 7–9 have a pair of brown bands.

The adults of *S. japonicus* are distinguished from the other known adults of *Sparbarus* as follows. In *S. japonicus*, vestiges of the posterolateral projections are absent on abdominal segment 2. In *S. corniger*, these vestiges are well-developed and distinct (Kluge, 1991). In *S. japonicus*, vestiges of the projections on segment 6 are directed posterolaterally (Fig. 123), whereas in *S. europaeus*, these vestiges are strongly curved dorsally (Kluge, per. comm.). In *S. japonicus*, diffuse black shading is absent on the thoracic sterna, whereas in *S. capnicus*, such shading is present. In *S. japonicus*, abdominal terga (Fig. 123) are pale, not stained with brown color patterns, as they are in all the North American *Sparbarus* (Fig. 164).

Among Palearctic and Oriental *Sparbarus* species, eggs of *S. japonicus*, *S. capnicus*, and *S. corniger* are similar in that the polar cap is one-third or more the total length of the egg (Fig. 562). In *S. europaeus*, the polar cap is about one-fourth the length of the egg (Fig. 578). The eggs of *S. japonicus* can be distinguished by having about 16 costae in the lateral half (Fig. 562). In *S. capnicus* and *S. corniger*, eggs have about 12 costae in the lateral half (Figs. 576, 577).

Distribution: Japan.

Material Examined: JAPAN: one larva (IIAS), five male adults, five female adults (PERC), Hirose (34° 40' N, 136° 05' E, 150m alt), Nabari-gawa R at Tsukigase-mura, Nara Prefecture, Honshu, IX-5-1998, K Tojo.

Sparbarus kabyliensis (Soldán), New Combination

Brachycercus kabyliensis Soldán: 1986:312.

Larva: Material of *B. kabyliensis* were not available to us for study; however, see formal description by Soldán (1986), figures 127–136, and diagnosis below.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Among *Sparbarus* species, larvae of the North African species *S. kabyliensis*, the eastern Palearctic species *S. corniger*, and the North American species *S. nasutus* differ from those of other *Sparbarus* in that they have strongly developed posterolateral projections on abdominal segment 2 that are as long as, or slightly shorter than, projections on segment 3 (Fig. 135). In other *Sparbarus* species, projections on segment 2 are distinctly shorter than those on segment 3 (Fig. 71). *Sparbarus kabyliensis*, however, can be distinguished from *S. corniger* and *S. nasutus* as follows. In *S. kabyliensis*, segment 2 of the maxillary palpi has long, stout setae in the distal three-fourths of the inner margin (Fig. 131), whereas in *S. corniger*, such setae are present only in the distal one-third to two-fifths of the inner margin of palp segment 2 (Fig. 89). In *S. kabyliensis*, the middle ocellar tubercle is shorter than the lateral tubercles, and the occiput lacks black bands posterior to the lateral ocellar tubercles. In *S. nasutus*, the middle ocellar tubercle is distinctly longer than the lateral tubercle is distinctly longer than the lateral tubercles (Fig. 175), and the occiput is stained with a distinct lateral band posterior to each of the lateral

Sparbarus lacustris (Needham), New Combination

Caenis lacustris Needham, 1918:249. Eurycaenis pallida Ide, 1930:218, nec Brachycercus pallidus Tshernova, 1928. Eurycaenis idei Lestage, 1931:119, replacement name for E. pallida Ide. Eurycaenis lacustris (Needham), 1918: Traver, 1932:139. Brachycercus idei (Lestage), 1931: Traver, 1935:641. Brachycercus lacustris (Needham), 1918: Traver, 1935:641. Brachycercus lacustris (Needham), 1918 [= B. idei (Lestage)]: Lyman, 1944:3.

Mature Larva: Body (Figs. 137, 138) length 4.7–7.5 mm. Caudal filaments length 3.0–4.5 mm. General coloration from pale yellow-brown to dark red-brown. Head: Frons stained with diffuse brown. Occiput (Figs. 138, 139) stained with diffuse brown patterns medially, with pair of somewhat oblique transverse dark brown bands posterior to lateral ocellar tubercle extending medially from eye to posterior margin; surface covered with several short and relatively long, fine setae; lateral margin posterior to compound eye parallel with long axis of body. Compound eye (Fig. 139) distinctly produced dorsally. Lateral ocellar tubercle (Fig. 139) slightly longer than basal width; distal half fingerlike and curved anteriorly; apex rounded to bluntly pointed. Middle ocellar tubercle (Fig. 139) elongate-conical in dorsal view, straight in lateral view; length slightly less than that of lateral ocellar tubercle, and about 2.0 X that of basal width; apex bluntly pointed. Antenna (Fig. 147) pale; scape with longitudinal black macula; pedicel 2.0 X length of scape, with less than 10 setae onehalf or more length of pedicel. Mouthparts as in Figures 141-146. Maxilla (Fig. 145) with galealacinia length 2.9 X basal width; palp segment 1 width 1.9 X width of segment 2; palp segment 2 1.3 X length of segment 1, with about 10 long, stout setae in distal one-third of inner margin, and less than 10 long, fine setae distally on outer margin. Thorax: Nota (Figs. 137, 138) without distinct black maculae except for few irregular maculae on mesonotum; sterna somewhat paler, with some diffuse black staining. Pronotum (Figs. 137, 139) subanterior transverse ridge not stained with diffuse black. Propleuron not visible or only narrowly visible in dorsal view, with few marginal setae (Fig. 137). Prosternum median transverse ridge with several fine setae shorter than one-fourth length of forefemur. Mesonotum (Figs. 137, 138) laterally with sparse marginal setae. Mesosternum (Fig. 140) anterior margin with only several scattered, fine setae shorter than one-fourth length of midfemur. Legs (Figs. 148, 149) pale; femora with basal half darker, forming distinct band in some individuals, and with small, black dorsodistal macula; tibiae with basal one-fourth to one-third somewhat darker. Ratios of length of body: foreleg: midleg: hindleg-4.0: 1.0: 1.7: 1.8. Ratios of length of forefemur: tibia: tarsus: claw—2.3: 1.2: 1.3: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.3: 1.7: 2.0: 1.0. Forefemur (Fig. 148) dorsal margin with row of very short setae in addition to some relatively long setae; ventral margin with row of short setae and about six setae as long as, or slightly longer than, width of femur. Foretibia (Fig. 148) ventral margin with row of five to eight short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus (Fig. 148) ventral margin with row of 10-12 short setae; anterior and posterior surfaces with some scattered setae as long as 2.0 X width of tarsus. Hindfemur (Fig. 149) length 5.0 X width; dorsal margin with row of short setae interspersed with some setae as long as 2.0 X width of femur; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 149) each dorsally with row of about 15 long, fine setae as long as about 3.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw (Fig. 149) slightly curved; length 5.6 X basal width. Abdomen: Terga (Fig. 137) with distinct dark brown markings as follows (absent in some): terga 1 and 2 with broad longitudinal stripe medially and narrow transverse stripe at posterior margin; terga 7–9 with pair of short transverse bands sublaterally at anterior margin, with broad longitudinal stripe medially, and with pair of narrow transverse stripes laterally at posterior margin except in tergum 9; tergum 10 darkened anteriomedially, with broad longitudinal stripe medially, and broad transverse stripe at posterior margin. Posterolateral projection 2 (Figs. 137, 138) moderately developed, with length as long as, or slightly longer than, basal width, and with apex forming angle clearly less than 90 degrees and bluntly pointed; projections 3–9 (Figs. 137, 138) apices pointed; projections 4–6 subequal in length, about 3.0 X basal width; projection 6 directed posteriorly; projection 7 length one-half or less that of projection 6; projections 8 and 9 small. Sterna unmarked, or with some diffuse black staining; sternum 9 posterior margin convexly produced. Operculate gill (Figs. 150, 151) yellow-brown except outer and posterior margins pale, with diffuse black staining at medial region in some individuals; length 1.2 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae up to one-third length of operculate gill; posterolateral corner with several very short setae; Y-ridge paler than adjacent areas in some individuals, with outer branch stained with black, forming patch in apical half of outer branch, or stripe along entire outer branch, and with few long setae. Caudal filaments pale yellow.

Male Adult: Northern populations (e.g., Michigan, Indiana, Iowa) body (Fig. 152) length 4.5–5.2 mm, caudal filaments length 15.0-16.0 mm, and wing length 4.5-5.0 mm. Southern populations (e.g., Texas, Alabama) body length 3.5-3.8 mm, caudal filaments length 11.0 mm, and wing length 3.4-3.6 mm. Head: Occiput (Fig. 152) pale yellow, with pair of diffuse, transverse brown stripes extending from eye to posterior margin (most posterior stripe indistinct or absent in some individuals). Epicranial suture and frons pale yellow. Antenna pale; scape with apical black macula; pedicel 2.1 X length of scape. Thorax: Pronotum (Fig. 152) pale vellow, without extensive black shading. Prosternum vellow, with median transverse ridge not blackened. Mesonotum (Fig. 152) yellow-brown. Mesosternum yellow, without diffuse black staining; sternacostal suture not blackened. Metanotum posteromedial projection broadly triangulate; apex bluntly pointed. Legs with coxae and trochanters brown; femora with black dorsodistal macula (Fig. 153). Forefemur pale brown, with longitudinal brown stripes; foretibia and foretarsus pale. Mid- and hindlegs pale. Ratios of length of body: foreleg: midleg: hindleg—2.5: 1.9: 1.0: 1.1. Ratios of length of forefemur: tibia: tarsus—1.0: 2.5: 1.8. Ratios of length of foretarsus segment I: II: III: IV: V-1.0: 4.0: 2.5: 2.3: 1.9. Forewing with ratio of length to greatest width—1.7; Sc, R₁ and adjacent area pale brown; other veins pale. Abdomen: Coloration (Fig. 152) generally pale, with brown maculae usually as follows: terga 1 and 2 with broad longitudinal stripe medially and narrow transverse stripe along posterior margin; terga 7–9 with pair of short transverse stripes sublaterally at anterior margin, broad longitudinal stripe medially, and pair of narrow transverse stripes laterally at posterior margin except in tergum 9; tergum 10 with longitudinal stripe medially and broad transverse stripe along posterior margin. Segments 3–7 with vestiges of posterolateral projections; vestige of posterolateral projection 7 short (Fig. 152). Genitalia (Fig. 154) with penes lobes moderately convex distolaterally; forceps distinctly angled at one-fifth to one-fourth distance from base. Caudal filaments pale.

Female Adult: Northern populations body length 5.0–5.5 mm, caudal filaments length 3.2–3.8 mm, and wing length 4.8–5.3 mm. Southern populations body length 4.0 mm, caudal filaments length 1.8 mm, wing length 3.8 mm. Ratio of wing length to greatest width—1.9. Ratio of length of body: foreleg: midleg: hind-leg—3.3: 1.0: 1.6: 1.7. Coloration and vestiges similar to males.

Egg: Habitus as in Figure 558. Length about 180 mm. Shape elongate-ovate. Polar cap about one-fourth length of entire egg, without tubercles. Chorion with 15–20 broad costae in lateral half.

Diagnosis: Among the larvae of Nearctic *Sparbarus*, which can be easily distinguished as a group by the presence of transverse brown bands on occiput and brown patterns on abdominal terga (Fig. 138), *S. lacustris* is most similar to *S. nasutus* and *S. choctaw*, in that they share a middle ocellar tubercle that is elongate-conical and as long as, or longer than, twice its basal width (Fig. 139), and posterolateral projections on abdominal segment 2 that are at least as long as, or longer than, their basal width and form a distal angle clearly less than 90 degrees (Fig. 137). In the other North American species *S. maculatus*, *S. coushatta*, and *S. miccosukee*, n. sp., the middle ocellar tubercle is short-triangulate and as long as its basal width in dorsal view (Fig. 156), and
the projections on segment 2 are not developed, being shorter than their basal width, and form a blunt right angle distally (Fig. 155). In *S. lacustris*, the middle ocellar tubercle is slightly shorter than the lateral ocellar tubercles (Fig. 139), whereas in *S. nasutus*, the middle ocellar tubercle is distinctly longer than the lateral tubercles (Fig. 175). In *S. lacustris*, the frons lacks transverse black bands, posterolateral projections on abdominal segment 7 are one-half or less of the length of those on segment 6 (Fig. 137), and the sublateral maculae at the anterior margins of abdominal terga 7–9 are short and nearly dotlike (Figs. 137, 138). In *S. choctaw*, there are transverse black bands dorsal to the middle ocellar tubercle (Fig. 78), projections on segment 7 are about two-thirds of the length of those on segment 6 (Fig. 78), and the sublateral maculae on the anterior margins of the terga 7–9 are elongate and nearly connected with the medial longitudinal stripe (Fig. 78).

Among known adults of North American *Sparbarus* species, adults of *S. lacustris* have an abdominal segment 2 that lacks vestiges of posterolateral projections, whereas such vestiges are distinct and developed in *S. nasutus*. In *S. lacustris*, the femora have a small, black dorsodistal macula (Fig. 153), and the forceps are distinctly angled at one-fifth to one-fourth the distance from the base (Fig. 154). In *S. maculatus*, the femora lack maculae, and forceps are not angled but are slightly and evenly bowed (Fig. 165).

Eggs of *S. lacustris* and *S. choctaw* do not have any tubercles on the polar cap, whereas in the other known eggs of North American *Sparbarus* including *S. nasutus*, *S. maculatus*, *S. coushatta* and *S. miccosukee*, n. sp., a number of tubercles are present on the polar cap (Fig. 565). In *S. lacustris*, there are 15–20 costae in the lateral half (Fig. 558), whereas in *S. choctaw*, there are 23–28 costae in the lateral half (Fig. 560).

Discussion: Sparbarus lacustris was the first species of Brachycercinae described from North America. Needham (1908) first recorded it from one larval specimen taken at Walnut Lake, Michigan and identified as Ephemerella sp. After examination of additional larval material from Oneida Lake, New York, Needham (1918) formally named the species *Caenis lacustris*, based on the similarity between it and the European (and herein shown to be Holarctic) species C. harrisella (= Brachycercus harrisella). Some years later, Ide (1930) described Eurycaenis pallida from male adults collected at Daventry, Ontario. That name, however, was preoccupied by a European species described by Tshernova (1928), and thus was given the new name, Eurycaenis idei, by Lestage (1931). Lyman (1944) reared what was then known as Brachycercus lacustris larvae from Douglas Lake, Michigan, showed that the adults were equivalent to those known as Brachycercus idei, and as a result, synonymized the latter. Unfortunately, the type material originally studied by Needham is lost. Materials studied by Lyman (1944) and Burks (1953) indicate that the larval characteristics of this species are distinct. For example, the relatively developed posterolateral projections on abdominal segment 2 and the color patterns of the occiput, abdominal terga, and operculate gills were illustrated by Burks (1953) and are confirmed by our study. Because types of S. lacustris are lost and because it is important to stabilize the species concept (see errors in literatures discussed below), we here designate a Neotype for the species (see Material Examined, below).

The treatment of *B. lacustris* in Michigan by Leonard and Leonard (1962) is in error and is actually referable to *B. harrisella*, as indicated by their Figure 21. Soldán (1986) presented descriptions and diagnoses for larvae and adults of *S. lacustris*, but his treatment of larvae from Maine is also in error, being actually referable to a northern population of *S. maculatus*. Soldán (1986) also treated larvae from Alabama, Georgia, Indiana, Mississippi, and South Carolina as *S. flavus*. *Sparbarus flavus*, as discussed above, is only referable to certain unidentifiable adult males from Louisiana, and there has never been any association of larvae and adults of that species by rearing. Among Soldán's ostensible *S. flavus* material we found larvae variously referable to the distinctive species *S. lacustris*, *S. maculatus*, *S. choctaw*, and *B. nitidus*. Essentially, Soldán's larval concept of *B. flavus* was based mainly on *S. lacustris*, and his larval concept of *S. lacustris* was based on *S. maculatus*. It is important to note that Soldán's (1986) use of the pronotal subanterior transverse ridge to distinguish *Sparbarus* species is of no use because that the ridge is present in all Brachycercinae and does not consistently vary among species. The Burian et al. (1997) key to larvae of four northeastern U.S.A. species is in error because it was based on Soldán's incorrectly applied species characteristics and concepts.

Distribution: Canada: Nova Scotia, Ontario, Quebec; U.S.A.: Alabama, Illinois, Indiana, Iowa, Maryland, Michigan, Minnesota, Missouri, North Dakota, Ohio, Oklahoma, Maine, New York, Texas, Wisconsin.

Material Examined: Larva NEOTYPE, Texas, Austin Co, San Bernard R at I-10, nr Sealy, V-9-1977, WP McCafferty, AV Provonsha, D Morihara (PERC). [There are an additional 41 larvae, two male adults, one female adult, and four exuviae from the same population as the neotype also deposited at PERC.] ONTARIO, two larvae, St Lawrence R below Brocksville, VII-28-1952, SS Roback (PERC). ALABAMA, Dallas Co: three larvae, Cedar Cr 5.5 mi N of Minter, VI-26-27-1968, WL Peters, P Tsui, M Pescador, M Makinde (FAMU). ILLINOIS, Will Co: five larvae, Braidwood Sta 1 L-C, Kankakee R nr Custer Pk, VI-20-1979, (CNC), two larvae, Braidwood Sta 1 R-B, Kankakee R nr Custer Pk, VI-20-1979, (CNC), six larvae, Mouth of Horse Cr 300 ft from KKK R VI-20-1979, Braidwood Sta 2A (INHS), one larva, Mouth of Horse Cr 300 ft from KKK R X-13-1979, Braidwood Sta 2A (INHS). INDIANA, Pulaski Co: one larva, Tippecanoe R 1.5 mi S of Tippecanoe R St Prk, VIII-4-1976, AV Provonsha, M Minno (PERC); Putnam Co: one larva, Deer Cr 0.5 mi S E Manhattan, VII-20-1978, M Minno, JH Hollis, (PERC). IOWA, Appanoose Co: three larvae, Shoal Cr nr Exline, T67N, R17W, Sec 19, VIII-23-1999 (UI); Bucanan Co: one larva, Bear Cr 2.5 mi SE Brandon, VIII-8-1996 (UI); Clinton Co: one larva, Elk Run Cr nr Andover, X-15-1999 (UI); Decatur Co: one larva, Elk Cr at St Rd 2, 40/43/4N, 93/56/53 W, IX-11-2001, WP McCafferty, AV Provonsha, RP Randolph (PERC); Howard Co: one larva, Crane Cr nr Lourdes, IX-7-1994 (UI); Madison Co: one larva, North Branch of North R 3.5 mi SW of De Soto, VIII-25-1995 (UI); Wright Co: one larva, Otter Cr nr Goldfield, VIII-11-2000 (UI). KANSAS, Barton Co: one larva exuviae, Arkansas R, 1 mi S Dundee Elevator, VIII-15-1975, Higgins (KU); Chautauqua Co: one larva, Big Caney R, 1.0 mi E Cedar Vale, N US 166 Br, VI-6-1980, P Liechti, DCH (KU); Harper Co: one larva, E Branch Ruch Cr, 3 mi SW Harper, IX-17-1974, D Higgins, (KU); Kingman Co: one larva, Ninnescah R, 1.3 mi S Murdock, VI-7-1977, D Higgins, PML (KU); Meade Co: one larva, Cimarron R, 8.7 mi W, 18.8 mi S Meade, K23 Hwy, VII-17-1980, P Liechti, MBD (KU), 26 larvae, Cimarron R, 8.7 mi W, 18.8 mi S Meade, VI-2-1981, P Liechti, DGH, DCR (KU); Ottawa Co: three male adults, Solomon R, 1.0 mi W, 1.0 mi S Bennington, IX-14-1977, P Liechti (KU); Reno Co: seven larvae, N fk Ninnescah R, 3.4 mi W, 3.0 mi S Castleton, V-22-1975, D Higgins (KU), one larva, N fk Ninnescah R, inflow to Cheney Res, VII-3-1979, FC Gilbert, MBD (KU); Russell Co: two larvae, Saline R on CR 3.5 mi N Russell, VII-12-1978, S Hamilton, GAS (KU). MARYLAND, Calvert Co: one larva, Patuxent R 2 mi N Lower Marlboro, VII-30-1970, S Fuller (PERC). MICHIGAN, seven male adults, one female adult, St Claire R [no further data] (PERC); Benzie Co: four larvae, Platte R, Sleeping Bear Dunes National Lakeshore, VII-20-1992, R Durfee (PERC); Cheboygan Co: four larvae, Douglas Lake, T37N/R3W/S33, VII-8-1938, FE Lyman (UM), four larvae, Douglas Lake, T37N/R3W/S28, VII-11-1938, FE Lyman (UM), one larva, Douglas Lake, T37N/ R3W/S22, VII-16-1938, FE Lyman (UM), six female adults, six exuviae, Douglas Lake, T37N/R3W/S33, VII-17-1938, FE Lyman (UM), two larvae, Douglas Lake, VII-17-1938, JM Moffett (UM), one larva, Douglas Lake, T37N/R3W/S18, VII-20-1938, FE Lyman (UM), three exuviae, Douglas Lake, T37N/R3W/S29, VII-21-1938, FE Lyman (UM), one exuviae, Douglas Lake, T37N/R3W/S22, VII-28-1938, FE Lyman (UM), two larvae, Douglas Lake, VIII-1-1938, JM Moffett (UM), two larvae, Douglas Lake, T37N/R3W/S33, VIII-1-1938, FE Lyman (UM), one larva, Douglas Lake, T37N/R3W/S22, VIII-4-1938, FE Lyman (UM), seven male adults, Douglas Lake, VII-25-1939, JM Moffett (UM), three larvae, two male adults, one female adult, Douglas Lake, T37N/R3W/S18, VII-27-1939, FE Lyman (UM), seven exuviae, Douglas Lake, VII-29-1939, FE Lyman (UM). MINNESOTA: one larva, Red R of the North, 11NC, VI-1993, USGS (CSU). MISSOURI, Nodaway Co: one larva, Honey Cr Sec Line 13/24, T65N, R34W, VIII-31-1993, RJ Sarver (CSU). NORTH CAROLINA: Caswell Co: three larvae, Hyco Cr, VII-1990 (PERC); Hertford Co: three larvae, Chowan R, VII-1988 (PERC); Jones Co: one larva, Trent R near Trenton, VI-1987 (NDNR). NORTH DAKOTA: one larva, Red R of the North, 11NC, VI-1993, USGS (CSU). OHIO: two larvae, Lake Erie, Put-in-Bay, VII-12-1937, INHS (INHS). OKLAHOMA, Comanche Co: one larva, Engineer Pond, Ft Sill West range, X-11-2002,

J Schmidt (CSU). TEXAS, Anderson Co: two larvae, Site 55-I, Box Cr VI-10-1998, DE Bowles (TAMU); Colorado Co: 15 larvae, San Bernard R at FM 3013, VII-18-1997, JR Davis (PERC); Kerr Co: one larva, Flat Rock Lake headwaters 200 m below low water crossing, XI-2-1983, JR Davis (PERC); Montgomery Co: one larva, Site 57-J, Peach Cr, VI-16-1998, DE Bowles (TAMU); Nacogdoches Co: one larva, Site 25-B, Legg Cr, VI-9-1998, DE Bowles (TAMU); Palo Pinto Co: five larvae, Ioni Cr at SH 16 N Strawn, VII-14-1988, S Twidwell (PERC); Travis Co: one larva, Austin, Brackenridge Field Laboratory, Town Lake, VIII-7-1997, CR Nelson (TAMU). WISCONSIN, Grant Co: three larvae, Wisconsin R above Milleville landing, VII-11-1991, RA Lillie (PERC), two larvae, Wisconsin R Milleville, VII-11-1991, RA Lillie (PERC); Marathon Co: one larva, Big Rib R Dahlke Rd access, VII-14-1992, RA Lillie (PERC).

Sparbarus maculatus (Berner), New Combination

Brachycercus maculatus Berner, 1946:78. Brachycercus pini Soldán, 1986:326. Brachycercus maculatus Berner, 1946 [= B. pini Soldán]: Berner and Pescador, 1988:356.

Mature Larva: Body (Fig. 155) length 4.0–6.4 mm. Caudal filaments length 1.6–3.0 mm. General coloration pale yellow-brown. Head: Frons stained with diffuse brown. Occiput (Figs. 155, 156) stained with diffuse brown patterns medially, with pair of somewhat oblique transverse dark brown bands posterior to lateral ocellar tubercle extending medially from eye to posterior margin; surface covered with several short, fine setae; lateral margin posterior to compound eye parallel with long axis of body. Compound eye (Fig. 156) distinctly produced dorsally. Lateral ocellar tubercle (Fig. 156) as long as, or slightly longer than basal width; distal half fingerlike and curved anteriorly; apex rounded to bluntly pointed. Middle ocellar tubercle (Figs. 155, 156) triangulate in dorsal view, straight in lateral view, slightly longer than basal width, and about two-thirds length of lateral tubercle; apex acutely pointed. Antenna (Fig. 157) pale; scape with longitudinal black macula; pedicel 2.5 X length of scape, with black macula at base, and with less than 10 setae one-half or more length of pedicel. Labrum as in Figure 158. Hypopharynx as in Figure 159. Maxilla (Fig. 160) with galealacinia length 3.1 X basal width; palp segment 1 width 1.9 X width of segment 2; palp segment 2 1.3 X length of segment 1, with about 10 long, stout setae along distal half of inner margin, and less than 10 long, fine setae distally on outer margin. Labial palp as in Figure 161. Thorax: Nota (Fig. 155) brown, with some irregular black maculae; sterna somewhat paler, stained with diffuse black shading. Pronotum (Fig. 155) anterior submarginal transverse ridge stained with black laterally. Propleuron not visible or only narrowly visible in dorsal view, with few marginal setae. Prosternum median transverse ridge with tuft of fine setae as long as one-third length of forefemur. Mesonotum (Fig. 155) laterally with sparse marginal setae. Mesosternum anterior margin with only several scattered, fine setae shorter than one-fourth length of midfemur. Legs (Fig. 155) pale; femora basally somewhat darker but not forming distinct band, without small, black dorsodistal macula; tibiae basally somewhat darker but not forming distinct band (Fig. 155). Ratios of length of body: foreleg: midleg: hindleg—3.4: 1.0: 1.5: 1.5. Ratios of length of forefemur: tibia: tarsus: claw—2.6: 1.4: 1.6: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.5: 1.9: 2.2: 1.0. Forefemur dorsal margin with row of very short setae in addition to some setae slightly longer than width of femur; ventral margin with row of short setae and less than 10 setae as long as, or slightly longer than, width of femur. Foretibia ventral margin with row of about eight short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus ventral margin with row of about 10 short setae; anterior and posterior surfaces with some scattered setae as long as 2.0 X width of tarsus. Hindfemur length 6.7 X width; dorsal margin with row of short setae interspersed with some setae slightly longer than width of femur; ventral margin with short setae. Hindtibia and hindtarsus each dorsally with about five long, fine setae as long as about 2.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw evenly curved; length 4.5-6.0 X basal width. Abdomen: Terga (Fig. 155) usually with

extensive dark brown staining and markings as follows (absent in some): terga 1 and 2 with pair of narrow transverse bands laterally at anterior margin, with broad longitudinal stripe medially, and transverse band at posterior margin; terga 7–9 with pair of short transverse bands sublaterally at anterior margin, with broad longitudinal stripe medially, and with pair of narrow transverse bands submedially at posterior margin; tergum 10 with longitudinal stripe medially and broad band on posterior margin. Posterolateral projection 2 (Fig. 155) shorter than basal width, with apex forming blunt or right angle; projections 3–9 (Fig. 155) apices pointed; projections 5 and 6 subequal in length, about 4.0 X basal width; projection 6 directed posteriorly; projection 7 length about one-third that of projection 6; projections 8 and 9 relatively small. Sterna stained with diffuse black shading; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 155) yellow-brown; length 1.2 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae up to one-third length of operculate gill; posterolateral corner with row of marginal setae about two-thirds length of those of posteromedial corner and intermixed with several very short setae; Y-ridge with adjacent areas extensively stained with diffuse pale black shading, and with outer branch stained with dark black at distal portion (absent in some). Caudal filaments pale yellow.

Male Adult: Body length 4.1–5.1 mm. Forewing length 3.8 mm. Caudal filaments length 13.0 mm. Head: Frons stained with diffuse brown. Occiput pale yellow. Epicranial suture bordered with diffuse brown, and with transverse broad, diffuse brown band posterior to lateral ocellus laterally extending from eye to posterior margin (Fig. 162). Antenna (Fig. 163) pale; scape with apical brown macula; pedicel 2.8 X length of scape. Thorax: Pronotum pale yellow, stained with extensive black shading. Prosternum yellow. Mesonotum yellowbrown. Mesosternum vellow, with extensive diffuse black shading; sternacostal suture not blackened. Metanotum posteromedial projection broadly triangulate; apex bluntly pointed. Coxae and trochanters brown; femora without black dorsodistal macula. Forefemur pale brown, with longitudinal brown stripes; foretibia and foretarsus pale. Mid- and hindlegs pale. Ratios of length of body: foreleg: midleg: hindleg—2.6: 1.6: 1.0: 1.0. Ratios of length of forefemur: tibia: tarsus—1.0: 2.1: 1.3. Ratios of length of foretarsus segment I: II: III: IV: V-1.0: 4.0: 2.5: 1.8: 2.2. Forewing with ratio of length to greatest width-1.7; Sc, R₁ and adjacent area pale brown; other veins pale. Abdomen: Coloration (Fig. 164) generally pale, with brown maculae as follows: terga 1 and 2 with broad longitudinal stripe medially and narrow transverse stripe along posterior margin; terga 7-9with pair of short transverse stripes sublaterally at anterior margin, broad longitudinal stripe medially, and pair of narrow transverse stripes laterally at posterior margin except in tergum 9; tergum 10 with longitudinal stripe medially and broad transverse stripe along posterior margin. Segments 3–7 with vestiges of posterolateral projections; vestige of posterolateral projection 7 very short (Fig. 164). Genitalia (Fig. 165) with penes lobes moderately convex distolaterally; forceps slightly and evenly curved, not angled. Caudal filaments pale.

Female Adult: Unknown.

Egg: Habitus as in Figure 563. Length about 230 mm. Shape elongate-ovate. Polar cap about one-fourth length of entire egg, with number of tubercles. Chorion with 11–15 broad costae in lateral half.

Diagnosis: Larvae of the North American *Sparbarus* species *S. maculatus, S. miccosukee*, n. sp., and *S. coushatta* are relatively similar. These three species share an apically pointed middle ocellar tubercle that is short-triangulate, about as long as its basal width (Fig. 156), and posterolateral projections on abdominal segment 2 that are shorter than their basal width and bluntly right angled apically (Fig. 155). In *S. lacustris, S. nasutus*, and *S. choctaw*, the middle ocellar tubercle is elongate-conical and as long as, or longer than, twice its basal width (Fig. 139), and the posterolateral projections on abdominal segment 2 are moderately to well developed, as long as, or longer than, their basal width (forming a distal angle clearly less than 90 degrees) (Figs. 137, 187). *Sparbarus maculatus* larvae are distinguished from *S. coushatta* and *S. miccosukee*, n. sp., by having femora that lack an apical black macula on the dorsal margin (Fig. 155).

Adults of *S. maculatus* can be distinguished from the other three North American *Sparbarus* species described as adult as follows. In *S. maculatus*, abdominal segment 2 lacks vestiges of posterolateral projections (Fig. 164), whereas such vestiges are distinct and developed in *S. maculatus*. In *S. maculatus*, femora lack

black dorsodistal maculae, and the male forceps are slightly and evenly bowed (Fig. 165), whereas in *S. lacustris*, black maculae are present dorsodistally on the femora (Fig. 153) and the male forceps are distinctly angled at one-fifth to one-fourth of the distance from their base (Fig. 154).

Eggs of the North American species *S. nasutus*, *S. maculatus*, *S. coushatta* and *S. miccosukee*, n. sp., have tubercles on the polar cap (Fig. 563), which are absent in the eggs of *S. lacustris* and *S. choctaw* (Fig. 558). Furthermore, the eggs of *S. maculatus* can be distinguished by the presence of 11–15 longitudinal costae in the lateral half (Fig. 563); whereas costae in the lateral half number seven to eight in *S. miccosukee*, n. sp., (Fig. 564) and 17–20 in *S. coushatta* and *S. nasutus* (Figs. 561, 565).

Distribution: U.S.A.: Alabama, Florida, Indiana, Maine, Maryland, New York, North Carolina, Virginia, and Wisconsin.

Material Examined: One male adult PARATYPE, Florida, Alachua Co, Santa Fe R, Cat No II-2839-1, II-28-1939, L Berner, No 1239.17 (FAMU). One male adult PARATYPE, Florida, Alachua Co, Santa Fe R, Cat No II-2839-1, II-28-1939, L Berner, No 1239.15 (FAMU). One larva PARATYPE of Brachycercus pini, Florida, Bay Co, Pine Log Cr at Hwy 79, VI-20-1971, PH Carlson, NE Farmer, RD Kaplan (FAMU). One larva PARATYPE of Brachycercus pini, Florida, Pasco Co, Withlacoochee R (southern), IV-7-1955, WM Beck (FAMU). ONTARIO, Hastings Co: one larva, Dungannon Tp, Egan Cr, STN 18, 45°03.6'N 77°43.5'W, VI-28-1977, J Williams and R Colden (ROM). LABAMA, Dallas Co: five larvae, Cedar Cr 5.5 mi N of Minter, VI-26-27-1968, WL Peters, P Tsui, M Pescador, M Makinde (FAMU). FLORIDA, Alachua Co: two male subimagos, two exuviae, Santa Fe R, V-8-1947, L Berner (FAMU). INDIANA: one larva, Greasy Cr, Arland, VII-10-1929, HT Spieth (PERC); Benton Co: one larva, Big Pine Cr at US 52, VII-3-1972, WP McCafferty, AV Provonsha, E Levine (PERC). MAINE, Washington Co: two larvae, Schoodie Br S, VIII-16-1973, T Mingo (FAMU). MARYLAND, Montgomery Co: one larva, Potomac R, 4 mi below mouth of Monocacy R, VIII-20-1957, SS Roback (PERC). NEW YORK, Saratoga Co: four larvae, Hudson R, Waterford, VII-7-1994 (NYEC); Warren Co: 11 larvae, Hudson R, Corinth, VII-7-1994 (NYEC). NORTH CAROLINA, Brunswick Co: one larva, Waccamaw R, VIII-1990 (PERC); Caswell Co: one larva, Country Line Cr, VIII-1994, ROA (PERC); three larvae Hyco Cr, VII-1990 (PERC); Duplin Co: one larva, NE Cape Fear R, X-1989 (PERC); Edgecombe Co: one larva, Tar R, VII-1992 (PERC); Harnett Co: one larva, U Little R, VIII-1993, CPF (PERC); Jones Co: two larvae, Island Cr, VIII-1995 (PERC); four larvae, Trent R, IX-1985 (PERC); one larva, Trent R nr Trenton, VI-1987 (PERC); Nash Co: two larvae, Swift Cr, 5600, VI-1991 (PERC); Onslow Co: one larva, New R at Gum Br, VII-1988 (PERC); Sampson Co: four larvae, Coharie Cr, VIII-1993, DR Lenat (PERC). TENNESSEE, two larvae, Big South Fork area, Black R at Clear Fork, IX-2-3 (PERC). VIR-GINIA, Louisa/Spotsylvania Co: two larvae, North Anna R, Rt 208, VI-25-1969, GM Simmons (PERC). WISCONSIN, Burnette Co: 10 larvae, St Croix R at Hwy 70, VI-16-1992, RA Lillie (PERC); Langlade Co: one larva, Wolf R, A99, East Bank - Alder, VI-29-1999, RA Lillie (PERC), two larvae, Wolf R, 99-4, VI-27-2000, RA Lillie (PERC); Rusk Co: 16 larvae, Chippewa R, above Hwy E, VII-14-1992, RA Lillie (PERC).

Sparbarus miccosukee, New Species

Mature Larva: Body (Fig. 166) length 4.6–5.4 mm. Caudal filaments length 2.5–2.8 mm. General coloration pale yellow-brown. *Head*: Frons stained with diffuse brown. Occiput (Fig. 166) stained with diffuse brown patterns medially, with pair of somewhat oblique transverse dark brown bands posterior to lateral ocellar tubercle extending medially from eye to posterior margin; surface covered with several short, fine setae; lateral margin posterior to compound eye nearly parallel with long axis of body. Compound eye (Fig. 167) distinctly produced dorsally. Lateral ocellar tubercle (Fig. 167) as long as, or slightly longer than, basal width; distal half slightly curved anteriorly; apex rounded to bluntly pointed. Middle ocellar tubercle (Figs. 166, 167) triangulate in dorsal view, straight in lateral view, slightly longer than basal width, and about two-thirds length

of lateral tubercle; apex acutely pointed. Antenna (Fig. 168) pale; scape with longitudinal black macula; pedicel about 2.0 X length of scape, and with less than 10 setae one-half or more length of pedicel. Labrum as in Figure 169. Hypopharynx as in Figure 170. Maxilla (Fig. 171) with galealacinia length 3.0 X basal width; palp segment 1 width 1.8 X width of segment 2; palp segment 2 1.2 X length of segment 1, with about eight long, stout setae along distal half of inner margin, and about 10 long, fine setae distally on outer margin. Labial palp as in Figure 172. Thorax: Nota (Fig. 166) brown, with some irregular black maculae; sterna somewhat paler, stained with diffuse black shading. Pronotum (Fig. 166) anterior submarginal transverse ridge stained with black laterally. Propleuron not visible or only narrowly visible in dorsal view, with some marginal setae. Prosternum median transverse ridge with several fine setae shorter than one-fourth length of forefemur. Mesonotum (Fig. 166) laterally with sparse marginal setae. Mesosternum anterior margin with only several scattered, fine setae shorter than one-fourth length of midfemur. Legs pale throughout except femora somewhat darker basally but not forming distinct band, and with small, black dorsodistal macula (Figs. 166, 173). Ratios of length of body: foreleg: midleg: hindleg-3.1: 1.0: 1.5: 1.5. Ratios of length of forefemur: tibia: tarsus: claw—2.5: 1.2: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—2.6: 1.3: 1.6: 1.0. Forefemur dorsal margin with row of very short setae in addition to some setae slightly longer than width of femur; ventral margin with row of short setae and about 10 setae as long as width of femur. Foretibia ventral margin with row of about eight short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus ventral margin with row of about 10 short setae; anterior and posterior surfaces with some scattered setae as long as 2.0 X width of tarsus. Hindfemur length 6.5 X width; dorsal margin with row of short setae interspersed with some setae slightly longer than width of femur; ventral margin with short setae. Hindtibia and hindtarsus each dorsally with row of about 12 long, fine setae as long as about 3.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw evenly curved; length 6.5–7.0 X basal width. Abdomen: Terga (Fig. 166) usually with distinct dark brown markings as follows (absent in some): terga 1 and 2 extensively stained with diffuse black at medial and posterior margin; terga 7–9 with pair of short transverse bands sublaterally at anterior margin, and pair of long, broad, triangulate longitudinal stripes submedially; tergum 10 with broad band on posterior margin. Posterolateral projection 2 (Fig. 166) shorter than basal width, with apex forming blunt angle; projections 3–9 (Fig. 166) apices pointed; projections 4–6 subequal in length, about 2.5 X basal width; projection 6 directed posteriorly; projection 7 length about onehalf that of projection 6; projections 8 and 9 small. Sterna stained with diffuse black shading; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 166) yellow-brown; length 1.3 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae up to one-half length of operculate gill; posterolateral corner with row of marginal setae about two-thirds length of those of posteromedial corner and intermixed with several very short setae; Y-ridge with adjacent areas extensively stained with diffuse pale black shading, and with outer branch darkened at distal portion. Caudal filaments pale yellow.

Adult: Unknown.

Egg: Habitus as in Figure 564. Length about 200 mm. Shape elongate-ovate. Polar cap about one-fourth length of entire egg, with tubercles. Chorion with seven to eight broad costae in lateral half.

Diagnosis: Larvae of North American species *S. miccosukee*, *S. coushatta*, and *S. maculatus* are relatively similar. These three species share an apically pointed middle ocellar tubercle that is short-triangulate and about as long as its basal width (Fig. 167), and posterolateral projections on abdominal segment 2 that are shorter than their basal width and form a blunt right angle apically (Fig. 166). In *S. lacustris, S. nasutus*, and *S. choctaw*, the middle ocellar tubercle is elongate-conical and as long as, or longer than, twice its basal width (Fig. 139), and the posterolateral projections on abdominal segment 2 are moderately to well developed, as long as, or longer than, their basal width and form a distal angle clearly less than 90 degrees (Figs. 138, 187). In *S. miccosukee*, the femora have an apical black macula on the dorsal margin (Fig. 173), whereas in *S. maculatus*, these markings are absent (Fig. 155). In *S. miccosukee*, abdominal terga 7–9 have a pair of long and broad submedially triangulate maculae (Fig. 166), and the pedicels are about twice the length of the scape

(Fig. 168). In *S. coushatta*, abdominal terga 7–9 have a medial longitudinal stripe (Fig. 94), and the pedicels are about two and one-half times of the length of the scape (Fig. 96).

Among the *Sparbarus* species that have eggs with a number of tubercles on the polar cap, those of *S. miccosukee* are distinguished by having only seven to eight costae in the lateral half (Fig. 564). This is the lowest number of costae known for a *Sparbarus* egg. In *S. maculatus*, *S. nasutus* and *S. coushatta*, the costae number more than nine in the lateral half (Fig. 565), and in particular, the evidently very closely related *S. maculatus* has 11–15 costae in the lateral half (Fig. 563).

Discussion: The specimen of *S. miccosukee* from Jackson County, Florida (see material examined, below) was actually part of the paratype series of *Brachycercus pini* Soldán (1986) (= *B. maculatus*) (Berner and Pescador, 1988).

Etymology: The specific epithet is a noun in apposition and is after the native North American people of the Miccosukee tribe, original occupants of the region that includes the type locality of the new species.

Distribution: U.S.A.: Florida.

Material Examined: Larva HOLOTYPE, Florida, Santa Rosa Co, Cat No 8-1254-1, L Berner (PERC). One larva PARATYPE, Florida, Escambia Co, Cat No 8-1254-2, L Berner (PERC). One larva PARATYPE of *Brachycercus pini*, Florida, Jackson Co, Waddells Mill Cr, 28-XI-1960, WM Beck (FAMU).

Sparbarus nasutus (Soldán), New Combination

Brachycercus nasutus Soldán, 1986:321.

Mature Larva: Body (Figs. 19, 174) length 4.5–8.1 mm. Caudal filaments length 2.8–4.2 mm. General coloration yellow-brown. Head: Frons stained with diffuse brown. Occiput (Figs. 174, 175) stained with diffuse brown patterns medially, with pair of somewhat oblique transverse dark brown bands posterior to lateral ocellar tubercle extending medially from eye to posterior margin; surface covered with several short and relatively long, fine setae; lateral margin posterior to compound eye parallel with long axis of body. Compound eye (Fig. 176) moderately produced dorsally. Lateral ocellar tubercle (Figs. 175, 176) longer than basal width; distal half fingerlike and curved anteriorly; apex rounded to bluntly pointed. Middle ocellar tubercle (Figs. 174, 175, 176) elongate-conical in dorsal view, and slightly curved dorsally in lateral view; length about 2.0 X that of lateral ocellar tubercle, and about 3.0 X basal width; apex bluntly pointed. Antenna (Fig. 179) pale; scape with longitudinal black macula; pedicel 2.2 X length of scape, with black macula at base, and with 20-25 setae one-half or more length of pedicel. Labrum as in Figure 180. Hypopharynx as in Figure 181. Maxilla (Fig. 182) with galealacinia length 2.5 X basal width; palp segment 1 width 1.8 X width of segment 2; palp segment 2 1.5 X length of segment 1, with about 10 long, stout setae along distal two-fifths of inner margin, and less than 10 long, fine setae distally on outer margin. Labial palp as in Figure 183. Thorax: Nota (Fig. 174, 177) without distinct black maculae except for few irregular maculae on mesonotum; sterna somewhat paler, stained with diffuse black shading. Propleuron not visible or only narrowly visible in dorsal view, with few marginal setae (Fig. 174). Prosternum median transverse ridge with several fine setae shorter than one-fourth length of forefemur. Mesonotum (Fig. 174) laterally with sparse marginal setae. Mesosternum anterior margin with only several scattered, fine setae shorter than one-fourth length of midfemur. Legs pale; femora with basal half darker, forming distinct band, and with small, black dorsodistal macula; tibiae with basal one-fourth to one-third darker (Figs. 174, 184, 185). Ratios of length of body: foreleg: midleg: hindleg-4.1: 1.0: 1.7: 1.7. Ratios of length of forefemur: tibia: tarsus: claw—2.6: 1.3: 1.5: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.5: 1.8: 2.1: 1.0. Forefemur (Fig. 184) dorsal margin with row of very short setae in addition to some relatively long setae; ventral margin with row of short setae and about eight setae as long as, or slightly longer than, width of femur. Foretibia (Fig. 184) ventral margin with row of about 10 short setae; posterior

surface with some scattered setae as long as width of tibia. Foretarsus (Fig. 184) ventral margin with row of about 12 short setae; anterior and posterior surfaces with some scattered setae as long as 2.0 X width of tarsus. Hindfemur (Fig. 185) length 6.0 X width; dorsal margin with row of short setae interspersed with some setae as long as 2.0 X width of femur; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 185) each dorsally with row of about 15 long, fine setae as long as about 3.0 X width of tibia, and ventrally with row of short, stout setae. Hindclaw (Figs. 178, 185) slightly curved; length 6.5 X basal width. Abdomen: Terga (Fig. 174) usually with distinct dark brown markings as follows (absent in some): terga 1 and 2 with transverse bands at both anterior and posterior margins, and with broad longitudinal stripe medially; terga 7–9 with pair of short transverse bands sublaterally at anterior margin, with broad longitudinal stripe medially, and with transverse stripe at posterior margin except in tergum 9; tergum 10 darkened anteriomedially, with broad longitudinal stripe medially, and broad transverse band at posterior margin. Posterolateral projections 2–9 (Figs. 174, 187) with apices bluntly pointed; projection 2 strongly developed, with apex forming angle clearly less than 90 degree; projections 2–6 subequal in length, about 2.5 X basal width; projection 6 directed posteriorly; projection 7 length about two-thirds that of projection 6; projections 8 and 9 relatively small. Sterna with diffuse black shading; sternum 9 (Fig. 188) posterior margin convexly produced. Operculate gill (Figs. 174, 186) yellow-brown; length 1.3 X width; dorsum laterally with some long setae; posteromedial corner with row of long marginal setae up to one-third length of operculate gill; posterolateral corner with row of marginal setae about two-thirds length of those of posteromedial corner and intermixed with several very short setae; Y-ridge with adjacent areas extensively stained with diffuse pale black shading, and with outer branch stained with dark black at distal portion, and with several long setae. Caudal filaments pale vellow.

Male Adult: Body length 4.9–5.2 mm. Forewing length 3.5–4.1 mm. General coloration pale yellow. Head: Occiput pale yellow, with pair of diffuse, transverse brown stripes extending from eye to posterior margin. Epicranial suture bordered with pale vellow-brown. Antenna pale; scape with black macula; pedicel length 3.0 X that of scape. Thorax: Pronotum pale yellow, margined with brown, without extensive black shading. Prosternum yellow; median transverse ridge stained with dark brown. Mesonotum yellow-brown. Mesosternum pale yellow, with extensive diffuse black shading; sternacostal suture not blackened. Metanotum posterior margin broadly and roundly protruding medially. Coxae and trochanters brown; femora with black dorsodistal macula. Forefemur pale brown, with longitudinal brown stripes; foretibia and foretarsus pale. Mid- and hindlegs pale. Forewing (Fig. 16) with ratio of length to greatest width—1.7; Sc, R₁ and adjacent area pale brown; other veins pale. Abdomen: Coloration (Fig. 189) generally pale, usually with brown maculae as follows: terga 1 and 2 with broad longitudinal stripe medially and transverse bands along anterior and posterior margins; terga 7–9 with pair of short transverse bands sublaterally at anterior margin, with broad longitudinal stripe medially, and with narrow transverse band on posterior margin except in tergum 9; tergum 10 with longitudinal stripe medially and broad transverse stripe along posterior margin. Segments 2-6 with distinct vestiges of posterolateral projections; segment 7 with very short vestige of posterolateral projection. Genitalia (Fig. 190) with penes lobes moderately convex distolaterally; forceps somewhat angled at one-fifth distance from base. Caudal filaments pale.

Female Adult: Body length 5.2–6.3 mm. Forewing length 5.5–6.2 mm. Caudal filaments length 3.2–3.6 mm. Ratio of length of body: foreleg: midleg: hindleg—3.5: 1.0: 1.7: 1.7. Coloration and vestiges similar to males.

Egg: Habitus as in Figure 565. Length about 240 mm. Shape elongate-ovate. Polar cap about one-fourth length of entire egg, with tubercles. Chorion with 17–20 broad costae in lateral half.

Diagnosis: Among the larvae of Nearctic *Sparbarus*, *S. nasutus* is most similar to *S. lacustris* and *S. choctaw*, in that they all share a middle ocellar tubercle that is elongate-conical and as long as, or longer than, twice its basal width (Fig. 175). They also have posterolateral projections on abdominal segment 2 that are as long as, or longer than, their basal width and forming a distal angle clearly less than 90 degrees (Fig. 187), although those of *S. nasutus* are considerably more developed than those of *S. choctaw* and *S. lacustris* (Figs.

78, 138). In the other North American species S. maculatus, S. coushatta, and S. miccosukee, the middle ocellar tubercle is short-triangulate and as long as its basal width in dorsal view (Fig. 156), and the projections on segment 2 are not developed, being shorter than their basal width and forming a blunt right angle distally (Fig. 155). Larvae of S. nasutus have a middle ocellar tubercle that is twice or more as long as the lateral ocellar tubercles and about three times the basal width (Fig. 175), making such middle ocellar tubercles among the most developed in the subfamily. This diagnostic feature readily distinguishes S. nasutus from all other Nearctic Sparbarus species. In the other regions, larvae of the eastern Asian species S. tubulatus and the eastern European species S. europaeus also have middle ocellar tubercles that are distinctly longer than the lateral tubercles (Figs. 101, 191), but are less than twice the length of lateral ones. Sparbarus nasutus can be additionally distinguished from the latter two species by the presence of pair of black bands posterior to the lateral ocellar tubercles on the occiput (Fig. 174), and strongly developed posterolateral projections on abdominal segment 2 (Fig. 187), which are as long as those on segment 3. In S. tubulatus and S. europaeus, the occiput does not have black bands posterior to lateral ocellar tubercles, and the projections on segment 2 are weakly developed, being distinctly shorter than projection 3 (Fig. 104). Another Palearctic species, S. corniger, has strongly developed posterolateral projections on the abdominal segment 2 that are similar to those in S. nasutus (Fig. 90), but it can be distinguished from the latter by the presence of a middle ocellar tubercle being subequal to the lateral tubercles in length (Fig. 85).

Adults of *S. nasutus* and *S. corniger* are distinguished from all other *Sparbarus* (and Brachycercinae) species known as adults by having distinct vestiges of posterolateral projections on the abdominal segment 2 (Fig. 189). Adults of *S. nasutus* have brown bands posterior to the lateral ocelli and brown medial stripes and lateral maculae on the abdominal terga (Fig. 189), whereas such markings are absent in *S. corniger*.

Among the eggs that have a number of tubercles on the polar cap, those of *S. nasutus* and *S. coushatta* are most similar and are difficult to distinguish (Figs. 565, 561). However they can be distinguished from other species by having 17–20 costae in the lateral half, whereas eggs of *S. miccosukee* have only seven to eight such costae in the lateral half (Fig. 564), and eggs of *S. maculatus* have 11–15 costae in the lateral half (Fig. 563).

Distribution: U.S.A.: Alabama, Florida, Indiana, Iowa, Nebraska, and Wisconsin.

Material Examined: FLORIDA, Escambia Co: one larva, 8-1254-2, L Berner (PERC). INDIANA, Pulaski Co: two larvae, Tippecanoe R, 1.5 mi S of Tipp R St Prk, VII-14-1976, AV Provonsha, M Minno (PERC), four male adults, eight female adults, two male subimagos, Tippecanoe R, 1.5 mi S of Tippecanoe R St Prk, VII-30-1976, AV Provonsha, M Minno (PERC), 13 larvae, two male subimagos, one female subimago, 14 exuviae, Tippecanoe R, 1.5 mi S of Tipp R St Prk, VIII-4-1976, AV Provonsha, M Minno (PERC), seven larvae, Tippecanoe R, at Co Rd 1.5 mi S of Tipp Riv St Prk, VI-30-1978, AV Provonsha, D Bloodgood, JH Hollis (PERC). IOWA, Kossuth Co: one larva, Buffalo Cr, N 43° 14.32', W 93° 59.17', VIII-24-2000 (UI). NEBRASKA, Sheridan Co: two larvae, Niobrara R, Gorden, VII-11-1984, R Lawson, K Brown, M Brohman (PERC), six larvae, Niobrara R, S Gorden, VII-27-1984, R Lawson, K Brown, M Brohman (PERC). WISCONSIN, Burnette Co: eight larvae, St Croix R, Seven Island Area, VII-17-1991, RA Lillie, J Lillie (PERC), 14 larvae, St Croix R, Hwy 70, VI-16-1992, RA Lillie (PERC); Columbia Co: three larvae, Wisconsin R, below Portage 2 mi, VII-12-1991, RA Lillie (PERC); Grant Co: nine larvae, Wisconsin R, Woodman, VI-9-1987, RA Lillie (PERC); Richland Co: two larvae, Wisconsin R, Gotham Boat Landing, VIII-31-1985, RA Lillie (PERC), one larva, Wisconsin R, nr Orion Boat Landing, VII-11-1991, RA Lillie (PERC); Rusk Co: 16 larvae, Chippewa R, above Hwy E, VII-14-1992, RA Lillie (PERC); Waupaca Co: three larvae, Embarrass R, Behuke Rd, VII-14-1992, RA Lillie (PERC).

Sparbarus tubulatus (Tshernova), New Combination

Brachycercus tubulatus Tshernova, 1952:285. *Brachycercus* KUa Yoon and Bae, 1988:184. *Brachycercus tubulatus* Tshernova, 1952 [= *B*. KUa Yoon and Bae]: Hwang and Bae, 1999:243.

Mature Larva: Body (Fig. 191) length 4.0–5.1 mm. Caudal filaments length 2.5 mm. General coloration pale yellow-brown. Head: Coloration pale yellow. Frons without distinct diffuse brown staining. Occiput (Figs. 191, 192) without distinct diffuse staining and dark brown bands posterior to lateral ocellar tubercles; surface with several short setae; lateral margin posterior to compound eye curved inward. Compound eye (Fig. 192) not strongly produced dorsally. Lateral ocellar tubercle (Fig. 192) slightly longer than basal width; distal portion fingerlike, slightly curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 191, 192) elongateconical in dorsal view, straight in lateral view; length 1.5 X that of lateral ocellar tubercle, and about 2.5 X basal width; apex rounded to bluntly pointed. Antenna (Fig. 193) pale, without maculae; pedicel 1.8 X length of scape, with less than 10 setae one-half or more length of pedicel. Labrum as in Figure 194. Hypopharynx as in Figure 195. Maxilla (Fig. 196) with galealacinia length 2.8 X basal width; palp segment 1 width 2.0 X width of segment 2; segment 2 1.2 X length of segment 1, with about eight long, stout setae along distal half of inner margin, and with less than 10 fine setae at apex and on outer margin. Labial palp as in Figure 197. Thorax: Nota (Fig. 191) yellow-brown, without distinct black maculae; sterna pale yellow, without diffuse black stain. Propleuron only narrowly visible in dorsal view, with sparse marginal setae. Prosternum median transverse ridge with several scattered setae shorter than one-third length of forefemur. Mesosternum anterior margin with several scattered setae shorter than one-fourth length of midfemur. Legs pale throughout, without basal band or apical macula (Fig. 191). Ratios of length of body: foreleg: midleg: hindleg, 4.0: 1.0: 1.6: 1.8. Ratios of length of forefemur: tibia: tarsus: claw, 4.5: 2.3: 2.5: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw, 4.1: 2.7: 2.8: 1.0. Forefemur dorsal margin with row of very short setae in addition to some relatively long setae; ventral margin with row of short setae and less than 10 setae as long as, or slightly longer than, width of femur. Foretibia ventral margin with row of about six short setae; posterior surface with some scattered setae as long as width of tibia. Foretarsus ventral margin with row of about 10 short setae; anterior and posterior surfaces and with some scattered setae as long as width of tarsus. Hindfemur length 5.0 X width; dorsal margin with row of short setae interspersed with some setae as along as 1.5 X width of femur; ventral margin with short setae. Hindtibia and hindtarsus each dorsally with row of about 10–20 long, fine setae as long as about 2.5 X width of tibia, and ventrally with row of short, stout setae. Hindclaw moderately curved; length 4.7 X basal width. Abdomen: Terga (Fig. 191) pale yellow, without distinct maculae or diffuse black shading. Posterolateral projection 2 (Fig. 191) triangulate and blunt, with length less than one-half that of segment 3; projections 3–7 (Fig. 191) with apices bluntly pointed; projections 5 and 6 subequal in length, about 2.5 X basal width; projection 6 slightly curved medially; projection 7 short, about one-half length of projection 6; projections 8 and 9 small. Sterna pale yellow, without diffuse black staining; sternum 9 posterior margin convexly produced. Operculate gill pale yellow-brown; length 1.2 X width; dorsum laterally with several long setae; posteromedial corner with row of long marginal setae one-fourth to one-third length of operculate gill; posterolateral corner with row of marginal setae two-thirds length of those at posteromedial corner and intermixed with several very short setae; Y-ridge without black staining, with several long setae. Caudal filaments pale yellow.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of *S. tubulatus* and the eastern European (western Russia) species *S. europaeus* are similar in that they share the presence of a middle ocellar tubercle that is distinctly longer than the lateral tubercles (Fig. 192). In all other Palearctic and Oriental species of *Sparbarus*, the middle ocellar tubercle is not longer than the lateral tubercles (Fig. 62). *Sparbarus tubulatus* is distinguished from *S. europaeus* by hav-

ing segment 2 of the maxillary palpi only slightly longer than segment 1 (Fig. 196). In *S. europaeus*, segment 2 of the maxillary palpi is one and one-half times the length of segment 1 (Fig. 103). The North American species *S. nasutus* also has a middle ocellar tubercle that is distinctly longer than the lateral tubercles (Fig. 175); however, it can be easily distinguished from *S. tubulatus* by the pair of black bands posterior to the lateral ocellar tubercles (Fig. 174) and the strongly developed posterolateral projections on abdominal segment 2 (Fig. 187).

Distribution: Eastern Asian region of Russia, Korea.

Material Examined: SOUTH KOREA: one larva, Hangang R at Ttuksom, Gwangjin-gu, Seoul, X-3-1981, JU Byun (SWU); one larva, no data (SWU).

Insulibrachini, New Tribe

Type genus: Insulibrachys Soldán

Diagnosis: The larvae of Insulibrachini are distinguished from those of all other tribes of Brachycercinae by the ocellar tubercles that are cylindrical and somewhat truncate apically and covered with dense, long setae distally (Figs. 198, 199). In other tribes, ocellar tubercles are conical or hemispherical and lack long setae (Fig. 400).

Insulibrachys

Insulibrachys Soldán, 1986:333. **Type species**: Insulibrachys needhami Soldán.

Species Included: I. needhami Soldán.

Mature Larva: *Head*: Head capsule anteriorly with transverse row of long setae dorsal to base of clypeus laterally (Fig. 199). Clypeus with long setae. Occiput (Fig. 198) without long, fine setae; lateral margin curved inward posterior to compound eye. Compound eye (Figs. 198, 200) not strongly produced dorsally, laterally positioned; female eye not anteriorly reaching middle ocellar tubercle, and with distance from posterior margin of head about one-half diameter of eye. Ocellar tubercles (Figs. 198, 199) cylindrical; apex somewhat truncate; distal portion with dense, long setae. Lateral and middle ocellar tubercles subequal in length. Pedicel (Fig. 208) about 2.0 X length of scape, with dense, long setae. Labrum (Fig. 202) subquadrate. Hypopharynx (Fig. 205) with superlingua ovate. Maxilla (Fig. 206) with galealacinia sickle shaped; length about 3.0 X width; maxillary palp two segmented; segment 1 wider than segment 2; segment 2 longer than segment 1, with row of long, stout setae along inner margin, and with long, fine setae at apex and along outer margin, and without dense, long setae on ventral surface. Labial palp (Fig. 207) two segmented; segment 1 ventrally with patch of setae as long as, or longer than, one-half length of segment 1. Thorax: Pronotum (Fig. 198) subquadrate; anterior margin nearly straight; lateral margin distinctly convexly produced. Median ridge of prosternum not produced medially, covered with some short setae, and laterally produced ventrally, forming ridge posterior to forecoxa in lateral view (Fig. 200). Mesosternum without apparent setae along anterior margin (Fig. 200). Meso- and metasternum without processes. Legs (Figs. 209, 210) without plate-shaped process on dorsal margin of coxa. Forefemur (Fig. 209) ventrally with some setae as long as, or shorter than, width of femur. Foretibia (Fig. 209) longer than tarsus; ventral margin with setae measuring in length 2.0 X width of tibia; posterior surface with short and long setae not arrayed in distinct row. Foretarsus (Fig. 209) ventrally with row of setae shorter than width of tarsus; dorsal margin, and anterior and posterior surfaces with dense setae not arrayed in distinct rows. Hindleg 1.4 X length of foreleg. Hindfemur (Fig. 210) dorsally with some setae measuring in length 1.5–2.0 X width of femur. Hindtibia and hindtarsus (Fig. 210) dorsally with row of long setae measuring in length 4.0–5.0 X width of tibia. Hindclaw (Fig. 210) evenly curved, with inner margin lacking armature. *Abdomen*: Tergum 1 (Fig. 198) without median process at posterior margin. Tergum 2 (Fig. 198) with posterior margin slightly protruding medially, and without process at base of operculate gill. Terga 7 and 8 (Fig. 198) with long, fine setae on posterior margin. Tergum 10 (Fig. 198) anterior margin strongly emarginated medially. Posterolateral projections (Figs. 198, 211) developed on segments 3–9, slightly bending dorsally; projection 6 directed posteriorly; projection 9 longer than three-fourths length of tergum 10. Sterna flat throughout. Operculate gill (Fig. 198, 201, 213) subquadrate and symmetrical, with posterolateral corner not produced; posterior margin with dense, long marginal setae; posteromedial and posterolateral corners with marginal setae of similar length; Y-ridge strongly developed; ventral multiple submarginal rows of hairlike microtrichia present and adjacent to lateral margin (Fig. 201).

Male adult: Unknown.

Female Adult: See formal description by Soldán (1986), and diagnosis below.

Egg: Unknown.

Diagnosis: The larvae of *Insulibrachys* are easily distinguished from those of all of other genera of Brachycercinae by the following exclusive characteristics. The ocellar tubercles are cylindrical and somewhat truncate apically and distally covered with dense, long setae (Figs. 198, 199), the entire lateral margin of the pronotum is continuously rounded (Fig. 198), and the lateral areas of the prosternal median ridge are strongly produced ventrally to form a ridge posterior to each forecoxa, as seen in lateral view (Fig. 200). Insulibrachys can be additionally distinguished by having maxillary and labial palpi that are two segmented (Figs. 206, 207), a labial palp segment 1 covered with a patch of long setae on the ventral surface (Fig. 207), thoracic sterna that are flat throughout, an abdominal tergum 2 (Fig. 198) without a process at the base of the operculate gills, a posterolateral projection 6 that is not curved medially (Fig. 198), and operculate gills with ventral submarginal rows of hairlike microtrichia (Fig. 201), but without a longitudinal ridge in the sublateral area nor a protruding edge at the posterolateral corner (Fig. 213). In *Caenoculis*, palpi are three segmented (Figs. 29, 30). In Sparbarus, labial palp segment 1 is not covered with long setae ventrally (Fig. 146). In Brachycercus, the abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In Oriobrachys, n. gen., operculate gills have a strongly developed longitudinal ridge in the sublateral area (Fig. 284). In Susperatus, n. gen., thoracic sterna have multiple conical processes (Fig. 361). In Latineosus, n. gen., Alloretochus, n. gen., and Cercobrachys, posterolateral projection 6 is more or less curved medially (Fig. 375), and ventral submarginal rows of microtrichia are lacking on operculate gills in most species (Fig. 428).

Adults of *Insulibrachys* can be distinguished from other Brachycercinae species by having a pronotum with the lateral margins continuously rounded throughout.

Distribution: Neotropical: Cuba.

Insulibrachys needhami (Soldán)

Insulibrachys needhami Soldán, 1986:334.

Mature Larva: Body (Fig. 198) length 7.6 mm. Caudal filaments 3.7 mm. General coloration yellow brown. *Head*: Occiput (Fig. 198) stained with brown in irregular patterns. Ocellar tubercles (Figs. 198, 199) with dense, long setae 1.5–2.0 X length of ocellar tubercle at distal portion. Lateral ocellar tubercle nearly hemispherical in lateral view, slightly shorter than width at base. Middle ocellar tubercle somewhat subquadrate in dorsal view; length subequal to basal width. Antenna (Fig. 208) pale brown; scape without macula; pedicel 1.9 X length of scape, with about 30 setae one-half or more length of pedicel. Mouthparts as in Figures 202–

207. Labrum (Fig. 202) distal margin slightly concave medially; lateral margin slightly and roundly produced. Hypopharynx (Fig. 205) with superlingua lateral margin moderately and roundly produced. Maxilla (Fig. 206) length 2.8 X width; palp segment 1 width 1.3 X width of segment 2; segment 2 1.6 X length of segment 1, with about 10 long, stout setae along entire length of inner margin, and with about 30 long, fine setae at apex and along entire length of outer margin. Thorax: Nota (Fig. 198) yellow brown, without black macula. Pronotum (Fig. 198) lateral margin with dense marginal setae. Propleuron (Fig. 198) narrowly visible in dorsal view, and with dense marginal setae. Prosternum median transverse ridge with some setae one-fourth or less length of forefemur. Mesonotum (Fig. 198) with dense marginal setae laterally. Mesosternum paler than notum, without diffuse black staining. Meso- and metasternum without medial processes. All legs pale brown, without basal band or black macula (Figs. 209, 210). Ratios of length of body: foreleg: midleg: hindleg-3.2: 1.0: 1.2: 1.3. Ratios of length of forefemur: tibia: tarsus: claw-4.5: 2.5: 1.9: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—4.0: 3.5: 1.6: 1.0. Forefemur (Fig. 209) dorsally with row of dense, short setae interspersed with some long setae as long as 2.0 X width of femur, and ventrally with row of dense, short setae interspersed with several long setae as long as 1.0 X width of femur. Foretibia (Fig. 209) ventrally with about 20 setae measuring in length about one-half width of tibia, and about 12 setae as long as 1.5–2.0 X width of tibia. Foretarsus (Fig. 209) ventrally with row of about 12 setae measuring in length about one-third width of tarsus. Foretibia and foretarsus with dense, stout setae and sparse, long, fine setae on anterior and posterior surfaces, but not arrayed in distinct rows. Hindfemur (Fig. 210) length 4.4 X width; dorsal margin with row of short setae interspersed with some long setae as long as 1.5–2.0 X width of femur; ventral margin with short setae; posterior surface with some long, fine setae in basal third. Hindtibia (Fig. 210) dorsally with row of about 50 long, fine setae as long as about 5.0 X width of tibia, and ventrally with row of short, stout setae and row of long, fine setae fewer and shorter than those on dorsal margin. Hindtarsus (Fig. 210) dorsally with row of about 30 long, fine setae, and ventrally with row of short, stout setae and row of long, fine setae fewer and shorter than those on dorsal margin. Hindclaw (Fig. 210) length 5.5 X basal width. Abdomen: Terga (Fig. 198) yellow brown, without black macula. Segment 2 with lateral margin only slightly and broadly produced, not forming distinct posterolateral projection (Figs. 198, 211); projections 3-9 (Figs. 198, 211) apices acutely pointed; projections 4–6 subequal in length, about 2.5 X basal width; projection 6 directed posteriorly; projection 7 about two-thirds length of projection 6; projections 8 and 9 subequal in length, about one-third length of projection 6. Sterna somewhat paler than terga, without diffuse black staining; sternum 9 posterior margin convexly produced (Fig. 212). Operculate gill (Fig. 213) yellow-brown, without black macula; length 1.1 X width; dorsum with some scattered setae; posterior margin with row of dense, long setae two-fifths length of operculate gill; Y-ridge without black macula, with row of some long setae. Caudal filaments pale yellowbrown.

Male Adult: Unknown.

Female Adult: See formal description by Soldán (1986).

Egg: Unknown.

Distribution: Cuba.

Material Examined: Larva HOLOTYPE, Cuba, Pinar del Río Prov, Santa Cruz de Los Baños, III-28-1939, JG Needham (PERC).

Brachycercini, New Tribe

Type genus: Brachycercus Curtis

Diagnosis: The larvae of Brachycercini are distinguished from those of all other tribes of Brachycercinae by having maxillary and labial palpi that are two-segmented (Figs. 234, 235), and abdominal tergum 2 without a

posteromedial process (Fig. 245), but with a finger-shaped process on either side immediately anterior to the base of operculate gills (Fig. 255). In Caenoculini, maxillary and labial palpi are three segmented (Figs. 29, 30), and abdominal terga 1 and 2 each have one posteromedial cone-shaped process (Fig. 35). In other tribes, abdominal tergum 2 does not have finger-shaped processes at the base of the operculate gills (Fig. 198).

Brachycercus

Brachycercus Curtis, 1834:122.
Oxycypha Burmeister, 1839:796, unnecessary name replacement.
Eurycaenis Bengtsson, 1917:186.
Brachycercus Curtis, 1834 [= Eurycaenis Bengtsson]: Campion, 1923:517.
Brachicercus: Grandi, 1951:174, orthographic error.
Type species: Brachycercus harrisella Curtis.

Species Included: B. berneri Soldán, B. harrisella Curtis, B. nitidus (Traver), and B. ojibwe, n. sp.

Mature Larva: Body length 5.3–8.5 mm. Caudal filaments length 2.1–4.7 mm. General coloration pale vellow-brown to dark red-brown. Head: Anterolateral head with transverse row of long setae between antenna and base of mandible (Fig. 259). Clypeus with long setae (Fig. 259). Occiput with or without dense, long, fine setae; lateral margin curved inward posterior to compound eye (Fig. 245). Compound eye laterally oriented, not strongly produced dorsally (Fig. 246); female compound eve not reaching anteriorly beyond base of middle ocellar tubercle, and with distance from posterior margin of head about one-half diameter of eye (Fig. 246). Ocellar tubercles without apparent setae or with only short setae no longer than one-half length of ocellar tubercle. Lateral ocellar tubercle (Figs. 215, 260) triangulate in lateral view; distal portion straight or slightly curved anteriorly; apex rounded or bluntly pointed. Middle ocellar tubercle (Figs. 215, 260) as long as, or shorter than, lateral tubercles, triangulate or elongate-conical in dorsal view. Pedicel (Fig. 219) 1.8–2.1 X length of scape, with more than 15 setae one-half or more length of pedicel. Labrum (Fig. 230) trapezoidal, distally slightly emarginate medially. Hypopharynx (Fig. 233) with superlingua ovate, not triangulate laterally. Maxilla (Fig. 234) with galealacinia sickle shaped, with ratio of length to basal width 2.4–2.9; maxillary palp two segmented; segment 1 width 1.6–1.7 X that of segment 2; segment 2 1.3–1.4 X length of segment 1, with row of 12-16 long, stout setae along distal three-fourths of inner margin, with more than 15 long, fine setae at apex and along distal half of outer margin, and without dense, long setae on ventral surface. Labial palp (Fig. 235) two segmented; segment 1 ventrally with patch of setae one-half or more length of segment 1. Thorax: Pronotum trapezoidal (Fig. 245); anterior margin slightly emarginate; lateral margin produced, forming angulate expansion in about anterior two-fifths (Fig. 246). Propleuron not visible or only narrowly visible in dorsal view (Fig. 245), with relatively dense marginal setae. Median transverse ridge of prosternum medially slightly or strongly produced (Figs. 216, 228), laterally not produced, covered with tuft of setae one-third or less length of forefemur, directed anteriorly or anterolaterally. Mesosternum (Figs. 228, 247) with or without produced processes on basisternum and sternellum, and with row of relatively dense setae along anterior margin shorter than one-fourth length of midfemur, directed anteriorly or anterolaterally. Metasternum (Fig. 228) without process. Legs without flat process on dorsal margin of coxa (Figs. 237, 238). Forefemur (Fig. 237) ventrally with mostly short setae and some setae as long as width of femur. Foretibia (Fig. 237) as long as, or slightly shorter than, foretarsus; ventral margin with row of setae as long as, or shorter than, width of tibia, sometimes also with some setae as long as 1.5 X width of tibia; posterior surface without distinct long setal row. Foretarsus (Fig. 237) ventral margin with row of setae as long as, or shorter than, width of tarsus; anterior and posterior surfaces with scattered setae, some 2.0-3.0 X as long as width of tarsus; dorsal marginal setae not arrayed in distinct row. Hindleg (Fig. 238) length 1.6-1.8 X that of foreleg. Hindfemur (Fig. 38) length greater than 5.0 X width, dorsally with some setae measuring in length 2.0 X or more width of femur. Hindtibia and hindtarsus (Fig. 238) dorsally with row of long setae measuring in length 3.0-4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Figs. 224, 238) evenly and moderately curved, longer than 5.0 X basal width; inner margin smooth, without armature. Abdomen: Tergum 1 (Fig. 226) with weakly developed, indistinct median process at posterior margin. Tergum 2 (Fig. 226) without median process at posterior margin, with finger-shaped process on either side immediately anterior to base of operculate gill (Figs. 217, 255). Terga 7 and 8 with row of long, fine setae along posterior margin (fewer on tergum 8). Tergum 10 anterior margin strongly emarginate medially (Fig. 226). Posterolateral projection not developed on segment 2 (Fig. 229), less than one-half length of projection 3, forming blunt angle; posterolateral projections 3–7 (Fig. 229) well developed; projections 3–6 strongly upturned; projection 5 length more than 3.5 X basal width; projection 6 directed posteriorly; projection 7 one-third to two-thirds length of projection 6; projection 9 less than one-half length of tergum 10. Sterna flat throughout. Operculate gill (Fig. 225) subquadrate, with length 1.2– 1.3 X width; posterolateral corner with distinctive produced edge (but hardly apparent in some B. harrisella populations from Central European, see Diagnosis below); dorsal surface covered with some long setae laterally; marginal setae at posteromedial and posterolateral corners subequal in length; Y-ridge strongly developed, with some long setae; ventral multiple submarginal rows of hairlike microtrichia present and relatively offset from lateral and posterior margins (Fig. 256).

Adult: Male body (Fig. 241) length 4.8–5.8 mm; wing length 4.5–5.8 mm; caudal filaments length 14.0–16.0 mm. Female body length 5.3–7.4 mm; wing length 5.7–6.3 mm; caudal filaments length 3.6–4.8 mm. General coloration dark brown. *Head*: Pedicel (Fig. 242) about 2.0 X length of scape. *Thorax*: Pronotum (Fig. 241) trapezoidal, with lateral margin not convexly produced. Prosternum flat or only slightly produced ventrally. Metanotum (Fig. 241) with medial process at posterior margin broadly triangulate. Male foreleg three-fourths to four-fifths length of body; foretibia about twice length of forefemur. Female foreleg about one-fourth length of body. *Abdomen*: Terga (Fig. 241) with or without diffuse brown shading. Segments 3–7 or 3–8 with vestiges of posterolateral projections (Fig. 243). Male genital forceps (Fig. 244) blade shaped, with longitudinal fold, slightly bowed; penes lobe (Fig. 244) subquadrate.

Egg: Shape ovate (Fig. 555). Chorion with 13–18 longitudinal costae in lateral half (Figs. 555, 557). Costa symmetrical in cross-section, overlapping inter-costal grooves equally along both sides (Fig. 558). Polar cap without tubercles (Fig. 555). One micropyle present at least in some species.

Diagnosis: The larvae of *Brachycercus* are distinguished from those of all other genera of Brachycercinae except *Caenoculis*, by having an abdominal tergum 2 with a finger-shaped process on either side immediately anterior to the base of operculate gills (Figs. 217, 255), and operculate gills with a protruding edge at the posterolater corner (Fig. 225). Such a posterolaterally protruding edge of *Brachycercus* is distinctive in all examined Nearctic and Palearctic specimens, however according to Malzacher (per. comm.), it may be difficult to detect in certain Central European B. harrisella individuals. In other genera, abdominal tergum 2 does not have such processes at the base of the operculate gills (Fig. 198), and the operculate gills are generally symmetrical, lacking a protruding edge at the posterolateral corner (Fig. 73). Brachycercus can also be distinguished by having ocellar tubercles without long setae (Fig. 227), a middle ocellar tubercle that is straight or has the apical portion curved dorsally in the lateral view (Fig. 225), maxillary and labial palpi that are twosegmented (Figs. 234, 235), a labial palp segment 1 covered with a patch of long setae ventrally (Fig. 235), a metasternum that is flat (Fig. 228), an abdominal tergum 1 with a low and indistinct posteromedial process, an abdominal tergum 2 without a posteromedial process (Fig. 245), a posterolateral projection 6 not curved medially (Fig. 245), and operculate gills without a longitudinal ridge in the sublateral area (Fig. 225). In Caenoculis, maxillary and labial palpi are three segmented (Figs. 29, 30), and abdominal terga 1 and 2 each have one posteromedial cone-shaped process (Fig. 35). In Insulibrachys, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In Sparbarus, long setae are absent on the ventral surface of labial palp segment 1 (Fig. 146). In Oriobrachys, n. gen., operculate gills have a strongly developed longitudinal ridge in the sublateral area (Fig. 284). In Susperatus, n. gen., the apical portion of the middle ocellar tubercle is curved ventrally in the lateral view (Fig. 360), and the metasternum has a conical process (Fig. 361). In *Latineosus*, n. gen., *Alloretochus*, n. gen., and *Cercobrachys*, posterolateral projection 6 is distinctly curved medially (Fig. 375).

Adults of *Brachycercus* can be distinguished from those of *Insulibrachys, Susperatus*, n. gen., *Alloretochus*, n. gen., and *Cercobrachys* by having a pronotum with nearly straight lateral margins (Fig. 241), a pedicel that is about twice as long as the scape (Fig. 242), a prosternal median ridge not distinctly produced (Fig. 242), and distinct vestiges of posterolateral projections on abdominal segments 3–7 or 3–8 (Fig. 243). In *Insulibrachys*, lateral margins of the pronotum are convexly produced. In *Susperatus*, n. gen., *Alloretochus*, n. gen., and *Cercobrachys*, the prosternal median ridge is distinctly produced medially (Fig. 349). Additionally, in *Cercobrachys* the pedicel length is one and one-half times that of the scape or shorter (Fig. 489), vestiges of posterolateral projections are usually present on no more than abdominal segments 3–6 (Fig. 430). There is no single characteristic that consistently distinguishes adults of all *Brachycercus* from those of all *Sparbarus*, but they can be separated on a species by species basis (see key).

The eggs of *Brachycercus* have 13–18 costae in the lateral half that are symmetrical in cross-section (Figs. 555, 556). The eggs of all other genera have various numbers of costae that are asymmetrical in cross-section (overlapping only one adjacent inter-costal groove) (Figs. 558, 559), or they lack costae (Fig. 567).

Distribution: Palearctic: Europe, eastern Asian regions of Russia, Mongolia, northern China; Nearctic: Canada, U.S.A.

Brachycercus berneri Soldán

Brachycercus berneri Soldán, 1986:298. Brachycercus floridicola Soldán, 1986:307. Brachycercus berneri Soldán, 1986 [= B. floridicola Soldán]: Berner and Pescador, 1988:352.

Mature larva: Body (Fig. 214) length 5.7–6.0 mm. Caudal filaments length 2.9–3.1 mm. Coloration pale yellow-brown. Head: Occiput (Figs. 214, 215) with patches of diffuse brown staining and with covering of several long, fine setae. Ocellar tubercles without apparent setae. Lateral ocellar tubercle (Fig. 215) length subequal to basal width; anterior margin slightly concave; apex bluntly pointed. Middle ocellar tubercle (Figs. 214, 215) short-triangulate in dorsal view, with length slightly longer than basal width and slightly shorter than lateral tubercle; lateral margins somewhat concave; apex rounded to bluntly pointed. Antenna (Fig. 219) pale; scape without maculae; pedicel 2.0 X length of scape, with 15–20 relatively long setae. Mouthparts as in Figures 202-207. Labrum as in Figure 220. Hypopharynx as in Figure 221. Maxilla (Fig. 222) with galealacinia ratio of length to width—2.9; palp segment 1 width 1.6 X width of segment 2; segment 2 1.4 X length of segment 1, with about 12 long, stout setae on inner margin. Thorax: Nota without distinct black maculae (Fig. 214). Pronotum (Fig. 215) with lateral expansion acutely pointed. Prosternum (Fig. 216) with median transverse ridge slightly protruding ventrally. Mesonotum (Fig. 214) with relatively dense, moderately long marginal setae laterally. Mesosternum (Fig. 216) without medial processes. Legs pale; without basal band or black macula (Figs. 214, 223, 224). Ratio of length of body: foreleg: midleg: hindleg-3.4: 1.0: 1.5: 1.6. Ratio of length of forefemur: tibia: tarsus: claw—2.5: 1.2: 1.3: 1.0. Ratio of length of hindfemur: tibia: tarsus: claw— 2.5: 1.7: 1.7: 1.0. Forefemur (Fig. 223) with row of relatively dense, long and short setae along dorsal margin. Foretibia (Fig. 223) ventral margin with row of about eight setae as long as, or shorter than, 1.5 X width of tibia; posterior surface with some setae measuring in length about 2.0 X width of tibia. Foretarsus (Fig. 223) ventral margin with row of about 12 relatively short setae; anterior and posterior surfaces with some setae about 3.0 X width of tarsus. Hindfemur (Fig. 224) length 6.1 X width; dorsal margin with row of relatively sparse short and long setae; ventral margin with short setae. Hindtibia (Fig. 224) dorsally with row of about 20 long, fine setae. Hindtarsus (Fig. 224) dorsally with row of about 15 long, fine setae. Hindclaw (Fig. 224) slightly and evenly curved; length 10.0 X basal width. Abdomen: Terga (Fig. 214) pale yellow-brown, without

distinct black or brown markings except terga 1 and 2 with some diffuse brown staining. Tergum 2 process anterior to operculate gill narrow (Fig. 217). Posterolateral projection 2 (Fig. 218) slightly produced into blunt angle; projections 3–9 (Fig. 218) apices bluntly pointed; projections 4–6 subequal in length, measuring about 3.6 X basal width; projection 7 about one-half length of projection 6; projections 8 and 9 relatively small. Sterna unmarked; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 225) length 1.2 X width; coloration brown, distinctly darker than posterior abdominal terga, except lateral and posterior margins pale and translucent, laterally with several long setae about one-fourth length of operculate gill; posteromedial corner with row of long marginal setae about one-third length of operculate gill; posterolateral corner with setae subequal in length to those at posteromedial corner and with some short setae; Y-ridge concolorous with adjacent area. Caudal filaments pale yellow.

Adult: See formal description by Soldán (1986), and diagnosis below.

Egg: Unknown.

Diagnosis: The larvae of *B. berneri* are distinguished from other *Brachycercus* species as follows: In *B. berneri*, the mesosternum lacks medial processes (Fig. 216), whereas *B. harrisella* larvae have a process on both the basisternum and sternellum (process on sternellum may be indistinct) (Fig. 228). In *B. berneri*, the apex of the middle ocellar tubercle is acutely pointed (Fig. 215), and the hindclaws are longer than one-fourth the combined length of the hindtibia and hindtarsus, and 10 times as long as their basal width (Fig. 224). In *B. nitidus* and *B. ojibwe*, the apex of the middle ocellar tubercle is blunt (Fig. 246), and the hindclaws are about one-fifth the combined length of the hindtibia and hindtarsus, and no longer than seven times their basal width (Fig. 253).

Adults of *B. berneri* are distinguished from those of *B. harrisella* and *B. nitidus* as follows: The mesosternum is yellow-brown, and the mesosternal basisternum does not have a slightly produced process medially, whereas in *B. harrisella*, the mesonotum is dark black-brown, and the mesosternal basisternum has a slightly produced process (Fig. 242). In *B. berneri*, the male caudal filaments length is 12 mm, and the female's 1.5 mm, whereas in *B. nitidus*, the male caudal filaments are longer than 15 mm, and the female caudal filaments are longer than 2.5 mm.

Discussion: Brachycercus berneri was originally reported by Berner (1950) as Brachycercus sp. A larvae from Sweetwater Creek, Liberty County, Florida. Although Berner (1950) clearly described the lateral expansion of the pronotum, which distinguished the species from *Brachycercus maculatus* (= Sparbarus maculatus), the illustration (plate 18, p. 192) was problematic. Soldán (1986) stated that Berner's illustration was referable to a new species Brachycercus pini Soldán, which he considered closely related to B. maculatus. Soldán (1986) also described a new species Brachycercus floridicola Soldán, which he considered closely related to B. berneri. Berner and Pescador (1988) clarified several critical characteristics associated with Soldán's (1986) Brachycercus species, including the presence of the pronotal lateral expansion in B. floridicola and the lack of a developed abdominal posterolateral projection 2 in B. berneri. As a result, they correctly synonymized B. floridicola with B. berneri. Berner and Pescador (1988) also synonymized B. pini with B. macu*latus*, and at the same time believed that plate 18 given by Berner (1950) was referable to *B. berneri*, although it incorrectly did not show the protruding edge at the posterolateral corner of the operculate gills. These protruding edges were added in their plate 23, which was labeled as *B. berneri* and basically repeated from plate 18 in Berner's (1950) study. Nonetheless, based on the present study, there are series of other characteristics demonstrated by Berner's illustration that indicate it is referable to S. maculatus, including compound eyes that are anteriorly positioned, lateral margins of head posterior to compound eyes that are parallel with the long axis of body, basally banded tibiae and tarsi, the absence of the pronotal lateral angulate expansion, the absence of a finger-shaped process at the base of operculate gills, and the presence of leg and abdominal tergum color patterns typical of North American Sparbarus species, not Brachycercus. Therefore, although the material described as Brachycercus sp. A by Berner (1950) are referable to B. berneri (specimens were examined in this study), the illustration labeled as B. sp. A by Berner (1950) is referable to S. maculatus, and the illustration labeled as *B. berneri* by Berner and Pescador (1988) was incorrectly depicted with a combination of characteristics from both of the two species.

Distribution: U.S.A.: Alabama, Florida, Georgia, South Carolina.

Material Examined: FLORIDA, Liberty Co: two larvae, Sweetwater Cr, Cat No IV-3046-1, IV-30-1946, L Berner (PERC), one exuvia, Sweetwater Cr, Cat No IV-1451-1, IV-14-1951, L Berner (PERC), one exuviae, Cat No I-349-3, L Berner (PERC).

Brachycercus harrisella Curtis

Brachycercus harrisella Curtis, 1834:3.
Caenis harrisella (Curtis), 1834: Stephens, 1835:61.
Caenis pennata Stephens, 1835:61.
Eurycaenis harrisella (Curtis), 1834: Bengtsson 1917:186.
Brachycercus pallidus Tshernova, 1928:114.
Brachycercus magnus Tshernova, 1952:284.
Brachycercus harrisella Curtis, 1834 [= C. pennata Stephens]: Kimmins, 1971:318.
Brachycercus harrisella Curtis, 1834 [= E. harrisella Bengtsson]: Jacob, 1974:96.
Brachycercus arcticus Soldán, 1986:297, new synonym.
Brachycercus harrisella Curtis, 1834 [= B. pallidus Tshernova = B. magnus Tshernova]: Kluge 1991:14.
Brachycercus YUa Quan et al., 2002:244.

Mature Larva: Body (Fig. 226) length 5.3–8.5 mm. Caudal filaments length 2.1–4.0 mm. Coloration pale grey-brown to dark black-brown. Head: Occiput (Figs. 226, 227) with patches of diffuse brown staining and with covering of more than 10 long, fine setae. Ocellar tubercles distally with some setae shorter than one-half length of tubercle. Lateral tubercle (Fig. 227) slightly longer to about 3.0 X basal width; distal portion fingerlike and slightly curved anteriorly; apex rounded to bluntly pointed. Middle ocellar tubercle (Figs. 226, 227) elongate-conical in dorsal view, and straight or slightly curved dorsally in lateral view, with length about 2.0 X basal width, and subequal to, or slightly shorter than, lateral tubercle; lateral margin straight or somewhat concave; apex rounded to bluntly pointed. Antenna (Fig. 236) pale; scape without macula; pedicel 2.1 X scape length, with 15–25 relatively long setae. Mouthparts as in Figures 230–235. Maxilla (Fig. 234) with galealacinia ratio of length to width—2.7; palp segment 1 width 1.6 X that of segment 2; segment 2 1.4 X length of segment 1, with about 15 long, stout setae on inner margin. Thorax: Nota without distinct black maculae (Fig. 226). Pronotum with lateral expansion bluntly pointed (Fig. 227). Prosternum (Fig. 228) with median transverse ridge strongly produced ventrally to form conical medial process. Mesonotum (Fig. 226) with relatively dense, moderately long marginal setae laterally. Mesosternal basisternum with developed, broad-based medial process with rounded to bluntly pointed apex; sternellum with medial process less produced, indistinct in some individuals (Fig. 228). Legs pale, without basal band or black macula (Figs. 226, 237, 238). Ratio of length of body: foreleg: midleg: hindleg—3.5: 1.0: 1.4: 1.5. Ratio of length of forefemur: tibia: tarsus: claw— 4.0: 2.1: 2.0: 1.0. Ratio of length of hindfemur: tibia: tarsus: claw-4.0: 2.4: 2.4: 1.0. Forefemur (Fig. 237) dorsally with row of relatively dense, long and short setae. Foretibia (Fig. 237) ventral margin with row of about eight setae subequal in length to width of tibia; posterior surface with some setae measuring in length about 2.0 X width of tibia. Foretarsus (Fig. 237) ventral margin with row of about 15 relatively short setae; anterior and posterior surfaces with some setae measuring in length about 2.0 X width of tarsus. Hindfemur (Fig. 238) length 5.6 X width; dorsal margin with row of relatively sparse short and long setae; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 238) each dorsally with row of about 40–50 long, fine setae. Hindclaw (Fig. 238) evenly curved; length 5.5-7.0 X basal width. Abdomen: Terga (Fig. 226) pale brown, without distinct macula; terga 1 and 2 stained with diffuse black; posterior terga stained less so or without black staining. Tergum 2 process anterior to base of operculate gill stout (Fig. 229). Posterolateral projection 2

(Fig. 229) slightly produced to form blunt angle; projections 3–9 (Fig. 229) apices bluntly pointed; projections 4–6 subequal in length, measuring about 4.5 X basal width; projection 7 one-half to two-thirds length of projection 6; projections 8 and 9 relatively small. Sterna unmarked; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 239) length 1.3 X width; coloration brown, somewhat darker than posterior abdominal terga, except lateral and posterior margins pale and somewhat translucent, laterally with several long setae about one-fourth length of operculate gill; posteromedial corner with row of long marginal setae about one-third length of operculate gill; posterolateral corner with setae subequal in length to those at posteromedial corner and with some short setae; Y-ridge concolorous with, or somewhat darker than, adjacent area. Caudal filaments pale yellow-brown.

Male adult: Body (Fig. 241) length 4.8–5.8 mm. Caudal filaments length 14.0–16.0 mm. Wing length 4.5-5.8 mm. Head: Yellow-brown. Frons and occiput stained with diffuse dark black-brown. Stem of epicranial suture and posterior margin of head bordered with black (Fig. 241). Antenna (Fig. 242) scape and pedicel brown, without distinct maculae; flagellum pale. Thorax: Pronotum (Fig. 241) yellow brown, with extensive black shading; longitudinal medial line and subanterior transverse ridge bordered with black. Prosternum yellow-brown, stained with black shading; median transverse ridge bordered with black, slightly produced medially. Mesonotum (Fig. 241) dark black-brown. Mesosternum (Fig. 242) yellow-brown, with extensive black shading; basisternum with slightly produced vestige of medial process somewhat darker or lighter than adjacent area; sternacostal suture stained with black. Ratio of length of Body: foreleg: midleg: hindleg-3.0: 2.4: 1.0: 1.1. Ratio of length of forefemur: tibia: tarsus—1.0: 2.0: 1.4. Ratio of length of foretarsus segment I: II: III: IV: V—1.0: 7.0: 4.3: 3.8: 3.3. Legs with coxa and trochanter brown. Forefemur pale brown, with longitudinal brown stripes; foretibia and foretarsus paler. Mid- and hindfemur pale brown; mid-and hindtibia and mid- and hindtarsus pale. Forewing (Fig. 240) ratio of length to greatest width—1.7; Sc, R₁ and adjacent area pale brown; other veins pale. Abdomen: terga (Fig. 241) pale brown; terga 1 and 2 stained with extensive diffuse black; posterior terga less stained. Sterna pale brown, stained with diffuse black. Segments 3–8 with distinct vestiges of posterolateral projections (Fig. 243). Penes lobe (Fig. 244) with lateral margin slightly convex distally, and ventrally with medial sclerotized area stained with brown. Forceps (Fig. 244) evenly curved. Caudal filaments pale.

Female adult: Body length 5.3–7.4 mm. Caudal filaments length 3.6–4.8 mm. Wing length 5.7–6.3 mm. Ratio of length of body: foreleg: midleg: hindleg—3.7: 1.0: 1.5: 1.7. Coloration and vestiges similar to male.

Egg: Habitus as in Figure 555. Length about 300 mm. Polar cap about one-fourth to one-third length of egg. Chorion with 13–18 broad costae in lateral half.

Diagnosis: The larvae of *B. harrisella* are distinguished from all other *Brachycercus* by the presence of a well-developed medial processes on the mesosternum (Fig. 228). The adults can be distinguished from other species as follows. The body length is 4.8 mm or longer in males, and 5.3 mm or longer in females. Caudal filaments are 14.0 mm or longer in male, and 3.5 mm or longer in female. *Brachycercus berneri* has a body length of 4.5 mm, male caudal filaments are 12.0 mm, and female caudal filaments are 1.5 mm. The mesosternal basisternum of *B. harrisella* has a slightly produced medial process (Fig. 242), which is absent in both *B. berneri* and *B. nitidus*. Eggs of *B. harrisella* are not consistently differentiated from the eggs of *B. nitidus* and *B. ojibwe*.

Discussion: The first representation of *B. harrisella* in North America was unintentionally given in Leonard and Leonard's (1962) publication on Michigan mayflies, by way of an illustration of a larva that was misidentified and labeled as *Brachycercus lacustris* (= *Sparbarus lacustris*). A number of important characters, including the shape of ocellar tubercles, pronotal lateral margins, and operculate gills, clearly indicate that the illustration was referable to *B. harrisella*. One year later, Edmunds et al. (1963) provided another illustration of a larva (from Idaho) labeled as *Brachycercus* sp. and stated that the species was possibly *B. prudens* (= *Susperatus prudens*). This larval illustration, however, is also referable to *B. harrisella*.

Soldán (1986) described B. arcticus Soldán from Alaska and B. edmundsi Soldán from northwestern and

southwestern U.S.A. The characteristics Soldán (1986) used to distinguish his species were as follows. In B. edmundsi, posterolateral projections 6 and 7 were said to overlap each other in dorsal view, but in B. arcticus and B. harrisella, they supposedly did not overlap. In B. harrisella, posterolateral projections 5 and 6 were said to be two and one-half times longer than wide, and contiguous in lateral view, and the posterior mesosternal process (on sternellum) was said to be as large as the anterior one (on basisternum); whereas in B. arcticus, posterolateral projections 5 and 6 were said to be four times longer than wide, and separated in lateral view, and the posterior mesosternal process was said to be strongly reduced. Based on the close examination of type materials of B. arcticus and B. edmundsi, as well as considerable additional materials previously attributable to those species, we have found Soldán's differentiation and resultant species concepts to be untenable. The overlapping status of posterolateral projections 4-6 are largely determined by the conditions of specimens and the angle of observation. In any case, they have been found to be variable among individuals and populations of the same species. The ratios of length to width in posterolateral projections 5 and 6 are also not consistent within species. Among populations of B. harrisella, the development of mesosternal process on the sternellum is variable. In some specimens it is as developed as the one on the basisternum, but almost indistinguishable in others (Kluge, per. comm.). Therefore, Brachycercus arcticus and B. edmundsi are here synonymized with B. harrisella because no consistent specific differences could be found.

Distribution: Europe; eastern Asian regions of Russia; Mongolia; northern China; Canada: Alberta, Saskatchewan; U.S.A.: Alaska, Colorado, Idaho, Michigan, Montana, Nebraska, Utah, Wisconsin, Wyoming.

Material Examined: Larva HOLOTYPE of Brachycercus arcticus, Alaska, Yukon-Koyukuk: Birch Cr between Big Cr and Preacher's Cr, 66°00' N, 144°50' W, VIII-17-1962, J Varley (PERC). CHINA: four larvae, Heilongjiang Prov, Heihe, Sijiazi, VI-26-1999, YT Quan, YH Jin (SWU). CZECHOSLOVAKIA: one larva, Topla R nr Hlinné (Presov), E Slovakia, 29-VI-1964, GF Edmunds (PERC). LITHUANIA: seven larvae, Vilnius, R Neris, 14-29-VI-1988, N Kluge (PERC). MONGOLIA: four male adults, one female adult, one male subimago, Övörhangay Aimak R, Tatsyn-gol 15 km W Bayanteeg, 24–26-VII-1980, V Zherikhin (PERC). ALBERTA: two larvae, site 42, Pembina R, 54°03' N, 114°19' W, VI-21-1979, LD Corkum (USK). SASKATCHEWAN: Two male adults, two female adults, North Saskatchewan R at Cecil Ferry, VI-11-1971, DM Lehmkuhl (USK); one female subimago, Saskatoon, South Saskatchewan R at Queen Elizabeth Power Station, VII-10-1999, JM Webb (PERC); one male adult, one exuvia, Battle R at Hwy 21, 52°50'26" N, 109°20'33" W, VII-1-2000, JM Webb (PERC). COLORADO, Yuma Co: one larva, Arikaree R, Black Wolf Cr, VI-6-2000, Scheurer. IDAHO, Lincoln Co: one larva, North Gooding Canal at Jct US Hwy 93, 6 mi N Shoshone, 4,190, 24-VII-1964, SL Jensen, PS Lombardi, FD Isenberg. KANSAS, Chevenne Co: one larva, S fk Republican R, 11 mi W, 7 mi S St Francis, VI-5-1979, D Higgins, PML (KU), three larvae, S fk Republican R, 11 mi W, 7 mi S St Francis, VI-5-1979, D Higgins, PL (KU); Philips Co: seven larvae, N fk Solomon R, 0.7 mi S Glade US hwy 183, V-19-1977, D Higgins, PML (KU), seven larvae, N fk Solomon R, 0.7 mi S Glade US hwy 183, V-19-1977, D Higgins, PML (KU). MICHIGAN, Lake Co: four female adults, one female subimago, five exuviae, T17NR13WS16, EX Leonard Coll L47-496, V-25-1947, JW Leonard, FA Leonard (UM), one larva, T17NR13WS16, EX Leonard Coll L47-481, VII-22-1947, JW Leonard, FA Leonard (UM), nine larvae, T17NR13WS16, EX Leonard Coll L47-482, VII-24-1947, JW Leonard, FA Leonard (UM), one female adult, T17NR13WS16, EX Leonard Coll L47-514, VII-26-1947, JW Leonard, FA Leonard (UM), one male subimago, one exuvia, T17NR13WS16, EX Leonard Coll L47-602, VIII-3-1947, JW Leonard, FA Leonard (UM). MONTANA, Blaine Co: two larvae, Milk R 16 mi W Havre at US Hwy 2 (MP469), 48°35'45" N, 109°21'48" W, VI-14-2000, WP McCafferty et al. (PERC). NEBRASKA, Blaine Co: one larva, Goose Cr, Co Rd 7 S of Koshopah, VI-13-2000, T Klubertanz (PERC); Dundy Co: one larva, Rock Cr, St Rec Area inflow area, V-18-1977, P Liechti, DGH (KU); Garden Co: 11 larvae, Blue Cr, Rackett Rd, V-22-1998, B Kondratieff (CSU); Hall Co: one larva, Platte R nr St Rd 11 and I-80, IV-26-1981, WP McCafferty, AV Provonsha, D Bloodgood (PERC); Hayes Co: one larva, Frenchman R at US Hwy 6, 4.7 mi E of Waunita, VI-12-1994, B Kondratieff (CSU); Hitchcock Co: seven larvae, Republican R below Swanson Reservoir, V-17-1977,

P Liechti, DGH (KU); Sheridan Co: four larvae, Niobrara R, 29-V-1984, R Lawson, K Brown, M Brohman (PERC), two larvae, Niobrara R, 8-VI-1984, R Lawson K Brown, M Brohman (PERC), five larvae, one male adult, (MP349) Niobrara R at St Rd 27, VI-16-1984, WP McCafferty, AV Provonsha (PERC), one larva, Niobrara R, Gorden, 11-VII-1984, R Lawson, K Brown, M Brohman (PERC); Wheeler Co: three larvae, (MP405) Cedar R at St Rd 70/91 E of Ericson, 41°47'00" N, 98°41'53" W, VI-6-2000, WP McCafferty et al. (PERC). WISCONSIN, Burnett Co: three larvae, St Croix R, Cliff area upriver Hwy 70, VI-12-1991, RA Lillie (PERC); Dunn Co: one larva, Chippewa R, Fooshrooke Rd, VI-15-1992, RA Lillie; Pepin Co: one larva, Chippewa R, Above Durand, VI-11-1991, RA Lillie (PERC); Richland Co: two larvae, Bear Cr, V-31-1988, RA Lillie (PERC), one larva, Mill Cr, V-31-1988, RA Lillie (PERC). WYOMING, Sweetwater Co: one larva and slides, Green R, Sta 7, R Mi 372 – K, VII-3-1959, G Smith, G Musser (PERC), one larva, Green R, R Mi 378 – R, VI-30-1959, G Smith, G Musser (PERC), 27 larvae, Green R at Green River City, Picnic Grds on Service Rd, W city, 6-VII-1968, R & D Koss (PERC), one larva, Black's Fork R at I-80, W Green River City, 2-VIII-1969, AV Provonsha (PERC).

Brachycercus nitidus (Traver)

Eurycaenis nitida Traver, 1932:139. *Brachycercus nitidus* (Traver), 1932: Traver, 1935:641.

Mature Larva: Body (Fig. 245) length 5.9–8.5 mm. Caudal filaments length 3.1–4.7 mm. Coloration pale yellow-brown. Head: Frons and vertex (Figs. 245, 246) extensively stained with black brown, distinctly darker than adjacent regions. Occiput (Figs. 245, 246) with patches of diffuse brown staining, and covered with several long, fine setae. Ocellar tubercles without apparent setae. Lateral tubercle (Fig. 246) length subequal to, or slightly longer than, basal width; distal half slightly curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 245, 246) triangulate in dorsal view, with length subequal to basal width, and subequal to, or slightly shorter than, lateral tubercle; lateral margin straight; apex rounded to bluntly pointed. Antenna (Fig. 248) pale; scape without maculae; pedicel 1.8 X length of scape, with 15–20 relatively long setae. Labrum as in Figure 249. Hypopharynx as in Figure 250. Maxilla (Fig. 251) with galealacinia ratio of length to width—3.0; palp segment 1 width 1.7 X width of segment 2; segment 2 1.4 X length of segment 1, with about 12 long, stout setae on inner margin. Thorax: Nota without distinct black maculae. Pronotum (Figs. 245, 246) with lateral expansion acutely pointed. Prosternum (Fig. 247) with median transverse ridge slightly produced. Mesonotum (Fig. 245) with relatively dense, moderately long marginal setae laterally. Meso- and metasternum (Fig. 247) without medial processes. Legs pale, without basal band or black macula (Figs. 245, 252, 253). Ratio of length of body: foreleg: midleg: hindleg-3.8: 1.0: 1.7: 1.8. Ratio of length of forefemur: tibia: tarsus: claw—3.4: 1.7: 1.7: 1.0. Ratio of length of hindfemur: tibia: tarsus: claw—4.2: 2.9: 2.6: 1.0. Forefemur (Fig. 252) dorsally with row of relatively dense, long and short setae. Foretibia (Fig. 252) ventral margin with row of about 10 setae subequal in length to width of tibia; posterior surface with some setae measuring in length about 2.0 X width of tibia. Foretarsus (Fig. 252) ventral margin with row of about 15 relatively short setae; anterior and posterior surfaces with some setae measuring in length about 3.0 X width of tarsus. Hindfemur (Fig. 253) length 6.2 X width; dorsal margin with row of relatively sparse short and long setae; ventral margin with short setae. Hindtibia (Fig. 253) dorsally with row of about 30-40 long, fine setae. Hindtarsus (Fig. 253) dorsally with row of about 20 long, fine setae. Hindclaw (Fig. 253) evenly curved; length 6.0 X basal width. Abdomen: Terga (Fig. 245) pale brown; terga 1 and 2 stained with diffuse black; posterior terga less stained or without black staining; tergum 10 bordered with dark brown, and stained with brown medially. Tergum 2 process anterior to base of operculate gill stout (Fig. 255). Posterolateral projection 2 (Fig. 245) slightly produced, forming blunt angle; projections 3–9 (Fig. 245) apices bluntly pointed; projections 4–6 subequal in length, measuring about 3.8 X basal width; projection 7 about one-half length of projection 6; projections 8 and 9 relatively small. Sterna unmarked; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 254) length 1.3 X width; coloration dark brown, distinctly darker than posterior abdominal terga, except lateral and posterior margins pale and somewhat translucent; lateral region with several long setae about one-fourth length of operculate gill; posteromedial corner with row of long marginal setae about one-third length of operculate gill; posterolateral corner with setae subequal in length to those at posteromedial corner and with some short setae; Y-ridge concolorous with adjacent area. Caudal filaments pale yellow-brown.

Male adult: See formal description by Soldán (1986), female description in part, and diagnosis below.

Female adult: Body (Fig. 257) length 5.2 mm. Caudal filaments length 3.5 mm. Wing length 5.8 mm. *Head:* Pale yellow-brown. Frons and epicranial suture (Fig. 257) stained with brown. Antenna scape and pedicel pale brown without macula; flagellum pale. *Thorax*: Pronotum (Fig. 257) pale brown; longitudinal medial line and subanterior transverse ridge bordered with diffuse brown. Prosternum pale brown; median transverse ridge bordered with brown, not distinctly produced ventrally. Mesonotum (Fig. 257) yellow-brown to red-brown. Mesosternum sternacostal suture stained with brown; basisternum without slightly produced medial process. Coxae and trochanters pale brown; femora pale; tibiae and tarsi pale. Forewing ratio of length to greatest width—1.9; Sc, R₁ and adjacent area pale grey; other veins pale. *Abdomen*: terga (Fig. 257) pale brown, stained with diffuse black. Segments 3–7 with developed vestiges of posterolateral projections. Caudal filaments pale.

Egg: See formal description by Soldán (1986), and diagnosis below.

Diagnosis: Larvae of *B. nitidus* are distinguished from larvae of other *Brachycercus* as follows: The mesosternum is flat, without central processes (Fig. 247), whereas in *B. harrisella*, a distinct process is present medially on mesosternal basisternum, and a second process may be present on the mesosternal sternellum (Fig. 228). In *B. nitidus*, the middle ocellar tubercle is very bluntly pointed or somewhat rounded at apex (Fig. 245), and the hindclaws are about one-fifth of the combined length of the hindtibiae and hindtarsi, and not longer than seven times their basal width (Fig. 253); whereas in *B. berneri*, the middle ocellar tubercle is acutely pointed (Fig. 214), and the hindclaws are longer than one-fourth of the combined length of the hindtibiae and hindtarsi, and about 10 times as long as their basal width (Fig. 224). In *B. nitidus*, the frons and the operculate gill are extensively stained with dark black-brown (Fig. 246), the middle ocellar tubercle is slightly longer than its basal width (Fig. 246), the galealaciniae are longer than two and one-half times their width (Fig. 251), and the femora are pale throughout and not darker than the tibiae and tarsi (Fig. 245). In *B. ojibwe*, n. sp., the frons and the operculate gill are not stained extensively with dark black-brown (there is a transverse diffuse brown band dorsal to middle ocellar tubercle) (Fig. 259), the middle ocellar tubercle length is twice or more its basal width (Fig. 260), the galealaciniae are shorter than two and one-half times the width (Fig. 265), and the femora are pale brown basally (darker than the tibiae and tarsi) (Fig. 258).

Adults of *B. nitidus* are distinguished from those of *B. harrisella* by having a yellow-brown to red-brown coloration of the mesonotum (Fig. 257), and by the absence of a slightly produced medial process on the mesosternal basisternum. In *B. harrisella*, the mesonotum is usually dark black-brown (Fig. 241), and the mesosternal basisternum has a slightly produced medial process (Fig. 242). Adults of *B. nitidus* and *B. berneri* are similar in appearance. However, in *B. nitidus*, the caudal filaments are longer than 15 mm in males, and longer than 2.5 mm in females, whereas in *B. berneri*, caudal filaments are about 12 mm in males, and 1.5 mm in females.

Eggs of *B. nitidus* are not consistently differentiated from those of *B. harrisella* and *B. ojibwe*, n. sp., (see above and below).

Distribution: Canada: Quebec; U.S.A.: Florida, Georgia, Massachusetts, North Carolina, South Carolina.

Material Examined: Female adult HOLOTYPE, North Carolina, Rocky Broad R, (Lecky Gap) 2-VII-1930 (CU). One larva PARATYPE, same data and deposition as holotype. One larva PARATYPE, North Carolina, Bald Cr, 6-VII-1930 (CU). One larva PARATYPE, North Carolina, Cedar Mt, 12-VII-1930 (CU). QUEBEC: two larvae, S Bolton, 1-VII-1930, LJ Milne (CNC); one larva, Mississquoi R, S Bolton, 3-VII-1929, GS Walley (CNC). GEORGIA, Dawson Co: three larvae, Cat No 6-2455-1, L Berner (PERC). MAS-SACHUSETTS: one larva, Amherst, 23-VI-1951, O Flint (PERC). NORTH CAROLINA, Cabarrus Co: 13 larvae, Coddle Cr, CC# 3467, VI-1985 (PERC), seven larvae, Coddle Cr, SR 1612, VI-1985 (PERC); Chero-kee Co: one larva, #112, Murphy, 27-VII-1930, HT Spieth (PERC); Iredell Co: three larvae, Rocky R, VI-1985 (PERC); Jackson Co: six larvae, Moses Cr, CC# 6594, VII-1994 (PERC); Madison Co: 10 larvae, Ivy Cr, CC# 5932, VII-1992, DR Lenat (PERC); Transylvania Co: one larva, Lake Toxaway, 25-VI-1936 (CU); Vance Co: nine larvae, L Island Cr, V-1988 (PERC); Watauga Co: one larva, Valle Crucis, Fall, 1934, L Thomsen (PERC), three larvae, Sawmill R, 9-VII-1959 (no other data) (PERC), four larvae, Brushy Cr, CC# 6804, V-1995 (PERC).

Brachycercus ojibwe, New Species

Mature Larva: Body (Fig. 258) length 5.6–7.0 mm. Caudal filaments length 2.8–4.0 mm. Coloration pale yellow-brown. Head: Frons (Fig. 259) with transverse brown band dorsal to middle ocellar tubercle. Occiput (Fig. 260) with some irregular diffuse brown staining, and covered with several long, fine setae. Lateral ocellar tubercle (Fig. 260) length subequal to, or slightly longer than, basal width; distal half slightly curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 258, 260) elongate-conical in dorsal view, and straight in lateral view, with length subequal to, or slightly longer than, 2.0 X basal width, and slightly shorter than lateral tubercle; lateral margin straight; apex rounded to bluntly pointed. Antenna (Fig. 262) pale; scape without maculae; pedicel 2.0 X length of scape, with 15–20 relatively long setae. Labrum as in Figure 263. Hypopharynx as in Figure 264. Maxilla (Fig. 265) with galealacinia ratio of length to width—2.3; palp segment 1 width 1.7 X width of segment 2; segment 2 1.4 X length of segment 1, with about 14 long, stout setae on inner margin. Thorax: Nota without distinct black maculae. Pronotum (Fig. 260) with lateral expansion bluntly pointed. Prosternum (Fig. 261) median transverse ridge slightly produced. Mesonotum with relatively dense, moderately long marginal setae laterally. Meso- and metasternum (Fig. 261) without medial processes. Femora (Fig. 258) pale brown except distally pale, without black macula; tibiae and tarsi pale. Ratio of length of body: foreleg: midleg: hindleg—3.2: 1.0: 1.5: 1.6. Ratio of length of forefemur: tibia: tarsus: claw—3.5: 1.4: 1.6: 1.0. Ratio of length of hindfemur: tibia: tarsus: claw-3.8: 2.4: 2.4: 1.0. Forefemur (Fig. 266) dorsally with row of relatively dense, long and short setae. Foretibia (Fig. 266) ventral margin with row of about eight setae as long as, or shorter than, width of tibia; posterior surface with some setae measuring in length about 3.0 X width of tibia. Foretarsus (Fig. 266) ventral margin with row of about 12 relatively short setae; anterior and posterior surfaces with some setae measuring in length about 3.0 X width of tarsus. Hindfemur (Fig. 267) length 6.5 X width; dorsal margin with row of relatively sparse short and long setae; ventral margin with short setae. Hindtibia (Fig. 267) dorsally with row of about 30-40 long, fine setae. Hindtarsus (Fig. 267) dorsally with row of about 20 long, fine setae. Hindclaw (Fig. 267) evenly curved; length 6.8 X basal width. Abdomen: Terga (Fig. 258) pale brown; terga 1 and 2 stained with diffuse black; posterior terga less stained or without black staining; terga 8 and 9 with transverse band of diffuse brown along anterior margin; tergum 10 anterior margin darkened with black-brown. Tergum 2 process anterior to base of operculate gill stout. Posterolateral projection 2 (Fig. 258) slightly produced, forming blunt angle; projections 3–9 (Fig. 258) apices bluntly pointed; projections 4–6 subequal in length, measuring about 4.0 X basal width; projection 7 about one-half length of projection 6; projections 8 and 9 relatively small. Sterna stained with diffuse black; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 268) length 1.3 X width; coloration brown, somewhat darker than posterior abdominal terga, except posterolateral corner pale and translucent; lateral region with several long setae about one-fourth length of operculate gill; posteromedial corner with row of long marginal setae about one-third length of operculate gill; posterolateral corner with setae subequal in length to those at

posteromedial corner and with some short setae; Y-ridge somewhat darker than adjacent area. Caudal filaments pale yellow.

Adult: Unknown.

Egg: Habitus as in Figure 557. Length about 200 mm. Polar cap about one-fourth length of egg. Chorion with 14–18 broad costae in lateral half.

Diagnosis: Larvae of *B. ojibwe* are distinguished from other *Brachycercus* larvae as follows: The mesosternum is flat, without medial processes (Fig. 261), whereas in B. harrisella, a distinct process is present medially on the mesosternal basisternum, and a second process may or may not be present on the mesosternal sternellum (Fig. 228). In B. ojibwe, the middle ocellar tubercle is twice as long as its basal width and bluntly pointed or somewhat rounded apically (Fig. 260), the hindclaws are about one-fifth of the combined length of the hindtibiae and hindtarsi, and not longer than seven times their basal width (Fig. 267). In B. berneri, the middle ocellar is subequal in length to its basal width, with the apex acutely pointed (Fig. 215), and the hindclaws are longer than one-fourth of the combined length of the hindtibiae and hindtarsi, and about 10 times as long as their basal width (Fig. 224). In B. ojibwe, the frons and vertex are not stained with extensive dark black-brown, there is a transverse diffuse brown band dorsal of the middle ocellar tubercle (Fig. 259), the middle ocellar tubercle is twice as long as its basal width (Fig. 260), the galealaciniae are shorter than two and one-half times their width (Fig. 265), and the femora are pale brown basally and darker than the tibiae and tarsi (Fig. 258). In B. nitidus, the frons and vertex are extensively stained with dark black-brown (Fig. 246), the middle ocellar tubercle is only slightly longer than its basal width (Fig. 246), the galealaciniae are longer than two and one-half times their width (Fig. 251), and the femora are as pale as the tibiae and tarsi (Fig. 245). Eggs of B. ojibwe are not consistently differentiated from those of B. harrisella and B. nitidus.

Etymology: The specific epithet is a noun in apposition and is after the native North American people of the Ojibwe tribe, inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: Wisconsin.

Material Examined: Larva HOLOTYPE, Wisconsin, Burnett Co, St Croix R, Hwy 70, VI-16-1992, RA Lillie (PERC). Seven larva PARATYPES, Wisconsin, Trempealeau Co, Trempealeau R, at Dodge, VI-11-1992, RA Lillie (PERC). ONTARIO, Nipissing District: one larva, Papineau Tp, Boom Cr, STN 11, 46°16.2'N 78°38.9'W, VII-8-1974, R Devost and J Picken (ROM); Renfrew District, three larvae, Hagarty and Richards Tp, NL Stream, STN 03/01, 45°35.9'N 77°31.5'W, VII-26-1984, J O'Neill and B Prange (ROM), two larvae, Hagarty and Richards Tp, Byers Cr, STN 04/01, 45°35.6'N 77°30.9'W, VII-31-1984, J O'Neill and B Prange (ROM), five larvae, Hagarty and Richards Tp, Byers Cr, STN 08/01, 45°32.3'N 77°32.2'W, VIII-9-1984, J O'Neill and B Prange (ROM), one larva, Hagarty and Richards Tp, Byers Cr, STN 07/01, 45°33.8'N 77°31.5'W, VII-30-1994, J O'Neill and B Prange (ROM), one larva, Hagarty and Richards Tp, Byers Cr, STN 07/01, 45°33.8'N 77°31.5'W, VII-30-1994, J O'Neill and B Prange (ROM), one larva, Hagarty and Richards Tp, Byers Cr, STN 01/01, 45°33.8'N 77°31.5'W, VII-30-1994, J O'Neill and B Prange (ROM). WISCONSIN, Ashland Co: five larvae, Flambeau R, Holts Landing, VI-17-1992, RA Lillie (PERC); Burnette Co: one larva, St Croix R, above Hwy 70, below island, VI-12-1991, RA Lillie (PERC); Eau Claire Co: seven larvae, Eau Claire R, Hwy 6, Channoy Rd, VI-17-1992, RA Lillie (PERC); Grant Co: two larvae, Wisconsin R, Woodman BL, V-23-1988, RA Lillie (PERC), two larvae, Wisconsin R, 1 mi upstr from Big Green R, VI-7-1990, RA Lillie (PERC), one larva, Wisconsin R, nr Woodman, VI-7-1990, RA Lillie (PERC), 17 larvae, Wisconsin R, nr Woodman, VI-7-1990, RA Lillie (PERC), 33 larvae, Wisconsin R, Big Green RBL, VI-5-1992, RA Lillie (PERC), five larvae, Wisconsin R, Milleville Side Channel, VI-5-1992, RA Lillie (PERC); Lacrosse Co: 12 larvae, Black R, Hwy 35, BL Eddg, VI-11-1992, RA Lillie (PERC); Marathon Co: three larvae, Big Rib R, Dahlke Rd Access, VI-10-1992, RA Lillie (PERC), two larvae, Eau Claire R at Hwy 52 in Hogarty, 45.029820N, 89.303050W, T29N R10E Sec33, sw4/sw4, VI-28-2000, W Smith, R Lillie (PERC); Outagamie Co: four larvae, Wolf R, Hwy 54, Shiocton, VI-9-1992, JD Lillie, RA Lillie (PERC); Pepin Co: one larva, Chippewa R, above Durand, VI-11-1991, RA Lillie (PERC); Richland Co: three larvae,

Wisconsin R, Port Andrew, VI-6-1988, RA Lillie (PERC), one larva, Wisconsin R, Port Andrew, VI-6-1988, RA Lillie (PERC); Rock Co: one larva, Sugar R, VI-4-1992, RA Lillie (PERC); Trempealeau Co: 22 larvae, Black R, nr Hwy 35, boat landing, VI-10-1991, RA Lillie (PERC), three larvae, Black R, upriver Hwy 35, VI-10-1991, RA Lillie (PERC), one larva, Black R, VI-10-1991, RA Lillie (PERC), 26 larvae, 1 exuviae, Black R, Above Hwy 35, VI-11-1992, RA Lillie (PERC), one larva, Black R, Below Beaver Cr, VII-10-1992, RA Lillie, J Barko (PERC); Waupaca Co: seven larvae, Wolf R, Above Dey Rd, BL, VI-9-1992, JD Lillie, RA Lillie (PERC).

Latineosini, New Tribe

Type genus: Oriobrachys, New Genus

Diagnosis: The larvae of Latineosini are distinguished from those of all other tribes of Brachycercinae by having the abdominal posterolateral projection 6 distinctly curved medially (Fig. 282) and foretibiae without a row of long setae on the posterior surface (Fig. 280). In morphologically similar Cercobrachini, n. trib., the posterior surface of foretibiae has a distinct row of 4–7 long setae (Fig. 383). In all other tribes, posterolateral projection 6 is directed posteriorly or only slightly curved medially (Fig. 137).

Oriobrachys, New Genus

Type species: Oriobrachys mahakam, n. sp.

Species Included: O. mahakam, n. sp.

Mature Larva: Head: Head capsule anterolaterally with transverse row of long setae between antenna and base of mandible (Fig. 270). Clypeus with long setae. Occiput without long, fine setae: lateral margin curved inward posterior to compound eye (Fig. 269). Compound eye anterolaterally oriented, not strongly produced dorsally; male compound eye with anterior margin anteriorly not extending beyond base of middle ocellar tubercle (Figs. 269, 270). Ocellar tubercles without apparent setae. Lateral ocellar tubercle (Fig. 270) triangulate in lateral view. Middle ocellar tubercle (Fig. 269) shorter than lateral ones, triangulate in dorsal view. Pedicel (Fig. 279) about 2.0 X length of scape, without apparent long setae one-half or more length of pedicel. Labrum (Fig. 273) nearly trapezoidal. Hypopharynx (Fig. 276) with superlingua ovate. Maxilla (Fig. 277) with galealacinia sickle shaped, with ratio of length to basal width about 2.5; maxillary palp two segmented; segment 1 slightly wider than segment 2; segment 2 about 2.0 X length of segment 1, with row of long, stout setae along distal three-fourths of inner margin, with long, fine setae at apex and along outer margin, and with some long setae on ventral surface. Labial palp (Fig. 278) two segmented; segment 1 ventrally with patch of setae longer than one-half length of segment 1. Thorax: Pronotum (Fig. 269) trapezoidal; anterior margin moderately emarginate; lateral margin broadly produced, forming blunt angulate expansion in anterior one-half, not strongly convex or arc shaped overall. Median ridge of prosternum broadly produced ventrally, covered with tuft of setae one-third or less length of forefemur, directed anteroventrally, lateroventrally, or posteroventrally; prosternum laterally not produced ventrally (Fig. 270). Mesosternum without process, and with row of setae one-fourth or less length of midfemur along anterior margin, directed anteriorly or anterolaterally (Fig. 270). Metasternum without process. Legs (Figs. 280, 281) without plate-shaped process on dorsal margin of coxa. Forefemur (Fig. 280) ventrally with short setae and long setae measuring in length 1.0–1.5 X width of femur. Foretibia (Fig. 280) slightly shorter than foretarsus; ventral margin with setae shorter than width of tibia; posterior surface without distinct row of long setae. Foretarsus (Fig. 280) ventral margin setae not longer than width of tarsus; dorsal margin with long setae but not in distinct setal row. Hindleg slightly longer than foreleg. Hindfemur (Fig. 281) length 4.3 X width, dorsally with some setae measuring in length up to 1.5 X width of femur. Hindtibia and hindtarsus (Fig. 281) dorsally with row of long setae measuring in length 3.0 X width of tibia. Hindclaw (Fig. 281) nearly straight; length 7.3 X basal width; inner margin lacking armature (Fig. 281). *Abdomen*: Terga 1 and 2 (Fig. 269) without median process at posterior margin. Tergum 2 without process anterior to base of operculate gill. Tergum 6 with long, fine setae on posterior margin. Terga 7–8 without long setae on posterior margin. Tergum 10 anterior margin strongly emarginate medially. Posterolateral projections 3–6 (Figs. 282, 283) strongly upturned; projection 6 distinctly curved medially; projections 7–8 (Fig. 282) short, less than one-fifth length of projection 6; projection 9 minute, shorter than one-half length of tergum 10. Sterna flat throughout. Operculate gill (Figs. 272, 283, 284) nearly subquadrate; posterolateral corner without protruding edge; dorsum with some long setae; sublateral area with strongly developed longitudinal ridge, and with area lateral to such ridge strongly folding ventrally (Figs. 283, 284); posteromedial corner with short marginal setae; posterior margin and posterolateral corner with marginal setae; sublateral corner with some indicateral corner with some indicateral corner with some indicateral corner with marginal setae; posterior margin and posterolateral corner with marginal setae; posterior margin and posterolateral corner with marginal setae; submargin and posterolateral corner with area lateral corner; Y-ridge weakly developed, with several setae; venter lacking submarginal rows of microtrichia (Fig. 272).

Adult: Unknown.

Egg: Unknown.

Diagnosis: The larvae of *Oriobrachys* are distinguished from those of other genera of Brachycercinae by having operculate gills with a longitudinal ridge in the sublateral area (Figs. 283, 284). They and larvae of Latineosus, n. gen., Alloretochus, n. gen., and Cercobrachys are also distinguished from all other genera by having the posterolateral projection 6 distinctly curved medially (Fig. 282). Additionally, they have compound eyes that are not produced dorsally (Fig. 270), an occiput with lateral margins posterior to the compound eye distinctly curved inward (Fig. 269), ocellar tubercles without long setae (Fig. 270), a middle ocellar tubercle that is straight in lateral view (Fig. 270), maxillary and labial palpi that are two segmented (Figs. 277, 278), a labial palp segment 1 with long setae ventrally (Fig. 278), thoracic sterna that are flat throughout, foretibiae without a row of long setae on the posterior surface (Fig. 280), an abdominal tergum 2 without a posteromedial process or a process at the base of the operculate gills, and operculate gills without a protruding edge at the posterolateral corner (Fig. 284). In Caenoculis, palpi are three segmented (Figs. 29, 30), and abdominal tergum 2 has one posteromedial cone-shaped process (Fig. 35). In Insulibrachys, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In Sparbarus, long setae are absent on the ventral surface of labial palp segment 1 (Fig. 146). In Brachycercus, abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In Latineosus, n. gen., long setae are absent on the ventral surface of labial palp segment 1 (Fig. 297), compound eyes are strongly produced dorsally (Fig. 286), and the lateral margins of the occiput posterior to the compound eyes are approximately parallel with the long axis of the body (Fig. 298). In Susperatus, n. gen., the apical portion of the middle ocellar tubercle is curved ventrally in lateral view (Fig. 360), and the thoracic sterna have multiple conical processes (Fig. 361). In Alloretochus, n. gen., and *Cercobrachys*, the posterior surface of foretibiae has a distinct row of 4–7 long setae (Fig. 383).

Etymology: The generic nomen is an arbitrary combination of letters alluding to a brachycercid group from the Oriental Region.

Distribution: Oriental: Indonesia.

Oriobrachys mahakam, New Species

Mature Larva: Body (Fig. 269) length 3.2 mm. Caudal filaments (Fig. 271) length 1.3 mm. Coloration yellow-brown. *Head*: Frons without black macula or diffuse staining. Occiput (Fig. 269) without black maculae or diffuse shading, covered with several short setae. Lateral ocellar tubercle (Fig. 270) shorter than basal

width by one-third, triangulate in lateral view; apex somewhat rounded. Middle ocellar tubercle (Figs. 269, 270) triangulate in dorsal view; length about two-thirds of basal width, and slightly shorter than lateral ocellar tubercle; apex bluntly pointed. Antenna (Fig. 279) pale; scape without macula; pedicel 1.9 X length of scape, with several setae shorter than one-half length of pedicel. Mouthparts as in Figures 273–278. Labrum (Fig. 273) trapezoidal; lateral margin slightly and roundly produced. Hypopharynx (Fig. 276) with superlingua lateral margin moderately and convexly produced. Maxilla (Fig. 277) with galealacinia length 2.5 X basal width; palp segment 1 width 1.2 X width of segment 2; segment 2 2.0 X length of segment 1, with about 12 long, stout setae along inner margin. Labial palp (Fig. 278) segment 1 ventrally with some long setae one-half to three-fourths length of palp segment 1. Thorax: Nota (Fig. 269) without distinct black maculae. Pronotum anterior margin moderately emarginate; lateral margin broadly produced, forming blunt angle in anterior half. Propleuron partially visible in dorsal view (Fig. 269). Prosternum median transverse ridge broadly produced ventrally, covered with tuft of setae one-fourth to one-third length of forefemur, directed anteroventrally, lateroventrally, or posteroventrally (Fig. 270). Mesosternum anterior margin covered with tuft of setae about one-fourth length of midfemur (Fig. 270). Legs (Figs. 269, 280, 281) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—2.6: 1.0: 1.1: 1.1. Ratios of length of forefemur: tibia: tarsus: claw—3.3: 1.7: 1.9: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.3: 2.5: 2.0: 1.0. Forefemur (Fig. 280) dorsally with relatively dense, long and short setae, ventrally with some short setae and basally with several long setae measuring in length 1.0–1.5 X width of femur in singular row but not well ordered. Foretibia (Fig. 280) ventral margin with row of about seven setae shorter than width of tibia; posterior surface with some setae subequal in length to width of tibia, but not in distinct row. Foretarsus (Fig. 280) ventral margin with row of 15–20 setae shorter than width of tarsus; dorsal margin and anterior and posterior surfaces with some setae measuring in length up to 3.0 X width of tarsus, not in distinct rows. Hindfemur (Fig. 281) length 4.3 X width, dorsally with row of short setae and some long setae measuring in length about 1.5 X width of femur, and ventrally with short setae. Hindtibia (Fig. 281) dorsally with row of about 30 long, fine setae measuring in length about 3.0 X width of tibia. Hindtarsus (Fig. 281) dorsally with row of about 25 long, fine setae. Hindtibia and hindtarsus ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 281) nearly straight; length 7.3 X basal width. Abdomen: Terga (Fig. 269) pale yellow; terga 1, 2, 7, and 8 stained with diffuse black shading, but without dark black macula; tergum 6 with row of relatively long setae on posterior margin; terga 7 and 8 without noticeable long setae on posterior margin. Segment 2 lateral margin slightly and nearly convexly produced (Fig. 282). Posterolateral projections 5 and 6 (Figs. 282, 283) longest; projection 5 length 2.0 X basal width; projection 6 distally strongly curved medially, becoming nearly parallel with posterior margin of tergum 6, with outer margin posterior to inner margin in dorsal view (Fig. 283), and with apex rounded; projections 7–9 minute and indistinct. Sterna stained with black shading; sternum 9 posterior margin convergently produced, truncate distally. Operculate gill (Figs. 283, 284) pale, unicolourous, and somewhat translucent; length 1.2 X width; dorsum laterally with several relatively long setae; posteromedial corner with row of relatively dense marginal setae less than one-sixth length of operculate gill; posterior margin and posterolateral corner with short, uniform marginal setae shorter than those at posteromedial corner by up to two-thirds; Yridge weakly developed, with several setae. Caudal filaments (Fig. 271) pale brown; median filament shorter than cerci by one-third.

Adult: Unknown.

Egg: Unknown.

Etymology: The specific epithet is a noun in apposition taken from the name of the river system from which the holotype is known.

Distribution: Indonesia.

Material Examined: Larva HOLOTYPE, Indonesia, E Kalimantan, Kelian R, Trib of Mahakam R, 250 km W of Samarinda, IX-6-1990, C Yule (FAMU).

Latineosus, New Genus

Type species: Cercobrachys colombianus Soldán

Species Included: L. cayo, n. sp., L. cibola n. sp., and L. colombianus (Soldán), n. comb.

Mature Larva: Body (Figs. 285, 298) length 4.0–5.9 mm. Caudal filaments length 1.3–3.0 mm. General coloration pale yellow to yellow-brown. Head: Head capsule anterolaterally with transverse row of long setae between antenna and base of mandible (Fig. 286). Clypeus with long setae. Occiput without long, fine setae (Fig. 299); lateral margin nearly parallel with long axis of body posterior to compound eye (Fig. 298). Compound eye anterolaterally oriented (Fig. 285), strongly produced dorsally (Figs. 286, 314); female compound eye with anterior margin extending beyond (Fig. 99) base of middle ocellar tubercle (Fig. 313) or not so, and with distance from posterior margin of head two-thirds or more diameter of compound eye (Fig. 285). Ocellar tubercles without apparent setae. Lateral ocellar tubercle (Fig. 286) triangulate in lateral view. Middle ocellar tubercle (Fig. 285) triangulate in dorsal view, shorter than lateral ones. Pedicel (Fig. 308) 1.5–2.5 X length of scape, with less than 10 setae one-half or more length of pedicel. Labrum (Fig. 302) nearly trapezoidal. Hypopharynx (Fig. 305) with superlingua ovate, not triangulate laterally. Maxilla (Fig. 306) with galealacinia sickle shaped, with ratio of length to basal width - 2.0-3.0; maxillary palp two segmented; segment 1 width 1.5–1.7 X width of segment 2; segment 2 1.5–1.8 X length of segment 1, with row of 8–12 long, stout setae along distal three-fourths of inner margin, with more than 15 long, fine setae at apex and along outer margin, and with some long setae on ventral surface. Labial palp (Fig. 307) two segmented; segment 1 ventrally without patch of long setae. Thorax: Pronotum (Fig. 313) trapezoidal; anterior margin slightly to strongly emarginate; lateral margin broadly produced, forming blunt angulate expansion in anterior two-fifths to one-half (Fig. 314), or slightly convexly produced (Fig. 286), but not strongly angulate or continuously rounded throughout. Prosternum median transverse ridge slightly produced ventrally, covered with tuft of setae shorter than onefourth length of forefemur, directed anteriorly or anterolaterally; prosternum laterally not produced ventrally. Mesosternum anterior margin with only scattered setae shorter than one-fourth length of midfemur. Meso- and metasternum without medial processes on basisternum or sternellum. Legs (Figs. 288, 289) without flat process on dorsal margin of coxa. Forefemur (Fig. 288) ventrally with short setae and some long setae as long as 1.0-1.5 X width of femur. Foretibia (Fig. 288) measuring three-fourths length of foretarsus to slightly shorter than foretarsus; ventral margin with setae length 1.0 X width of tibia or shorter; posterior surface with some setae as long as width of tibia, but not arrayed in distinct row. Foretarsus (Fig. 288) ventral margin setae as long as width of tarsus or shorter; dorsal margin and anterior and posterior surfaces with long setae length 2.0–4.0 X width of tarsus, but not in distinct setal row. Hindleg length about 1.5 X that of foreleg. Hindfemur (Fig. 289) length 4.3–5.9 X width, dorsally with some setae slightly longer than width of femur to 1.5 X width of femur. Hindtibia and hindtarsus (Fig. 289) dorsally with row of long setae measuring in length 3.0-4.0 X width of tibia. Hindclaw (Fig. 289) slightly and evenly curved; length 3.5–5.8 X basal width; inner margin lacking armature. Abdomen: Terga 1 and 2 (Fig. 313) without median process at posterior margin. Tergum 2 without process anterior to base of operculate gill. Tergum 7 with row of long setae on posterior margin; tergum 8 with scattered and fewer long setae. Tergum 10 anterior margin strongly emarginate medially (Fig. 313). Segment 2 lateral margin slightly produced into blunt angle (Fig. 290). Posterolateral projections 3-6 (Fig. 290) strongly upturned; posterolateral projection 5 length 3.0–3.6 X basal width; projection 6 distally strongly curved medially, becoming nearly parallel with posterior margin of tergum 6; projections 7–9 (Fig. 313) short to minute; projection 7 less than one-fifth length of projection 6; projection 9 shorter than one-half length of tergum 10. Sterna flat throughout. Operculate gill (Fig. 312) nearly subquadrate; length 1.3–1.4 X width; posterolateral corner without protruding edge; dorsum with short to long setae; posteromedial corner with dense, long marginal setae distinctly longer than those at posterolateral corner; Y-ridge moderately or weakly developed, without long setae; venter lacking submarginal rows of microtrichia or with few rows of

hairlike microtrichia offset from posterior margin (Fig. 291).

Adult: Unknown.

Egg: Shape elongate-ovate (Fig. 566). Polar cap without tubercles. Chorion with less than 10 costae in lateral half (Fig. 566). Costae asymmetrical in cross-section (overlapping adjacent inter-costal groove on one side only) (Fig. 566).

Diagnosis: The larvae of *Latineosus* are distinguished from those of all other genera of Brachycercinae except Sparbarus by having a labial palp segment 1 that lacks a patch of long setae on the ventral surface (Fig. 307). They and larvae of Oriobrachys, Alloretochus, n. gen., and Cercobrachys are also distinguished from all others by having a posterolateral projection 6 distinctly curved medially (Figs. 311, 318). Additionally, they can be distinguished by having ocellar tubercles without long setae (Fig. 286), a middle ocellar tubercle that is straight in the lateral view (Fig. 285), maxillary and labial palpi that are two segmented (Figs. 296, 297), thoracic sterna that are flat throughout, foretibiae without a row of long setae on the posterior surface (Fig. 288), an abdominal tergum 2 without a posteromedial process or processes at the base of the operculate gills (Fig. 313), an abdominal posterolateral projection 7 that is minute or indistinctive (Fig. 318), and operculate gills without a longitudinal ridge in the sublateral area nor a protruding edge at the posterolateral corner (Fig. 312). In Caenoculis, maxillary and labial palpi are three segmented (Figs. 29, 30), and abdominal tergum 2 has one posteromedial cone-shaped process (Fig. 35). In Insulibrachys, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In Sparbarus, the abdominal posterolateral projection 7 is distinct and as long as, or longer than, one-third of the projection 6 (Fig. 71). In Brachycercus, abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In Oriobrachys, operculate gills have a longitudinal ridge in the sublateral area (Fig. 284). In Susperatus, n. gen., the apical portion of the middle ocellar tubercle is curved ventrally in the lateral view (Fig. 360), and thoracic sterna have multiple conical processes (Fig. 361). In Alloretochus, n. gen., and Cercobrachys, the posterior surface of foretibiae has a distinct row of 4–7 long setae (Fig. 383).

The eggs of *Latineosus* can be distinguished from those of *Brachycercus* and *Susperatus*, n. gen., by having multiple costae that are asymmetrical in cross-section (Fig. 566). In *Brachycercus*, the costae are symmetrical in cross-section (Figs. 555, 556), and in *Susperatus*, n. gen., costae are absent on the eggs (Fig. 567). There is no single character that distinguishes eggs of *Latineosus*, *Cercobrachys*, and *Sparbarus*. However, in *Latineosus* and *Cercobrachys*, the polar cap does not have tubercles, and the number of costae is less than 10 in the lateral half of the eggs of most species. In *Sparbarus*, most species have more than 10 costae in the lateral half of the eggs (Fig. 558), and a number of North American species have tubercles on the polar cap (Fig. 563).

Etymology: The generic nomen is a compound Latinized word in the masculine gender that alludes to a Latin American grouping.

Distribution: Nearctic: southwestern; Neotropical: Belize, Colombia.

Latineosus cayo, New Species

Mature Larva: Body (Fig. 285) length 5.9 mm. Caudal filaments length 2.1 mm. Coloration pale yellow. *Head*: Frons and occiput with diffuse pale brown staining, without black maculae (Fig. 286). Occiput covered with some short setae. Compound eye (Figs. 285, 286) moderately produced dorsally; anterior margin not extending anteriorly beyond base of middle ocellar tubercle. Lateral ocellar tubercle (Fig. 286) slightly longer than basal width, triangulate in lateral view, with distal portion somewhat finger shaped and slightly curved anteriorly; apex bluntly pointed. Middle ocellar tubercle (Figs. 285, 286) triangulate in dorsal view; length slightly shorter than basal width, and about half length of lateral ocellar tubercle; apex rounded. Antenna (Fig.

287) pale; scape without macula; pedicel 2.0 X length of scape, with 5-10 setae one-half or more length of pedicel. Mouthparts as in Figures 292–297. Labrum (Fig. 292) lateral margin slightly produced and convex. Hypopharynx (Fig. 295) with superlingua lateral margin moderately produced and convex. Maxilla (Fig. 296) with galealacinia length 2.6 X basal width; palp segment 1 width 1.5 X width of segment 2; segment 2 1.5 X length of segment 1, with about eight long, stout setae along inner margin. Thorax: Nota (Fig. 285) with brown markings as follows: pronotum with longitudinal stripe medially and short, medial transverse stripe at anterior and posterior margins; and with anterolateral corner bordered with brown; propleuron bordered with brown; mesonotum with area anterior to wingpads with about 10 pairs of small, irregular-shaped maculae; metanotum anterior and posterior margins with broad, transverse stripe. Pronotum anterior margin moderately emarginate; lateral margin slightly produced, forming blunt angle in anterior third (Fig. 286). Propleuron partially visible in dorsal view (Fig. 285). Legs (Figs. 285, 288, 289) pale, coxae dorsally darker, and with brown markings as follows: Forefemur with dorsal margin with large, basal macula measuring about one-fourth length of femur, and short, subdistal macula; tibia dorsal margin with small, basal macula; tarsus dorsal margin with large, basal macula measuring about one-third length of tarsus; mid- and hindfemur with dorsal margin somewhat darker basally, and with small, subdistal macula; tibia dorsal margin somewhat darker basally; tarsus dorsal margin with large, basal macula measuring about one-fourth length of tarsus. Ratios of length of body: foreleg: midleg: hindleg—3.6: 1.0: 1.4: 1.4. Ratios of length of forefemur: tibia: tarsus: claw—2.4: 1.5: 1.7: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.8: 2.3: 2.1: 1.0. Forefemur (Fig. 288) dorsally with sparse, long and short setae, ventrally with row of dense, short setae and several setae as long as 1.0 X width of femur, generally in singular row. Foretibia (Fig. 288) ventral margin with row of about four setae as long as, or shorter than, width of tibia; posterior surface with some setae subequal in length to width of tibia, but not arrayed in distinct row. Foretarsus (Fig. 288) ventral margin with row of about 12 setae slightly shorter than width of tarsus; dorsal margin and anterior and posterior surfaces with some setae as long as 2.0 X width of tarsus, not in distinct rows. Hindfemur (Fig. 289) length 5.9 X width, dorsally with row of short setae and some setae slightly longer than width of femur, and ventrally with short setae. Hindtibia (Fig. 289) dorsally with row of about 15 long, fine setae measuring in length about 4.0 X width of tibia. Hindtarsus (Fig. 289) dorsally with row of about 12 long, fine setae. Hindtibia and hindtarsus ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 289) length 5.8 X basal width. Abdomen: Terga (Fig. 285) pale yellow, with brown markings as follows: Tergum 1 with short longitudinal stripe medially; tergum 2 with longitudinal stripe medially and large, irregularshaped macula sublaterally; tergum 6 with area posterior to posterolateral projection stained with diffuse brown; terga 7–9 with short longitudinal stripe medially; tergum 10 anterior margin darkened medially. Posterolateral projection 5 (Fig. 290) length 3.0 X basal width; projection 6 (Fig. 290) with distal half with outer margin posterior to inner margin in dorsal view, and with apex rounded, pair of projections not overlapping medially; projections 7–9 (Figs. 285, 290) small but distinct, acute at apex. Sterna pale yellow; sterna 1–8 with longitudinal diffuse, brown stripe sublaterally; sternum 9 posterior margin convex, somewhat truncate at apex. Operculate gill (Fig. 291) pale and somewhat translucent, without maculae; length 1.3 X width; dorsum covered with some short setae; posteromedial corner with row of dense, long marginal setae measuring up to two-fifths length of operculate gill; posterolateral corner with marginal setae shorter than those at posteromedial corner by about one-half, and intermixed with some short setae; Y-ridge moderately developed; venter with short, hairlike microtrichia offset from posterior margin, and arrayed in two or three rows but not well ordered. Caudal filaments pale; segment posterior margin darkened on every other 2–4 segments.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of *L. cay*o can be distinguished from all other species of *Latineosus* by having hairlike microtrichia in rows offset from the posterior margin on the venter of the operculate gills (Fig. 291). Ventral microtrichia are not present in *L. colombianus* and *L. cibola*, n. sp. (Fig. 301). *Latineosus cay*o larvae can be

additionally distinguished from *L. colombianus* by having compound eyes that are not extended anteriorly beyond the base of middle ocellar tubercle (Fig. 285), and by apices of posterolateral projections on abdominal segment 6 that do not overlap medially as seen in dorsal view (Fig. 290). In *L. colombianus*, the anterior margin of the compound eyes is distinctly extended anteriorly beyond the base of the middle ocellar tubercle (Fig. 313), and the apices of posterolateral projections on abdominal segment 6 distinctly overlap medially (Fig. 318). *Latineosus cay*o can be distinguished from *L. cibola*, n. sp., by having lateral ocellar tubercles that are longer than their basal width and somewhat finger shaped in the distal portion (Fig. 286), and abdominal posterolateral projections 7 and 8 that are small but distinct and acute (Fig. 290). In *L. cibola*, n. sp., lateral ocellar tubercles are simple-triangulate and slightly shorter than their basal width (Fig. 299), and projections 7 and 8 (Fig. 311) are indistinct.

Etymology: The specific epithet a noun in apposition and is based on the Cayo District, Belize, from where the type specimen was collected.

Distribution: Belize.

Material Examined: Larva HOLOTYPE, Belize, Cayo District, Macal R at Black lodge, 10 mi S of San Ignacio, III-13-14-2005, DE Baumgardner (TAMU).

Latineosus cibola, New Species

Mature Larva: Body (Fig. 298) length 4.0–4.8 mm. Caudal filaments length 1.7 mm. Coloration pale yellow. Head: Frons (Fig. 299) without black maculae or diffuse staining. Occiput (Fig. 299) without black maculae or diffuse shading, covered with some short setae. Compound eye (Figs. 298, 299) moderately produced dorsally; anterior margin not extending anteriorly beyond base of middle ocellar tubercle. Lateral ocellar tubercle (Fig. 299) slightly shorter than basal width, triangulate in lateral view; apex bluntly pointed. Middle ocellar tubercle (Figs. 298, 299) triangulate in dorsal view; length slightly shorter than basal width, and about twothirds length of lateral ocellar tubercle; apex bluntly pointed. Antenna (Fig. 308) pale; scape without macula; pedicel 2.5 X length of scape, with about five setae one-half or more length of pedicel. Mouthparts as in Figures 302–307. Labrum (Fig. 302) lateral margin slightly and roundly produced. Hypopharynx (Fig. 305) with superlingua lateral margin moderately and convexly produced. Maxilla (Fig. 306) with galealacinia length 3.0 X basal width; palp segment 1 width 1.5 X width of segment 2; segment 2 1.5 X length of segment 1, with about 12 long, stout setae along inner margin. Thorax: Nota (Fig. 298) without distinct black maculae. Pronotum (Figs. 298, 299) anterior margin moderately emarginate; lateral margin slightly produced, forming blunt angle in anterior third. Propleuron partially visible in dorsal view (Fig. 298). Legs (Figs. 298, 309, 310) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg-2.9: 1.0: 1.5: 1.5. Ratios of length of forefemur: tibia: tarsus: claw-3.2: 1.7: 1.8: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.8: 2.0: 2.6: 1.0. Forefemur (Fig. 309) dorsally with sparse, long and short setae, and ventrally with row of dense, short setae and several setae as long as 1.5 X width of femur in singular row. Foretibia (Fig. 309) ventral margin with row of about six setae as long as, or shorter than, width of tibia; posterior surface with some setae subequal in length to width of tibia, but not in distinct row. Foretarsus (Fig. 309) ventral margin with row of about 10 setae slightly shorter than width of tarsus; dorsal margin and anterior and posterior surfaces with some setae measuring up to 2.0 X width of tarsus, not arrayed in distinct rows. Hindfemur (Fig. 310) length 4.3 X width, dorsally with row of short setae and some long setae measuring in length about 1.5 X width of femur, and ventrally with short setae. Hindtibia (Fig. 310) dorsally with row of about 10–20 long, fine setae measuring in length about 3.0 X width of tibia. Hindtarsus (Fig. 310) dorsally with row of about 20 long, fine setae. Hindtibia and hindtarsus ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 310) stout; length 3.5 X basal width. Abdomen: Terga (Fig. 298) pale yellow, without black macula; tergum 10 anterior margin

darkened medially. Posterolateral projection 5 (Fig. 311) length 3.0 X basal width; projection 6 (Fig. 311) with distal half with outer margin posterior to inner margin in dorsal view, and with apex rounded; pair of projections 6 not overlapping medially; projections 7–9 (Figs. 298, 311) minute and indistinct. Sterna pale yellow, without black staining; sternum 9 posterior margin convex, somewhat truncate at apex. Operculate gill (Fig. 312) pale and somewhat translucent, without maculae; length 1.3 X width; dorsum covered with some short, spatulate setae (Fig. 300), and laterally with several setae as long as one-third length of operculate gill; posteromedial corner with row of dense, long marginal setae measuring about one-third length of operculate gill; posterolateral corner with marginal setae shorter than those at posteromedial corner by about one-third, and intermixed with some short setae; Y-ridge weakly developed; venter lacking submarginal rows of microtrichia. Caudal filaments pale.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of *L. cibola* can be distinguished from *L. cay*o by having lateral ocellar tubercles that are simple-triangulate and slightly shorter than their basal width (Fig. 299), and abdominal posterolateral projections 7 and 8 that are minute and indistinct (Fig. 311). In *L. cay*o, lateral ocellar tubercles are longer than their basal width and somewhat finger shaped in the distal portion (Fig. 286), and projections 7 and 8 are small but distinct and acute (Fig. 290). *Latineosus cibola* can be easily distinguished from *L. colombianus* by the presence of compound eyes that are not extended anteriorly beyond the base of middle ocellar tubercle (Fig. 299), and by the apices of posterolateral projections on abdominal segment 6 not overlapping medially as seen in dorsal view (Fig. 311). In *L. colombianus*, the anterior margin of compound eyes is distinctly extended anteriorly beyond the base of middle ocellar tubercle projections 6 distinctly overlap medially (Fig. 318).

Etymology: The specific epithet a noun in apposition and is after the native North American people of the Cibola tribe, inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: Texas.

Material Examined: Larva HOLOTYPE, Texas, Val Verde Co, San Felipe Cr, 1.5 km upstr mouth, X-8-1996, JR Davis (PERC). One larva PARATYPE, same data as holotype (TAMU). One larva exuviae PARATYPE, Texas, Webb Co, Rio Grande at Laredo Water Treatment Plant, upstr Laredo, III-24-1993, JR Davis (PERC).

Latineosus colombianus Soldán

Cercobrachys colombianus Soldán, 1986:340.

Larva: Body (Fig. 313) length 4.1 mm. Caudal filaments length unknown (filaments broken). Coloration pale yellow. *Head*: Frons without black maculae or diffuse staining. Occiput (Fig. 313) without black maculae or diffuse shading, and without apparent setae. Compound eye (Figs. 313, 314) strongly produced dorsally; anterior margin extending anteriorly beyond base of middle ocellar tubercle. Lateral ocellar tubercle (Fig. 314) length subequal to basal width, triangulate in lateral view; apex bluntly pointed. Middle ocellar tubercle (Figs. 313, 314) triangulate in dorsal view; length subequal to basal width, and about two-thirds length of lateral ocellar tubercle; apex pointed. Antenna (Fig. 315) pale; scape without macula; pedicel 1.5 X length of scape, with about five setae one-half or more length of pedicel. Mouthparts as in Figures 321–326. Labrum (Fig. 321) lateral margin slightly produced. Hypopharynx (Fig. 324) with superlingua lateral margin moderately convex. Maxilla (Fig. 325) with galealacinia length 2.0 X basal width; palp segment 1 width 1.7 X width of segment 2; segment 2 1.8 X length of segment 1, with about 12 long, stout setae along inner margin. *Thorax*: Nota without distinct maculae. Pronotum (Figs. 313, 314) anterior margin moderately emarginate; lateral margin margin margin margin margin margin margin margin.

gin slightly and broadly produced, forming blunt angle in anterior half. Propleuron partially visible in dorsal view (Fig. 313). Legs (Figs. 316, 317) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.3: 1.0: 1.4: 1.5. Ratios of length of forefemur: tibia: tarsus: claw—3.2: 1.5: 2.0: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-4.1: 2.4: 2.5: 1.0. Forefemur (Fig. 316) dorsally with sparse, long and short setae, ventrally with row of dense, short setae and several long setae as long as 1.0-1.5X width of femur. Foretibia (Fig. 316) ventral margin with row of about six setae as long as, or shorter than, width of tibia; posterior surface with several setae measuring in length about 3.0 X width of tibia, not arrayed in distinct row. Foretarsus (Fig. 316) ventral margin with row of about 20 setae as long as, or shorter than, width of tarsus; dorsal margin and anterior and posterior surfaces with several setae measuring in length about 4.0 X width of tarsus but not arrayed in distinct rows. Hindfemur (Fig. 317) length 5.7 X width; dorsal margin with row of short setae and some setae slightly longer than width of femur; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 317) each dorsally with row of about 20 long, fine setae measuring in length about 3.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 317) length 5.0 X basal width. Abdomen: Terga (Fig. 313) pale yellow, without black macula. Posterolateral projection 5 (Figs. 318, 319) length 3.6 X basal width; projection 6 (Figs. 318, 319) longest, broad, with distal half with outer margin anterior to inner margin in dorsal view, and with rounded apices of pair overlapping at medial line of abdomen in dorsal view; projections 7–9 (Fig. 313) minute and indistinct. Sterna pale yellow, without black staining; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 320) pale and unicolourous; length 1.4 X width; dorsum laterally with several setae as long as one-fourth length of operculate gill; posteromedial corner with row of dense, long marginal setae measuring about two-fifths length of operculate gill; posterolateral corner with marginal setae shorter than those at posteromedial corner by up to two-thirds, and intermixed with some short setae; Y-ridge weakly developed; venter lacking submarginal rows of microtrichia. Caudal filaments apparently pale.

Adult: Unknown.

Egg: Habitus as in Figure 566. Length about 160 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with two or three costae in lateral half. Costa width less than one-half of distance between adjacent costae.

Diagnosis: Larvae of *L. colombianus* can be easily distinguished from other species of *Latineosus* as follows. The compound eyes are strongly produced dorsally and extend anteriorly beyond the base of middle ocellar tubercle (Fig. 313); and the apices of the posterolateral projections on abdominal segment 6 overlap medially, and are twisted in such a way that the outer margins appear anterior to the inner ones in dorsal view (Figs. 318, 319). In *L. cay*o and *L. cibol*a, the compound eyes are moderately produced dorsally and do not extend anteriorly beyond the base of middle ocellar tubercle (Figs. 285, 298); projections on abdominal segment 6 have outer margins appearing posterior to the inner margins in dorsal view, and their apices do not meet or overlap medially (Figs. 290, 311).

Distribution: Colombia.

Material Examined: Larva HOLOTYPE, Colombia, Tolima Prov, Quebrada between Armero and Lerida, 11.7 km from Lerida, 4-IV-1969, WP McCafferty (PERC).

Cercobrachini, New Tribe

Type genus: Cercobrachys Soldán

Diagnosis: The larvae of Cercobrachini are distinguished from those of all other tribes of Brachycercinae by the presence of the labrum that has moderately to strongly produced lateral margins (Fig. 394), superlinguae

that have strongly and convergently produced lateral margins (Fig. 397), and foretibiae that have a distinct row of long setae on the posterior surface (Fig. 535). In other tribes, labrum is trapezoidal and has nearly straight lateral margins (Fig. 158), superlinguae are subovate and have moderately and convexly produced lateral margins (Fig. 159), and the foretibiae do not have a distinct row of long setae on the posterior surface (Fig. 288).

Susperatus, New Genus

Type Species: Eurycaenis prudens McDunnough.

Species Included: S. prudens (McDunnough), n. comb., S. tonkawa, n. sp., and S. tuberculatus, (Soldán) n. comb.

Mature Larva: Body (Fig. 327) length 4.5–7.7 mm. Caudal filaments (Fig. 327) length 2.1–3.0 mm. General coloration pale yellow-brown. Head: Head capsule anterolaterally with transverse row of long setae between antenna and base of mandible (Fig. 328). Clypeus with long setae. Occiput (Fig. 341) without long, fine setae; lateral margin curved inward posterior to compound eye. Compound eye (Figs. 328, 341) anterolaterally oriented, not distinctly produced dorsally; anterior margin not extending beyond base of middle ocellar tubercle anteriorly, and with distance from posterior margin of head two-thirds or more diameter of compound eye. Ocellar tubercles without apparent setae (Fig. 341). Lateral ocellar tubercle (Fig. 328) triangulate in lateral view. Middle ocellar tubercle (Figs. 328, 341) elongate-conical in dorsal view, slightly longer than lateral ones, and with distal portion curved ventrally in lateral view. Pedicel (Fig. 337) about 1.5 X length of scape, with 10 or less setae one-half or more length of pedicel. Labrum (Fig. 331) lateral margin moderately produced and convex. Hypopharynx (Fig. 334) with superlingua lateral margin strongly produced and somewhat triangulate. Maxilla (Fig. 335) with galealacinia sickle shaped, with ratio of length to basal width - 2.3–2.6; maxillary palp two segmented; segment 1 width 1.2–1.3 X width of segment 2; segment 2 about 2.0 X length of segment 1, with row of more than 15 long, stout setae along distal three-fourths of inner margin, with more than 15 long, fine setae at apex and along outer margin, and with some long setae on ventral surface. Labial palp (Fig. 336) two segmented; segment 1 ventrally with patch of setae one-half or more length of segment 1. Thorax: Pronotum (Figs. 327, 342) trapezoidal; anterior margin slightly emarginate; lateral margin produced, forming angulate expansion in anterior one-half. Prosternum (Figs. 329, 343) median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of dense setae about one-third length of forefemur, directed anteriorly or anterolaterally; prosternum laterally not produced ventrally. Mesosternum (Figs. 329, 343) with processes on basisternum and sternellum, and with row of dense setae shorter than one-fourth length of midfemur along anterior margin. Metasternum (Figs. 329, 343) with process. Legs (Figs. 327, 338, 339) without flat process on dorsal margin of coxa. Forefemur (Fig. 338) ventrally with short setae and row of long setae measuring in length 2.0 X width of femur. Foretibia (Fig. 338) measuring about three-fourths length of foretarsus; ventral margin with setae length as long as 2.0 X width of tibia; posterior surface with distinct row of long setae as long as, or longer than, tibia. Foretarsus (Fig. 338) ventral margin setae length 1.0 X width of tarsus or shorter; dorsal margin with row of long setae measuring in length about 4.0 X width of tarsus. Hindleg length about 1.5 X that of foreleg. Hindfemur (Fig. 339) length 4.7–5.0 X width, dorsally with some setae as long as 1.5 X width of femur. Hindtibia and hindtarsus (Fig. 339) dorsally with row of long setae measuring in length 3.0-4.0 X width of tibia. Hindclaw (Fig. 344) nearly straight or slightly and evenly curved; length 5.0–6.0 X basal width; inner margin lacking armature. Abdomen: Terga 1 and 2 without median process at posterior margin. Tergum 2 without process anterior to base of operculate gill. Tergum 7 with row of relatively dense, long setae along posterior margin; tergum 8 with fewer setae on posterior margin. Tergum 10 anterior margin strongly emarginate medially. Segment 2 lateral margin produced into short, bluntly pointed projection (Fig. 327). Posterolateral projections 3–6 (Fig. 345) strongly upturned; posterolateral projection 5 length 2.5–3.0 X basal width; projection 6 directed posteriorly; projection 7 (Fig. 345) one-half to two-thirds length of projection 6; projections 8 and 9 (Fig. 327) small; projection 9 shorter than one-half length of tergum 10. Sterna of at least several segments broadly produced vertically (Fig. 330). Operculate gill (Figs. 340, 346) somewhat rectangulate; length about 1.4 X width; posterolateral corner without protruding edge; posteromedial corner with dense, long marginal setae distinctly longer than those at posterolateral corner; Y-ridge strongly developed; venter lacking submarginal rows of microtrichia.

Adult: Male body (Fig. 353) length 3.5–5.1 mm; wing length 3.3–5.0 mm; caudal filaments length 10.0–20.0 mm. Female body length 5.0–5.7 mm; wing length about 4.8 mm; caudal filaments length about 2.3 mm. General coloration pale yellow. *Head*: Pedicel (Fig. 354) 1.6–2.0 X length of scape. *Thorax*: Pronotum (Fig. 353) trapezoidal; lateral margin not convexly produced. Prosternum median transverse ridge strongly produced medially into conical process (Fig. 349). Mesosternum flat (Fig. 349). Metanotum with medial, triangulate process at posterior margin. Male foreleg (Fig. 350) three-fourths to four-fifths length of body; foretibia 2.5–2.8 X length of forefemur. *Abdomen*: Terga without distinct brown or black maculae. Segments 3–6 or 4–6 with distinct vestiges of posterolateral projections (Fig. 347). Male genital forceps (Fig. 352) blade shaped, with longitudinal fold, and pointed at apex; subgenital plate (Fig. 352) with posterior margin truncate or slightly convexly produced; penes lobe (Fig. 352) subquadrate.

Egg: Shape ovate (Fig. 567). Polar cap without tubercles (Fig. 565). Chorion without costae (Fig. 567). Two micropyles present in at least some species (Fig. 568).

Diagnosis: The larvae of *Susperatus* are distinguished from those of all other genera of Brachycercinae by having the apical portion of the middle ocellar tubercle curved ventrally, as seen in lateral view (Fig. 328). In other genera, the middle ocellar tubercle is either straight or curved dorsally in the apical portion, as seen in lateral view (Figs. 31, 62). Susperatus larvae are also distinguished from all other Brachycercinae, except certain species of *Brachycercus*, by having conical processes on thoracic sterna (Fig. 329). Susperatus can be additionally distinguished by having ocellar tubercles without long setae (Fig. 341), maxillary and labial palpi that are two-segmented (Figs. 335, 336), a labial palp segment 1 covered with a patch of long setae ventrally (Fig. 336), an abdominal tergum without a posteromedial process or processes at the base of the operculate gills, a posterolateral projection 6 not curved medially (Fig. 345), and operculate gills without a longitudinal ridge in the sublateral area nor a protruding edge at the posterolateral corner (Fig. 340). In *Caenoculis*, palpi are three segmented (Figs. 29, 30), and abdominal tergum 2 has one posteromedial cone-shaped process (Fig. 35). In *Insulibrachys*, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In *Sparbarus*, long setae are absent on the ventral surface of labial palp segment 1 (Fig. 146). In Brachycercus, the abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In Oriobrachys, operculate gills have a strongly developed longitudinal ridge in the sublateral area (Fig. 284). In Latineosus, Alloretochus, n. gen., and Cercobrachys, posterolateral projection 6 is distinctly curved medially (Fig. 375).

Adults of *Susperatus*, *Alloretochus*, n. gen., and *Cercobrachys* can be distinguished from those of *Sparbarus*, *Insulibrachys*, and *Brachycercus* by having a prosternum conically produced ventrally (Fig. 355). Furthermore, *Susperatus* has a pronotum with nearly straight lateral margins (Fig. 353) and vestiges of posterolateral projections on abdominal segments 3–6 or 4–6. In *Insulibrachys*, the lateral margins of the pronotum are continuously rounded throughout. In *Brachycercus* and *Sparbarus*, vestiges of posterolateral projections are usually present on at least abdominal segments 3–7 (Fig. 243). Adults of *Susperatus* can be distinguished from known adults of *Cercobrachys* by having a pedicel longer than one and one-half times the length of the scape (Fig. 354), In *Cercobrachys*, the pedicel is as long as, or only slightly longer than, the scape (Fig. 489). Male adults of *Susperatus* can be distinguished from those of *Susperatus* n. gen., by their subgenital plate that has a convexly produced or truncate posterior margin (Fig. 352). In *Alloretochus*, n. gen., the posterior margin of subgenital plate is broadly emarginate (Fig. 387). Female adults of *Susperatus* and

Alloretochus, n. gen., cannot be consistently distinguished morphologically at the genus level at present although it should be kept in mind that *Alloretochus*, n. gen., is only found in Neotropical.

The eggs of *Susperatus* can be distinguished from known eggs of all other Brachycercinae by a chorion that does not have any costae (Fig. 567). In all others, multiple longitudinal costae are present on the chorion (Fig. 555).

Etymology: The generic nomen is a Latin masculine compound word (*sus*: under, *aspera*: rough), alluding to the thoracic sterna that have developed processes in this genus.

Distribution: Nearctic: Canada, U.S.A.

Susperatus prudens (McDunnough), New Combination

Eurycaenis prudens McDunnough, 1931:264. *Brachycercus prudens* (McDunnough), 1931: Traver, 1935:642.

Mature Larva: Body (Fig. 327) length 4.5–7.7 mm. Caudal filaments length 2.3–3.0 mm. Coloration pale yellow-brown. Head: Frons with irregular diffuse brown staining. Occiput (Figs. 328, 341) with irregular diffuse brown staining, and with some short setae. Lateral ocellar tubercle (Figs. 328, 341) longer than basal width; distal portion finger shaped, slightly curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 328, 341) length 2.5 X basal width, and longer than lateral tubercle by about one-fourth to one-third; apex rounded to bluntly pointed. Antenna (Fig. 337) pale; scape without macula; pedicel 1.4 X length of scape, with 10 or less setae one-half or more length of pedicel. Mouthparts as in Figures 331–336. Maxilla (Fig. 335) with galealacinia length 2.3 X basal width; palp segment 1 width 1.3 X width of segment 2; segment 2 2.0 X length of segment 1, with more than 20 long, stout setae along inner margin. Labial palp (Fig. 336) segment 1 ventrally with patch of setae subequal in length to palp segment 1. Thorax: Nota (Fig. 327) without distinct black maculae. Pronotum (Figs. 327, 342) with some diffuse black staining; lateral margin broadly produced, forming blunt angle in anterior half. Propleuron narrowly visible in dorsal view (Fig. 342). Mesosternal basisternum with medial process rounded or bluntly pointed; sternellum with medial process more produced than process on basisternum, appearing triangulate in lateral view, and papillate or bluntly pointed at apex (Figs. 329, 343). Metasternum with medial process similar to process on mesosternal sternellum (Fig. 329). Legs (Figs. 327, 338, 339) pale brown, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.3: 1.0: 1.3: 1.4. Ratios of length of forefemur: tibia: tarsus: claw—4.0: 1.8: 2.4: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-4.5: 2.6: 3.0: 1.0. Forefemur (Fig. 338) dorsally with dense, long and short setae, and ventrally with row of about 15 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 338) ventral margin with row of setae shorter than width of tibia and several setae longer than 2.0 X width of tibia; posterior surface with distinct row of about six setae as long as, or longer than, tibia. Foretarsus (Fig. 338) ventral margin with row of setae subequal in length to, or shorter than, width of tarsus; dorsal margin with row of about 10 long setae as long as up to 4.0 X width of tarsus; anterior and posterior surfaces with several scattered long setae. Hindfemur (Fig. 339) length 5.0 X width, dorsally with dense, long and short setae, and ventrally with rows of short setae. Hindtibia and hindtarsus (Fig. 339) each dorsally with row of 40–50 long, fine setae as long as 3.0–4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 344) evenly curved; length 5.0 X basal width. Abdomen: Terga (Fig. 327) pale brown, without black macula; terga 1 and 2 somewhat darker. Segment 2 lateral margin angulate, and produced into short lateral projection, with apex bluntly pointed (Fig. 327). Posterolateral projections 5 and 6 (Fig. 345) longest; length 2.5 X basal width; projection 6 directed posteriorly; projection 7 (Fig. 345) length about one-half of projection 6. Sterna pale brown, without maculae; sterna 1-4 each produced ventrally, appearing nearly hemispherical in lateral view (Fig. 330); sternum 9 posterior margin convexly produced.
Operculate gill (Figs. 340, 346) pale brown except posterior margin pale; length 1.4 X width; dorsum laterally with some long setae; posteromedial corner with row of dense, long marginal setae one-fourth to one-third length of operculate gill; posterolateral corner with marginal setae three-fourths length of those at posteromedial corner and intermixed with some short setae; Y-ridge with row of several long setae. Caudal filaments pale brown.

Male Adult: Body length 4.2–5.1 mm. Forewing length 4.5–5.0 mm. Caudal filaments length 17.0–20.0 mm. General coloration pale yellow. *Head*: Frons without dark brown staining. Occiput without black maculae or diffuse shading, with some diffuse brown shading. Scape (Fig. 348) pale brown, without black macula; pedicel (Fig. 348) paler, 1.6 X length of scape; flagellum pale. *Thorax*: Pronotum pale yellow. Mesonotum brown. Mesosternum pale and somewhat translucent, not stained with diffuse black; sternacostal suture not stained with dark black-brown. Coxae and trochanters brown. Forefemur (Fig. 350) pale brown, with brown stripes; foretibia and foretarsus (Fig. 350) paler. Mid- and hindlegs pale yellow. Ratios of length of body: foreleg: midleg: hindleg—2.5: 2.0: 1.0: 1.0. Ratios of length of forefemur: tibia: tarsus—1.0: 2.8: 1.4. Ratios of length of foretarsus segment I: II: III: IV: V—1.0: 6.6: 4.0: 3.0: 2.4. Forewing (Fig. 351) with ratio of length to greatest width—1.7. *Abdomen*: Terga and sterna pale and somewhat translucent, without black macula or diffuse shading. Segments 3–6 or 4–6 with distinct vestiges of posterolateral projections (Fig. 347); vestige of projection 6 not strongly curved medially. Genitalia (Fig. 352) with forceps with apical two-thirds curved medially; subgenital plate with posterior margin broadly truncate; penes lobe moderately convex distolaterally. Caudal filaments pale.

Female Adult: See formal description by Burks (1953), and diagnosis below.

Egg: Habitus as in Figure 567. Length about 180 mm. Polar cap one-fourth to one-third length of entire egg. Chorion smooth, non-punctate.

Diagnosis: Larvae of *S. prudens* can be distinguished from those of *S. tuberculatus* by having lateral margins of the pronotum that are slightly produced, forming a low, bluntly angulate expansion (Fig. 342), and the ventral process on the mesosternal basisternum that is rounded or bluntly pointed apically and usually shorter than the posterior processes (Fig. 329). In *S. tuberculatus*, the lateral margins of the pronotum are strongly produced, forming a broad, right-angled expansion (Fig. 360), and the mesosternal basisternum process is strongly produced with a papillate or less bluntly pointed apex, and is as long as the posterior processes (Fig. 361).

Adults of *S. prudens* are distinguished from those of *S. tonkawa*, n. sp., by a larger size (body length is over 4.0 mm in males), the male genital forceps that are curved medially in the apical two-thirds, and the posterior margin of the subgenital plate that is broadly truncate. In *S. tonkawa*, n. sp., the body length of male adults is 3.5 mm, male genital forceps are nearly straight in the apical two-thirds, and the posterior margin of the subgenital plate is convexly produced.

The eggs of *S. prudens* have a chorion that is smooth, and without punctures (Fig. 567), whereas in *S. tonkawa*, n. sp., the chorion is punctate (Fig. 568).

Distribution: Canada: Alberta, Saskatchewan; U.S.A.: Kansas, Montana, Nebraska, North Dakota, Utah, Wyoming.

Material Examined: ALBERTA: Eight larvae, Milk R, N of Aden, 1999-VII-31, JM Webb (PERC). SASKATCHEWAN: nine larvae, North Saskatchewan R at Borden Bridge, X-2-1999, JM Webb (PERC); one larva, South Saskatchewan R at Lemsford Ferry, 51 01'23" N, 109 07'56"W, IX-16-2000, JM Webb (PERC). MONTANA, Rosebud Co: one larva, Tongue R, Ashland, VII-17-1990, DL Gustafson (PERC). UTAH: one larva, Green R, Hideout Canyon, IX-5-1948, G Edmunds (PERC). WYOMING, Sweetwater Co: one larva, one male subimago, Black's Fork R, W Green River City, VIII-3-1968, R Koss, WP McCafferty (PERC), one larva, Green R at Green River City, Picnic Grds, on service Rd W city, VIII-3-1968, R Koss, WP McCafferty (PERC), 60 larvae, Black's Fork R at I-80, W Green River City, VIII-2-1969, AV Provonsha (PERC), 21 male adults,

Black's Fork R at jct I-80, VIII-29-1969, SL Jensen, AV Provonsha (PERC), one larva, Black's Fork R at I-80, 6 mi E Little America, VII-21-1971, SL Jensen, AV Provonsha (PERC).

Susperatus tonkawa, New Species

Larva: Unknown.

Male Adult: Body length 3.5 mm. Forewing length 3.3 mm. Caudal filaments length 10.0 mm. General coloration pale yellow. *Head*: Occiput (Fig. 353) pale yellow. Frons somewhat darker than occiput. Epicranial suture bordered with pale brown. Antenna (Fig. 354) pale, without black macula; pedicel 2.0 X length of scape. *Thorax*: Pronotum (Fig. 353) pale yellow, without black shading. Mesonotum (Fig. 353) yellow-brown. Mesosternum pale and somewhat translucent, not stained with diffuse black; sternacostal suture not stained with dark black-brown. Coxae and trochanters brown. Forefemur (Fig. 356) pale brown; foretibia and foretarsus paler. Mid- and hindlegs pale yellow. Ratios of length of body: foreleg: midleg: hindleg—2.3: 1.8: 1.0: 1.1. Ratios of length of forefemur: tibia: tarsus—1.0: 2.5: 2.0. Ratios of length of foretarsus segment I: II: III: IV: V—1.0: 6.4: 3.4: 3.0: 2.0. Forewing (Fig. 357) with ratio of length to greatest width—1.9. *Abdomen*: Terga and sterna pale and somewhat translucent, without black maculae or diffuse shading. Segments 3–6 with distinct vestiges of posterolateral projections; vestige of projection 6 strongly curved medially. Genitalia (Fig. 358) with forceps with apical two-thirds nearly straight; subgenital plate with posterior margin convexly produced; penes lobe moderately convex distolaterally. Caudal filaments pale.

Female adult: Body length 5.0–5.7 mm. Caudal filaments length 2.3 mm. Wing length 4.8 mm. Ratios of length of body: foreleg: midleg: hindleg-4.0: 1.0: 1.4: 1.5. Coloration and vestiges similar to males.

Egg: Habitus as in Figure 568. Length about 140 mm. Polar cap one-fifth to one-fourth length of entire egg. Chorion punctate. Two micropyles present.

Diagnosis: Adults of *S. tonkawa* can be distinguished from those of *S. prudens* by being shorter (body length is 3.5 mm in males) and by having male genital forceps that are nearly straight in the apical two-thirds, and the posterior margin of the subgenital plate that is convexly produced. In *S. prudens*, the body length of male adults is over 4.0 mm, male genital forceps are curved medially in the apical two-thirds, and the posterior margin of the subgenital plate is broadly truncate.

Eggs of *S. tonkawa* are distinguished by the presence of numerous small punctures on the chorion (Fig. 568). In *S. prudens*, eggs do not have punctures on the chorion (Fig. 567).

Discussion: Soldán (1986) described *S. tuberculatus* from Utah based on larva specimens. The adult stage of that species remains unknown. *Susperatus tuberculatus* is similar to *S. prudens* in that they share some larval characteristics. *Susperatus tonkawa*, on the other hand, which shows certain similarity to *S. prudens* in the egg and adult stages, is not known as larva. Although it would appear possible from this that *S. tonkawa* represents the adult stage of *S. tuberculatus*, it is not plausible because vestiges of the posterolateral projections 6 in *S. tonkawa* adults are strongly oriented medially, and the projections 6 of *S. tuberculatus* larvae are oriented posteriorly. Thus, the known stages of the two species do not correlate.

Etymology: The specific epithet is a noun in apposition and is after the native North American people of the Tonkawa tribe, inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: Texas.

Material Examined: Male adult HOLOTYPE, Texas, Milam Co, Little R (Site 19), IV-14-1994, RJ Garono (PERC). One male adult and one female adult PARATYPES, same data and deposition as holotype. One male adult and one female adult PARATYPES, same data as holotype (TAMU).

Susperatus tuberculatus (Soldán), New Combination

Brachycercus tuberculatus Soldán, 1986:330.

Mature Larva: Body (Fig. 359) length 4.8–5.5 mm. Caudal filaments length 2.1–2.8 mm. Coloration pale yellow-brown. Head: Frons without black macula or diffuse staining. Occiput (Fig. 359) with irregular diffuse brown staining, and covered with some short setae. Lateral ocellar tubercle (Fig. 360) longer than basal width; distal portion finger shaped, curved anteriorly; apex rounded. Middle ocellar tubercle (Figs. 359, 360) length 2.5 X basal width, and slightly longer than lateral tubercle; apex bluntly pointed. Antenna (Fig. 369) pale; scape without macula; pedicel 1.5 X length of scape, with less than 10 setae one-half or more length of pedicel. Mouthparts as in Figures 363-368. Maxilla (Fig. 367) with galealacinia length 2.6 X basal width; palp segment 1 width 1.2 X width of segment 2; segment 2 2.0 X length of segment 1, with more than 20 long, stout setae along inner margin. Labial palp (Fig. 368) segment 1 ventrally with patch of long setae as long as palp segment 1. Thorax: Nota (Fig. 359) without distinct black maculae or diffuse black staining. Pronotum (Fig. 360) lateral margin strongly produced, forming pointed right angle in anterior half. Propleuron narrowly visible in dorsal view (Fig. 359). Mesosternal basisternum and sternellum and metasternum with medial processes subequal in length, appearing triangulate in lateral view, and papillate or bluntly pointed at apex (Fig. 361). Legs (Figs. 359, 370, 371) pale brown, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.1: 1.0: 1.4: 1.5. Ratios of length of forefemur: tibia: tarsus: claw—3.4: 1.6: 2.1: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-4.0: 2.3: 2.5: 1.0. Forefemur (Fig. 370) dorsally with dense, long and short setae, and ventrally with row of about 10 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 370) ventral margin with row of setae as long as width of tibia and several setae longer than 2.0 X width of tibia; posterior surface with distinct row of about six long setae as long as, or longer than, tibia. Foretarsus (Fig. 370) ventral margin with row of setae as long as, or shorter than, width of tarsus; dorsal margin with row of about 10 long setae measuring in length about 4.0 X width of tarsus; anterior and posterior surfaces with several scattered long setae. Hindfemur (Fig. 371) length 4.7 X width, dorsally with dense, long and short setae, and ventrally with rows of short setae. Hindtibia and hindtarsus (Fig. 371) each dorsally with row of 40-50 long, fine setae as long as 3.0-4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 371) nearly straight; length 6.0 X basal width. Abdomen: Terga (Fig. 359) pale brown, without black maculae. Segment 2 lateral margin produced into short lateral projection; apex bluntly pointed (Fig. 359). Posterolateral projections 5 and 6 (Fig. 359) longest; length 3.0 X basal width; projection 6 directed posteriorly; projection 7 (Fig. 359) length about two-thirds that of projection 6. Sterna pale brown, without maculae; sterna 1–6 each produced ventrally, forming nearly hemispherical profile in lateral view (Fig. 362); sternum 9 posterior margin convexly produced. Operculate gill (Fig. 372) pale brown except posterior margin paler; length 1.4 X width; dorsum laterally with some long setae; posteromedial corner with row of dense, long marginal setae one-fourth to one-third length of operculate gill; posterolateral corner with marginal setae two-thirds length of those at posteromedial corner; Y-ridge with row of several long setae. Caudal filaments pale brown.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of *S. tuberculatus* can be distinguished from those of *S. prudens* by having lateral margins of the pronotum that are strongly produced, forming a right-angled and pointed expansion (Fig. 360), and a mesosternal basisternum process that is as long as the posterior processes and is papillate or bluntly pointed at the apex (Fig. 361). In *S. prudens*, the lateral margins of the pronotum are slightly produced to form a blunt angle (Fig. 342), and the mesosternal basisternum process is broadly produced, shorter than the posterior processes, and is rounded or very bluntly pointed at the apex (Fig. 329).

Discussion: George Edmunds (per. comm.) and in Soldán (1986) has indicated that the type material of S.

tuberculatus was mislabeled. Thus, it was not taken at the Provo River, Wasatch County, Utah as originally labeled and recorded by Soldán (1986). The Provo River is a large, high-gradient, mountain, trout stream in the Great Basin. This habitat and location are not predictably associated with Brachycercinae. The large substrate size and fast currents that typify the Provo River do not provide the appropriate sand-silt habitat for psammophilous larvae. Edmunds has stated that *S. tuberculatus* was much more likely taken in the large and flatter riverine habitat provided by the Yampa and Green Rivers in far northwestern Colorado, which were visited by the collector, V. Landa, on the same trip that the Provo River was sampled. The type locality for *S. tuberculatus* is therefore amended here, as seen in the Material Examined, below.

Distribution: U.S.A.: Colorado.

Material Examined: Larva HOLOTYPE, Colorado, Moffat Co, Dinosaur National Monument, Echo Prk, VI-1965, V Landa (PERC). One larva PARATYPE, no data (PERC). COLORADO, Routt Co: one larva, Yampa R, Hayden, 1975, E Ames (PERC).

Alloretochus, New Genus

Type Species: Cercobrachys peruanicus Soldán.

Species Included: A. peruanicus (Soldán), n. comb.

Mature Larva: Head: Head capsule anterolaterally with transverse row of long setae between antenna and base of mandible (Fig. 374). Clypeus with long setae. Occiput (Fig. 374) without long, fine setae; lateral margin curved inward posterior to compound eye. Compound eye (Figs. 373, 374) anterolaterally oriented, not strongly produced dorsally; with anterior margin not extending anteriorly beyond base of middle ocellar tubercle, and with distance from posterior margin of head two-thirds or more diameter of compound eye. Ocellar tubercles without apparent setae. Lateral ocellar tubercle (Fig. 374) triangulate in lateral view. Middle ocellar tubercle (Figs. 373, 374) triangulate in dorsal view, shorter than lateral ones. Pedicel (Fig. 382) about 1.4 X length of scape, with less than 10 setae one-half or more length of pedicel. Labrum (Fig. 376) lateral margin moderately produced. Hypopharynx (Fig. 379) with superlingua lateral margin moderately produced. Maxilla (Fig. 380) with galealacinia sickle shaped, with ratio of length to basal width about 2.3; maxillary palp two segmented; segment 1 width about 1.3 X width of segment 2; segment 2 about 2.3 X length of segment 1, with row of more than 15 long, stout setae along distal three-fourths of inner margin, with more than 15 long, fine setae at apex and along outer margin, and with some long setae on ventral surface. Labial palp (Fig. 381) two segmented; segment 1 ventrally with patch of setae one-half or more length of segment 1. Thorax: Pronotum (Fig. 373) trapezoidal; anterior margin moderately emarginate; lateral margin (Fig. 374) slightly and broadly produced, forming blunt angle in anterior half. Prosternum median transverse ridge strongly produced ventrally, forming rounded projection in lateral view and covered with tuft of setae about one-half length of forefemur, directed anteriorly or anterolaterally; prosternum laterally not produced ventrally. Mesosternum without medial processes on basisternum or sternellum, and with dense setae along anterior margin longer than one-fourth length of midfemur, directed anteriorly or anterolaterally. Metasternum without medial process. Legs (Figs. 373, 383, 384) without plate-shaped process on dorsal margin of coxa. Forefemur (Fig. 383) ventrally with short setae and row of long setae about 3.0 X width of femur. Foretibia (Fig. 383) about three-fourths length of foretarsus; ventral margin with setae as long as 1.0 X width of tibia; posterior surface with distinct row of long setae as long as, or longer than, tibia. Foretarsus (Fig. 383) ventral margin setae length about 1.0 X width of tarsus, with some shorter setae intermixed; dorsal margin with long setae about 5.0 X width of tarsus, roughly arrayed in setal row. Hindleg length about 1.3 X that of foreleg. Hindfemur (Fig. 384) length 5.3 X width, dorsally with some setae measuring in length 1.5–2.0 X width of femur. Hindtibia and hindtarsus (Fig. 384) dorsally with row of long setae about 4.0 X width of tibia. Hindclaw (Fig. 384) nearly straight, length about 5.0 X basal width; inner margin lacking armature. *Abdomen*: Terga 1 and 2 without median process at posterior margin. Tergum 2 without process anterior to base of operculate gill (Fig. 375). Terga 7 and 8 with short setae along posterior margin. Tergum 10 anterior margin strongly emarginate medially. Segment 2 lateral margin slightly produced into broad and blunt angle (Fig. 375). Posterolateral projections 3–6 (Fig. 375) strongly upturned; posterolateral projection 5 length about 4.0 X basal width; projection 6 curved medially; projection 7–9 (Fig. 373) short; projection 7 shorter than onefifth length of projection 6; projection 9 shorter than one-half length of tergum 10. Sterna flat throughout. Operculate gill (Fig. 385) nearly subquadrate; length about 1.5 X width; posterolateral corner without protruding edge; dorsum with some long setae; posteromedial corner with dense, long marginal setae distinctly longer than those at posterolateral corner; Y-ridge weakly developed, with several long setae; venter lacking submarginal rows of microtrichia.

Male and female adults: See formal descriptions by Molineri and Goitia (2006), figures 386, 387, and diagnosis below.

Egg: Unknown.

Diagnosis: The larvae of *Alloretochus* are distinguished from those of all other genera of Brachycercinae by having a maxillary palp segment 2 that is as long as about 2.3 X the length of the segment 1 (Fig. 380). In all other genera maxillary palp segment 2 is no longer than 2.0 X the length of the segment 1 (Fig. 234). Larvae of Alloretochus, Oriobrachys, Latineosus, and Cercobrachys are also distinguished from all others by having a posterolateral projection 6 curved medially (Figs. 375, 403). Additionally, they can be distinguished by having ocellar tubercles that do not have long setae (Fig. 374), a middle ocellar tubercle that is straight in lateral view (Fig. 374), a labrum with moderately produced lateral margins (Fig. 376), maxillary and labial palpi that are two segmented (Figs. 380, 381), a labial palp segment 1 with long setae ventrally (Fig. 381), a pronotum anterior margin that is moderately emarginate (lateral margin length is about 1.5 X midline length) (Fig. 374), thoracic sterna that are flat throughout, a foretarsus dorsal margin with several long setae but not forming a distinct row (Fig. 383), hindclaws with no armature on the inner margin (Fig. 384), an abdominal tergum 2 without a posteromedial process or processes at the base of the operculate gills (Fig. 375), a posterolateral projection 7 shorter than one-fifth length of the projection 6 (Fig. 373), and operculate gills without a longitudinal ridge in the sublateral area nor a protruding edge at the posterolateral corner (Fig. 385). In Caenoculis, palpi are three segmented (Figs. 29, 30), and abdominal tergum 2 has one posteromedial cone-shaped process (Fig. 35). In Insulibrachys, ocellar tubercles are covered with dense, long setae distally (Fig. 198). In Sparbarus, long setae are absent on the ventral surface of labial palp segment 1 (Fig. 146), and the abdominal posterolateral projection 7 is as long as, or longer than, one-third of the projection 6 (Fig. 71). In Brachycercus, abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In Oriobrachys, operculate gills have a longitudinal ridge in the sublateral area (Fig. 284). In Latineosus, long setae are absent on the ventral surface of the labial palp segment 1 (Fig. 297), and the foretibiae lack a row of long setae on the posterior surface (Fig. 288). In *Susperatus*, the apical portion of the middle ocellar tubercle is curved ventrally in lateral view (Fig. 360), and thoracic sterna have multiple conical processes (Fig. 361). In Cercobrachys, labrum lateral margins are strongly produced and rounded (Fig. 394), the pronotum anterior margin is strongly emarginate (lateral margin length is 2.0 X or more midline length) (Fig. 471), the dorsal margin of foretarsus has a well-ordered row of long setae (Fig. 495), and the hindclaw has some nodules on the inner margin (Fig. 472).

Adults of *Alloretochus*, *Susperatus*, and *Cercobrachys* can be distinguished from those of *Sparbarus*, *Insulibrachys*, and *Brachycercus* by having a prosternum conically produced ventrally (Fig. 386). In the latter three genera, the adult prosternum is flat or only slightly produced. In addition, *Alloretochus* has a pronotum with nearly straight lateral margins and vestiges of posterolateral projections on abdominal segments 3–6. In *Insulibrachys*, the lateral margins of the pronotum are continuously rounded throughout. In *Brachycercus* and

Sparbarus, vestiges of posterolateral projections are usually present on at least abdominal segments 3–7 (Fig. 243). Male adults of *Alloretochus* can be distinguished from those of *Susperatus* and *Cercobrachys* by their subgenital plate that has a broadly emarginate posterior margin (Fig. 387). In *Susperatus* and *Cercobrachys*, the posterior margin of subgenital plate is convexly produced or truncate (Fig. 352). Female adults of *Alloretochus* cannot be consistently distinguished morphologically from those of *Susperatus* and *Cercobrachys* at the genus level at present although it should be kept in mind that of the three genera, only *Alloretochus* is Neotropical.

Etymology: The generic nomen is a Latinized Greek masculine compound noun alluding to another ("all") from Loreto (the department of Peru from where the type of the genus is described) that is supported ("ochus").

Distribution: Neotropical: Bolivia, Peru.

Alloretochus peruanicus (Soldán), New Combination

Cercobrachys peruanicus Soldán, 1986:343.

Mature Larva: Body (Fig. 373) length 4.2 mm. Caudal filaments length 1.4 mm. Coloration pale yellowbrown. Head: Frons without black macula or diffuse staining. Occiput (Figs. 373, 374) with some irregular brown staining, without apparent setae. Lateral ocellar tubercle (Fig. 374) as long as basal width, triangulate in lateral view; apex bluntly pointed. Middle ocellar tubercle (Figs. 373, 374) triangulate in dorsal view; length subequal to basal width, and about one-half length of lateral tubercle; apex pointed. Antenna (Fig. 382) pale; scape without macula; pedicel 1.4 X length of scape, with less than five setae one-half or more length of pedicel. Mouthparts as in Figures 376-381. Labrum (Fig. 376) lateral margin moderately produced and somewhat angulate. Hypopharynx (Fig. 379) with superlingua lateral margin strongly produced to give hypopharynx somewhat triangulate shape. Maxilla (Fig. 380) with galealacinia length 2.3 X basal width; palp segment 1 width 1.3 X width of segment 2; segment 2 2.3 X length of segment 1, with more than 20 long, stout setae along inner margin. Labial palp (Fig. 381) segment 1 ventrally with patch of dense, long setae as long as palp segment 1. Thorax: Nota (Fig. 373) without distinct black maculae. Propleuron partially visible in dorsal view (Fig. 373). Mesosternum anterior margin covered with tuft of dense setae about one-third length of midfemur. Legs (Figs. 373, 383, 384) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—2.5: 1.0: 1.2: 1.3. Ratios of length of forefemur: tibia: tarsus: claw—2.9: 1.5: 2.1: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-4.1: 2.8: 2.9: 1.0. Forefemur (Fig. 383) dorsally with dense, long and short setae, ventrally with about 15 long setae measuring in length up to 3.0 X width of femur and arrayed in single row. Foretibia (Fig. 383) ventral margin with row of about 10 setae as long as, or shorter than, width of tibia and one long basal setae measuring in length 5.0 X width of tibia; posterior surface with distinct row of about five long setae as long as, or longer than, tibia; anterior surface with row of long setae subequal in length to tibia. Foretarsus (Fig. 383) ventral margin with row of about 10 setae as long as width of tarsus intermixed with about 20 short setae measuring in length one-third width of tarsus; anterior and posterior surfaces with some scattered setae longer than 5.0 X width of tarsus; dorsal margin with several such long setae roughly arrayed in row. Hindfemur (Fig. 384) length 5.3 X width; dorsal margin with dense, long and short setae; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 384) each dorsally with row of 15-20 long, fine setae as long as 4.0 X width of tibia, and ventrally with row of short, stout setae and some relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 384) nearly straight; length 5.0 X basal width. Abdomen: Terga (Fig. 373) pale yellow, without dark black macula; terga 7 and 8 with scattered, short setae along posterior margin. Segment 2 lateral margin slightly produced into broad and blunt angle (Fig. 373). Posterolateral projection 5 (Fig. 375) length 4.0 X basal width; projection 6 (Fig. 375)

distally moderately curved medially, forming 45 degree angle with posterior margin of tergum 6, rounded at apex; projections 7–9 (Fig. 373) minute and indistinct. Sterna pale; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 385) pale brown and unicolourous; length 1.5 X width; dorsum laterally with several long setae; posteromedial corner with row of dense, long marginal setae up to about one-half length of operculate gill; posterolateral corner with marginal setae shorter than those at posteromedial corner by up to two-thirds and intermixed with some short setae; Y-ridge weakly developed, with several long setae. Caudal filaments pale brown.

Male and female adults: See formal descriptions by Molineri and Goitia (2006), figures 386, 387, and the key below.

Egg: Unknown.

Distribution: Bolivia, Peru.

Material Examined: One larva PARATYPE, Peru, Loreto Prov, Rio Yurac, 1 km S Aguaytia, 16-VII-1963, WL Peters (PERC).

Cercobrachys

Cercobrachys Soldán, 1986:336. **Type species:** *Cercobrachys etowah* Soldán.

Species Included: C. cree Sun, Webb and McCafferty, C. etowah Soldán, C. fox, n. sp., C. minutus (Tshernova), C. lilliei, n. sp., C. petersorum Soldán, C. pomeiok, n. sp., C. serpentis Soldán, and C. winnebago, n. sp.

Mature Larva: Body length 3.3–6.8 mm. Caudal filaments length 1.7–2.5 mm. General coloration pale yellow to yellow-brown. Head: Head capsule anterolaterally with transverse row of long setae between antenna and base of mandible (Fig. 528). Clypeus with long setae (Fig. 528). Occiput (Fig. 527) without long, fine setae; lateral margin curved inward posterior to compound eye. Compound eye (Figs. 527, 528) anterolaterally oriented, not strongly produced dorsally; female compound eye with anterior margin not anteriorly extending beyond base of middle ocellar tubercle, and with distance from posterior margin of head two-thirds or more diameter of compound eye. Ocellar tubercles without apparent setae (Fig. 527). Lateral ocellar tubercle triangulate (Fig. 527) or rounded (Fig. 544) in lateral view. Middle ocellar tubercle shorter than lateral ones, triangulate (Fig. 527) or rounded (Fig. 544) in dorsal view. Pedicel (Fig. 389) 1.0–1.6 X length of scape, with less than 10 setae one-half or more length of pedicel. Labrum (Fig. 394) nearly ovate, with lateral margin strongly and convexly produced. Hypopharynx (Fig. 397) superlingua somewhat triangulate, with lateral margin strongly produced. Maxilla with galealacinia stout and triangulate (Fig. 398) to sickle shaped (Fig. 484), with ratio of length to basal width 1.3-2.5; maxillary palp (Fig. 398) two segmented; segment 1 width 1.0-1.2 X width of segment 2; segment 2 1.8–2.0 X length of segment 1, with row of more than 20 long, stout setae along distal three-fourths of inner margin, with more than 15 long, fine setae at apex and along outer margin, and with some long setae on ventral surface. Labial palp (Fig. 399) two segmented; segment 1 ventrally with patch of setae as long as segment 1. Thorax: Pronotum trapezoidal; anterior margin strongly emarginate (Fig. 545); lateral margin broadly produced, forming blunt angulate expansion in anterior two-fifths to one-half (Fig. 452), or slightly convexly produced (Fig. 545), but not continuously rounded throughout. Prosternal median ridge produced ventrally, usually forming conspicuous process, covered with tuft of setae one-half or more length of forefemur, directed anteriorly or anterolaterally; prosternum laterally not produced ventrally. Mesosternum usually with row of dense setae along anterior margin longer than one-fourth length of midfemur, directed anteriorly or anterolaterally (Fig. 546). Meso- and Metasternum without medial processes on basisternum or sternellum (Fig. 546). Legs (Figs. 535, 536) without flat process on dorsal margin of coxa. Forefemur (Fig. 535) ventrally with short setae and row of setae as long as, or longer than, 2.0 X width of femur. Foretibia (Fig. 535) measuring one-third to three-fourths length of foretarsus; ventral margin with setae

length 2.0-4.0 X width of tibia; posterior surface with distinct row of long setae as long as, or longer than, tibia. Foretarsus (Fig. 535) ventral margin setae length 2.5-5.0 X width of tarsus, with or without much shorter setae intermixed with long setae; dorsal margin with row of long setae measuring in length 4.0–6.0 X width of tarsus. Hindleg length 1.2–1.5 X that of foreleg. Hindfemur (Fig. 536) length 3.7–5.0 X width, dorsally with some setae measuring in length 1.5–2.0 X width of femur. Hindtibia and hindtarsus (Fig. 536) dorsally with row of dense, long setae measuring in length 3.0–4.0 X width of tibia. Hindclaw (Fig. 547) nearly straight or slightly and evenly curved; length 3.5–6.3 X basal width; inner margin with number of minute rounded nodules. Abdomen: Terga 1 and 2 (Fig. 533) without median process at posterior margin. Tergum 2 without process on either side anterior to base of operculate gill. Terga 6-8 with or without long, fine setae on posterior margin (Figs. 455, 475, 548). Tergum 10 anterior margin strongly emarginate medially (Fig. 549). Segment 2 lateral margin nearly straight, or produced into short, weak, bluntly pointed projection (Figs. 439, 516). Posterolateral projections 3–6 (Figs. 415, 454) strongly upturned; posterolateral projection 5 length 1.5– 3.8 X basal width; projection 6 more or less curved medially; projection 7 (Fig. 439) short, less than one-fifth length of projection 6 in most species; projections 8–9 (Fig. 404) minute; projection 9 shorter than one-half length of tergum 10. Sterna (Fig. 550) flat throughout. Operculate gill subquadrate (Fig. 481) to somewhat ovate (Fig. 405); length 1.2–1.5 X width; posterolateral corner without protruding edge; dorsum with or without long setae; posteromedial corner usually with dense, long marginal setae distinctly longer than those at posterolateral corner (Fig. 463), or with only very short marginal setae (Fig. 537); Y-ridge weakly or strongly developed (Figs. 405, 444), with or without long setae; venter lacking submarginal rows of microtrichia (Figs. 428).

Adult: Male body length 3.0–4.5 mm; wing length 2.9–3.6 mm; caudal filaments length 10.0–13.0 mm. Female body length 3.6–4.5 mm; wing length 3.8–4.1 mm; caudal filaments length 1.8–2.2 mm. General coloration pale yellow. *Head*: Pedicel (Fig. 489) 1.5 X or less length of scape. *Thorax*: Pronotum (Fig. 406) trapezoidal; lateral margin not rounded produced. Prosternum median transverse ridge produced, forming distinct process in lateral view (Fig. 433). Metanotum with medial, convex to triangulate process at posterior margin (Fig. 406). Male foreleg (Fig. 490) about two-thirds length of body to as long as body; foretibia about 2.0–3.0 X length of forefemur. *Abdomen*: Terga (Fig. 551) usually without distinct brown or black maculae. Segments 4–6 with distinct vestiges of posterolateral projections in most species (Fig. 430). Male genital forceps (Fig. 409) blade shaped, with longitudinal fold, and pointed at apex; subgenital plate (Figs. 409, 438) with posterior margin convexly produced or truncate; penes lobe (Fig. 409) subquadrate.

Egg: Shape ovate to elongate-ovate (Figs. 573, 575). Polar cap without tubercles (Fig. 571). Chorion with less than 10 costae in lateral half in most species (Fig. 572), or with 15 or more costae in lateral half in at least one species (Fig. 571). Costa asymmetrical in cross-section (overlapping adjacent inter-costal groove on one side only) (Fig. 575). One micropyle present in at least some species (Fig. 570).

Diagnosis: The larvae of *Cercobrachys* are distinguished from those of all other genera of Brachycercinae by having the foretarsus with a distinct, well ordered row of long setae on the dorsal margin (Fig. 535), and by having hindclaws with round, minute nodules on the inner margin (Fig. 547). *Oriobrachys, Alloretochus*, and *Cercobrachys* are distinguished from all other genera by having a posterolateral projection 6 more or less curved medially (Figs. 531, 548). *Cercobrachys* can be further distinguished by having ocellar tubercles without long setae (Fig. 544), a middle ocellar tubercle that is straight in the lateral view, a labrum with strongly produced lateral margins (Fig. 394), maxillary and labial palpi that are two segmented (Figs. 398, 399), a labial palp segment 1 with long setae ventrally (Fig. 399), a pronotum anterior margin strongly emarginate (lateral margin length is 2.0 X or more midline length) (Fig. 545), meso- and metasternum that are flat throughout (Fig. 546), an abdominal tergum 2 without a posteromedial process or processes at the base of the operculate gills (Fig. 533), and operculate gills without a longitudinal ridge in the sublateral area nor a protruding edge at the posterolateral corner (Fig. 405). In *Caenoculis*, palpi are three segmented (Figs. 29, 30), and abdominal tergum 2 has one posteromedial cone-shaped process (Fig. 35). In *Insulibrachys*, ocellar tuberc

cles are covered with dense, long setae distally (Fig. 198). In *Sparbarus*, long setae are absent on the ventral surface of labial palp segment 1 (Fig. 146), and the abdominal posterolateral projection 7 is as long as, or longer than, one-third of projection 6 (Fig. 71). In *Brachycercus*, abdominal tergum 2 has a process at the base of the operculate gills (Fig. 217), and the posterolateral corner of the operculate gills is distinctly more developed than the posteromedial corner (Fig. 225). In *Oriobrachys*, the operculate gills have a longitudinal ridge in the sublateral area (Fig. 284). In *Latineosus*, long setae are absent on the ventral surface of labial palp segment 1 (Fig. 297), and the foretibiae lack a row of long setae on the posterior surface (Fig. 288). In *Susperatus*, the apical portion of the middle ocellar tubercle is curved ventrally in lateral view (Fig. 360), and the meso- and metasternum have multiple conical processes (Fig. 361). In *Alloretochus*, lateral margins of the labrum are moderately produced (Fig. 376), and the anterior margin of the pronotum is moderately emarginate (lateral margin length is about 1.5 X midline length) (Fig. 374).

Adults of *Cercobrachys*, *Alloretochus*, and *Susperatus* can be distinguished from those of *Sparbarus*, *Insulibrachys*, and *Brachycercus* by having a prosternum conically produced ventrally (Fig. 433). Furthermore, *Cercobrachys* has a pronotum with nearly straight lateral margins (Fig. 430) and vestiges of posterolateral projections on abdominal segments 3–6 or 4–6. In *Insulibrachys*, the lateral margins of the pronotum are continuously rounded throughout. In *Brachycercus* and *Sparbarus*, vestiges of posterolateral projections are usually present on at least abdominal segments 3–7 (Fig. 243). Adults of *Cercobrachys* can be distinguished from known adults of *Susperatus* by having a pedicel as long as, or only slightly longer than, the scape (Fig. 489), In *Susperatus*, the pedicel is longer than one and one-half times the length of the scape (Fig. 354). Male adults of *Cercobrachys* can be distinguished from those of *Alloretochus* by their subgenital plate that has a convexly produced or truncate posterior margin (Figs. 409, 438). In *Alloretochus*, the posterior margin of subgenital plate is broadly emarginate (Fig. 387). Female adults of *Cercobrachys* and *Alloretochus* cannot be consistently distinguished morphologically at the genus level at present although it should be kept in mind that *Alloretochus* is only found in Neotropical.

The eggs of *Cercobrachys* can be distinguished from those of *Brachycercus* and *Susperatus* by having multiple costae that are asymmetrical in cross-section (Fig. 575). In *Brachycercus*, the costae are symmetrical in cross-section (Figs. 555, 556), whereas in *Susperatus*, costae are absent on eggs (Fig. 567). There is no single character that distinguishes eggs of *Cercobrachys*, *Latineosus*, and *Sparbarus*. However, in *Cercobrachys* and *Latineosus*, the polar cap does not have tubercles (Fig. 571), and the number of costae is less than 10 in the lateral half of the eggs in most species (Fig. 572). In *Sparbarus*, most species have more than 10 costae in the lateral half of the eggs (Fig. 558), and a number of North American species have tubercles on the polar cap (Fig. 565).

Distribution: Palearctic: Kazakhstan, eastern Asian region of Russia; Oriental: Thailand; Nearctic: Canada, U.S.A.

Cercobrachys cree Sun, Webb, and McCafferty

Cercobrachys cree Sun, Webb, and McCafferty, 2002:80.

Mature Larva: Body (Fig. 388) length 3.8–5.5 mm. Caudal filaments (Fig. 393) length 2.0–2.3 mm. Coloration pale yellow-brown. *Head*: Frons without black maculae or diffuse staining. Occiput (Figs. 388, 400) without black maculae or diffuse shading, without apparent setae. Epicranial suture stem bordered with pale brown. Lateral ocellar tubercle (Fig. 400) slightly shorter than basal width, triangulate in lateral view; apex bluntly pointed or rounded. Middle ocellar tubercle (Fig. 400) hemispherical in dorsal view; length slightly less than basal width, and about two-thirds length of lateral ocellar tubercle; apex rounded. Antenna (Fig. 389) pale; scape without macula; pedicel 1.3–1.5 X length of scape, with about five setae one-half or more length

of pedicel. Mouthparts as in Figures 394–399. Maxilla (Fig. 398) with galealacinia length 1.3 X basal width; palp segment 1 width 1.1 X width of segment 2; segment 2 1.8 X length of segment 1. Thorax: Nota without distinct black maculae. Pronotum (Fig. 401) lateral margin slightly and convexly produced. Propleuron mostly visible in dorsal view (Fig. 401). Prosternum median transverse ridge strongly produced ventrally, forming rounded process and covered with tuft of setae about one-half length of forefemur. Mesosternum anterior margin covered with tuft of setae as long as two-fifths length of midfemur. Legs (Figs. 390, 391) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg-2.9: 1.0: 1.3: 1.3. Ratios of length of forefemur: tibia: tarsus: claw—3.3: 1.5: 2.6: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-2.9: 2.3: 2.0: 1.0. Forefemur (Fig. 390) dorsally with dense, long and short setae, ventrally with about 20–25 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 390) ventral margin with row of about eight setae as long as 2.0 X width of tibia and with several shorter setae: posterior surface with distinct row of about seven setae as long as, or longer than, tibia. Foretarsus (Fig. 390) ventral margin with row of about 17 long setae as long as 4.0–5.0 X width of tarsus, and without short setae; dorsal margin with distinct row of about 20 long setae as long as 6.0 X width of tarsus. Hindfemur (Fig. 391) length 4.2 X width; dorsal margin with dense, long and short setae; ventral margin with short setae. Hindtibia and hindtarsus (Fig. 391) each dorsally with row of about 50 long, fine setae as long as about 4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 402) nearly straight; length 6.3 X basal width; inner margin roughened with series of minute, rounded nodules. Abdomen: Terga (Fig. 388) without black maculae; terga 1 and 2 pale brown; terga 3–6 pale; terga 7 and 8 pale brown, but paler than terga 1 and 2; terga 9 and 10 pale. Terga 6–8 without apparent setae on posterior margins (Fig. 404). Segment 2 lateral margin slightly convex, not forming conspicuous posterolateral projection (Fig. 388). Posterolateral projection 5 (Fig. 403) length about 2.0 X basal width; projection 6 (Fig. 403) longest, distally strongly curved medially, becoming nearly transversely oriented, with outer margin posterior to inner margin in dorsal view, and bluntly pointed at apex; projections 7–9 (Fig. 404) minute. Sterna pale brown, without black staining; sternum 9 (Fig. 392) posterior margin convexly produced. Operculate gill (Figs. 388, 405) pale, unicolourous and somewhat translucent; length 1.3 X width; dorsum without apparent long setae; posteromedial corner with row of dense, long marginal setae measuring about one-third length of operculate gill; posterolateral corner with marginal setae one-half length of those at posteromedial corner, and intermixed with some short setae; Y-ridge weakly developed, without long setae. Caudal filaments (Fig. 393) pale.

Male Adult: Body (Fig. 406) length 4.5 mm. Forewing (Fig. 407) length 3.2 mm. Forelegs and caudal filaments length unknown. General coloration pale yellow. *Head*: Epicranial suture narrowly bordered with diffuse black. Frons and vertex pale brown. Occiput pale yellow. Antenna (Fig. 406) pale, without black macula; pedicel slightly longer than scape. *Thorax*: Pronotum (Fig. 406) pale, with diffuse brown along anterior margin. Prosternum pale; median transverse ridge convexly produced ventrally. Mesonotum (Fig. 406) yellowbrown. Mesosternum pale; sternacostal suture not stained with black-brown. Metanotum posteromedial process (Figs. 406, 408) nearly triangulate, rounded apically. Forecoxa and foretrochanter pale brown; forefemur with brown stripes; foretibia and foretarsus pale. Mid- and hindlegs pale. Forewing (Fig. 407) with ratio of length to greatest width—1.8; Sc, R₁ and adjacent area stained with pale brown; other veins pale. *Abdomen*: Terga (Fig. 406) and sterna generally pale, except tergum 10 bordered with brown, without black maculae or diffuse shading. Segments 4–6 with distinct vestiges of posterolateral projections (Fig. 406); vestige of projection 6 strongly curved medially. Genitalia (Fig. 409) with forceps slightly bowed; subgenital plate with posterior margin convexly produced; penes lobe moderately convex distolaterally. Caudal filaments pale.

Female Adult: Unknown.

Egg: Habitus as in Figure 571. Length about 170 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with 15–18 costae in lateral half. Costa width subequal to one-half of distance between adjacent costae.

Diagnosis: Larvae of *C. cree* are relatively similar to those of North American species *C. serpentis* and *C. lilliei*, n. sp., in that they all have a ventral margin of the foretarsi that has a row of only long setae (Fig. 390), a strongly medially curved posterolateral projection 6 (Fig. 403), and a posterior margin of the operculate gills that has long marginal setae (Fig. 405). In C. etowah, C. fox, n. sp., and C. minutus, the ventral margin of the foretarsi has a row of setae consisting of both long and short setae (Fig. 441); and in C. petersorum, C. pomeiok, n. sp., and C. winnebago, n. sp., the projection 6 is moderately curved medially, forming an angle with the posterior margin of the tergum 6 that is about 45 degrees (Fig. 548), and the marginal setae on the posterior margin of the operculate gills are shorter than one-sixth of the length of the operculate gills (Fig. 537). In C. cree and C. serpentis, posterolateral projections 6 are curved to the extent that they are distally transversely oriented (Fig. 403), and abdominal terga are not stained with brown patterns (Fig. 388), whereas in C. lilliei, n. sp., projection 6 forms an angle of about 30 degrees with the posterior margin of the tergum 6 (Fig. 473), and abdominal terga 7-8 are stained with brown bands at the anterior margins (Fig. 459). Larvae of C. cree can be distinguished from those of C. serpentis by having a middle ocellar tubercle that is hemispherical (Fig. 400), and foretarsi that have a row of about 17 long setae on the ventral margin and a row of about 20 long setae on the dorsal margin (Fig. 390). In C. serpentis, the middle ocellar tubercle is triangulate (Fig. 527), and the foretarsi have a row of about 12 long setae on the ventral margin and a row of about 15 long setae on the dorsal margin (Fig. 518).

Adults of *C. cree* can be distinguished from other *Cercobrachys* species that are known as adults as follows. In *C. cree*, distinct vestiges of posterolateral projections are present on abdominal segment 6 and are about one-half the length of tergum 6, whereas in *C. winnebago*, n. sp., vestiges of projection 6 are indistinct. In *C. cree*, the thoracic and abdominal sterna are not stained with diffuse black, whereas in *C. fox*, n.sp., and *C. minutus*, the thoracic and abdominal sterna are extensively stained with diffuse black (Fig. 458). In *C. cree*, the mesosternum sternacostal suture is slightly darkened with yellow-brown and not distinctly darker than the adjacent area, whereas in *C. etowah*, the sternacostal suture is stained with dark black-brown and is much darker than the adjacent area (Fig. 432).

Eggs of *C. cree* can be distinguished from those of other *Cercobrachys* species with known eggs by having 15–18 costae in the lateral half of the chorion (Fig. 571). In others, the chorion has less than 10 costae in the lateral half (Fig. 572).

Distribution: Canada: Alberta, Saskatchewan; U.S.A.: Montana, North Dakota.

Material Examined: Larva HOLOTYPE, Saskatchewan, North Saskatchewan R at Borden Bridge, VII-27-1999, JM Webb (PERC). One male adult PARATYPE (reared), Saskatchewan, South Saskatchewan R at Lemsford Ferry, 51 01'23"N, 109 07'56"W, VIII-19-2001, JM Webb (PERC). Three larva PARATYPES, Saskatchewan, South Saskatchewan R at Lemsford Ferry, 51 01'23"N, 109 07'56"W, VIII-20-2001, JM Webb (PERC). ALBERTA: two larvae, Milk R N Aden, VII-31-1999, JM Webb (PERC). SASKATCHEWAN: eight larvae, South Saskatchewan R at Lemsford Ferry, 51 01'23"N, 109 07'56"W, VII-30-2000, JM Webb (PERC). MONTANA, Custer Co: five larvae, Powder R at US 12, E Miles City, 46°25'41"N, 105°18'37"W (WGS 84), VII-31-2002, WP McCafferty, LM Jacobus (PERC); Dawson Co: one larva, Yellowstone R at Intake, X-12-1998, R Newell and C Allen (PERC); Hill Co: eight larvae, Milk R at St Johns Bridge, VII-31-1999, JM Webb (PERC); Powder River Co: 10 larvae, Powder R at Hwy 212, VII-17-1990, DL Gustafson (PERC); Richland Co: one larva, Missouri R at St Rd 16, SE of Culbertson, 48°7'21"N, 104°28'32"W (WGS84), 27-VII-2002, WP McCafferty, LM Jacobus (PERC).

Cercobrachys etowah Soldán

Cercobrachys etowah Soldán, 1986:339.

Mature Larva: Body (Fig. 410) length 4.5-6.8 mm. Caudal filaments length 1.3-2.0 mm. Coloration pale vellow-brown. Head: Frons without black macula or diffuse staining. Occiput (Figs. 410, 424) without black maculae or diffuse shading, and without apparent setae. Lateral ocellar tubercle (Fig. 424) about as long as basal width, triangulate in lateral view; apex bluntly pointed. Middle ocellar tubercle (Figs. 410, 424) triangulate in dorsal view; length subequal to basal width, and slightly shorter than lateral tubercle; apex acutely pointed. Antenna (Fig. 411) pale; scape without macula; pedicel subequal in length to scape, with less than five setae one-half or more length of pedicel. Mouthparts as in Figures 418–423. Maxilla (Fig. 422) with galealacinia length 2.6 X basal width; palp segment 1 width 1.3 X width of segment 2; segment 2 2.0 X length of segment 1. Thorax: Nota (Fig. 410) without distinct black maculae. Pronotum (Fig. 425) lateral margin broadly produced, forming blunt angle in anterior half. Propleuron mostly visible in dorsal view (Fig. 410). Prosternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae about one-half length of forefemur. Mesosternum anterior margin covered with tuft of setae one-third to one-half length of midfemur. Legs (Figs. 412, 413) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg-3.7: 1.0: 1.4: 1.5. Ratios of length of forefemur: tibia: tarsus: claw-3.2: 1.5: 2.1: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.6: 3.0: 2.2: 1.0. Forefemur (Fig. 412) dorsally with dense, long and short setae, ventrally with about 10 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 412) ventral margin with row of about five setae measuring in length 2.0–3.0 X width of tibia; posterior surface with distinct row of about five long setae as long as, or longer than, tibia. Foretarsus (Fig. 412) ventral margin with row of about six long setae measuring in length 3.0–4.0 X width of tarsus and intermixed with about 20 short setae measuring one-half width of tarsus; dorsal margin with distinct row of about eight long setae as long as 6.0 X width of tarsus. Hindfemur (Fig. 413) length 5.0 X width; dorsal and ventral margins with dense, long and short setae. Hindtibia and hindtarsus (Fig. 413) each dorsally with row of 40–50 long, fine setae as long as 4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 426) nearly straight; length 5.0 X basal width; inner margin roughened with series of minute, rounded nodules. Abdomen: Terga (Fig. 410) pale yellow, without black macula; tergum 2 with anterior margin somewhat darkened medially; tergum 10 with anterior margin darkened medially. Tergum 6 with row of fine setae along posterior margin; terga 7 and 8 without setal row (Fig. 427). Segment 2 lateral margin slightly produced into low and blunt angle (Figs. 414, 415). Posterolateral projection 5 (Figs. 414, 415) with length 2.5 X basal width; projection 6 (Figs. 414, 415) longest, distally strongly curved medially, becoming nearly transversely oriented, with outer margin posterior to inner margin in dorsal view, and bluntly pointed at apex; projections 7–9 (Figs. 410, 427) minute and indistinct. Sterna pale, without black staining; sternum 9 posterior margin convexly produced; apex somewhat truncate and with small notch medially (inconspicuous in some) (Fig. 416). Operculate gill (Figs. 417, 428) pale and unicolourous; length 1.3 X width; dorsum without long setae; posteromedial corner with row of dense, long marginal setae measuring in length one-fourth to one-third length of operculate gill; posterolateral corner with marginal setae shorter than those at posteromedial corner by up to two-thirds, and intermixed with some short setae; Y-ridge weakly developed, without long setae. Caudal filaments pale except basal joint and several basal segments stained with dark black-brown (Fig. 410).

Male Adult: Body (Fig. 430) length 3.2–4.0 mm. Forewing (Fig. 435) length 2.9–3.0 mm. Caudal filaments length 10.0–11.0 mm. General coloration pale yellow. *Head*: Frons (Fig. 431) with large patch of brown staining. Occiput (Fig. 430) pale yellow, with some diffuse pale brown shading. Scape (Fig. 432) pale brown, without black macula; pedicel (Fig. 432) paler, slightly longer than scape. *Thorax*: Pronotum (Fig. 430) pale yellow, bordered with brown and stained with diffuse black. Prosternum (Figs. 432, 433) median transverse ridge convexly produced ventrally, darkened with brown. Mesonotum (Figs. 430, 433) yellow-brown. Mesosternum (Fig. 432) pale; sternacostal suture stained with dark black-brown. Metanotum (Fig. 430) posteromedial process blunt-triangulate to hemispherical. Coxae and trochanters brown. Forefemur (Fig. 434) pale

brown, with brown stripes; foretibia (Fig. 434) pale except basal joint brown; foretarsus (Fig. 434) pale. Midand hindfemur pale brown; mid- and hindtibia and mid- and hindtarsus pale. Ratios of length of body: foreleg: midleg: hindleg—2.1: 1.5: 1.0: 1.0. Ratios of length of forefemur: tibia: tarsus—1.0: 1.9: 1.3. Ratios of length of foretarsus segment I: II: III: IV: V—1.0: 3.7: 1.7: 1.0: 1.0. Forewing (Fig. 435) ratio of length to greatest width—1.9; Sc, R_1 and adjacent area stained with pale brown; other veins pale. *Abdomen*: Terga (Fig. 430) and sterna generally pale except tergum 10 bordered with brown (Fig. 437), without black macula. Segments 4–6 with distinct vestiges of posterolateral projections; vestige of projection 6 strongly curved medially (Figs. 430, 436). Genitalia (Figs. 429, 438) with forceps slightly bowed; subgenital plate with posterior margin convexly produced; penes lobe slightly convex distolaterally. Caudal filaments pale.

Female Adult: See formal description by Soldán (1986), and diagnosis below.

Egg: Habitus as in Figure 569. Length about 200 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with three to five broad costae in lateral half. Costa width about one-half of distance between adjacent costae.

Diagnosis: An acutely pointed middle ocellar tubercle (Fig. 424) and the darkened basal segments of the caudal filaments (Fig. 410) easily distinguish larvae of *C. etowah* from those of all other *Cercobrachys*. This species is relatively similar to *C. fox*, n. sp., and *C. minutus*, in that they all have a ventral margin of foretarsi that has a row of setae including some long setae (length twice or more the width of the foretarsi) and some short setae (length one-half or less the width of the foretarsi) (Fig. 412). In other *Cercobrachys*, the setal row on the ventral margin of foretarsi is made up of only long setae (length three to five times the width of the foretarsi) (Fig. 461). Additionally, in *C. etowah*, the ventral margin of foretarsi has about six longer setae that are three to four times as long as the width of the foretarsi (Fig. 412), the Y-ridge on the operculate gills is weakly developed (Fig. 417), and projections on abdominal segment 6 are strongly curved medially (Fig. 414). In *C. fox*, n. sp., the ventral margin of foretarsi has about 10 longer setae that are about two and one-half times as long as the width of the foretarsi (Fig. 441), and the Y-ridge is strongly developed (Fig. 444). In *C. minutus*, the longer setae on the ventral margin of foretarsi are shorter than twice the width of the foretarsi (Fig. 478), and the posterolateral projection 6 is not strongly curved medially but forming a 30–40 degree angle with the long axis of the abdomen (Fig. 480).

In the adult stage, *C. etowah* can be distinguished from other *Cercobrachys* species as follows. In *C. etowah*, distinct vestiges of the posterolateral projections of abdominal segment 6 are one-half or more of the length of tergum 6 (Fig. 436), whereas in *C. winnebago* n. sp., such vestiges are indistinct. In *C. etowah*, thoracic and abdominal sterna are not stained with diffuse black (Fig. 432), whereas such staining is present in *C. fox*, n. sp., and *C. minutus*, (Fig. 458). In *C. etowah*, the sternacostal suture on the mesosternum is distinctly darkened with black-brown and much darker than the adjacent area (Fig. 432), whereas in *C. cree*, the sternacostal suture is yellow-brown and not distinctly darker than the adjacent area.

Eggs of *C. etowah* are similar with those of *C. minutus*, *C. pomeiok*, n. sp. and *C. winnebago*, n. sp., in that they have a chorion that has five or less costae in the lateral half (Fig. 569). In *C. fox*, n. sp., *C. lilliei*, n. sp., and *C. serpentis*, the chorion has seven to eight costae in the lateral half (Fig. 570); and in *C. cree*, the chorion has 15–18 costae in the lateral half (Fig. 571).

Distribution: U.S.A.: Georgia, Florida, Indiana, North Carolina, South Carolina, and Wisconsin.

Material Examined: Five larva PARATYPES, Georgia, Cherokee Co, Etowah R, at junc of St Rd S 861, 6 1/2 mi ESE of Ball Ground, 22–25-VI-1971, WLP, JGP, L Berner, WM Beck, PTPT, MLP (FAMU). Three larva PARATYPES, Florida, Gadsden Co, Monroe Cr at bridge on St Hwy 268, 27-VI-1967, G Cooper, J Jones, B Owens (FAMU). Seven male adult PARATYPES, Florida, Dixie-Levy Co, Suwanee R at Alt Hwy 27, 9-V-1975, PH Carlson (FAMU). NORTH CAROLINA, Edgecombe Co: one larva, Fishing Cr, VII-1992 (NDNR); INDIANA, Pulaski Co: one larva, Tippecanoe R at Tippecanoe R St Prk, VII-2-1973, AV Provonsha, B Huff, K Black (PERC). SOUTH CAROLINA, Allendale Co: one larva, Lower Three Runs Cr, between Mullettville, Martin, VI-1-1960, SS Roback (PERC). WISCONSIN, Burnett Co: 17 larvae, St Croix R, Hwy

70, VI-16-1991, RA Lillie (PERC), two larvae, St Croix R, above 7th Island, VII-17-1991, RA Lillie, J Lillie (PERC); Green Co: one larva, Pecatonica R, upstr Martin Town, VII-6-1992, RA Lillie (PERC); Langlade Co: three larvae, Wolf R, Site 99A-Tran 9 (= above dredging), VI-27-2000, RA Lillie (PERC).

Cercobrachys fox, New Species

Cercobrachys sp. 1 McCafferty et al., 2003:88; Cercobrachys sp. A Guenther and McCafferty, 2005: 498.

Mature Larva: Body (Fig. 439) length 4.2–5.7 mm. Caudal filaments length 1.8–2.3 mm. Coloration yellowbrown to red-brown. Head: Frons without black macula or diffuse staining. Occiput (Figs. 439, 451) without black maculae or diffuse shading, and without apparent setae. Lateral ocellar tubercle (Fig. 451) slightly shorter than basal width, triangulate in lateral view; apex bluntly pointed. Middle ocellar tubercle (Fig. 451) triangulate in dorsal view; length slightly less than basal width and about two-thirds that of lateral ocellar tubercle; apex bluntly pointed. Antenna (Fig. 440) pale; scape without macula; pedicel subequal in length to scape, with about five setae one-half or more length of pedicel. Mouthparts as in Figures 445-450. Maxilla (Fig. 449) with galealacinia length 2.3 X basal width; palp segment 1 width 1.0 X width of segment 2; segment 2 2.0 X length of segment 1. Thorax: Nota (Fig. 439) without distinct black maculae. Pronotum (Fig. 452) lateral margin broadly produced, forming blunt angle in anterior half. Propleuron mostly visible in dorsal view (Fig. 439). Prosternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae about one-half length of forefemur. Mesosternum anterior margin covered with dense setae one-third to one-half length of midfemur. Meso- and metasternum stained with diffuse black. Legs (Figs. 441, 442) pale brown, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.4: 1.0: 1.4: 1.4. Ratios of length of forefemur: tibia: tarsus: claw—3.2: 1.6: 2.3: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.7: 2.2: 2.2: 1.0. Forefemur (Fig. 441) dorsally with dense, long and short setae, ventrally with about 15 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 441) ventral margin with row of about six setae as long as about 2.0 X width of tibia and some shorter setae; posterior surface with distinct row of about six long setae as long as, or longer than, tibia. Foretarsus (Fig. 441) ventral margin with row of about 10 setae as long as about 2.5 X width of tarsus intermixed with about 15 short setae measuring in length about one-half width of tarsus; dorsal margin with distinct row of about eight long setae as long as 4.0 X width of tarsus. Hindfemur (Fig. 442) length 4.0 X width; dorsal and ventral margins with dense, long and short setae. Hindtibia and hindtarsus (Fig. 442) each dorsally with row of about 30 long, fine setae as long as 4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 453) evenly curved; length 3.5 X basal width; inner margin with some inconspicuous, minute, rounded nodules. Abdomen: Terga (Fig. 439) without black macula; terga 1, 2, 7, and 8 pale brown, terga 9 and 10 paler. Tergum 2 with anterior margin somewhat darkened medially; tergum 7 with several scattered, short, fine setae on posterior margin (Fig. 455). Segment 2 lateral margin produced into blunt angle (Fig. 439). Posterolateral projection 5 (Fig. 454) length 2.8 X basal width; projection 6 (Figs. 454, 455) longest; apical portion strongly curved medially, becoming nearly transversely oriented, with outer margin posterior to inner margin in dorsal view, and bluntly pointed at apex; projection 7 (Fig. 439) relatively small; projections 8–9 (Fig. 439) minute and indistinct. Sterna pale brown, stained with diffuse black; sternum 9 posterior margin convexly produced; apex somewhat truncate and with small notch medially (inconspicuous in some) (Fig. 443). Operculate gill (Fig. 444) pale brown and unicolourous; length 1.3 X width; dorsum laterally with some long setae; posteromedial corner with row of dense, long marginal setae measuring about one-third length of operculate gill; posterolateral corner with marginal setae one-half length of those at posteromedial corner and intermixed with some short setae; Y-ridge strongly developed, with row of some long setae. Caudal filaments

pale brown.

Male Adult: Unknown.

Female Adult: Body (Fig. 458) length 4.0 mm. Forewing length 3.8 mm. Caudal filaments length 1.8 mm. General coloration pale yellow. *Head*: Frons without brown staining. Epicranial suture bordered with diffuse brown. Occiput pale yellow, with some diffuse pale brown shading. Scape and pedicel pale yellow, without black macula; pedicel subequal to scape in length. *Thorax*: Pronotum pale yellow. Prosternum (Fig. 458) without diffuse black shading; median transverse ridge convexly produced, not darkened with brown. Mesonotum yellow-brown. Mesosternum (Fig. 458) paler, extensively stained with diffuse black shading; sternacostal suture not stained with black. Metanotum posteromedial process blunt-triangulate. Metasternum (Fig. 458) extensively stained with diffuse black. Foreleg pale yellow; forefemur with diffuse brown shading. Mid- and hindlegs pale yellow. Ratios of length of body: foreleg: midleg: hindleg—2.7: 1.0: 1.4: 1.4. Forewing with ratio of length to greatest width—2.0; Sc, R1 and adjacent area stained with pale brown; other veins pale. *Abdomen*: Terga and sterna pale yellow; sterna 1–4 extensively stained with diffuse black shading (Fig. 458). Segments 4–6 with distinct vestiges of posterolateral projections.

Male Subimago: Body (Fig. 456) length 3.9 mm. Forewing length 3.1 mm. Caudal filaments length 2.2 mm. Genitalia (Fig. 457) with forceps slightly bowed; subgenital plate with posterior margin convexly produced; penes lobe moderately convex distolaterally. Coloration similar to adults.

Egg: Habitus as in Figure 570. Length about 525 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with seven to eight broad costae in lateral half. Costa width about one-half distance between adjacent costae.

Diagnosis: A yellow-brown operculate gill with a broad, strongly-developed Y-ridge (Fig. 444) distinguishes larvae of *C. fox* readily from those of all other North American *Cercobrachys* that are generally similar. The others have a Y-ridge that is narrow and less prominent, and even indistinct in some (Fig. 405). *Cercobrachys fox* is relatively similar to *C. etowah* and *C. minutus*, in that they all have a ventral margin of foretarsi that has a row of setae, including some long setae (length twice or more the width of the foretarsi) and some short setae (length one-half or less the width of the foretarsi) (Fig. 441). In other *Cercobrachys*, the setal row on the ventral margin of foretarsi is made up of only long setae (length three to five times the width of the foretarsi) (Fig. 461). Additionally, in *C. fox*, the apex of the middle ocellar tubercle is bluntly pointed (Fig. 451), the ventral margin of foretarsi has about 10 longer setae that are about two and one-half times as long as the width of the foretarsi (Fig. 441), and projections on the abdominal segment 6 are strongly curved medially (Fig. 454). In *C etowah*., the apex of the middle ocellar tubercle is acutely pointed (Fig. 424), and the ventral margin of foretarsi has about six longer setae that are three to four times as long as the width of the foretarsi (Fig. 478), and the posterolateral projection 6 is not strongly curved medially but forming a 30–40 degree angle with the long axis of the abdomen (Fig. 480).

Among the known adults of *Cercobrachys*, *C. fox* and the eastern Palearctic species *C. minutus* are the only species that have extensive diffuse black shading on the thoracic and abdominal sterna (Fig. 458). In *C. fox*, the abdominal terga are pale and lack black staining (Fig. 456), whereas in *C. minutus*, a pair of large patches of diffuse black staining are present on terga 1–8 (Fig. 488).

Eggs of *C. fox* are similar with those of *C. lilliei*, n. sp., and *C. serpentis*, in that they have a chorion that has seven to eight costae in the lateral half (Fig. 570). In *C. etowah*, *C. minutus*, *C. pomeiok*, n. sp., and *C. winnebago*, n. sp., the chorion has five or less costae in the lateral half (Fig. 569); and in *C. cree*, the chorion has 15–18 costae in the lateral half (Fig. 571). Eggs of *C. fox* and *C. lilliei*, n. sp., can be distinguished from those of *C. serpentis* by the width of the costa being subequal to, or greater than, one-half the distance between the two adjacent costae (Figs. 570, 572). In *C. serpentis*, the width of the costa is less than one-half the distance between the two adjacent costae (Fig. 573).

Etymology: The specific epithet a noun in apposition and is after the native North American people of the

Fox tribe, originally inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: Indiana, Iowa, Nebraska, North Dakota, and Wisconsin.

Material Examined: Larva HOLOTYPE, Iowa, Monona Co, Soldier R, 1 mi SW Ute at St Rd 183, IX-12-2001, WP McCafferty, AV Provonsha, RP Randolph (PERC). Two larva PARATYPES, same data as holotype (PERC). One male subimago PARATYPE, Indiana, Martin Co, W Fork White R at Hindostan Falls Pub Fish Site, VII-26-1982, AV Provonsha, M Doub (PERC). One female adult and one exuviae PARATYPES, Nebraska, Furnas Co, Republican R at Oxford, VIII-11-1982, AV Provonsha, V Van Alan (PERC). INDI-ANA, Martin Co: eight larvae, W Fork White R at Hindostan Falls Pub Fish Site, VII-26-1982, AV Provonsha, M Doub (PERC); Warren Co: one larva, Big Pine Cr, 3 mi SW Rainsville, VII-16-1973, AV Provonsha, K Black (PERC). IOWA, Greene Co: one larva, Buttrick Cr, 42/01/40N, 94/17/58W, VIII-30-1995 (PERC); Hardin Co: one larva, Tipton Cr, T87N R20W Sec 21 QTR NW QTRQTR NE UTMs Northing 4685918 Easting 484228, VIII-2-1999 (PERC); Kossuth Co: one larva, Buffalo Cr, 43/14/32N 93/59/17W, VIII-24-2000 (PERC); Poweshiek Co: one larva, North Skunk R, site 1, VIII-6-2001 (UI). KANSAS, Douglas Co: 11 larvae, Kansas R at Eudora Br, VIII-21-1978, P Liechti (KU), one larva, Kansas R below dam Lawrence, US 59 Hwy Br, IX-3-1981, P Liechti (KU), one larva, Kansas R at Lecompton, se1/4 sec 34, T11S, R18E, VII-28-1982, P Liechti (KU); Kingman Co: one larva, S fk Chikaskia R, 2.0 mi W jct SR 42 and CR, 3 mi E, 2 mi W Nashville, VI-19-1978, G Schuster, SWH (KU); Smith Co: one larva, N fk Solomon R, 2 mi E Cedar, VI-5-1974, D. Higgins, (KU); Reno Co: one larva, N fk Ninnescah R, 3 mi S, 3.2 mi E Castleton, VI-6-1977, P Liechti, DGH (KU). NEBRASKA, Furnas Co: one larva, Republican R at Oxford (on logs in river), VIII-11-1982, AV Provonsha, V Van Alan (PERC); Pawnee Co: three larvae, North Fork of the Big Nemaha R, 1 mi E of Table Rock on Hwy 4, VIII-12-1997, T Klubertanz, D Jones (PERC); Sheridan Co: one larva, Niobrara R, S Gorden, VII-27-1984, R Lawson, K Brown (PERC). WISCONSIN, Green Co: four larvae, Sugar R, Hwy 11-BL, VI-4-1992, RA Lillie (PERC), three larvae, Sugar R, Hwy 11-BL, VII-6-1992, RA Lillie (PERC); Richland Co: two larvae, Wisconsin R, Port Andrew, VI-6-1988, RA Lillie (PERC), three larvae, Wisconsin R, nr Riverview CK Hwy 60, VIII-3-1993, RA Lillie (PERC); Rock Co: eight larvae, Sugar R, VI-5-1991, RA Lillie, K Webster (PERC), one larva, Sugar R, above Nelson Rd, VII-10-1991, RA Lillie (PERC), one larva, Sugar R, Shoreline D-Frame Net above Nelson Rd, VII-10-1991, RA Lillie (PERC), two larvae, Sugar R at Nelson Rd, VI-4-1992, RA Lillie (PERC); Sauk Co: one larva, Honey Cr, above Hwy 60, VII-20-1991, RA Lillie (PERC); Trempealean Co: one larva, Black R, below Beaver Cr, VI-11-1992, RA Lillie (PERC), one larva, Black R, above Hwy 35, VI-10-1992, R Lillie, J Barko (PERC), four larvae, Trempealean R at Dodge, VI-11-1992, RA Lillie (PERC).

Cercobrachys lilliei, New Species

Mature Larva: Body (Fig. 459) length 4.7–6.2 mm. Caudal filaments length 2.2–2.5 mm. Coloration pale yellow-brown. *Head:* Frons without black macula or diffuse staining. Occiput (Figs. 459, 470) without black maculae or diffuse shading, and without apparent setae; lateral margin curved inward posterior to compound eye. Compound eye (Fig. 470) not distinctly produced dorsally; anterior margin reaching but not distinctly extending anteriorly beyond base of middle ocellar tubercle. Lateral ocellar tubercle (Fig. 470) slightly shorter than basal width, triangulate in lateral view; apex bluntly pointed to rounded. Middle ocellar tubercle (Figs. 459, 470) nearly triangulate in dorsal view; length about one-half of basal width, and one-half length of lateral tubercle; apex bluntly pointed to rounded. Antenna (Fig. 460) pale; scape without macula; pedicel 1.3 X length of scape, with about five setae one-half or more length of pedicel. Mouthparts as in Figures 464–469. Maxilla (Fig. 468) with galealacinia length 1.5 X basal width; palp segment 1 width 1.1 X width of segment 2; segment 2 1.8 X length of segment 1. *Thorax*: Nota (Fig. 459) without distinct black maculae. Pronotum (Fig. 471) lateral margin slightly and convexly produced. Propleuron mostly visible in dorsal view (Fig. 459). Pros-

ternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae about one-half length of forefemur. Mesosternum anterior margin covered with tuft of setae two-fifths length of midfemur. Legs (Figs. 461, 462) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.2: 1.0: 1.5: 1.5. Ratios of length of forefemur: tibia: tarsus: claw—3.6: 1.6: 2.7: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.5: 3.1: 2.4: 1.0. Forefemur (Fig. 461) dorsally with dense, long and short setae, ventrally with about 15 long setae measuring in length 2.0 X or more width of femur and arrayed in two distinct rows. Foretibia (Fig. 461) ventral margin with row of about six setae as long as 2.0 X width of tibia intermixed with several shorter setae; posterior surface with distinct row of about seven long setae as long as, or longer than, tibia. Foretarsus (Fig. 461) ventral margin with row of about 15 long setae measuring in length 4.0-5.0 X width of tarsus, without short setae; dorsal margin with distinct row of about 18 long setae measuring in length about 5.0 X width of tarsus. Hindfemur (Fig. 462) length 4.0 X width, dorsally with dense, long and short setae, and ventrally with short setae. Hindtibia (Fig. 462) dorsally with row of about 70 long, fine setae as long as about 4.0 X width of tibia. Hindtarsus (Fig. 462) dorsally with row of about 60 long setae. Hindtibia and hindtarsus ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 472) nearly straight; length 5.0 X basal width; inner margin roughened with series of minute, rounded nodules. Abdomen: Terga (Fig. 459) pale yellow-brown; terga 1, 2 and 6–10 stained with diffuse brown shading; terga 7–9 with brown band along anterior margin and pair of medial stripes (indistinct in some); tergum 8 more extensively stained than other terga; tergum 6 with row of short, fine setae along posterior margin (Fig. 473); terga 7 and 8 without apparent setae (Fig. 474). Segment 2 lateral margin slightly convex, not forming conspicuous posterolateral projection (Fig. 459). Posterolateral projection 5 (Fig. 473) length about 2.0 X basal width; projection 6 (Fig. 473) longest, distally strongly curved medially, forming angle less than 30 degrees with posterior margin of tergum 6, but not transversely oriented, with outer margin posterior to inner margin in dorsal view, and bluntly pointed at apex; projections 7–9 (Fig. 474) minute and indistinct. Sterna pale, without black staining; sternum 9 posterior margin convexly produced; apex somewhat truncate. Operculate gill (Fig. 463) pale, unicolourous and somewhat translucent; length 1.3 X width; dorsum without apparent long setae; posteromedial corner with row of dense, long marginal setae about one-third length of operculate gill; posterolateral corner with marginal setae one-half length of those at posteromedial corner and intermixed with some short setae; Yridge weakly developed, without long setae. Caudal filaments pale except basal intersegmental joints stained with brown in some individuals.

Adult: Unknown.

Egg: Habitus as in Figure 572. Length about 200 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with seven to eight costae in lateral half. Costa width subequal to one-half of distance between bases of adjacent costae.

Diagnosis: Larvae of *C. lilliei* are relatively similar to those of the North American species *C. cree* and *C. serpentis*, in that they all have a ventral margin of foretarsi that has a row of only long setae (Fig. 461), a strongly medially curved posterolateral projection 6 (Fig. 473), and a posterior margin of the operculate gills that has long marginal setae (Fig. 463). In *C. etowah*, *C. fox*, n. sp., and *C. minutus*, the ventral margin of the foretarsi has a row of setae consisting of both long and short setae (Fig. 441); and in *C. petersorum*, *C. pomeiok*, n. sp., and *C. winnebago*, n. sp., the projection 6 is moderately curved medially, forming an angle with the posterior margin of the tergum 6 that is about 45 degrees (Fig. 548), and the marginal setae on the posterior margin of the operculate gills are shorter than one-sixth of the length of the operculate gills (Fig. 537). In *C. lilliei*, hindtibiae have about 70 long, fine setae along the dorsal margin (Fig. 462), the abdominal terga 7–9 are stained with diffuse brown and usually have an anterior band and medial stripes (Fig. 459), and the posterior margin of the tergum 6 (Fig. 473). In *C. serpentis* and *C. cree*, hindtibiae have about 50 long, fine setae along the dorsal margin (Fig. 391), abdominal terga are not stained with brown shading or patterns (Fig. 388),

and the projections on abdominal segment 6 are curved to the extent that they have become transversely oriented, being distally parallel with the posterior margin of tergum 6 (Fig. 403).

Eggs of *C. lilliei* are similar with those of *C. fox* and *C. serpentis*, in that they all have the chorion with seven to eight costae in the lateral half (Fig. 572). In *C. etowah*, *C. minutus*, *C. pomeiok*, n. sp., and *C. winnebago*, n. sp., the chorion has five or less costae in the lateral half (Fig. 575); and in *C. cree*, the chorion has 15–18 costae in the lateral half (Fig. 571). Eggs of *C. lilliei* and *C. fox* can be distinguished from those of *C. serpentis* by the width of the costa, which is subequal to, or greater than, one-half the distance between the two adjacent costae (Fig. 572). In *C. serpentis*, the width of the costa is less than one-half the distance between the two adjacent costae (Fig. 573).

Etymology: The species is named in honor of Richard Lillie, who collected the type specimens from Wisconsin, and has contributed a great number of Brachycercinae specimens to our study.

Distribution: U.S.A.: Wisconsin.

Material Examined: Larva HOLOTYPE, Wisconsin, Trempealean Co, Black R, below Beaver Cr, VII-10-1992, R Lillie, J Barko (PERC). Fourteen larva PARATYPES, same data as holotype (PERC). WISCON-SIN, Grant Co: one larva, Wisconsin R, VI-6-1987, RA Lillie (PERC), eight larvae, Wisconsin R, Mileville, VII-11-1987, RA Lillie (PERC), two larvae, Wisconsin R, Mileville, VII-11-1991, RA Lillie (PERC), four larvae, Wisconsin R, Woodman, VI-20-1986, RA Lillie (PERC), three larvae, Wisconsin R, Woodman, VI-9-1987, RA Lillie (PERC); Pepin Co: four larvae, Chippewa R, upriver Hwy 35, below 2nd Island, VII-11-1991, R Lillie (PERC); Rock Co: 30 larvae, Sugar R, Avon Wildlife Area, VII-6-1992, RA Lillie (PERC); Trempealean Co: 16 larvae, Black R, above Hwy 35, main channel, VII-16-1991, R Lillie, J Lillie (PERC), three larvae, Black R, above Hwy 35, Main channel, VII-16-1991, R Lillie, J Lillie (PERC), three larvae, Black R, above Hwy 35, Main channel, VII-16-1991, R Lillie, J Lillie (PERC), three larvae, Black R, above Hwy 35, Main channel, VII-16-1991, R Lillie, J Lillie (PERC), three larvae, Black R, above Hwy 35, NI-11-1992, RA Lillie (PERC).

Cercobrachys minutus (Tshernova)

Brachycercus minutus Tshernova, 1952:285.

Eurycaenis minutus (Tshernova), 1952: Kazlauskas, 1962:147. *Cercobrachys minutus* (Tshernova), 1952: Soldán, 1986:342.

Mature Larva: Body (Fig. 475) length 4.4–5.4 mm. Caudal filaments length 1.9–2.1 mm. Coloration yellowbrown. Head: Frons without black macula or diffuse staining. Occiput (Figs. 475, 476) without black maculae or diffuse shading, covered with several short setae. Compound eye (Figs. 475, 476) not distinctly produced dorsally; anterior margin reaching but not distinctly extending anteriorly beyond base of middle ocellar tubercle. Lateral ocellar tubercle (Figs. 475, 476) slightly shorter than basal width, triangulate in lateral view; apex bluntly pointed to somewhat rounded. Middle ocellar tubercle (Figs. 475, 476) triangulate in dorsal view; length subequal to basal width, and about two-thirds length of lateral ocellar tubercle; apex bluntly pointed. Antenna (Fig. 477) pale; scape without macula; pedicel 1.5 X length of scape, with 5–10 setae one-half or more length of pedicel. Mouthparts as in Figures 482–487. Maxilla (Fig. 486) with galealacinia length 2.5 X basal width; palp segment 1 width 1.2 X width of segment 2; segment 2 2.0 X length of segment 1. Thorax: Nota (Fig. 475) without distinct black maculae. Pronotum (Fig. 475) lateral margin slightly produced, forming blunt angle in anterior half. Propleuron partially visible in dorsal view (Fig. 475). Prosternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae about onehalf length of forefemur. Mesosternum anterior margin covered with tuft of setae one-fourth to one-third length of midfemur. Legs (Figs. 478, 479) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.3: 1.0: 1.3: 1.3. Ratios of length of forefemur: tibia: tarsus: claw—3.5: 1.8: 2.3: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.9: 2.3: 2.5: 1.0. Forefemur (Fig. 478) dorsally with dense, long and short setae, ventrally with about 10 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 478) ventral margin with row of about five setae measuring in

length about 2.0 X width of tibia and some setae shorter than width of tibia; posterior surface with distinct row of about six long setae as long as, or longer than, tibia. Foretarsus (Fig. 478) ventral margin with row of about six long setae measuring in length about 1.5 X width of tarsus and intermixed with about 12 short setae measuring in length about one-half width of tarsus; dorsal margin with distinct row of about 10 long setae as long as 4.0 X width of tarsus. Hindfemur (Fig. 479) length 4.5 X width; dorsal and ventral margins with dense, long and short setae. Hindtibia and hindtarsus (Fig. 479) each dorsally with row of 30-40 long, fine setae as long as 4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 479) nearly straight; length 6.3 X basal width; inner margin with some inconspicuous, rounded nodules. Abdomen: Terga pale yellow; terga 1, 2, 7, and 8 stained with diffuse black shading, but without dark black macula; tergum 7 with row of long setae on posterior margin (Fig. 475); tergum 8 with scattered and fewer long setae. Segment 2 lateral margin slightly produced into low and blunt angle (Fig. 480). Posterolateral projections 5 and 6 (Fig. 480) longest; projection 5 length 3.8 X basal width; projection 6 distally curved medially, forming angle of 30–40 degrees with long axis of abdomen, rounded at apex; projections 7–9 (Figs. 475, 480) minute and indistinct. Sterna stained with black shading; sternum 9 posterior margin convexly produced, with apex somewhat truncate. Operculate gill (Fig. 481) pale brown and unicolourous; length 1.5 X width; dorsum laterally with several long setae onefourth length of operculate gill; posteromedial corner with row of dense, long marginal setae one-third to onehalf length of operculate gill; posterolateral corner with marginal setae shorter than those at posteromedial corner by up to two-thirds and intermixed with some short setae; Y-ridge strongly developed, with several long setae. Caudal filaments pale brown.

Male Adult: Body (Fig. 488) length 3.0–3.2 mm. Forewing length 3.0–3.6 mm. Caudal filaments length 10.0-12.0 mm. General coloration pale brown. Head: Frons with patch of brown staining medially. Stem of epicranial suture bordered with brown (Fig. 488). Scape (Fig. 489) pale brown, without black macula; pedicel (Fig. 489) paler; about 1.5 X length of scape. Thorax: Pronotum (Fig. 488) pale brown, stained extensively with diffuse black. Prosternum median transverse ridge convexly produced ventrally, darkened with brown. Mesonotum (Fig. 488) dark red-brown. Mesosternum paler; sternacostal suture stained with dark blackbrown, and stained with diffuse black. Metanotum posteromedial process triangulate. Coxae and trochanters brown. Forefemur (Fig. 490) pale brown, with brown stripes; foretibia (Fig. 490) pale except basal joint brown; foretarsus (Fig. 490) pale. Mid- and hindfemur pale brown; mid- and hindtibia paler; mid- and hindtarsus pale. Ratios of length of body: foreleg: midleg: hindleg-2.0: 2.0: 1.0: 1.0. Ratios of length of forefemur: tibia: tarsus—1.0: 2.9: 2.1. Ratios of length of foretarsus segment I: II: III: IV: V—1.0: 9.0: 4.5: 3.5: 2.5. Forewing with ratio of length to greatest width—1.8; Sc, R₁ and adjacent area stained with pale brown; other veins pale. Abdomen: Terga (Fig. 488) pale; terga 1–8 with large patch of diffuse black staining laterally, usually connected. Segments 4-6 with distinct vestiges of posterolateral projections; vestige of projection 6 directed posteriorly. Sterna 1–8 with large patch of diffuse black staining laterally. Genitalia (Fig. 491) with forceps slightly bowed; subgenital plate with posterior margin convexly produced; penes lobe strongly convex distolaterally. Caudal filaments pale.

Female Adult: Body length 3.6 mm. Forewing length 4.1 mm; ratio of forewing length to greatest width—1.8. Caudal filaments length 1.8 mm. Ratios of length of body: foreleg: midleg: hindleg—2.9: 1.0: 1.5: 1.5. Coloration and vestiges similar to males.

Egg: See formal description by Kluge (1991), figures 580, 581, and diagnosis below.

Diagnosis: Larvae of *C. minutus* are relatively similar to those of *C. etowah* and *C. fox* in that they all have a ventral margin of the foretarsi that has a row of setae, including some long setae (length twice or more the width of the foretarsi) and some short setae (length one-half or less the width of the foretarsi) (Fig. 478). In other *Cercobrachys*, the setal row on the ventral margin of foretarsi is made up of only long setae (length three to five times the width of the foretarsi) (Fig. 461). Additionally, *C. minutus* has the longer setae on the ventral margin of foretarsi shorter than twice the width of the foretarsi (Fig. 478), and the posterolateral projections

on abdominal segment 6 are not strongly curved medially, but forming a 30–40 degree angle with the long axis of the abdomen (Fig. 480). In *C. etowah* and *C. fox*, the longer setae on the ventral margin of foretarsi are as long as, or longer than, two and one-half times of the width of the foretarsi (Fig. 441), and posterolateral projection 6 is strongly curved medially (Fig. 454).

Adults of *C. minutus* are easily distinguished by the presence of a pair of large patches of diffuse black staining on abdominal terga 1–8 (Fig. 488). Such patches are absent in all other known *Cercobrachys* adults.

The eggs of *C. minutus* are the only eggs of *Cercobrachys* outside the Western Hemisphere with less than five costae in the lateral half of the chorion (Fig. 580). Nearctic species *C. etowah*, *C. pomeiok*, n. sp., and *C. winnebago*, n. sp., are also known to have less than five costae in the lateral half of the chorion (Fig. 569).

Distribution: Kazakhstan, eastern Asian region of Russia.

Material Examined: RUSSIA: five male adults, one female adult, Moskovskaya Oblast' Kashira, R Oka, 25-VI-1963, I Kalugina (PERC). KAZAKHSTAN: four larval exuviae, R. Chu nr mouth of R Kuragaty, 17–18-VI-1986, N Kluge (PERC).

Cercobrachys petersorum Soldán

Cercobrachys petersorum Soldán, 1986:344.

Mature Larva: Body (Fig. 493) length 5.7 mm without head. Caudal filaments length 1.8 mm. Coloration pale yellow-brown. Head: head missing on holotype except for antenna and mouthparts on slide. According to previous description and illustration, ocellar tubercle rounded; lateral tubercle shorter than width of compound eye; middle ocellar tubercle length about one-half length of lateral tubercle (Soldán 1986) (Fig. 492). Antenna (Fig. 494) pale; scape without macula; pedicel 1.6 X length of scape, with less than five setae onehalf or more length of pedicel. Mouthparts as in Figures 498-503. Maxilla (Fig. 502) with galealacinia length 1.8 X basal width; palp segment 1 width 1.1 X width of segment 2; segment 2 1.8 X length of segment 1. Thorax: Nota (Fig. 493) without distinct black maculae. Pronotum (Fig. 493) lateral margin slightly and convexly produced. Propleuron mostly visible in dorsal view (Fig. 493). Prosternum median transverse ridge slightly and broadly produced ventrally, with several short setae near or shorter than one-third length of forefemur. Mesosternum anterior margin with some setae about one-fourth length of forefemur. Mid- and hindleg missing on holotype. Foreleg (Fig. 495) pale, without basal band or black macula. Ratios of length of body: foreleg—2.6: 1.0. Ratios of length of forefemur: tibia: tarsus: claw—2.3: 0.7: 2.2: 1.0. According to previous description, ratios of length of hindfemur: tibia: tarsus-4.2: 2.0: 3.2 (Soldán 1986). Forefemur (Fig. 495) dorsally with dense, long and short setae, ventrally with some short setae and basally with about 20 long setae measuring in length 2.0–3.0 X or more width of femur in singular row but not well ordered. Foretibia (Fig. 495) ventral margin with about four setae measuring in length up to 4.0 X width of tibia; posterior surface with distinct row of about five long setae as long as, or longer than, tibia. Foretarsus (Fig. 495) ventral margin with row of about 14 long setae measuring in length 5.0 X width of tarsus, without short setae; dorsal margin with distinct row of about 15 long setae as long as about 6.0 X width of tarsus. Foreclaw (Fig. 495) nearly straight; length 10.0 X basal width; inner margin without nodules. Abdomen: Segment 9 missing on holotype. Terga (Fig. 493) pale yellow, without maculae; terga 7–10 with brown band laterally along anterior margin, and some diffuse shading. Tergum 6 posterior margin without apparent setae; tergum 7 with row of short, fine setae along posterior margin (Fig. 493); tergum 8 without apparent setae. Segment 2 lateral margin produced into low, right angle (Fig. 493). Posterolateral projection 5 (Figs. 493, 496) with length about 2.5 X basal width; projection 6 (Figs. 493, 496) longest, distally directed posteromedially, forming angle about 45 degrees with posterior margin of tergum 6, with apex bluntly pointed; projection 7 (Figs. 493, 496) developed, as long as one-half of projection 6; projection 8 indistinct (Fig. 493). Sterna pale, without black staining. Operculate

gill (Figs. 496, 497) pale yellow; length 1.2 X width; dorsum without apparent long setae; posteromedial corner with row of only short marginal setae shorter than one-tenth length of operculate gill; posterolateral corner with short marginal setae and some setae slightly longer than those at posteromedial corner; Y-ridge weakly developed, without long setae. Caudal filaments pale.

Adult: Unknown.

Egg: Unknown.

Diagnosis: Larvae of C. petersorum are relatively similar to those of the North American species C. pomeiok, n. sp., and C. winnebago, n. sp., in that they all have a ventral margin of the foretarsi that has a row of only long setae (Fig. 495), posterolateral projections on the abdominal tergum 6 that are not strongly curved medially but form an angle with the posterior margin of tergum 6 that is 45 degrees or greater (Fig. 493), and operculate gills whose marginal setae on the posteromedial corner are shorter than one-sixth length of the gill (Fig. 497). In C. etowah, C. fox, and C. minutus, the ventral margin of foretarsi has a row of setae consisting both long and short setae (Fig. 497). In C. cree, C. lilliei, and C. serpentis, posterolateral projections on abdominal tergum 6 are strongly curved medially to form an angle with the posterior margin of tergum 6, that is subequal to, or less than, 30 degrees (Figs. 414, 454), and the marginal setae on the posteromedial corner of operculate gills are longer than one-fourth of the gill length (Fig. 444). Cercobrachys petersorum can be distinguished from C. pomeiok, n. sp., and C. winnebago, n. sp., by having a prosternal median transverse ridge that is only slightly produced ventrally, a mesosternum anterior margin with only short setae, and an abdominal posterolateral projection 7 that is developed and longer than one-half length of the abdominal tergum 7 (Fig. 493). In C. pomeiok, n. sp., and C. winnebago, n. sp., the prosternal median transverse ridge is strongly produced ventrally, becoming more and less conical, the mesosternum anterior margin has tuft of long setae as long as, or longer than, one-half length of forefemur (Fig. 546), and abdominal projection 7 is minute (Fig. 549).

Distribution: Thailand.

Material Examined: Larva HOLOTYPE, Thailand, Chiengmai Prov, Mae Ping, Chiengmai, XI-17-1964 WL Peters and JG Peters (FAMU).

Cercobrachys pomeiok, New Species

Mature Larva: Body (Fig. 504) length 5.7-5.9 mm. Caudal filaments length 1.7-1.9 mm. Coloration pale yellow-brown. Head: Frons without black macula or diffuse staining. Occiput (Fig. 504) without black maculae or diffuse shading, and without apparent setae. Lateral ocellar tubercle (Fig. 504) hemispherical in lateral view; length one-half of basal width; apex rounded. Middle ocellar tubercle (Fig. 504) hemispherical in dorsal view; length about one-half of basal width, and about one-half length of lateral tubercle; apex rounded. Antenna (Fig. 505) pale; scape without macula; pedicel 1.3 X length of scape, with about five setae one-half or more length of pedicel. Mouthparts as in Figures 510–515. Maxilla (Fig. 514) with galealacinia length 1.5 X basal width; palp segment 1 width 1.0 X width of segment 2; segment 2 1.9 X length of segment 1. Thorax: Nota (Fig. 504) without distinct black maculae. Pronotum (Fig. 504) lateral margin slightly and convexly produced. Propleuron mostly visible in dorsal view (Fig. 504). Prosternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae longer than one-half length of forefemur. Mesosternum anterior margin covered with tuft of setae one-half or more length of midfemur. Legs (Figs. 506, 507) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.0: 1.0: 1.2: 1.2. Ratios of length of forefemur: tibia: tarsus: claw—3.3: 1.3: 2.8: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.4: 2.8: 2.1: 1.0. Forefemur (Fig. 506) dorsally with dense, long and short setae, ventrally with about 16 long setae measuring in length 2.0 X or more width of femur and arrayed in two distinct rows. Foretibia (Fig. 506) ventral margin with row of about three setae as long as 2.0 X width of tibia

and several shorter setae; posterior surface with distinct row of about five long setae as long as, or longer than, tibia. Foretarsus (Fig. 506) ventral margin with row of about 11 long setae measuring in length 4.0 X width of tarsus, without short setae; dorsal margin with distinct row of about 12 long setae as long as about 6.0 X width of tarsus. Hindfemur (Fig. 507) length 4.1 X width, dorsally with dense, long and short setae, and ventrally with short setae. Hindtibia (Fig. 507) dorsally with row of about 75 long, fine setae as long as 4.0 X width of tibia. Hindtarsus (Fig. 507) dorsally with row of about 50 long setae. Hindtibia and hindtarsus ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 507) nearly straight; length 5.3 X basal width; inner margin roughened with series of minute, rounded nodules. Abdomen: Terga (Fig. 504) pale yellow; terga 1 and 2 stained with diffuse brown; terga 7–10 with brown band laterally along anterior margin and some diffuse shading in certain individual. Tergum 6 with row of short, fine setae along posterior margin (Fig. 504); terga 7 and 8 without apparent setae. Segment 2 lateral margin slightly produced into low, right angle (Figs. 504, 508). Posterolateral projection 5 (Figs. 504, 508) with length about 1.5 X basal width; projection 6 (Figs. 504, 508) longest, distally directed posteromedially, forming angle about 60 degrees with posterior margin of tergum 6; projections 7–9 (Figs. 504, 508) minute and indistinct. Sterna pale, without black staining; sternum 9 posterior margin convexly produced, with small median notch at apex. Operculate gill (Fig. 509) pale yellow, slightly stained with some diffuse brown; length 1.2 X width; dorsum without apparent long setae; posteromedial corner with row of only short marginal setae about one-tenth length of operculate gill; posterolateral corner with short marginal setae and some longer setae about 2.0–3.0 X length of those at posteromedial corner; Y-ridge weakly developed, without long setae. Caudal filaments pale.

Adult: Unknown.

Egg: Habitus as in Figure 574. Length about 180 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with about three broad costae in lateral half. Costa width about one-half of distance between adjacent costae.

Diagnosis: Larvae of *C. pomeiok* are relatively similar to those of *C. petersorum* and *C. winnebago*, n. sp. in that they all have a ventral margin of the foretarsi with a row of only long setae (Fig. 506), posterolateral projections on the abdominal tergum 6 that are not strongly curved medially but form an angle with the posterior margin of tergum 6, that is 45 degrees or greater (Fig. 508), and operculate gills whose marginal setae on the posteromedial corner are shorter than one-sixth length of the gill (Fig. 509). In C. etowah, C. fox, and C. minutus, the ventral margin of foretarsi has a row of setae consisting both long and short setae (Fig. 497). In C. cree, C. lilliei, and C. serpentis, posterolateral projections on the abdominal tergum 6 are strongly curved medially to form an angle with the posterior margin of tergum 6 that is subequal to, or less than, 30 degrees (Figs. 414, 454), and the marginal setae on the posteromedial corner of operculate gills are longer than onefourth of the gill length (Fig. 444). Cercobrachys pomeiok can be distinguished from C. petersorum and C. winnebago, n. sp., by having foretarsi with about 12 long setae on the dorsal margin (Fig. 506), hindtibiae with about 75 long setae on the dorsal margin (Fig. 507), and an abdominal posterolateral projection 7 that is minute and indistinct (Fig. 508). In C. petersorum, the abdominal posterolateral projection 7 is developed and longer than one-half length of the abdominal tergum 7 (Fig. 493). In C. winnebago, n. sp., the foretarsi have about 25 long setae on the dorsal margin (Fig. 535), hindtibiae have about 100 long setae on the dorsal margin (Fig. 536), and posterolateral projection 7 is very small but distinct and acutely pointed (Fig. 549).

Eggs of *C. pomeiok* are similar with those of *C. etowah*, *C. minutus*, and *C. winnebago*, n. sp., in that they share the chorion with five or less costae in the lateral half (Fig. 574). In *C. fox*, *C. lilliei*, and *C. serpentis*, the chorion has seven to eight costae in the lateral half (Fig. 570); and in *C. cree*, the chorion has 15–18 costae in the lateral half (Fig. 571).

Etymology: The specific epithet a noun in apposition and is after the native North American people of the Pomeiok tribe, inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: North Carolina, South Carolina.

Material Examined: Larva HOLOTYPE, North Carolina, Edgecombe Co, Tar R, Tarboro, VII-1990 (PERC). Two larva PARATYPES, South Carolina, Laurens Co, Beaver Dam Cr, 7 mi NE of Gray Court, VII-20-1995, Glover, Renfrew, Guymon (PERC).

Cercobrachys serpentis Soldán

Cercobrachys serpentis Soldán, 1986:346.

Mature Larva: Body (Fig. 516) length 3.3–5.9 mm. Caudal filaments length 1.7–2.2 mm. Coloration pale yellow-brown. Head: Frons without black macula or diffuse staining. Occiput (Figs. 516, 527) without black maculae or diffuse shading, and without apparent setae. Lateral ocellar tubercle (Fig. 528) slightly shorter than basal width, triangulate in lateral view; apex bluntly pointed to rounded. Middle ocellar tubercle (Fig. 527) triangulate in dorsal view; length slightly less than basal width, and about two-thirds length of lateral ocellar tubercle; apex bluntly pointed. Antenna (Fig. 517) pale; scape without macula; pedicel only slightly longer than scape, with less than five setae one-half or more length of pedicel. Mouthparts as in Figures 521– 526. Maxilla (Fig. 525) with galealacinia length 1.7 X basal width; palp segment 1 width 1.2 X width of segment 2; segment 2 1.8 X length of segment 1. Thorax: Nota without distinct black maculae. Pronotum (Figs. 516, 529) lateral margin slightly and convexly produced. Propleuron mostly visible in dorsal view (Fig. 516). Prosternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae about one-half length of forefemur. Mesosternum anterior margin covered with tuft of setae one-third length of midfemur. Legs (Figs. 518, 519) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—2.7: 1.0: 1.1: 1.2. Ratios of length of forefemur: tibia: tarsus: claw—3.2: 1.5: 2.2: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw—3.8: 2.9: 2.4: 1.0. Forefemur (Fig. 518) dorsally with dense, long and short setae, and ventrally with row of about 15–20 long setae measuring in length 2.0 X or more width of femur and arrayed in single row. Foretibia (Fig. 518) ventral margin with row of about five setae as long as 2.0 X width of tibia and several shorter setae; posterior surface with distinct row of about five long setae as long as, or longer than, tibia. Foretarsus (Fig. 518) ventral margin with row of about 12 long setae as long as 3.0 X width of tarsus, without short setae; dorsal margin with distinct row of about 15 long setae as long as about 6.0 X width of tarsus. Hindfemur (Fig. 519) length 4.1 X width, dorsally with dense, long and short setae, and ventrally with short setae. Hindtibia and hindtarsus (Fig. 519) each dorsally with row of about 50 long, fine setae as long as about 3.0–4.0 X width of tibia, and ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 530) nearly straight; length 5.0 X basal width; inner margin roughened with series of minute, rounded nodules. Abdomen: Terga (Fig. 516) without black macula; terga 1 and 2 pale brown; terga 3-6 pale; terga 6-8 without apparent setae on posterior margins (Fig. 532); terga 7 and 8 pale brown, paler than terga 1 and 2; terga 9 and 10 pale. Segment 2 lateral margin slightly convex, not forming conspicuous posterolateral projection (Fig. 516). Posterolateral projection 5 (Fig. 531) length about 2.0 X basal width; projection 6 (Fig. 531) longest, distally strongly curved medially, becoming nearly transversely oriented, bluntly pointed at apex; projections 7-8 (Fig. 532) small; projection 9 (Fig. 532) minute and indistinct. Sterna pale brown, without black staining; sternum 9 posterior margin convexly produced. Operculate gill (Fig. 520) pale brown except posterior margin pale; length 1.3 X width; dorsum laterally with several long setae; posteromedial corner with row of dense, long marginal setae about one-third length of operculate gill; posterolateral corner with marginal setae one-half length of those at posteromedial corner, and intermixed with some short setae; Y-ridge weakly developed, without long setae. Caudal filaments pale.

Adult: Unknown.

Egg: Habitus as in Figure 573. Length about 170 mm. Shape elongate-ovate. Polar cap less than one-

fourth length of entire egg. Chorion with 7–8 costae in lateral half. Costa width less than one-half of distance between adjacent costae.

Diagnosis: Larvae of C. serpentis are relatively similar to those of the North American species C. cree and C. lilliei, in that they all have a ventral margin of the foretarsi with a row of only long setae (Fig. 518), a strongly medially curved posterolateral projection 6 (Fig. 531), and a posterior margin of the operculate gills with long marginal setae (Fig. 520). In C. etowah, C. fox, n. sp., and C. minutus, the ventral margin of the foretarsi has a row of setae consisting of both long and short setae (Fig. 441); and in C. petersorum, C. pomeiok, n. sp., and C. winnebago, n. sp., the projection 6 is moderately curved medially, forming an angle with the posterior margin of the tergum 6 that is about 45 degrees (Fig. 548), and the marginal setae on the posterior margin of the operculate gills are shorter than one-sixth of the length of the operculate gills (Fig. 537). In C. serpentis and C. cree, posterolateral projections 6 are curved to the extent that they are distally transversely oriented (Fig. 531), and abdominal terga are not stained with brown patterns (Fig. 516). In C. lilliei, abdominal projection 6 forms an angle of about 30 degrees with the posterior margin of the tergum 6 (Fig. 473), and abdominal terga 7–8 are stained with brown bands at the anterior margins (Fig. 459). Larvae of C. serpentis can be distinguished from C. cree by having a middle ocellar tubercle that is triangulate (Fig. 527), and foretarsi with a row of about 12 long setae on the ventral margin and a row of about 15 long setae on the dorsal margin (Fig. 518). In C. cree, the middle ocellar tubercle is hemispherical (Fig. 400), and foretarsi have a row of about 17 long setae on the ventral margin and a row of about 20 long setae on the dorsal margin (Fig. 390).

Eggs of *C. serpentis* are similar with those of *C. fox* and *C. lilliei*, in that they share a chorion that has seven to eight costae in the lateral half (Fig. 573). In *C. etowah*, *C. minutus*, *C. pomeiok*, and *C. winnebago*, n. sp., the chorion has five or less costae in the lateral half (Fig. 569); and in *C. cree*, the chorion has 15–18 costae in the lateral half (Fig. 571). In *C. serpentis*, the width of the costa is less than one-half the distance between the two adjacent costae (Fig. 573); whereas in *C. fox* and *C. lilliei*, the width of the costa is subequal to, or greater than, one-half the distance between the two adjacent costae (Figs. 570, 572).

Distribution: U.S.A.: Idaho, Montana, Nebraska, and Wyoming.

Material Examined: Larva HOLOTYPE, Idaho, Payette Co, Snake R at Payette, VIII-7-1965, GF Edmunds (PERC). IDAHO, Owyhee Co: one larva, Snake R at Payette, VII-30-1998, B Alcorn, R Piston (PERC); Payette Co: one larva, Snake R at Payette, VIII-7-1965, GF Edmunds (PERC). MONTANA, Rosebud Co: four larvae, Tongue R, Ashland, VII-17-1990, DL Gustafson (PERC). WYOMING, Sweetwater Co: one larva, Black's Fork R at I-80, W Green River City, VIII-2-1969, AV Provonsha (PERC).

Cercobrachys winnebago, New Species

Cercobrachys sp. 2 McCafferty et al., 2003:88.

Mature Larva: Body (Fig. 533) length 3.8–6.4 mm. Caudal filaments length 1.8–2.5 mm. Coloration pale yellow-brown. *Head*: Frons without black macula or diffuse staining. Occiput (Figs. 533, 544) without black maculae or diffuse shading, and without apparent setae. Lateral ocellar tubercle (Fig. 544) length one-half of basal width, hemispherical in lateral view; apex rounded. Middle ocellar tubercle (Fig. 544) hemispherical in dorsal view; length about one-half of basal width, and about one-half length of lateral tubercle; apex rounded. Antenna (Fig. 534) pale; scape without macula; pedicel subequal to scape in length, with about five setae one-half or more length of pedicel. Mouthparts as in Figures 538–543. Maxilla (Fig. 542) with galealacinia length 1.5 X basal width; palp segment 1 width 1.2 X width of segment 2; segment 2 1.9 X length of segment 1. *Thorax*: Nota (Fig. 533) without distinct black maculae. Pronotum (Figs. 533, 545) lateral margin slightly and convexly produced. Propleuron mostly visible in dorsal view (Fig. 533). Prosternum median transverse ridge strongly produced ventrally, forming cylindrical process and covered with tuft of setae longer than one-half

length of forefemur. Mesosternum (Fig. 546) anterior margin covered with tuft of setae longer than one-half length of midfemur. Legs (Figs. 535, 536) pale, without basal band or black macula. Ratios of length of body: foreleg: midleg: hindleg—3.6: 1.0: 1.4: 1.5. Ratios of length of forefemur: tibia: tarsus: claw—3.3: 1.3: 2.5: 1.0. Ratios of length of hindfemur: tibia: tarsus: claw-3.2: 2.8: 2.1: 1.0. Forefemur (Fig. 535) dorsally with dense, long and short setae, ventrally with about 20 long setae measuring in length 2.0 X or more width of femur and arrayed in two distinct rows. Foretibia (Fig. 535) ventral margin with row of about eight setae as long as 2.5 X width of tibia and several shorter setae; posterior surface with distinct row of about seven long setae as long as, or longer than, tibia. Foretarsus (Fig. 535) ventral margin with row of about 16 long setae measuring in length 4.0 X width of tarsus, and without short setae; dorsal margin with distinct row of about 25 long setae measuring in length about 4.0 X width of tarsus. Hindfemur (Fig. 536) length 3.7 X width, dorsally with dense, long and short setae, and ventrally with short setae. Hindtibia (Fig. 536) dorsally with row of about 100 long, fine setae as long as about 4.0 X width of tibia. Hindtarsus (Fig. 536) dorsally with row of about 80 long setae. Hindtibia and hindtarsus ventrally with row of short, stout setae and row of relatively long, fine setae much shorter and fewer than those on dorsal margin. Hindclaw (Fig. 547) nearly straight; length 5.3 X basal width; inner margin roughened with series of minute, rounded nodules. Abdomen: Terga (Fig. 533) pale yellow-brown, unicolorous, without black macula or diffuse shading; tergum 6 with row of short, fine setae along posterior margin (Fig. 548); terga 7 and 8 (Fig. 549) without apparent setae. Segment 2 lateral margin slightly produced into shallow, right angle (Fig. 533). Posterolateral projection 5 (Fig. 548) length about 2.3 X basal width; projection 6 (Fig. 548) longest, distally directed posteromedially, forming angle about 45 degrees with posterior margin of tergum 6, bluntly pointed at apex; projection 7 (Fig. 549) very small but distinct and acutely pointed, projections 8 and 9 minute (Fig. 549). Sterna (Fig. 550) pale, without black staining; sternum 9 posterior margin convexly produced, somewhat truncate at apex. Operculate gill (Fig. 537) pale, unicolourous and somewhat translucent; length 1.3 X width; dorsum without apparent long setae; posteromedial corner with only row of short marginal setae shorter than one-six length of operculate gill; posterolateral corner with short setae and some longer setae about 1.5 X length of those at posteromedial corner; Y-ridge weakly developed, without long setae. Caudal filaments pale.

Male Adult: Body (Fig. 551) length 3.5–4.2 mm. Forewing length 3.2–3.5 mm. Caudal filaments length 12.0-13.0 mm. General coloration pale yellow. Head: Vertex and occiput (Fig. 551) slightly stained with diffuse brown. Epicranial suture (Fig. 551) bordered with pale brown. Antenna (Fig. 552) with scape pale brown, without black macula; pedicel paler, slightly longer than scape. Thorax: Pronotum (Figs. 551, 552) pale yellow, slightly stained with diffuse black. Prosternum median transverse ridge convexly produced, margined with pale brown. Mesonotum (Fig. 551) yellow-brown. Mesosternum paler, without diffuse black shading; sternacostal suture not stained with dark black-brown. Metanotum posteromedial process blunt triangulate. Coxae and trochanters brown. Forefemur pale brown, with brown stripes; foretibia pale except basal joint brown; foretarsus pale. Mid- and hindfemur pale brown; mid- and hindtibia and mid- and hindtarsus pale. Ratios of length of body: foreleg: midleg: hindleg—2.5: 1.7: 1.0: 1.0. Ratios of length of forefemur: tibia: tarsus-1.0: 2.0: 1.3. Ratios of length of foretarsus segment I: II: III: IV: V-1.0: 4.6: 2.4: 2.0: 1.8. Forewing with ratio of length to greatest width—2.1; Sc, R₁ and adjacent area stained with pale brown; other veins pale. Abdomen: Terga (Fig. 551) and sterna generally pale except tergum 10 bordered with brown, without black macula or diffuse shading. Segments without distinct vestiges of posterolateral projections except minute vestige of projection 6 in some individuals. Genitalia (Fig. 553) with forceps slightly bowed; subgenital plate with posterior margin convexly produced; penes lobe slightly convex distolaterally. Caudal filaments pale.

Female Adult: Body (Fig. 554) length 3.8–4.5 mm. Forewing length 3.9–4.1 mm; ratio of forewing length to greatest width—2.0. Caudal filaments length 2.0–2.2 mm. Ratios of length of body: foreleg: midleg: hindleg—3.4: 1.0: 1.3: 1.4. Coloration and vestiges similar to males.

Egg: Habitus as in Figure 575. Length about 250 mm. Shape elongate-ovate. Polar cap less than one-fourth length of entire egg. Chorion with about four broad costae in lateral half. Costa width about one-half of

distance between adjacent costae.

Diagnosis: Larvae of C. winnebago are relatively similar to those of C. petersorum and C. pomeiok in that they all have a ventral margin of the foretarsi with a row of only long setae (Fig. 535), posterolateral projections on the abdominal tergum 6 that are not strongly curved medially but form an angle with the posterior margin of tergum 6, that is 45 degrees or greater (Fig. 548), and operculate gills whose marginal setae on the posteromedial corner are shorter than one-sixth length of the gill (Fig. 537). In C. etowah, C. fox, and C. minutus, the ventral margin of foretarsi has a row of setae consisting both long and short setae (Fig. 497). In C. cree, C. lilliei, and C. serpentis, posterolateral projections on the abdominal tergum 6 are strongly curved medially to form an angle with the posterior margin of tergum 6, that is subequal to, or less than, 30 degrees (Figs. 414, 454), and the marginal setae on the posteromedial corner of operculate gills are longer than onefourth of the gill length (Fig. 444). Cercobrachys winnebago can be distinguished from C. petersorum and C. pomeiok by having foretarsi with about 25 long setae on the dorsal margin (Fig. 535), hindtibiae with about 100 long setae on the dorsal margin (Fig. 536), and an abdominal posterolateral projection 7 that is very small but distinct and acutely pointed (Fig. 549). In C. petersorum, abdominal posterolateral projection 7 is developed and longer than one-half length of the abdominal tergum 7 (Fig. 493). In C. pomeiok, foretarsi have about 12 long setae on the dorsal margin (Fig. 506), hindtibiae have about 75 long setae on the dorsal margin (Fig. 507), and posterolateral projection 7 is minute and indistinct (Fig. 508).

Adults of *C. winnebago* are distinguished from all other known adults of *Cercobrachys* by having abdominal terga 4–6 that lack apparent vestiges of posterolateral projections or have only minute vestiges on segment 6. In other *Cercobrachys*, segments 4–6 usually have distinct vestiges of posterolateral projections, and the vestiges on the segment 6 are one-half or more of the length of the tergum 6.

Furthermore, adult *C. winnebago* has a yellow-brown sternacostal suture on the mesosternum, whereas in *C. etowah*, the sternacostal suture is distinctly darkened with black-brown and much darker than the adjacent area (Fig. 432). In *C. winnebago*, thoracic and abdominal sterna are not stained with diffuse black (Fig. 554), whereas such staining is present in *C. fox* and *C. minutus* (Fig. 458).

Eggs of *C. winnebago* are similar with those of *C. etowah*, *C. minutus*, and *C. pomeiok*, in that they share a chorion with five or less costae in the lateral half (Fig. 575). In *C. fox*, *C. lilliei*, and *C. serpentis*, the chorion has seven to eight costae in the lateral half (Fig. 570); and in *C. cree*, the chorion has 15–18 costae in the lateral half (Fig. 571).

Etymology: The specific epithet a noun in apposition and is after the native North American people of the Winnebago tribe, inhabitants of a region in the vicinity of the species range.

Distribution: U.S.A.: Iowa, Nebraska, Texas, and Wisconsin.

Material Examined: Larva HOLOTYPE, Nebraska, Furnas Co, Republican R at Oxford (River channel), VIII-11-1982, AV Provonsha, V Van Alan (PERC). Eight larva, four male imago, four female imago PARATYPES, same data and deposition as holotype. IOWA, Adair Co: one larva, West Fk, Middle Nodaway R at Co Rd G61, IX-12-2001, WP McCafferty, AV Provonsha, RP Randolph (PERC); Kossuth Co: one larva, Buffalo Cr, 43/14/32N 93/59/17W, VIII-24-2000 (PERC); Monona Co: five larvae, Soldier R, 1 mi SW Ute at St Rd 183, IX-12-2001, WP McCafferty, AV Provonsha, RP Randolph (PERC); Poweshiek Co: eight larvae, North Skunk R, site 2, VIII-6-2001 (UI); Tama Co: one larva, Richland Cr, 0.5 mi N of Haven, 41.899N, 92.475W, IX-8-1995 (PERC); Van Buren Co: eight larvae, Fox R at St Rd 2, IX-10-2001, WP McCafferty, AV Provonsha, RP Randolph (PERC). KANSAS, Douglas Co: 50 male adults, two female adults, Kansas R, Lawrence, SW ¼ sec 30, T12S, R20E, VIII-20-1982, P Liechti (KU); Jefferson Co: two larvae, Delaware R, 0.5 mi W Halfmound, VI-17-1980, A Slater, DGH (KU); McPherson Co: one larva, Smoky Hill R, 3.0 mi S, 1.5 mi W Lindsborg, IX-6-1982, P Liechti, DCR (KU); Meade Co: one larva, N fk Solomon R, 0.25 mi S Portis, VII-6-1977, SW Hamilton, (KU); Russell Co: four larvae, Smoky Hill R, 5.5 mi S Bunke Hill, VII-5-1977, SW Hamilton, (KU). NEBRASKA, Antelope Co: two larvae, Elkhorn R, Hwy 14 S of Neligh, VII-25-

2001, Kondratieff, Zuellig (CSU); Buffalo Co: two larvae, Kearney, IX-6-1951 (PERC); Furnas Co: 50 larvae, 10 male imagos, 4 female imagos, four male subimagos, three female subimagos, 13 exuviae, Republican R at Oxford (River channel), VIII-11-1982, AV Provonsha, V Van Alan (PERC), 11 larvae, Republican R at Oxford, VIII-11-1982, AV Provonsha, V Van Alan (PERC); Nance Co: two larvae, Cedar R, Hwy 14/22 N Fullerton, VII-25-2001, Kondratieff, Zuellig (CSU); Sheridan Co: five larvae, Niobrara R, Gorden, VII-11-1984, R Lawson, K Brown (PERC), three larvae, Niobrara R, S Gorden, VII-27-1984, R Lawson, K Brown (PERC), 12 larvae, Niobrara R, VIII-9-1984, R Lawson, K Brown, M Brohman (PERC). TEXAS, Lipscomb Co: one larva, Wolf Cr at FM 1454 Lipscomb, VII-18-1990, S Twidwell (PERC). WISCONSIN, Green Co: 18 larvae, Sugar R, Hwy 11-BL, VII-6-1992, RA Lillie (PERC); Rock Co: four larvae, Sugar R, Above Nelson Bridge, VI-5-1991, R Lillie, K Webster (PERC), four larvae, Sugar R, vicinity Nelson Rd, below logjam, VI-5-1991, R Lillie, K Webster (PERC), four larvae, Sugar R, above Nelson Rd, VII-10-1991, R Lillie (PERC), 11 larvae, Sugar R at Nelson Rd, VII-6-1992, RA Lillie (PERC).

Keys to Species

Known Larvae

1	Operculate gill asymmetrical, with protruding edge at posterolateral corner (Figs. 37, 254). [Palearctic,	
	Oriental, Nearctic]	
1′	Operculate gill generally symmetrical, without protruding edge at posterolateral corner (Figs.	
	150, 444). [Nearctic, Palearctic, Oriental, Neotropical]	
2	Maxillary and labial palpi three segmented (Figs. 29, 30). [Oriental] Caenoculis, 3	
2'	Maxillary and labial palpi two segmented (Figs. 234, 235). [Palearctic, Nearctic] Brachycercus, 5	
3	Posterolateral projections developed on abdominal segments 4-7 (Fig. 52) Caenoculis bishopi	
3'	Posterolateral projections developed on five or more abdominal segments (Fig. 24) 4	
4	Posterolateral projections developed on abdominal segments 4-8	
4'	Posterolateral projections developed on abdominal segments 3-9 (Fig. 24) Caenoculis acutalis	
5	Apex of middle ocellar tubercle acutely pointed (Fig. 215). Hindclaw length more than one-fourth com-	
	bined length of hindtibia and hindtarsus (Fig. 224). [Nearctic] Brachycercus berneri	
5'	Apex of middle ocellar tubercle very bluntly pointed or somewhat rounded (Fig. 246). Hindclaw length	
	less than one-fourth combined length of hindtibia and hindtarsus (Fig. 253). [Palearctic, Nearctic] 6	
6	Basisternum of mesosternum with medial process (Fig. 228). [Palearctic, Nearctic]	
	Brachycercus harrisella	
6'	Basisternum of mesosternum without medial process (Fig. 261). [Nearctic]7	
7	Frons stained with black (Fig. 246). Middle ocellar tubercle length slightly longer than basal width (Fig.	
	246). Galealacinia length greater than 2.5 X basal width (Fig. 251). Operculate gill black-brown (Fig.	
	245) Brachycercus nitidus	
7'	Frons yellow brown (Fig. 259). Middle ocellar tubercle length about 2.0 X or more basal width (Fig. 260).	
	Galealacinia length less than 2.5 X basal width (Fig. 265). Operculate gill paler brown (Fig. 258)	
	Brachycercus ojibwe	
8	Ocellar tubercles broadly cylindrical, with apex somewhat truncate, and with apical portion covered with	
	dense, long setae (1.5–2.0 X length of ocellar tubercle) (Fig. 198). [West Indies]	
	Insulibrachys, Insulibrachys needhami	
8'	Ocellar tubercles conical (Fig. 156), finger shaped (Fig. 328), or hemispherical (Fig. 400), with apex	

	ridge strongly bent ventrally (Figs. 283, 284). [Oriental] Oriobrachys, Oriobrachys mahakam
9'	Operculate gill without sublateral longitudinal ridge [Nearctic, Palearctic, Oriental, Neotropical] (Figs. 496, 497)
10	Medial processes present on both meso- and metasternum (Fig. 329). [Nearctic] Susperatus, 11
10'	Medial processes absent on meso- and metasternum (Fig. 140). [Palearctic, Oriental, Nearctic, Neotropical]
11	Process on basisternum of mesosternum broadly produced, shorter than processes on sternellum of mesos-
	ternum and on metasternum, and with apex rounded or very bluntly pointed (Fig. 329). Lateral margin of
	pronotum anterioriy only moderately produced into bluntly pointed expansion (Fig. 528)
11,	Process on basisternum of mesosternum strongly produced as long as other ventral processes, and with
11	apex papillate or pointed (Fig. 361). Lateral margin of pronotum anteriorly strongly produced into trian-
	gulate, pointed expansion (Fig. 360)
12	Abdominal posterolateral projection 6 with apical portion not curved medially, but directed nearly posteri-
	orly (Fig. 137). Operculate gill ventral surface with submarginal rows of hairlike microtrichia in lateral
10,	and posterior areas (Fig. 151). [Palearctic, Oriental, Nearctic]
12	Abdominal posterolateral projection 6 with apical portion distinctly curved medially (Fig. 3/5). Opercu-
	late gill ventral surface lacking submarginal rows of microtricnia in most species (Fig. 428), or if present,
12	Only in posterior area (Fig. 291). [Palearctic, Oriental, Nearctic, Neotropical]
15	tell
13'	Occipit with one or two transverse black hands posterior to lateral ocellar tubercle (Fig. 155). [Nearctic]
15	20
14	Middle ocellar tubercle distinctly longer than lateral ocellar tubercles (Fig. 101). [Palearctic]
14'	Middle ocellar tubercle as long as, or shorter than, lateral ocellar tubercles. (Fig. 62) [Palearctic, Oriental]
15	Maxillary palp segment 2 subequal to segment 1 in length (Fig. 196). [eastern Palearctic]
15'	Maxillary palp segment 2 about 1.5 X length of segment 1 (Fig. 103). [western Palearctic]
	Sparbarus europaeus
16	Abdominal posterolateral projection 2 as long as, or slightly shorter than, posterolateral projection 3 (Fig. 90). [Palearctic]
16'	Abdominal posterolateral projection 2 one-half or less length of posterolateral projection 3 (Fig. 71).
17	[eastern Palearctic, Oriental]
1/	margin (Fig. 131). [northern Africa]
17'	Maxillary palp segment 2 with long, stout setae present along approximately distal one-third of inner mar- gin (Fig. 89). [eastern Palearctic]
18	Pedicel longer than 3.0 X length of scape, with more than 20 setae one-half or more length of pedicel (Fig.
	108). [Oriental]
18'	Pedicel about 2.0 X length of scape, with about 10 or less setae one-half or more length of pedicel (Fig.
	63). [eastern Palearctic, Oriental]
19	Middle ocellar tubercle as long as 1.5 X basal width, and about two-thirds length of lateral tubercles (Fig.
	62). Abdominal sterna stained with diffuse black shading. [Oriental]
19'	Middle ocellar tubercle as long as 2.5 X basal width, and subequal in length to lateral tubercles (Fig. 117).
	Abdominal sterna without diffuse black shading. [eastern Palearctic]
20	Middle ocellar tubercle 2.0 X or more length of lateral tubercles (Fig. 175) Sparbarus nasutus

20'	Middle ocellar tubercle as long as, or shorter than, lateral tubercles (Figs. 139, 156)
21	Middle ocellar tubercle short-triangulate, as long as basal width (Fig. 155). Lateral projection of abdomi-
	nal tergum 2 not developed, with length less than basal width, and with apex forming blunt right angle
	(Fig. 155)
21'	Middle ocellar tubercle relatively elongate, with length about 1.5-2.0 X basal width (Fig. 139). Abdomi-
	nal tergum 2 with moderately developed triangulate lateral projection, with length subequal to basal
	width, and with apex forming acute angle (Fig. 137) 24
22	Femora without black apical macula on dorsal margin (Fig. 155) Sparbarus maculatus
22'	Femora with black apical macula on dorsal margin (Fig. 173)
23	Abdominal terga 7–9 with medial longitudinal brown stripe (Fig. 94). Pedicel about 2.5 X length of scape
	(Fig. 96)
23'	Abdominal terga 7–9 with submedial triangulate brown maculae (Fig. 166). Pedicel about 2.0 X length of
	scape (Fig. 168) Sparbarus miccosukee
24	Posterolateral projection 7 about two-thirds length of projection 6 (Fig. 78). Abdominal terga 7–9 anterior
	margin with narrow, submedial elongate bands narrowly separated from medial stripe (Fig. 78)
24'	Posterolateral projection 7 one-half or less length of projection 6 (Fig. 137). Abdominal terga 7–9 anterior
	margin with short, dotlike marks laterally and widely separated from medial stripe (Fig. 137)
25	Labrum nearly trapezoidal, with lateral margin nearly straight to moderately produced (Fig. 302).
	Hypopharynx superlingua with lateral margin moderately and convexly produced (Fig. 305). Foretarsus
	dorsal margin without long setae (Fig. 309), or with several long setae but not forming distinct row (Fig.
	383). [southwestern Nearctic, Neotropical]
25'	Labrum nearly ovate, with lateral margin strongly produced and rounded (Fig. 394). Hypopharynx super-
	lingua with lateral margin strongly produced and somewhat triangulate (Fig. 397). Foretarsus dorsal mar-
	gin with well-ordered row of long setae (Fig. 390). [eastern Palearctic, Oriental, Nearctic]
26	Maxillary palp segment 2 more than 2.0 X length of segment 1 (Fig. 380). Labial palp segment 1 with
	ventral patch of setae as long as or longer than segment 1 (Fig. 381). Posterolateral projection 6 moder-
	ately curved medially but not nearly parallel with posterior margin of tergum 6 (Fig. 375). [Neotropical] .
	Alloretochus, Alloretochus peruanicus
26'	Maxillary palp segment 2 1.5–1.8 X length of segment 1 (Fig. 296). Labial palp segment 1 lacking ventral
	patch of long setae (Fig. 297). Posterolateral projection 6 distally nearly parallel with posterior margin of
	tergum 6 (Fig. 311). [southwestern Nearctic, Neotropical] Latineosus, 27
27	Anterior margin of compound eye extended anterior of base of middle ocellar tubercle (Fig. 314). Apices
	of posterolateral projection 6 pair overlapping medially in dorsal aspect (Fig. 318). [Neotropical]
	Latineosus colombianus
27'	Anterior margin of compound eye not extended anterior of base of middle ocellar tubercle (Fig. 299). Api-
	ces of posterolateral projection 6 pair not meeting medially (Fig. 311). [southwestern Nearctic, Neotropi-
	cal]
28	Lateral ocellar tubercle longer than basal width and somewhat finger shaped in distal portion (Fig. 286).
	Abdominal posterolateral projections 7 and 8 small but distinct and acute (Fig. 290). [Neotropical]
	Latineosus cayo
28'	Lateral ocellar tubercle slightly shorter than basal width and simple-triangulate (Fig. 299). Abdominal
	posterolateral projections 7 and 8 minute and indistinct (Fig. 311). [southwestern Nearctic]
	Latineosus cibola
29	Foretibia short, about one-third length of foretarsus (Fig. 495). Posterolateral projection 7 longer than

	one-half length of abdominal tergum 7 (Fig. 493). [Oriental] Cercobrachys petersorum
29'	Foretibia as long as about one-half length of foretarsus or longer (Fig. 535). Posterolateral projection 7
	minute (much shorter than one-third length of abdominal tergum 7) (Fig. 549). [Palearctic, Nearctic] 30
30	Galealacinia sickle shaped, subequal to, or longer than, 2.3 X basal width (Fig. 422). Ventral margin of
	foretarsus with row of long and short setae, with long setae subequal to, or longer than, 1.5 X width of
	foretarsus and short setae shorter than width of foretarsus (Fig. 412). [eastern Palearctic, Nearctic] 31
30'	Galealacinia stout and subtriangulate, subequal to, or shorter than, 1.7 X basal width (Fig. 542). Ventral
	margin of foretarsus with row of long setae only (3.0 X or more width of foretarsus) (Fig. 535). [Nearctic]
31	Middle ocellar tubercle acutely pointed (Fig. 424). Long setae on ventral margin of foretarsus subequal to,
	or longer than, 3.0 X width of foretarsus (Fig. 412). [Nearctic] Cercobrachys etowah
31	Middle ocellar tubercle bluntly pointed (Fig. 451). Long setae on ventral margin of foretarsus shorter than
22	3.0 X width of foretarsus (Fig. 4/8) [eastern Palearctic, Nearctic]
32	Posterolateral projection 6 strongly curved medially, distally parallel with posterior margin of tergum 6
22,	(Fig. 454). [Nearctic]
32	Posterolateral projection 6 not strongly curved medially, distally forming an angle with posterior margin
22	Undtibie with shout 50 long setes along dersel menoin (Fig. 510). Desterior menoin of shdominal tergum
33	Finduloia with about 50 long setae along dorsar margin (Fig. 519). Posterior margin of abdominal terguin 6 without row of fine setae (Fig. 402).
	margin of torgum 6 (Fig. 403) Posterolateral projection o distanty hearty parallel with posterior
22,	Hindtibia with 70 or more long setae along dorsal margin (Fig. 536). Posterior margin of abdominal ter
55	aum 6 with row of fine setae (Fig. 548). Posterolateral projection 6 distally forming an angle with poster-
	rior margin of tergum 6 subequal to or more than 30 degrees (Fig. 548)
34	Middle ocellar tubercle triangulate with apex bluntly pointed (Fig. 527)
34'	Middle ocellar tubercle hemispherical with apex rounded (Fig. 400)
35	Operculate gill with long marginal setae on posteromedial corner (one-fourth to one-third length of oper-
	culate gill) (Fig. 463).
35'	Operculate gill with short marginal setae on posteromedial corner (less than one-sixth length of operculate
	gill) (Fig. 537)
36	Foretarsus with about 25 long setae on dorsal margin (Fig. 535). Hindtibia with about 100 long setae on
	dorsal margin (Fig. 536). Posterolateral projection 7 very small but distinct and acutely pointed (Fig. 549)
36'	Foretarsus with about 12 long setae on dorsal margin (Fig. 506). Hindtibia with about 75 long setae on
	dorsal margin (Fig. 507). Posterolateral projection 7 minute and indistinct (Fig. 508)
	Cercobrachys pomeiok

Known Adults

1 Pronotum lateral margin continuously rounded throughout. [West Indies]	
	Insulibrachys, Insulibrachys needhami
1'	Pronotum lateral margin not continuously rounded, nearly straight (Fig. 430). [Palearctic, Oriental, Nearc-
	tic, Neotropical]
2	Prosternum with median ridge strongly produced, forming conical process (Fig. 349). [Palearctic, Nearc-
	tic, Neotropical]
2'	Prosternum flat or only slightly produced ventrally, not forming distinct medial process. [Palearctic, Ori-
	ental, Nearctic]10
3	Male subgenital plate with posterior margin broadly emarginated medially (Fig. 387). [Neotropical]
	Alloretochus, Alloretochus peruanicus

3'	Male subgenital plate with posterior margin convexly produced (Fig. 409) or truncate (Fig. 438). [Palearc- tic Nearctic]	
4	Pedicel longer than 1.5 X length of scape (Fig. 348). [Nearctic]	
4′	Pedicel not longer than 1.5 X length of scape (Fig. 406). [eastern Palearctic, Nearctic]	
~	Cercobrachys, 6	
5	Male body length more than 4.0 mm $(4.2-5.1 \text{ mm})$; genitalia forceps with apical two-thirds curved medi-	
Ξ,	ally (Fig. 352); styliger plate with posterior margin truncate	
5	traight (Eig. 258)) stylicer plate with posterior morein conveyly produced	
6	Thereasis and and eminal storms stained with diffuse black (Fig. 458) [asstern Delegratic Negratical 7	
0 6'	Thoracic and abdominal sterna pala, not stained with diffuse black (Fig. 554). [Nearetic]	
07	Abdominal targe 1, 8 each stained with two patches of diffuse black laterally (Fig. 488) [castern Deleare	
/	ticl	
7,	Abdominal terga without black shading [Nearctic]	
/ 8	Abdominal segment 6 without distinct vestige of posterolateral projection, or if present then vestige less	
0	than one-half length of tergum 6	
8'	Abdominal segment 6 with distinct vestige of posterolateral projection subequal in length to one-half of	
0	tergum 6 or longer (Fig. 436)	
9	Mesosternum with sternacostal suture darkened with black-brown distinctly darker than adjacent area	
-	(Fig. 432).	
9'	Mesosternum with sternacostal suture vellow-brown, not distinctly darker than adjacent area	
-	Cercobrachvs cree	
10	Abdominal segment 2 with distinct vestige of posterolateral projection. [eastern Palearctic, Nearctic] 11	
10'	Abdominal segment 2 without vestige of posterolateral projection. [eastern Palearctic, Oriental, Nearctic]	
11	Occiput with transverse black hand posterior to lateral occilus [Nearetic] Sparbarus nasutus	
11	Occipit with transverse, black band posterior to lateral ocellus. [Nearctic]	
12	Occipit without black band posterior to lateral ocellus (Fig. 162) [Nearctic]	
12	Occipit with one of two transverse, black bands posterior to lateral ocellus (Fig. 123). [Pelearctic Oriental	
12	Nearctic]	
13	Male with forceps distinctly angled at one-fifth to one-fourth distance from base (Fig. 154)	
13'	Male with forceps nearly straight or evenly curved near base (Fig. 165) Sparbarus maculatus	
14	Mesonotum dark red-brown to black-brown (Fig. 241). Mesosternal basisternum medially with slight pro-	
	trusion, representing vestige of well-developed larval process (Fig. 242). [Palearctic, Nearctic]	
	Brachycercus harrisella	
14'	Mesosternum yellow-brown to red-brown. Mesosternal basisternum without produced vestige of medial	
15	Male with forcers with dorsal and ventral margins curving linearly to meet only at base (ventral view)	
15	[Nearctic]	
15'	Male with forceps with dorsal and ventral margins curving linearly to meet at one-third or more distance	
16	from base (ventral view) (Fig. 126). [Patearctic, Oriental]	
10	Sinaher species with caudal mainent 12 mm long in male, and 1.5 mm long in female	
16,	Brachycercus Derneri	
10	Larger species with caudal manient more than 15 mm long in male, and more than 2.5 mm long in female.	
17	Vestige of posterolateral projection 6 strongly curved medially. [western Palearctic] <i>Sparbarus europaeus</i>	

17'	Vestige of posterolateral projection 6 not curved medially. [eastern Palearctic,	Oriental] 18
18	Thoracic sterna stained with diffuse black. [Oriental]	Sparbarus capnicus
18'	Thoracic sterna pale, not stained with diffuse black. [eastern Palearctic]	Sparbarus japonicus

Known Eggs

1	Chorion without longitudinal costae (Fig. 567). [Nearctic]
1'	Chorion with longitudinal costae (Fig. 555). [Palearctic, Oriental, Nearctic, Neotropical]
2	Chorion punctate (Fig. 568)
2'	Chorion entirely smooth (Fig. 567)
3	Costa symmetrical in cross-section (Fig. 556), overlapping adjacent inter-costal grooves on both sides of
	costa (Fig. 555)
	Brachycercus harrisella, B. nitidus, B. ojibwe
3'	Costa asymmetrical in cross-section (Fig. 559), overlapping adjacent inter-costal grooves only on one side
	of costa (Fig. 558). [Palearctic, Oriental, Nearctic, Neotropical]
4	Polar cap tuberculate (Fig. 565). [Nearctic]
4'	Polar cap without tubercles (Fig. 562). [Palearctic, Oriental, Nearctic, Neotropical]7
5	Chorion with about seven costae in lateral half (Fig. 564)
5'	Chorion with more than 10 costae in lateral half (Fig. 561)
6	Chorion with about 11–15 costae in lateral half (Fig. 563)
6'	Chorion with about 17-20 costae in lateral half (Figs. 561, 565) Sparbarus nasutus, S. coushatta
7	Chorion with less than 10 costae in lateral half (Fig. 572). [Palearctic, Nearctic, Neotropical]
7'	Chorion with more than 10 costae in lateral half (Fig. 558). [Palearctic, Nearctic, Neotropical]
8	Chorion with less than five costae in lateral half (Figs. 566, 569, 574, 575, 580).
	[Palearctic] Cercobrachys minutus
	[Nearctic]
	[Neotropical] Latineosus colombianus
8'	Chorion with seven to eight costae in lateral half (Fig. 570). [Nearctic]9
9	Costa width subequal to, or greater than, one-half distance between two adjacent costae (Figs. 570, 572)
	Cercobrachys fox, C. lilliei
9'	Costa width less than one-half distance between two adjacent costae (Fig. 573).
10	Chorion with more than 20 costae in lateral half (Fig. 560). [Nearctic] Sparbarus choctaw
10'	Chorion with less than 20 costae in lateral half (Fig. 562). [Palearctic, Oriental, Nearctic] 11
11	Polar cap one-fourth or less total length of egg (Fig. 558). [western Palearctic, Nearctic] 12
11'	Polar cap one-third or more total length of egg (Fig. 562). [eastern Palearctic, Oriental] 13
12	Egg with numerous round granules among costae and on cap (Fig. 571). [Nearctic] Cercobrachys cree
12'	Egg surface without round granules (Fig. 558)
	[western Palearctic]
	[Nearctic]
13	About 16 costae in lateral half (Fig. 562). [eastern Palearctic] Sparbarus japonicus
13'	About 12 costae in lateral half (Figs. 576, 577)
	[eastern Palearctic]
	[Oriental]

Phylogeny and Phylogenetic Classification

One hundred and two morphological characters were used for cladistic analysis (Table 1). Outgroup comparisons were the primary source for hypothesizing polarities (e.g., Ross 1974). The Caeninae, particularly genera *Caenis* and *Callistellina* Sun and McCafferty served as the primary outgroup. Caenoidea, particularly Neoephemeridae, the sister family of Caenidae (Wang and McCafferty 1997), constituted the secondary outgroup, and all other Pannota constituted the tertiary outgroup. Character states distributed among thirty-two well-described species of Brachycercinae, as well as Caeninae species, *Caenis youngi* Roemhild and *Callistellina panda* Sun and McCafferty, were encoded and recorded in a character matrix (Table 2), and input into MacClade 4.01 and PAUP* 4.0b programs for phylogenetic analysis using Maximum Parsimony criterion. Thirty-two best trees (score of best trees found = 315) rooted with the outgroup taxa, *Caenis youngi* and *Callistellina panda*, were obtained by the Heuristic Search method. The disagreements among these trees were limited to the arrangements of certain species within *Sparbarus*, and of certain derived species within *Cercobrachys*. A 50% majority-rule consensus of the best trees with bootstrap support values is shown in Figure 582.

In the cladogram shown in Figure 582, a number of groupings of species are monophyletic within Brachycercinae. In order to derive a strict phylogenetic classification and one concurrently of practical use, sequencing conventions of Nelson (1973) were used in recognizing certain of the clades at the tribe and genus levels of classification. As such, six sequentially derived clades of Brachycercinae species are recognized as appropriate tribes, and nine infra-categories are recognized at the genus level (Fig. 583, Table 3). Besides the previously established genera *Caenoculis, Insulibrachys, Brachycercus*, and *Cercobrachys*, they also include the new genera *Sparbarus* and *Susperatus* to accommodate some new species and a number of species previously placed in *Brachycercus*, the new genera *Alloretochus* and *Latineosus* to accommodate some other new species and several species previously placed in *Cercobrachys*, and the new genus *Oriobrachys* to accommodate one additional new species. The hypothesized generic phylogeny within the subfamily is shown in Figure 583.

Five species could not be included in the initial cladistic analysis because material could not be secured. They are *Caenoculis nhahoensis*, *Sparbarus corniger*, *S. europaeus*, *S. gilliesi*, and *S. kabyliensis*. *Susperatus tonkawa* was also not included because its larval stage, where the preponderance of characters resides, remains unknown. These species are provisionally placed in the phylogenetic tree at hypothetical positions, which are based on previous descriptions indicating or suggesting that certain critical characteristics fit new generic concepts. Deductions regarding their likely phylogenetic relationships among other species are given in detail below. The resultant cladogram of all known Brachycercinae species (with tribe and genus concepts) is shown in Figure 584. A revised hierarchical classification of the subfamily is shown in Table 3, and followed in the account of taxa given above.

Integrity of Subfamily Brachycercinae

The cladistic analysis strongly supports the monophyletic status of Brachycercinae. Previously, certain synapomorphies for the Brachycercinae had been suggested in studies of Caenidae and Pannota. Malzacher's (1997) use of mainly larval characteristics, i.e., the presence of ocellar tubercles and upturned abdominal posterolateral projections proved to be sound apomorphic characteristics for Brachycercinae. The apomorphic two-segmented maxillary and labial palpi, although common among many unrelated mayfly clades, evidently were commonly derived in *Brachycercus, Cercobrachys* and *Insulibrachys*, but excluded *Caenoculis* in Malzacher's (1997) scheme. The single adult characteristic given by Malzacher (1997) for the subfamily was the presence of the strongly developed, functional male genitalia, and this was his sole basis for including the genera *Afrocercus* and *Madecocercus* in Brachycercinae. This characteristic, however, is untenable for defining Brachycercinae because it is found in at least six variously related genera in Caenidae, including *Brachycercus*.

ercus, Cercobrachys, Afrocercus, Madecocercus, Tasmanocoenis Lestage, and Wundacaenis Suter. Although Malzacher included Insulibrachys as having such genitalia, the male adult of that genus remains unknown. Malzacher's conclusion that segmented forceps without any function represent an ancestral state within Caenidae when compared with the outgroup, genus Potamanthellus Lestage (Neoephemeridae) is logical. However, derived genitalia appear to have evolved two or more times in Caenidae based on compelling evidence, for example, when the larva of Madecocercus (as Provonshaka) was discovered by McCafferty and Wang (1995), it was shown not to possess any of the unique larval apomorphies associated with Brachycercinae, just as is the case in other non-Brachycercinae with derived forceps.

McCafferty and Wang (2000) removed *Afrocercus* and *Madecocercus* from Brachycercinae based on the synapomorphies found on larvae of *Madecocercus* and the overall similarity between the two genera. The synapomorphies that supported their grouping of Brachycercinae (including *Brachycercus, Cercobrachys,* and *Insulibrachys*) were all larval characteristics. Besides the presence of ocellar tubercles, two-segmented labial palpi, and the upturned abdominal posterolateral projections, they added the presence of highly reduced forelegs and the robust last segment of the labial palpi. The latter characteristic is actually equivalent to the reduced segmentation of the labial palpi, in that segment 2 in such Brachycercinae apparently represents the fused segments 2 and 3 of Caeninae and some primitive Brachycercinae. Kluge (2004) added several other synapomorphies for this Brachycercinae concept (equivalent to his Brachycercus clade), which included slender legs with femora that are not widened medially, long, slightly curved claws without denticles, abdominal tergum 2 that lacks a median projection, and eggs with longitudinal crests (costae). Most of the above synapomorphies of Brachycercinae were generally adopted by Malzacher and Staniczek (2006).

None of the above studies placed the genus *Caenoculis* in the Brachycercinae. Malzacher (1997) and McCafferty and Wang (2000) suggested two apomorphies that were shared by *Caenoculis* and Caeninae genera: the presence of a narrow prosternum and the ventral submarginal microtrichia row of the operculate gills. Soldán (1986) had previously claimed that the forecoxae were nearly contiguous in *Caenoculis*; however, the present study has shown the prosternum of *Caenoculis* to be as widely separated as in other Brachycercinae. Also, the present study, utilizing SEMs, revealed that the ventral submarginal microtrichia row of the operculate gills is present in numerous Brachycercinae. Thus, the placement of *Caenoculis* in Caeninae is not effectively supported. Kluge (2004) and Malzacher and Staniczek (2006) proposed another synapomorphy for Caeninae, i.e., the metanotum of adults having a transverse ridge on the dorsal surface. This characteristic cannot be verified at present for *Caenoculis* due to lack of adult specimens.

The development of ocellar tubercles in the larval stage as the primary synapomorphy for Brachycercinae is well represented in *Caenoculis*. In addition, although the abdominal posterolateral projections of *Caenocu*lis were described as not being upturned by Soldán (1986), the present study shows they are indeed somewhat upturned in all specimens we examined. Because the three-segmented palpi state apparently represents a plesiomorphy it cannot be used to remove *Caenoculis* from Brachycercinae. This study has demonstrated synapomorphies in addition to the above two that clearly place *Caenoculis* in Brachycercinae. They include the following larval character states: anterior transverse rows of long setae present dorsal to the base of the mouthparts, a patch of long setae present ventrally posterior to the base of the glossae, a patch of long setae present ventrally on labial palp segment 1 (with reversion), shortened forelegs, vertically oriented forecoxae, anterior surface of the hindleg being anterior to the posterior surface, ventral setae of the forefemur being half or more the width of the forefemur, inner margin of the hindclaws lacking tooth-shaped denticles, abdominal posterolateral projection 5 length being 2.0 X or more basal width (with reversion), and posterolateral projection 7 being distinctly shorter than posterolateral projection 6. All the above characteristics are therefore assumed to be present on the hypothetical ancestor A (Fig. 583). The appearance of costae on the egg chorion may also represent a synapomorphy for the subfamily (with reversion); however, it is not clear yet since eggs of *Caenoculis* remain unknown. There are additional apomorphies of Brachycercinae present in primitive taxa that were reversed in some apotypic lineages, and they are significant in supporting the origin and integrity of the subfamily although they do not appear as consistent synapomorphies throughout. One species previously placed in *Caenoculis* (not the type of the genus) apparently does not possess the apomorphies required to place it in Brachycercinae. Thus, *Caenoculis dangi* was recombined with *Caenis* in this study (see previous discussion).

By incorporating *Caenoculis* in the Brachycercinae, two synapomorphies previously recognized for the hypothesized Brachycercinae + Madecocercinae clade may require re-evaluation. McCafferty and Wang (2000) considered the male forceps with longitudinal fold as a shared synapomorphy for the two subfamilies, although the grooved forceps in Brachycercinae are structurally different from those in Madecocercinae, which have a longitudinal ridge shaped process. Malzacher and Staniczek (2006) also recognized this synapomorphy, suggesting that the grooved forceps in Brachycercinae could be interpreted as a more apotypic stage of the ridged ones. The male subimago genitalia dissected from a last instar larva of C. acutalis showed forceps lacking of a longitudinal groove or fold. Such forceps, similar to those of male adult *Caenis*, may appear in the adult stage, although it is not certain if much additional developmental transformation will occur. In this case, the retention of relatively ancestral male genitalia in *Caenoculis* indicates that the ridged forceps of Madecocercinae are not homologous with grooved forceps in Brachycercinae, but evolved independently. Nevertheless, comprehensive studies on the adult stage of *Caenoculis* are needed for confirming the character states. The reduction of the maxillary palpi was another synapomorphy proposed for a Brachycercinae + Madecocercinae clade by Malzacher and Staniczek (2006), who suggested that the greatly reduced maxillary palpi of Madecocercinae was a further apotypic state of the two segmented palpi in Brachycercinae. However, the three-segment state of the maxillary palpi in *Caenoculis* suggests that the different reductions in Madecocercinae and certain Brachycercinae are independently evolved.

Evolution of Brachycercinae

Caenoculini Clade and the Origin of Brachycercinae

The tribe Caenoculini, consisting of single genus *Caenoculis*, is characteristically somewhat intermediate between Caeninae and other Brachycercinae. It shares a series of critical apomorphies with other Brachycercinae, while at the same time retaining certain plesiomorphies common to Caeninae. Besides the three-segmented maxillary and labial palpi and the male forceps that possibly lack longitudinal fold, symplesiomorphies of *Caenis* and *Caenoculis* also include, e.g., a pronotum strongly produced laterally in the anterior fourth to form a distinct angulate expansion and a well-developed posteromedial projection on the tergum 2. The retention of such plesiomorphies and lack of certain apomorphies found in more derived lineages of Brachycercinae make it clear that *Caenoculis* represents an ancestral branch of Brachycercinae. It is hypothesized that the ancestor species, ancestor A (Fig. 583), of all Brachycercinae was most similar to Cae*noculis*. In addition to the appearance of apomorphies and plesiomorphies described previously, one significantly derived complex of features for this ancestor involves the relatively setaceous condition of the larvae that typifies Brachycercinae. For example, the head possesses rows of long setae on the anterior margin; there are dense, long setae on the maxillary palpi, the labium, and the labial palpi; and the legs have well-developed series of setae that are longer and denser than those in Caeninae (Caenoculis bishopi larvae do not have hairlike setae on their body and legs that are as dense and long as in C. acutalis, instead the above areas are covered with dense, toad-stool shaped setae, which may be modified from the hairlike setae).

The origin of Brachycercinae can be viewed mainly as four phases of larval evolution: 1) the appearance of elevated ocelli as ocellar tubercles, 2) development of setation, 3) modification of leg orientation and movement, and 4) development of abdominal projections for gill protection. These changes are associated with the type of larval habitat being exploited by Brachycercinae, essentially life at the surface or subsurface of sand, sand-silt, or silt substrates. The respiratory organs requires extra protections from abrasive granules by, e.g., the developed and upturned posterolateral projections; long setae may offer some protection, cleaning ability, and filter-feeding adaptations; elevation of visual sense organs (ocellar tubercles, compound eyes)

may be related to remaining exposed while the head is partially buried in substrate; and long, adenticulate claws are typical of sand and silt dwellers (McCafferty 1991). The modification of legs and claws of Brachycercinae can be compared to that in some long-clawed sand dwellers among the Pisciforma mayflies; and the ocellar tubercle and gill basket development can be compared to convergences in two other distantly related psammophilous clades of Pannota [the Afrotropical family Machadorythidae and the Neotropical subfamily Coryphorinae, Leptohyphidae (see Jacobus and McCafferty 2006)] (McCafferty and Wang 2000). These characters, e. g., the various developmental levels of the gill basket, especially the orientation of the posterolateral projection 6 and the development of the posterior setae rows on abdominal terga 6–8 that apparently provide auxiliary protection to the posterior opening of the gill basket, may have a close relationship with particular larval habitat adaptation.

Although some or all species of *Caenoculis* in this study have various apomorphies, many of them are shared with at least some species of other genera, especially *Brachycercus*, which include, e.g., the presence of the ocellar tubercles that possess short setae distally, an occiput that is covered with some long setae, an abdominal tergum 1 that possesses a posteromedial projection, an abdominal tergum 2 that possesses a process anterior to the operculate gills, and operculate gills that possess a protruding edge at the posterolateral corner. Although it is possible that these characteristics were present in the original Brachycercinae, and became modified or reversed variously in apotypic lineages, deductions from the most likely cladogram under the Maximum Parsimony criteria suggest they are results of convergence in the two genera.

Given the above, the presence of a developed and cone-shaped posteromedial process on the abdominal tergum 1 and operculate gills that possess a protruding edge at the posterolateral corner are strong candidate as the synapomorphy for *Caenoculis*, for they not only are present in *C. acutalis* and *C. bishopi*, but also were recorded in the previous description of *C. nhahoensis* (Soldán 1986), although only simply referred as "medial teeth apparent" and "gill cover asymmetrical", respectively. Another candidate of synapomorphy is the presence of the long marginal setae on the posterolateral corner of operculate gills that are longer than those at the posteromedial corner. Unfortunately, this character state has only been confirmed for *C. acutalis* and *C. bishopi*, because the character was not recorded in the previous descriptions of *C. nhahoensis*.

Although specimens of *C. nhahoensis* were not examined in this study, it is considered to be in a more apotypic lineage together with *C. bishopi* within the genus (Fig. 584). Abdominal posterolateral projections 3 and 9 are absent in *C. bishopi*, which are also absent in *C. nhahoensis* according to Soldán (1986). Whereas in *C. acutalis*, both projections 3 and 9 are well developed, representing a relatively more plesiotypic state.

Sparbarini Clade

In Brachycercinae, a number of apomorphies are shared by non-*Caenoculis* lineages. The most significant include the presence of two-segmented maxillary and labial palpi, the absence of apparent lateral angulation on the pronotum, the absence of a medial process on the posterior margin of abdominal tergum 2, and an anterior margin of abdominal tergum 10 that is emarginate. Therefore, all above mentioned characteristics are presumed to be present in the hypothetical ancestor B (Fig. 583). In adults, another significant characteristic is the presence of longitudinal groove on male forceps that may also have evolved from this node. Evidence from the imago genitalia of *Caenoculis* is needed to prove this hypothesis as indicated above.

Sparbarini, being represented by single genus *Sparbarus*, is the first basally derived clade within the non-*Caenoculis* lineages. Significant apomorphies for *Sparbarus* involve particular reductions of body setae. Even though increased setation is a general evolutionary trend exhibited by Brachycercinae, subsequent reduction of setae associated with various parts of the body compared to the setation in plesiotypic genera of Brachycercinae occurred in certain lineages according to the cladistic results. These important events, which are mostly partial reversions, provided important information for cladistic analysis.

Sparbarus lost the patch of long, fine setae on the ventral surface of labial palp segment 1, which is present in all other Brachycercinae except a more derived genus, *Latineosus*. The absence of such long setae
in these two genera is apparently due to convergence. In the vast majority of *Sparbarus* species, reduction of setae also occurred on the distal segment of the maxillary palpi. As such, the inner margin of this segment has a row of stout setae only in the distal one-half or less, and the outer margin has only 10 or fewer long, fine setae apically. According to Kluge (1991), *Sparbarus europaeus*, which could not be included in the cladistic analysis, has instead a row of setae along the distal three-fourths of inner margin, and more than 15 long, fine setae on outer margin apically. Therefore, reductions of setation on the maxillary palpi apparently cannot be used as synapomorphies for the entire genus. Nevertheless, important information suggesting the possible ancestral nature of *S. europaeus* within the genus is provided. Another apomorphy common to all *Sparbarus* is the presence of marginal setae at the posteromedial corner of operculate gills that are significantly longer than those at the posterolateral corner. Such an evolutionary tendency is also found in more apotypical clades, i.e., descendents of the hypothetical ancestor E (Fig. 583), which appears to be a result of convergence. In all *Sparbarus* species, setae are reduced on the head capsule, ocellar tubercles, prosternal median ridge, and mesosternal anterior margin. On the legs, setae are reduced, e.g., on the posterior surface of foretibiae and the dorsal margin of hindtibiae. Setae on many other parts of the body are also relatively short and few, but appear to be symplesiomorphic with more ancestral genera.

In some *Sparbarus* species, the middle ocellar tubercle is as long as, or slightly shorter than, the lateral tubercles, as is the case in most of *Caenoculis, Insulibrachys, Brachycercus, Oriobrachys,* and *Susperatus*. In other *Sparbarus* species, the middle ocellar tubercle evolved in two directions, becoming either shorter than the lateral tubercles by at least one-third or becoming significantly longer than the lateral tubercles, providing some evidence of species groups within the genus. In most *Cercobrachys*, the middle ocellar tubercle also became shorter, reflecting another apparent convergence.

Specimens of S. corniger, S. europaeus, S. gilliesi, and S. kabyliensis could not be secured for the cladistics analysis. We here hypothesize their phylogenetic relationships among Sparbarus (Fig. 584) as follows. Sparbarus europaeus is likely a rather primitive species in the genus as discussed above. Sparbarus gilliesi larvae have a distinct diagnostic pedicel with dense, relatively long setae. This feature is characteristic of Caenoculis and Insulibrachys, suggesting another relatively ancestral position. Sparbarus gilliesi however is perhaps more derived than S. europaeus because of the apomorphic reduced setae on the maxillary palpi. Furthermore, S. capnicus and S. gilliesi are similar according to Soldán and Landa (1991), in that they share a middle ocellar tubercle that is distinctively shorter than the lateral ones. They are also found in the same geographic region (S. gilliesi from Sri Lanka, S. capnicus from southern China) and thus may represent sister species near the base of Sparbarus. Sparbarus corniger and S. kabyliensis larvae are morphologically similar to each other according to Soldán (1986) and Kluge (1991). These two species share the apomorphic well-developed abdominal posterolateral projection 2 and therefore are considered to be sister species here. Sparbarus *japonicus* and *S. tubulatus* larvae likely represent another clade because their larvae share a relatively elongate middle ocellar tubercle, relatively short forelegs, and slender hindfemora (states of the latter two characters are uncertain in the four species not included in the analysis). Because of lack of additional data for these species, a more comprehensive study of Palearctic Sparbarus species is needed.

Nearctic species of *Sparbarus* form a monophyletic subgroup as shown in all best MP trees, and supported by a Bootstrap value of 56% (Fig. 582). Evidential synapomorphies include the presence of compound eyes that are extended more anteriorly and are produced more dorsally, the relatively straight lateral margins of the occiput posterior to the compound eyes, and a distinct color pattern of one or two transverse black bands posterior to the lateral ocellar tubercles, and a broad, brown, medial stripe and pair of anterolateral maculae on the abdominal terga. (Similar modifications of the compound eyes of *Latineosus* are considered to be convergent.) A pair of sister groups are included in this lineage (Fig. 584). The first group includes S. *nasutus*, S. *lacustris*, and S. *choctaw*, which share a elongated middle ocellar tubercle, and a relatively well-developed lateral projection on the abdominal segment 2. The most apomorphic states of the above two characters are present in S. *nasutus*, and they suggest it is the most derived species among the three. *Sparbarus lacustris* and

S. choctaw can be treated as sister species because they share a relatively more anterior position of compound eyes, and longer marginal setae at the posteromedial corner of the operculate gills. The second group includes S. *coushatta*, *S. miccosukee*, and *S. maculatus*, which share a middle ocellar tubercle that is distinctively shorter than the lateral ones. Among these, *S. miccosukee* and *S. maculatus* comprise a more derived clade as evidenced by sharing a middle ocellar tubercle that is acutely pointed, and a pedicel that is 2.5 X or more the length of the scape.

Insulibrachini Clade

A hypothetical ancestor C is shown (Fig. 583) for the non-*Caenoculis*, non-*sparbarus* genera. The apomorphies gained by this ancestor and all descendant genera primarily involved the development of body setae, which included the setae tuft on the prosternal median ridge and setae rows on the foretarsus ventral margin and the hindtibia dorsal margin. Relatively long setae are present on the prosternum and ventral margin of foretarsi in *Caenoculis acutalis*. Such setae are also observed on the foretarsus in two *Sparbarus* species. Within the apotypical clades, one or more cases of reduction to various extents in above setae are found in *Brachycercus berneri*, *Alloretochus peruniacus*, *Cercobrachys petersorum*, and certain *Latineosus* species. These phenomena are interpreted as being subject to convergence and reversion, respectively.

Genus *Insulibrachys* represents the tribe Insulibrachini, and the first basally derived clade within the descendant lineages of the ancestor C. A number of autapomorphies characterize this genus, making it quite different from other Brachycercinae. The most significant include the long setae distally on the ocellar tubercles, the cylindrical ocellar tubercles, extremely dense setae on the antennal pedicel, an overall strongly convex lateral pronotal margin, produced lateral areas of the prosternal median ridge, and very long setae along the foretibia ventral margin and hindtibia dorsal margin. Setae on the ocellar tubercles and antennae are present in *Caenoculis*, but are fewer and shorter. Short setae are also present on the ocellar tubercles of *Brachycercus harrisella*, and are on the pedicels in *Brachycercus* species and *Sparbarus gilliesi*, but less dense. The other genera in the subfamily only have very few and short setae on the pedicel, and no apparent setae on ocelli, as in the Caeninae outgroups. Furthermore, *Insulibrachys* have two ancestral character states, i.e., the presence of a pronotum with a straight anterior margin and foretibiae that are distinctly longer than the foretarsi, which are shared with the Caeninae outgroups but not with any other Brachycercinae genera and thus can only be explained as evolutionary reversions.

Brachycercini Clade

A clade including *Brachycercus*, *Oriobrachys*, *Latineosus*, *Susperatus*, *Alloretochus*, and *Cercobrachys* represents a sister group to Insulibrachini. Shared apomorphies among these lineages mainly involved a prosternum that is produced ventrally in the medial region, and a mesosternum that possesses relatively long setae on the anterior margin. Such characteristics of the latter clades are therefore assumed to appear in the hypothetical ancestor D (Fig. 583). The medial development of the prosternum is observed in one of the outgroups, *Callistellina panda*, and the relatively long setae on the mesosternum are also present in *Caenoculis acutalis*, which must be due to convergence. Two cases of reversion involving the reduction of mesosternal setae are found in *Latineosus colombianus* and *L. cibola*. Another apomorphic feature that was possibly gained by the ancestor D is the marginally offset position of the ventral microtrichia rows of the operculate gills, which is shared by all species of *Brachycercus*. Such a characteristic, also observed in the outgroup *Caenis*, is likely to be subject to reversion. In genera *Caenoculis, Sparbarus*, and *Insulibrachys*, the ventral microtrichia rows are adjacent to the gill margin.

Brachycercini (genus *Brachycercus*) is a sister clade to the other descendants of ancestor D and a relatively apotypic position cladistically, despite some characteristics shared with *Caenoculis* as discussed above. Brachycercini synapomorphies include a pedicel with dense, relatively long setae, a pronotum with distinct angulate expansion on the lateral margin (a reversion), further shortened forelegs, the presence of a fingershaped process anterior to the operculate gill on the each side of the abdominal tergum 2, further elongated posterolateral projections, operculate gills with a produced edge at the posterolateral corner, and egg costae with a symmetric cross-sectional shape. Among these characteristics, a setaceous pedicel is present in *Caeno-culis acutalis, Insulibrachys*, and certain *Sparbarus* species; a pronotum with distinct lateral angulate expansion is observed in *Susperatus tuberculatus*, significantly shortened forelegs are present in most *Sparbarus* species; the presence of finger-shaped processes on the abdominal tergum 2 and operculate gills with a produced edge at the posterolateral corner are found in *Caenoculis*; and significantly elongated posterolateral projections are also present in several species of various genera within the subfamily. These instances are considered to be convergent.

Among the four known species, *B. harrisella* represents a basal lineage as exemplified by its possession of conical ventral processes on the mesosternum; whereas *B. ojibwe*, *B. nitidus*, and *B. berneri* form a separate clade evidenced by sharing a relatively long foreclaw and a low posteromedial process on abdominal tergum 1. *Brachycercus nitidus* and *B. berneri* are a pair of sister species supported by the presence of foreclaws that are even longer than those in *B. ojibwe*. *Brachycercus berneri* has the longest fore- and hindclaws among the four species. It also has setae on the ventral margin of foretibiae that are longer than those in all other congeners, suggesting a most apotypic position in the genus.

Latineosini Clade

Genera Oriobrachys, Latineosus, Susperatus, Alloretochus, and Cercobrachys shared synapomorphies which include the position of the compound eves that is relatively offset from the posterior margin of the head, an elongated maxillary palp segment 2, further elongated setae on the margin and surfaces of foretarsi and on the posteromedial margin of operculate gills, and the absence of ventral submarginal microtrichia, or in the case of Latineosus cayo, only in the posterior submarginal area of operculate gills. These derived characteristics are assumed to be present in the hypothetical common ancestor E (Fig. 583) of the above genera. The relatively anterior position of the compound eyes and a relatively long maxillary palp segment 2 are also present in certain Sparbarus species and are considered to be results of convergence. Relatively short maxillary palp segment 2 and short setae on foretarsi are observed in two Latineosus species, L. cibola and L. cayo; relatively short marginal setae at the posteromedial corner of operculate gills are also found in *Latineosus*, Susperatus, and several highly apotypic Cercobrachys species. Such instances apparently represent reversions. Another synapomorphy of this clade involves the reduction of egg costae, with certain reversions occurring in the derived species groups. Such reduction may have been present in ancestor E, but unfortunately that cannot be verified at present because the eggs of Oriobrachys remain unknown. Generally, there are relatively few plesiomorphies shared by the descendants of the ancestor E with the more plesiotypic genera *Caenoculis*, *Sparbarus*, and *Insulibrachys*, suggesting their relative apotypic status within the subfamily.

The two tribal clades Latineosini and Cercobrachini are descendants of ancestor E. Latineosini consists of two genera, *Oriobrachys* and *Latineosus*. The synapomorphies shared between them include a posterolateral projection 6 that is strongly curved medially, becoming nearly parallel with the posterior margin of the tergum 6, and operculate gills that have an only weakly developed Y-ridge without apparent long setae. These derived characteristics are assumed to appear in the hypothetical common ancestor F (Fig. 583) of the two genera. A posterolateral projection 6 that is very strongly curved medially or a weakly developed Y-ridge is observed in certain *Cercobrachys*; also, a Y-ridge lacking apparent long setae is found in several species of various genera. All such instances are likely due to convergence.

Oriobrachys represents a unique Oriental lineage separated at the base of the clade descended from hypothetical ancestor F (Fig. 583). The autapomorphic characteristic of this genus involves operculate gills with a well-developed sublateral longitudinal ridge and that are slanted ventrally lateral to that ridge. In all other genera of the subfamily, the only longitudinal ridge on operculate gills is the Y-ridge, and the operculate gills are not slanted ventrally near the lateral edge. The next sequentially derived clade includes *Latineosus* (*L. cayo, L. cibola* and *L. colombianus*) (Fig. 584). Synapomorphies shared by these three species are the presence of compound eyes moderately to strongly elevated, the presence of lateral margins of the occiput posterior to compound eyes that are approximately parallel with the long axis of the body, the middle ocellar tubercle that is distinctively shorter than lateral ones, and the absence of the patch of long, fine setae on the ventral surface of labial palp segment 1. A shortened middle ocellar tubercle is also found in *Alloretochus, Cercobrachys*, and some species in plesiomorphic *Caenoculis* and *Sparbarus*, but is likely due to convergence. The convergence with such characteristics found within *Sparbarus* was discussed above. Comparatively, *L. colombianus* is the most apotypic among the congeners, possessing autapomorphies such as the more anteriorly extended compound eyes and a significantly elongated and uniquely twisted posterolateral projection 6.

Cercobrachini Clade

The second clade among the descendants of ancestor E represents Cercobrachini, which is a sister tribe to Latineosini, and consists of three genera: *Susperatus*, *Alloretochus*, and *Cercobrachys*. A hypothetical common ancestor G shared by these three genera is shown in Figure 583. This more apotypic clade is supported by a series of synapomorphies, primarily involving the modification of shapes of mouthpart (i.e., the labrum and superlingua both have lateral margins strongly produced), the further shortening of the foretibia, and the overall development of body setae. The three genera share a generally setaceous condition, e.g., the inner margin of the maxillary palp segment 2 has more than 20 setae, the forefemora and tibiae have long setae on the ventral margins, and the posterior surface of the foretibiae has a distinct setae row consisting of 4–7 very long setae. In addition, the prosternum is strongly produced ventrally. A relatively shortened foretibia is found in *L. colombianus*, and long marginal setae on foretibiae are also found in *Insulibrachys needhami* and are evidently convergent. All above apomorphic characteristics are presumed to be present in the hypothetical ancestor G (Fig. 583).

A relatively basal branch among the descendents of the hypothetical ancestor G is *Susperatus*, represented by *S. prudens*, *S. tuberculatus*, and *S. tonkawa* (Fig. 584). *Susperatus prudens* and *S. tuberculatus* share a number of synapomorphies exclusively, including a much elongated and apically curved, ventrally directed middle ocellar tubercle (a curved middle ocellar tubercle is also present in *Caenoculis*, *Brachycercus*, and *Sparbarus*, but it is directed dorsally). The two species also have medial processes on the meso- and metasterna, and transverse ridges on at least abdominal sterna 1–4. The eggs of *S. prudens* are highly unusual for the subfamily because they lack costae. The only other species with such an egg is *S. tonkawa*, whose larval stage remains unknown. This is the basis for hypothesizing that *S. tonkawa* is also a member of this branch (Fig. 584). A number of plesiomorphies are retained in *Susperatus*. Certain symplesiomorphies or homoplasic similarities that are shared with *Brachycercus* (such as the presence of an unshortened middle ocellar tubercle and a long posterolateral projection 7) led Soldán (1986) to place the previously described species of *Susperatus* in *Brachycercus*.

Synapomorphies of *Alloretochus* and *Cercobrachys* include a middle ocellar tubercle that is shorter than the lateral ones by one-third or more, setae on the pro- and mesosternum that are relatively long (one case of general reduction of these setae is discussed below), and the posterolateral projection 6 that is distinctively curved medially. These characteristics are presumed to be present in hypothetical ancestor H (Fig. 583).

Alloretochus peruanicus, which was previously placed in *Cercobrachys* by Soldán (1986), is shown by the cladistics analysis to represent a most basal lineage among the descendents of the ancestor H, and thus a sister group to a more apotypic *Cercobrachys* clade. The autapomorphic characteristics of Alloretochus include a maxillary palp segment 2 that is considerably elongated and much more than twice the length of the segment 1, and posterior marginal setae of operculate gills that are as long as one-half length of the gill. These derived characteristics are not found among any other Brachycercinae lineages, with the exception that two *Sparbarus* species also convergently have long marginal setae on their operculate gills. As discussed above,

the derived condition of weakly developed Y-ridge on the operculate gills also present in *A. peruanicus*, which may serve as another apomorphy for this genus.

All *Cercobrachys* species constitute a relatively apotypic monophyletic group (Figs. 582–584). A number of synapomorphies are shared in this clade, including a subovate labrum with progressively produced lateral margins (one case of reversion is discussed below), a pronotum with the anterior margin strongly emarginate, foretarsi with long setae on the ventral margin and a well-ordered row of long setae on the dorsal margin, and hindclaws with minute nodules on the inner margin. Larvae of the genus are generally more setaceous. Setal development reflects a number of gradational stages represented in different species and species groups within the genus. Furthermore, reduction related convergence of *Cercobrachys* or of some *Cercobrachys* species and various subgroups or species of *Sparbarus* were discussed above under the *Sparbarus* clade.

Cercobrachys minutus, C. fox, and *C. etowah* represent the first three basal sequential lineages of the clade (Fig. 582). Some character states shared by them are transitional between their ancestor and more derived lineages of *Cercobrachys.* For example, they have somewhat robust galealaciniae, and their foretarsi have long and short setae in the ventral marginal setal row. In the more derived *Cercobrachys*, galealaciniae became even more robust, and the ventral marginal setal row of foretarsi is made up of only long setae. The order of sequence among these three species (Fig. 582) is based on the relative setal length on the ventral margin of foretarsi, and the relative reduction of setae along the posterior margins of abdominal terga 7 and 8. Also, *C. etowah* is hypothesized to be the most apotypical among the three because it shares more developed nodules on the hindclaws with other species of the genus.

Cercobrachys cree, *C. lilliei*, *C. petersorum*, *C. pomeiok* and *C. winnebago* form a monophyletic clade (Fig. 582), which is relatively more apotypic than *C. serpentis* in that they share apomorphic extremely shortened foretibiae. Within these species, *C. lilliei*, *C. petersorum*, *C. pomeiok* and *C. winnebago* make up a more apotypic clade (Fig. 582) supported by the synapomorphy involving posterolateral projections 6 that are not strongly curved medially (reversing to more plesiomorphic condition). Another possible synapomorphy for this clade is the presence of 70 or more long, fine, setae on the dorsal margin of the hindtibiae, although this characteristic cannot be verified in *C. petersorum* because the hindlegs of the examined specimen are lost.

Three significant reversions serve as the synapomorphies shared by the hypothesized most derived C. petersorum, C. pomeiok and C. winnebago (Fig. 582). These include lateral ocellar tubercles that are hemispherical and distinctly short, posterolateral projections 6 that are only slightly curved medially (straighter than in C. lilliei), and operculate gills that have only very short marginal setae at the posteromedial corner. Cercobrachys petersorum is hypothesized to be at the base of C. pomeiok-C. winnebago branch (Fig. 584). Being from Thailand, C. petersorum is the only apotypic Cercobrachys species that is found outside of North America. It shows a number of characteristics differing from the other two species, which suggest a relatively long period of separation between the Oriental and Nearctic lineages. We suggest that there are additional undiscovered species of Cercobrachys in the Orient. Comparatively, C. pomeiok and C. winnebago have a labrum with more protruding lateral margins, more stout maxillary galealaciniae, and a more protruding prosternum with denser and longer setae. In C. petersorum, the labrum is only moderately produced laterally, the maxillary galealaciniae are relatively slender, and the thoracic sternal setae are relatively short and sparse. Besides these reversions, C. petersorum also has some other autapomorphic characteristics, including relatively long foreclaws, and a posterolateral projection 7 that is distinctively longer than that of other Cercobrachys but similar to that of certain Susperatus and Sparbarus species. The sister species C. pomeiok and C. winnebago are the most apotypic species in *Cercobrachys*. They are morphologically similar and share close geographic distributions.

Biogeography Discussion

Certain general deductions concerning the biogeographic history of Brachycercinae can be made when the distributions of each genus and species of this subfamily are superimposed on the cladogram, as shown in Figure 584. Given the theorized Pangaean origin of the Caenidae, as outlined by Wang and McCafferty (2000), Brachycercinae clearly shows a Northern Hemisphere origin. By the time that Laurasia and Gondwanaland were substantially separated by the mid-Cretaceous, the subfamily had become established in Laurasia. The most primitive genus *Caenoculis* is presently confined to southeastern Asia. Such a distributional pattern suggests that it has resulted from an early dispersal event of the subfamily and is now refugial. The relatively primitive genera *Sparbarus* and *Brachycercus* are widely and almost exclusively distributed across the Northern Hemisphere. In *Sparbarus*, two species, however, are found in the Oriental Region, *S. capnicus* (southern China) and *S. gilliesi* (Sri Lanka), apparently resulting from dispersal from the Palearctic to the southern edge of Asia. Among the other species of *Sparbarus*, vicariance events are associated with the separation of a Nearctic clade and a Palearctic clade. Such vicariance is also apparent within *Brachycercus*, where a clade consisting of three species is found exclusively in the Nearctic. In addition, the monospecific *Insulibrachys*, which has become isolated in the Caribbean Islands, is related to these ancestral Holarctic clades as evidenced by its phylogenetic position (Fig. 582).

Two small yet relatively derived genera, Oriobrachys and Latineosus apparently involved dispersals and subsequent isolations. Oriobrachys was likely to have dispersed ancestrally from the Palearctic to the Orient, and Latineosus ancestrally from North America to Central and South America possibly involving an early Pliocene land bridge (see McCafferty 1998). More derived Brachycercinae, represented by ancestor G (Fig. 583) and its descendants including the genera Susperatus, Alloretochus, and Cercobrachys are essentially Nearctic. This phenomenon might be explained by Pleistocene glaciation events that presumably eliminated a considerably large portion of the subfamily in Palearctic region, while at the same time, the Nearctic element survived due to the north-south orientation of the mountain chains of North America that made periodic retreats to more amenable southern climates possible. Within this clade, there are several apparent instances of dispersal from the Nearctic to other regions. The Genus Alloretochus in Peru is another example of probable migration from North to South America, and may have occurred more recently than that of Latineosus. This fits the common model of Southern Pleistocene migration shown by McCafferty (1998), although he also showed that overall northern migration during the American Interchange was more prevalent in mayflies. Two species of Cercobrachys, C. minutus and C. petersorum, are found in northeastern Asia and southeastern Asia, respectively. Their dispersals into the Eastern Hemisphere may have occurred via the Arcto-Tertiary Forests connecting North America and Asia. Such trans-Beringia dispersals have also been proposed for other mayflies (McCafferty 1983, Peters 1988).

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Literature Cited

- Bae, Y.J. (1997) A Historical Review of Ephemeroptera Systematics in Northeast Asia. In: Landolt, P. & Sartori, M. (Eds), Ephemeroptera & Plecoptera: Biology-Ecology-Systematics. Mauron+Tinguely & Lachat SA, Fribourg, pp. 405–417.
- Barnard, K.H. (1932) South African mayflies (Ephemeroptera). *Transactions of the Royal Society of South Africa*, 20, 201–259.
- Belfiore, C., Girolamo, I.D. & Mancini, L. (1996) Reperti, Ephemeroptera, Caenidae. *Bollettino dell'Associazione Romana di Entomologia*, 50, 83–87.
- Bengtsson, S. (1917) Weitere Beiträge zur Kenntnis der nordischen Eintagsfliegen. Entomologisk Tidskrift, 38, 174–194.
- Berner, L. (1946) New species of Florida Mayflies (Ephemeroptera). Florida Entomologist, 28, 60-82.
- Berner, L. (1950) The Mayflies of Florida. University of Florida Press, Gainesville, 267 pp.
- Berner, L. & Pescador, M.L. (1988) *The Mayflies of Florida, Revised Edition*. University Presses of Florida, Gainesville, 415 pp.
- Bogoescu, C. (1958) *Ephemeroptera. Fauna Republicii Populare Romîne. Insecta VII (3)*, Editura Academiei Republicii Populare Romîne, Buccuresti, 187 pp.
- Brittain, J.E. (1972) Brachycercus harrisella Curtis (Ephemeroptera) new to Norway. Norsk Entomologiskl Tidsskrift, 19, 171.
- Burian, S.K., Novak, M.A., Bode, R.W. & Abele, L. (1997) New record of *Brachycercus maculatus* Berner (Ephemeroptera: Caenidae) from New York and a key to larvae of northeastern species. *The Great Lakes Entomologist*, 30, 85–88.
- Burks, B.D. (1953) The mayflies, or Ephemeroptera, of Illinois. *Bulletin of the Illinois Natural History Survey*, 26, 1–216.
- Burmeister, H. (1839) Ephemerina. In: Handbuch der Entomologie, II. Band 2. Enslin, Berlin, pp. 788-804.
- Campion, H. (1923) On the use of the generic name of *Brachycercus* in Plectoptera and Orthoptera. *Annals and Magazine of Natural History*, 11, 515–518.
- Curtis, J. (1834) Description of some nondescript British species of may-flies of anglers. *London and Edinburgh Philosophical Magazine and Journal of Science*, 4, 120–122.
- Demoulin, G. (1955) Les Brachycercidae Australiens. Le genre *Tasmanocoenis* Lestage. *Bulletin of Institut Royal des Sciences Naturelles de Belgique*, 31, 1–7.
- Eaton, A.E. (1868) On some points in the anatomy of the immature *Caenis macrura* Stephens. *Transactions of the Ento*mological Society of London, 1868, 279–282.
- Eaton, A.E. (1883–88) A revisional monograph of recent Ephemeridae or mayflies. *The Transactions of the Linnean Society of London. Second Series, Zoology*, 3, 1–352.
- Edmunds, G.F., Jr., Allen, R.K. & Peters, W.L. (1963) An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). *University of Utah Biological Series*, 13, 1–55.
- Edmunds, G.F., Jr., Jensen, S.L. & Berner, L. (1976) *The Mayflies of North and Central America*. University of Minnesota Press, Minneapolis, 330 pp.
- Edmunds, G.F., Jr. & McCafferty, W.P. (1988) The mayfly subimago. Annual Review of Entomology, 33, 509-529.
- Edmunds, G.F., Jr. & Waltz, R.D. (1996) Ephemeroptera. *In*: Merritt, R.W. & Cummins, K.W. (Eds), *An Introduction to the Aquatic Insects of North America. Third Edition.* Kendall/Hunt Publishing Company, Dubuque, pp. 126–163.
- Elouard, J.-M. & Sartori, M. (2001) A revision of the Malagasy genus *Madecocercus* Malzacher, 1995 (Ephemeroptera, Caenidae). *Bulletin de la Société Vaudoise des Sciences Naturelles*, 87, 229–235.
- Gose, K. (1980) The mayflies of Japan, No. 11. Kaiyou to Seibutsu, 2, 454–457. (in Japanese)

Grandi, M. (1951) Contributi allo studio degli Efemeroidei esotici. I. Un nuove Cenide africano: *Caenis hoggariensis* sp. n. *Bollettino dell'Istituto di Entomologia della Università di Bologna*, 18, 173–180.

Guenther, J.L. & McCafferty, W.P. (2005) Mayflies (Ephemeroptera) of the Great Plains. III: North Dakota. *Transactions of the American Entomological Society*, 131, 491–508.

Hagen, H. (1863) Neuroptera. Synopsis of the British Ephemeridae. Entomologist's Annual, 1863, 1–35.

Hennig, W. (1966) *Phylogenetic Systematics*. University of Illinois Press, Urbana, 263 pp.

Hwang, J.M. & Bae, Y.J. (1999) Systematics of the Caenidae (Ephemeroptera) in Korea. *Korean Journal of Entomology*, 29, 239–245.

- Ide, F.P. (1930) Contribution to the biology of Ontario mayflies with description of new species. *The Canadian Entomologist*, 62, 204–213, 218–231.
- Itämies, J., Kuusela, K. & Savolainen, E. (1979) *Brachycercus harisella* (Ephemeroptera, Caenidae) found in Finland. *Notulae Entomologicae*, 59, 89–90.
- Jacob, U. (1974) Zur Kenntnis zweier Oxycypha-Arten Hermann Burmeisters (Ephemeroptera: Caenidae). Reichenbachia, 15, 93–97.
- Jacobus, L.M. & McCafferty, W. P. (2006) Reevaluation of the phylogeny of the Ephemeroptera Infraorder Pannota (Furcatergalia), with adjustments to higher classification. *Transactions of the American Entomological Society*, 132, 81– 90.
- Kazlauskas, R. (1962) Novye dannye po faune podenok (Ephemeroptera) Pribaltiki. *Gidrobiologicheskie Issledovaniia*, 3, 147–150.
- Kimmins, D.E. (1971) A list of the type-specimens of Ephemeroptera in the British Museum (Natural History). *Bulletin of the British Museum (Natural History) Entomology*, 25, 309–324.

Klapálek, F. (1909) Ephemerida, Eintagsfliegen. Die Süsswasserfauna Deutschlands, 8, 1–32.

Kluge, N.J. (1991) Mayflies of the genus *Brachycercus* (Ephemeroptera, Caenidae) of the fauna USSR. *Vestnik Zoologii*, 1991 (2), 14–23. (in Russian)

- Kluge, N.J. (2004) *The Phylogenetic System of Ephemeroptera*. Kluwer Academic Publishers, Dortrecht/Boston/London, 442 pp.
- Koss, R.W. & Edmunds, G.F., Jr. (1974) Ephemeroptera eggs and their contribution to phylogenetic studies of the order. *Zoological Journal of the Linnean Society*, 55, 267–349.
- Leonard, J.W. &. Leonard, F.A. (1962) *Mayflies of Michigan Trout Streams*. Cranbrook Institute of Science, Bloomfield Hills, 139 pp.
- Lestage, J.-A. (1917) Contribution a l'étude des larvaes des Éphémères Paléarctiques. Annale de Biologie Lacustre, 8, 213–457.
- Lestage, J.-A. (1919) Contribution a l'étude des larvaes des Éphémères Paléarctiques (Serie 2). Annale de Biologie Lacustre, 9, 79–182.
- Lestage, J.-A. (1924) A propos du genre *Coenis* Steph. = *Brachycercus* Curt. (Ephemeroptera). *Annales de la Société Entomologique de Belgiqe*, 64, 61–62.
- Lestage, J.-A. (1931) Notes sur le premier Brachycercidien découvert dans la faune Australienne *Tasmanocaenis tonnoiri* sp. n. (Ephemeroptera) et remarques sur la famille des Brachycercidae. *Memoires de la Societe Entomologique de Belgique*, 23, 49–60.
- Lyman, F.E. (1944) Taxonomic notes on *Brachycercus lacustris* (Needham) (Ephemeroptera). *Entomological News*, 55, 3–4.
- Maddisson, D.R. & Maddisson, W.P. (2000) *MacClade 4: Analysis of Phylogeny and Character Evolution. Version 4.0.* Sinauer Associates, Sunderland.
- Malzacher, P. (1987) Eine neue Caeniden-Gattung Afrocercus gen. nov. und Bemerkungen zu Tasmanocaenis tillyardi (Insecta: Ephemeroptera). Stuttgarter Beiträge zur Naturkunde Serie A (Biologie), 407, 1–10.
- Malzacher, P. (1995) Caenidae from Madagascar (Insecta: Ephemeroptera). *Stuttgarter Beiträge zur Naturkunde Serie A* (*Biologie*), 530, 1–12.
- Malzacher, P. (1997) Relationships in the Caenidae (Insecta: Ephemeroptera). In: Landolt, P. & Sartori, M. (Eds), Ephemeroptera & Plecoptera: Biology-Ecology-Systematics. Mauron + Tinguely & Lachat SA, Fribourg, pp. 550– 553.
- Malzacher, P. & Staniczek, A. (2006) Revision of the Madecocercinae (Ephemeroptera: Caenidae). *Aquatic Insects*, 28, 165–193.
- McCafferty, W.P. (1981) Aquatic Entomology. Jones and Bartlett Publishers, Sudbury, Massachusetts, 448 pp.
- McCafferty, W.P. (1983) *Litobrancha* from the Oligocene in eastern Asia. *Annals of the Entomological Society of America*, 76, 205–208.
- McCafferty, W.P. (1991) Comparison of Old and New World *Acanthametropus* (Ephemeroptera: Acanthametropodidae) and other psammophilous mayflies. *Entomological News*, 102, 205–214.
- McCafferty, W.P. (2001a) The gentle quest: 200 years in search of North American mayflies. *In*: Domínguez, E. (Ed), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic/Plenum Publishers, New York, pp. 21–35.
- McCafferty, W.P. (2001b) Status of some historically unfamiliar American mayflies (Ephemeroptera). *Pan-Pacific Ento*mologist, 77, 210–218.
- McCafferty, W.P. & Edmunds, G.F., Jr. (1979) The higher classification of the Ephemeroptera and its evolutionary basis. *Annals of the Entomological Society of America*, 72, 5–12.

- McCafferty, W.P., Hubbard, T., Klubertanz, T.H., Randolph, R.P. & Birmingham, M. (2003) Mayflies (Ephemeroptera) of the Great Plains. II: Iowa. *Transactions of the American Entomological Society*, 129, 77–105.
- McCafferty, W.P. & de Moor, F.C. (1995) South African Ephemeroptera: problems and priorities. *In*: Corkum, L.D. & Ciborowski, J.J.H. (Eds), *Current Directions in Research on Ephemeroptera*. Canadian Scholars' Press, Toronto, pp. 463–476.
- McCafferty, W.P. & Wang, T.-Q. (1995) A new genus and species of Tricorythidae (Ephemeroptera: Pannota) from Madagascar. *Annales de Limnologie*, 31, 179–183.
- McCafferty, W.P. & Wang, T.-Q. (2000) Phylogenetic systematics of the major lineages of pannote mayflies (Ephemeroptera: Pannota). *Transactions of the American Entomological Society*, 126, 9–101.
- McDunnough, J. (1931) New North American Caeninae with notes (Ephemeroptera). *The Canadian Entomologist*, 63, 254–268.
- Molineri, C. & Goitia, E. (2006) Description of the adult stage of *Cercobrachys peruanicus* (Ephemeroptera: Caenidae). *Revista de la Sociedad Entomológica Argentina*, 65, 63–67.
- Navás, L. (1932) Insectos de la Argentina. Revista de la Academia de Ciencias de Zaragoza, 16, 87-120.
- Needham, J.G. (1908) Notes on the aquatic insects of Walnut Lake. With especial reference to a few species of considerable importance as fish food. *In*: Hankinson, T.L. *et al. Report of the Board of Geological Survey of Michigan for 1907 on the Biology of Walnut Lake*. Wynkoop Hallenbeck Crawford Company, State Printers, Lansing, Michigan, pp. 252–271.
- Needham, J.G. (1918) A new mayfly, *Caenis*, from Oneida Lake, New York. *New York State College of Forestry Technical Publication*, 9, 249–251.
- Nelson, G.J. (1973) Classification as an expression of phylogenetic relationships. Systematic Zoology, 22, 344–359.
- Peters, W.L. (1988) Origins of the North American Ephemeroptera fauna, especially the Leptophlebiidae. *Memoirs of the Entomological Society of Canada*, 144, 13–24.
- Pictet, F.J. (1843–1845) *Histoire naturelle générale et particulière des insectes névroptères, Famille des Éphémérines.* Chez J. Kessmann et Ab. Cherbuliz, Geneva, 300 pp.
- Provonsha, A.V. (1990) A revision of the genus *Caenis* in the North America (Ephemeroptera: Caenidae). *Transactions* of the American Entomological Society, 116, 801–884.
- Provonsha, A.V. & McCafferty, W. P. (1995) New brushlegged caenid mayflies from South Africa (Ephemeroptera: Caenidae). Aquatic Insects, 17, 241–251.
- Quan, Y.-T., Bae, Y.J., Jung, J.-C. & Lee, J.-W. (2002) Ephemeroptera fauna of Northeast China. *Insecta Koreana*, 19, 241–269.
- Ross, H.H. (1974) Biological Systematics. Addison-Wesley, Reading, Massachusetts, 345 pp.
- Schoenemund, E. (1930) Eintagsfliegen oder Ephemeroptera. Die Tierwelt Deutschlands und der angrenzenden Meeresteile, 19, 1–106.
- Soldán, T. (1986) A revision of the Caenidae with ocellar tubercles in the nymphal stage (Ephemeroptera). *Acta Universitatis Carolinae Biologica*, 1982–1984, 289–362.
- Soldán, T. & Landa, V. (1991) Two new species of Caenidae (Ephemeroptera) from Sri Lanka. In: Alba-Tercedor, J. & Sanchez-Ortega, A. (Eds), Overview and Strategies of Ephemeroptera and Plecoptera. Sandhill Crane Press, Gainesville, Florida, pp. 235–243.
- Spieth, H.T. (1933) The phylogeny of some mayfly genera. *Journal of the New York Entomological Society*, 41, 55–86, 327–391.
- Stephens, J.F. (1835) Family III. Ephemeridae, Leach. In: Illustration of British Entomology. Mandibulata, 6. Baldwin and Cradock, London, pp 54–70.
- Sun, L., Webb, J.M. & McCafferty, W.P. (2002) Cercobrachys cree: a new species (Ephemeroptera: Caenidae) from western North America. Entomological News, 113, 80–86.
- Swofford, D. (2002) PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland.
- Thew, T.B. (1960) Revision of the genera of the family Caenidae (Ephemeroptera). *Transactions of the American Entomological Society*, 86, 187–205.
- Tojo, K. (2001) Redescription of *Brachycercus japonicus* Gose, 1980 (Ephemeroptera, Caenidae). *Entomological Science*, 4, 369–377.
- Traver, J.R. (1932) Mayflies of North Carolina. Journal of the Elisha Mitchell Scientific Society, 47, 84-236.
- Traver, J.R. (1935) Part II. Systematics. *In*: Needham, J.G., Traver, J.R. & Hsu Y.-C. *The Biology of Mayflies*. Comstock Publishing Co., Ithaca, New York, pp. 237–739.
- Tshernova, O.A. (1928) Beitrag zur Kenntnis der Ephemeropteren des Oka-Bassins. Arbeiten der Biologischen Oka-Statition zu Murom, Russland, 5, 113–115.
- Tshernova, O.A. (1952) Mayflies (Ephemeroptera) of the Amur River Basin and adjacent waters and their role in the nutrition of Amur fishes. *Trudy Amurskoj Ichtiologicheskoy Ekspedicii*, 1945–1949, 230–360. (in Russian)
- Tshernova, O.A. (1964) Ephemeroptera. In: Opredelitel nasekomykh Evropeyskoy chasti SSSR. Nauka, Moskva, pp. 110-

136. (in Russian)

- Ulmer, G. (1920) Übersicht über die Gattungen der Ephemeropteren, nebst Bemerkungen über einzelne Arten. *Stettiner Entomologische Zeitung*, 81, 97–144.
- Ulmer, G. (1924) Ephemeropteren von den Sunda-Inseln und den Philippinen. Treubia, 6, 28-91.
- Walker, F. (1853) Ephemerinae. In: List of the Specimens of Neuropterous Insects in the Collection of the British Museum, Part III (Termitidae- Ephemeridae). British Museum, London, pp. 533–585.
- Wang, T.-Q. & McCafferty, W. P. (1997) Sister relationship of the Neoephemeridae and Caenidae (Ephemeroptera: Pannota). *Entomological News*, 108, 52–56.
- Westwood, J.O. (1840) The family Ephemeridae. In: An Introduction to the Modern Classification of Insects Found on Natural Habit and Corresponding Organization of the Different Families. Volume 2. Longman, Orme, Brown, Green, and Longmans, London, pp 24–34.
- Wiley, E.O. (1981) *Phylogenetics: the Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, Inc., New York, 439 pp.
- Yoon, I.B. & Bae, Y.J. (1988) I. Order Ephemeroptera. *In: Illustrated Encyclopedia of Fauna and Flora of Korea. Vol.* 30. Animals (Aquatic Insects). Ministry of Education, Korea, pp. 95–184. (in Korean)
- Zhou, C.-F., Sun, L. & McCafferty, W.P. (2003a) A New Species of *Caenoculis* Soldán from China (Ephemeroptera: Caenidae). *The Pan-Pacific Entomologist*, 79, 185–191.
- Zhou, C.-F., Sun, L. & McCafferty, W.P. (2003b) A New Species of *Brachycercus* Curtis (Ephemeroptera: Caenidae) from China. *Proceedings of the Entomological Society of Washington*, 106, 312–318.

TABLE 1. Encoded characters and character states used in the cladistic analysis of Brachycercinae (0 = plesiomorphic state; $0^* =$ only found in outgroup; characters refer to larval stage, unless noted differently; bracketed number denotes different directional states within the same character).

- 1. Female compound eye position. $(0)^{*}$ Posterior margin at, or very close to, posterior margin of head (Fig. 11). Posterior margin separated from posterior margin of head by about one-half diameter of eye (Fig. 24). (1)Posterior margin separated from posterior margin of head by two-thirds or more diameter of eye (Fig. 175). (2)2. Female compound eye relative anterior extension. (0)Anterior margin not extending anterior of base of middle ocellar tubercle (Fig. 175). Anterior margin extending anterior of base of middle ocellar tubercle (Fig. 313). (1)3. Compound eye elevation. (0)Not strongly produced dorsally (Fig. 246). Strongly produced dorsally (Fig. 139). (1)4. Occiput posterior shape. (0)Lateral margin posterior to compound eye distinctly curved inward (Fig. 214). Lateral margin posterior to compound eye approximately parallel with long axis of body (Fig. 175). (1)5. Occiput color pattern. (0)Transverse black band absent (Fig. 116). (1)Transverse black band(s) present posterior to lateral ocellar tubercle (Fig. 155). 6. Occiput setation. Occiput without, or with less than 10 long setae (Fig. 400). (0)Occiput covered with relatively dense, long setae (Fig. 31). (1)7. Head anterior transverse row of long setae dorsal to base of mouthparts. $(0)^{*}$ Absent (Fig. 1). Present (Fig. 31). (1)8. Clypeus transverse row of setae measuring in length one-half or more width of clypeus. $(0)^{*}$ Absent (Fig. 1). Present (Fig. 528). (1)9. Ocellar tubercles development. $(0)^{*}$ Not developed (Fig. 11). (1) Developed (Fig. 24). 10. Ocellar tubercles setation. Absent or not apparent (Fig. 400). (0)(1)With some short setae (shorter than one-half length of ocellar tubercle) (Fig. 31). With dense, long setae (1.5 X or more length of ocellar tubercle) (Fig. 198). (2)11. Lateral ocellar tubercles shape [1]. (0)Tapered-conical (Fig. 31). Cylindrical (Fig. 198). (1)12. Lateral ocellar tubercles shape [2].
- (0) Tapered-conical (Fig. 31).
- (1) Hemispherical (Fig. 544).

- 13. Middle ocellar tubercle length to basal width ratio in dorsal view.
- (0) Less than 1.5 (Fig. 155).
- (1) Near 2.0 (Fig. 260).
- (2) 2.5 or more (Fig. 175).
- 14. Middle ocellar tubercle length relative to lateral tubercle length [1].
- (0) Approximately subequal (Fig. 117).
- (1) One-half to two-thirds lateral tubercle (Fig. 156).
- 15. Middle ocellar tubercle length relative to lateral tubercle length [2].
- (0) Approximately subequal (Fig. 117).
- (1) 1.2–1.5 X lateral tubercle (Fig. 192).
- (2) 2.0 X or more lateral tubercle (Fig. 175).
- 16. Middle ocellar tubercle orientation in lateral view.
- (0) Straight or with apical portion curved dorsally (Figs. 31, 192).
- (1) With apical portion curved ventrally (Fig. 360).
- 17. Middle ocellar tubercle shape in dorsal view.
- (0) Hemispherical (Fig. 400).
- (1) Tapered-conical (Fig. 451).
- 18. Middle ocellar tubercle apex shape.
- (0) Not acutely pointed (Fig. 451).
- (1) Acutely pointed (Fig. 424).
- 19. Pedicel length to scape length ratio [1].
- (0) 1.8–2.2 (Fig. 236).
- (1) 2.5 or more (Fig. 157).
- 20. Pedicel length to scape length ratio [2].
- (0) 1.8–2.2 (Fig. 236).
- (1) 1.5 or less (Fig. 440).
- 21. Pedicel number of long setae (one-half or more length of pedicel).
- (0) About 10 or less (Fig. 147).
- (1) 15–25 (Fig. 32).
- (2) > 30 (Fig. 208).
- 22. Labrum shape.
- (0) Trapezoidal with lateral margin nearly straight (Fig. 158).
- (1) Subquadrate with lateral margin moderately produced (Fig. 376).
- (2) Subovate with lateral margin strongly convexly produced (Fig. 394).
- 23. Superlingua shape.
- (0) Subovate with lateral margin moderately and convexly produced (Fig. 159).
- (1) Subtriangulate with lateral margin strongly and convergently produced (Fig. 397).
- 24. Galealacinia length to width ratio [1].
- (0) 2.3–2.6 (Fig. 234).
- (1) 2.8 or more (Fig. 160).
- 25. Galealacinia length to width ratio [2].

(0)	2.3–2.6 (Fig. 234).
(1)	ca. 2.0 (Fig. 325).
(2)	ca 1.7 or less (Fig. 525)
(2)	ou. 1.7 of 1055 (116. 525).
26.	Maxillary palp segments number.
20.	Three (Fig. 20)
(0) (1)	Two (Fig. 29).
(1)	Two (Fig. 200).
27	Maxillary pain segment 2 length to segment 1 length ratio (when 2 segmented)
(0)	1.6 or loss (Fig. 222)
(0)	1.0 of ress (Fig. 222).
(1)	1.8–2.0 (Fig. 325).
(2)	ca. 2.3 (Fig. 380).
28	Maxillary palp segment 1 width to segment 2 width ratio (when 2 segmented)
20.	1.8 or more (Fig. 160)
(0)	1.5 17 (E. 202)
(1)	1.5-1.7 (Fig. 222).
(2)	1.3 or less (Fig. 502).
29.	Maxillary palp segment 2 (or $2 + 3$ if 3 segmented) inner margin location of stout setae
(0)	In distal two-thirds or more (Fig. 206)
(0)	In distal one half or loss (Fig. 145)
(1)	In distal one-mail of less (Fig. 145).
30	Maxillary nalp segment 2 (or $2 + 3$ if 3 segmented) inner margin number of stout setae
(0)	15 or fewer (Fig. 206)
(0)	> 20 (Fig. 422)
(1)	20 (11 <u>8</u> . 1 22).
31.	Maxillary palp terminal segment outer distal number of long, fine setae.
(0)	10 or fewer (Fig. 9).
(1)	15 or more (Fig. 29).
32.	Labium ventral long setae posterior to glossa base.
(0)*	Absent (Fig. 10).
(1)	Present (Fig. 381).
33.	Labial palp segments number.
(0)	Three (Fig. 30).
(1)	Two (Fig. 207).
24	Lakiel nelp account 1 control actation
J4.	Laurai parp segment i ventrai setation. With r_{2} or prove that a state $(T' = 10)$
(0)	with no apparent setae or very short setae (Fig. 10).
(1)	With long, fine setae (one-half or more length of palp segment 1) (Fig. 381).
35	Pronotum anterior margin shape
(0)	Straight (Fig. 24)
(0)	Subagin (11g. 24). Moderately emerginate (lateral length 1.5 V midling length) (Fig. 259)
(1)	Stearth and the second
(2)	Strongly emarginate (lateral length 2.0 X or more midline length) (Fig. 4/1).
36	Pronotum lateral margin convexity
(0)	Not forming distinctly convex ridge (Fig. 24)
(1)	Forming distinctly convex ridge (Fig. 108)
(1)	Forming distillency convex huge (Fig. 170).
37.	Pronotum lateral margin angulation.
(0)	With distinct angulate expansion (Fig. 24).
(1)	Without angulate expansion or not apparent (Fig. 545).
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- 38. Position of anterior pronotum lateral margin angulation.
- (0) Far forward, anterior one-fifth to one-fourth (Fig. 24).
- (1) Moderately forward, anterior two-fifths to one-half (Fig. 215).
- 39. Prosternum medial development.
- (0) Not produced ventrally (Fig. 31).
- (1) Slightly produced ventrally (Fig. 247).
- (2) Distinctly produced ventrally, forming cylindrical or conical process in lateral view (Fig. 361).
- 40. Prosternum median ridge lateral development.
- (0) Not produced ventrally (Fig. 247).
- (1) Produced ventrally, forming distinct ridge posterior to forecoxa in lateral view (Fig. 200).
- 41. Prosternum median ridge setation.
- (0) None apparent, or with scattered setae less than one-fourth length of forefemur (Fig. 140).
- (1) With tuft of setae as long as one-fourth to one-third length of forefemur (Fig. 361).
- (2) With tuft of setae as long as, or longer than, one-half length of forefemur (Fig. 546).
- 42. Mesosternum anterior margin setation.
- (0) None apparent, or with scattered setae less than one-fourth length of midfemur (Fig. 140).
- (1) Row of setae measuring less than one-fourth length of midfemur (Fig. 361).
- (2) Row of setae longer than one-fourth length of midfemur (Fig. 546).
- 43. Mesosternal basisternum medial process development.
- (0) Absent (Fig. 140).
- (1) Present (Fig. 361).
- 44. Mesosternal sternellum medial process development.
- (0) Absent (Fig. 546).
- (1) Indistinctly or moderately produced, with apex rounded or bluntly pointed (Fig. 228).
- (2) Strongly produced, with apex bluntly pointed or papillate (Fig. 361).
- 45. Metasternum medial process development.
- (0) Absent (Fig. 546).
- (1) Present (Fig. 361).

46. Forecoxa orientation.

- (0)* Horizontally (anterolaterally) directed (Fig. 13).
- (1) Vertically (ventrally) directed (Fig. 343).
- 47. Mid- and hindleg orientation.
- (0)* with ventral margins anteriorly or ventroanteriorly directed (Fig. 1).
- (1) with ventral margins ventrally or posteroventrally directed (Fig. 19).
- 48. Hindleg length to foreleg length ratio.
- (0) 1.1–1.2 (Figs. 2, 3).
- (1) 1.3–1.5 (Figs. 441, 442).
- (2) 1.6–1.8 (Figs. 148, 149).
- 49. Hindcoxa dorsal process development.
- (0) Present (Fig. 34).
- (1) Absent (Fig. 70).
- 50. Foretibia length to foretarsus length ratio.

- (0) > 1.3 (Fig. 2).
- (1) 0.9–1.1 (Fig. 237).
- (2) 0.7–0.8 (Fig. 441).
- (3) 0.6 or less (Fig. 495).
- 51. Hindfemur length to width ratio.
- $(0)^*$ 3.0 or less (Fig. 3).
- (1) 3.7–4.7 (Fig. 210).
- (2) 5.0 or more (Fig. 224).
- 52. Forefemur ventral margin setae length.
- (0)* Shorter than one-third width of forefemur (Fig. 2).
- (1) 0.5-1.5 X width of forefemur (Fig. 69).
- (2) 2.0 X or more width of forefemur (Fig. 412).
- 53. Forefemur ventral margin setal rows.
- (0) One row (Fig. 412).
- (1) Two rows (Fig. 461).
- 54. Foretibia ventral margin setae length.
- (0) All subequal to, or shorter than, width of foretibia (Fig. 33).
- (1) Some ca. 1.5 X width of foretibia (Fig. 223).
- (2) Some 2.0 X or more width of foretibia (Fig. 390).
- 55. Foretibia posterior surface setation.
- (0) All setae subequal to, or shorter than, width of foretibia (Fig. 288).
- (1) With some scattered setae measuring 1.5 X or more width of foretibia (Fig. 370).
- (2) With 4–7 long setae in distinct row, and subequal to, or longer than, foretibia (Fig. 535).
- 56. Foretarsus ventral margin setae length.
- (0) All short (subequal to, or shorter than, width of foretarsus) (Fig. 2).
- (1) Some 1.5–2.5 X width of foretarsus, intermixed with short setae (Fig. 478).
- (2) Some 3.0 X or more width of foretarsus, intermixed with short setae (Fig. 412).
- (3) All 3.0 X or more width of foretarsus (Fig. 535).
- 57. Foretarsus dorsal margin and anterior and posterior surfaces setation.
- (0) Scattered setae (Fig. 69).
- (1) Rowed on dorsal margin but not well ordered (Fig. 383).
- (2) Rowed on dorsal margin and well ordered (Fig. 535).
- 58. Foretarsus dorsal margin and anterior and posterior surfaces setae length.
- (0) Subequal to, or slightly longer than, width of foretarsus (Fig. 2).
- (1) About 2.0 X width of foretarsus (Fig. 209).
- (2) 2.5–3.0 X width of foretarsus (Fig. 223).
- (3) 4.0 X or more width of foretarsus (Fig. 412).
- 59. Hindfemur dorsal setae length.
- (0) Subequal to, or shorter than, 1.5 X width of hindfemur (Fig. 210).
- (1) Subequal to, or longer than, 2.0 X width of hindfemur (Fig. 536).
- 60. Hindtibia dorsal setae number.
- (0) about 20 or less (Fig. 224).
- (1) 30–50 (Fig. 442).
- (2) about 70 or more (Fig. 536).

- 61. Hindtibia dorsal setae length.
- (0) 2.0 X or less width of hindtibia (Fig. 70).
- (1) 2.5–4.0 X width of hindtibia (Fig. 536).
- (2) 5.0 X or more width of hindtibia (Fig. 210).
- 62. Hindclaw Shape.
- $(0)^*$ Strongly hooked in apical third (Fig. 3).
- (1) Slightly and evenly curved or nearly straight (Fig. 344).
- 63. Foretibia + foretarsus length to foreclaw length ratio.
- (0) > 4.0 (Fig. 3).
- (1) 3.4–3.9 (Fig. 518).
- (2) 2.8–3.3 (Fig. 338).
- (3) £ 2.7 (Fig. 223).
- 64. Hindclaw length to basal width ratio.
- (0) About 7.0 or less (Fig. 339).
- (1) About 10.0 (Fig. 224).
- 65. Hindclaws inner marginal topography.
- $(0)^*$ With row of triangulate denticles (Fig. 3).
- (1) Entirely without armature (Fig. 344).
- (2) Roughened with few indistinct, round, minute nodules (Fig. 453).
- (3) With series of distinct, round, minute nodules (Fig. 547).
- 66. Abdominal tergum 1 posteromedial process development.
- (0) Entirely absent (Fig. 14).
- (1) Low and indistinct.
- (2) Well developed and cone shaped (Fig. 35).
- 67. Abdominal tergum 2 posteromedial process development.
- (0) Present (Fig. 14).
- (1) Absent (Fig. 226).
- 68. Abdominal tergum 2 process anterior to operculate gill development.
- (0) Absent (Fig. 14).
- (1) Present (Fig. 24).
- 69. Abdominal tergum 6 posteromarginal setal row development.
- (0) Absent (Fig. 403).
- (1) Present (Fig. 473).
- 70. Abdominal tergum 7 posteromarginal setation.
- (0) With dense, long setae (Fig. 24).
- (1) With scattered setae, or one row of relatively sparse long or short setae (Fig. 455).
- (2) Without apparent setae (Fig. 532).
- 71. Abdominal tergum 8 posteromarginal setation.
- (0) With setal row or several scattered setae (Fig. 24).
- (1) Without apparent setae (Fig. 532).
- 72. Developed posterolateral projections orientation.
- (0)* Horizontal (flat) throughout (Fig. 1).

- (1) Slightly upturning (Fig. 211).
- (2) Strongly upturning (Fig. 415).
- 73. Abdominal segment 2 lateral development.
- (0) Not produced to form projection, if margin extended the process shorter than basal width, with apex nearly rounded or forming blunt right angle (Fig. 459).
- (1) Moderately produced to form triangulate projection, as long as basal width, but much shorter than projection 3, with apex forming acute angle (Fig. 137).
- (2) Strongly produced to form triangulate projection longer than basal width, and subequal to projection 3, with apex forming acute angle (Fig. 187).
- 74. Posterolateral projection 5 length to basal width ratio.
- (0)* 1.5 or less (Fig. 14).
- (1) 1.8–3.0 (Fig. 415).
- (2) 3.5 or more (Fig. 24).
- 75. Posterolateral projection 6 distal direction.
- (0) Not curved medially, or with only slight curve medially forming less than 20 degree angle with long axis of body (Fig. 345).
- (1) With medial curve, forming about 30–45 degree angle with long axis of body (Fig. 548).
- (2) With moderate medial curve, forming about 60 degree angle with long axis of body (Fig. 473).
- (3) With strong medial curve, becoming parallel or nearly so with posterior margin of tergum 6 (Fig. 454).
- 76. Posterolateral projection 6 distal twist.
- (0) Not twisted (Fig. 345).
- (1) Slightly twisted, with outer margin remaining posterior to inner margin in dorsal view (Figs. 283, 454).
- (2) Strongly twisted, with outer margin appearing anterior to inner margin in dorsal view (Figs. 318, 319).
- 77. Posterolateral projection 6 apex condition.
- (0) Pointed or bluntly pointed (Fig. 319).
- (1) Nearly rounded (Fig. 480).
- 78. Posterolateral projection 7 length relative to projection 6 length.
- (0)* Subequal to projection 6 (Fig. 1).
- (1) Three-fifths to three-fourths of projection 6 (Fig. 24).
- (2) About one-half of projection 6 (Fig. 218).
- (3) About one-third of projection 6 (Fig. 137).
- (4) Less than one-fifth of projection 6 or indistinct (Fig. 533).
- 79. Posterolateral projection 9 length relative to tergum 10 midlength.
- (0) Greater than three-fourths length of tergum 10 (Fig. 24).
- (1) One-half or less length of tergum 10 (Fig. 549).
- 80. Abdominal tergum 10 anterior margin shape.
- (0)* Straight or only slightly emarginate (Fig. 1).
- (1) Strongly emarginate (Fig. 549).
- 81. Abdominal sterna ventral topography.
- (0) Flat, not developed ventrally (Fig. 550).
- (1) Sterna 1-4 or more with ventrally produced transverse ridges (Fig. 330).
- 82. Operculate gill length to width ratio.
- (0) 1.3: 1 or less (Fig. 463).
- (1) Greater than 1.3: 1 (Fig. 385).

- 83. Operculate gill posterolateral corner development.
- (0) Not more developed than posteromedial corner (Fig. 463).
- (1) With produced edge, more protruding than posteromedial corner (Fig. 225).
- 84. Operculate gill sublateral longitudinal ridge development.
- (0) Absent; operculate gill generally flat (Fig. 496).
- (1) Present; operculate gill with area lateral to such ridge strongly folding ventrally (Fig. 283).
- 85. Operculate gill dorsal hairlike setation.
- (0) Absent or with only very short setae (Fig. 405).
- (1) With lateral region with some long setae one-fifth to one-third length of operculate gill (Fig. 444).
- 86. Operculate gill dorsal flat setation.
- (0) Absent (Fig. 405).
- (1) With lateral region covered with some short, flat setae (Fig. 300).
- 87. Operculate gill Y-ridge development.
- (0) Strongly developed, broad, robust (Fig. 186).
- (1) Weakly developed, narrow, indistinct (Fig. 405).
- 88. Y-ridge long setation.
- (0) At least several long setae along Y-ridge (Fig. 4).
- (1) No apparent long setae along Y-ridge (Fig. 405).
- 89. Operculate gill posterior margin longest setae length [1].
- (0) One-sixth to one-fourth length of gill (Fig. 4).
- (1) One-third to two-fifths length of gill (Fig. 444).
- (2) One-half length of gill (Fig. 385).
- 90. Operculate gill posterior margin longest setae length [2].
- (0) One-sixth to one-fourth of length of gill (Fig. 4).
- (1) Less than one-sixth length of gill (Fig. 537).
- 91. Operculate gill posteromedial corner margin setae length.
- (0) Not distinctly longer than posterolateral corner setae (Fig. 4).
- (1) 1.3–1.5 X length of posterolateral corner setae (Fig. 312).
- (2) 1.6–1.8 X length of posterolateral corner setae (Fig. 73).
- (3) 2.0 X or more length of posterolateral corner setae (Fig. 463).
- 92. Operculate gill posterolateral corner marginal setae length.
- (0) One-sixth to one-fourth length of gill and not longer than posteromedial corner setae (Fig. 4).
- (1) More than one-fourth length of gill and longer than posteromedial corner setae (Fig. 37).
- 93. Operculate gill ventral submarginal microtrichia presence.
- (0) Present on lateral submarginal area and present or absent on posterior submarginal area (Fig. 15).
- (1) Present exclusively on posterior submarginal area (Fig. 291).
- (2) Absent (Fig. 428).
- 94. Operculate gill ventral submarginal microtrichia type.
- (0) Palmate microtrichiae absent; most microtrichiae simple, hairlike (Fig. 151).
- (1) Palmate microtrichiae present (Fig. 39).
- 95. Operculate gill ventral submarginal microtrichia row development.

- (0) In multiple rows (Fig. 39).
- (1) In single row (Fig. 16).
- 96. Operculate gill ventral submarginal microtrichia row(s) position.
- (0) Offset from lateral margin (Fig. 15).
- (1) Adjacent to lateral margin (Fig. 38).
- 97. Forceps structure in male adults.
- (0) Without longitudinal groove (fold) (Fig. 41).
- (1) With longitudinal groove (fold) (Fig. 244).
- 98. Egg chorion costa development.
- (0) Not present (Fig. 18).
- (1) Present (Fig. 555).
- 99. Costae number in lateral half [1].
- (0) 9–20 (Fig. 555).
- (1) 23 or more (Fig. 560).
- 100. Costae number in lateral half [2].
- (0) 9–20 (Fig. 555).
- (1) 6–8 (Fig. 570).
- (2) 3–4 (Fig. 575).
- 101. Costae cross-sectional shape.
- (0) Asymmetric (costa overlapping adjacent inter-costal grooves only on one side of costa) (Figs. 558, 559).
- (1) Symmetrical (overlapping adjacent inter-costal grooves on both sides of costa) (Figs. 555, 556).
- 102. Egg polar cap tubercles presence.
- (0) Without tubercles (Fig. 555).
- (1) With tubercles (Fig. 563).

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Character number	Character state	Species	Caenis youngi	Callistellina panda	acutalis	berneri	bishopi	capnicus	cayo	choctaw	cibola	colombianus	coushatta	стее	etowah	fox	harrisella	japonica	lacustris	lilliei	maculatus	mahakam	miccosukee	minutus	nasutus	needhami	nitidus	ojibwe	peruanicus	petersorum	pomeiok	prudens	serpentis	tuberculatus	tubulatus	winnebago
	1		0	0	1	1	1	1	2	2	2	2	2	2	2	2	1	1	2	2	2		2	2	1	1	1	1	2		2	2	2	2	1	2
	2		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0		0	0	0	0	0	0
	3		0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0		0	0	0	0	0	0
	4		0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
	5		0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
	6		0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
	7		0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1
	8		0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1
	9		0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	10		N/A	N/A	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0		0	0	0	0	0	0
	11		N/A	N/A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	N/A	0	0	0	0	N/A
	12		N/A	N/A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	N/A	0	0	0	1	1	0	0	0	0	1
	13		N/A	N/A	0	0	0	0	0	1	0	0	0	0	0	0	1	2	1	0	0	0	0	0	2	0	0	1	0	0	0	2	0	2	2	0
	14		N/A	N/A	0	0	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	0	1	1	N/A	0	0	0	1	1	1	0	1	0	N/A	· 1
	15		N/A	N/A	0	0	N/A	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A	N/A	0	0	0	N/A	N/A	0	N/A	N/A	2	0	0	0	N/A	N/A	N/A	0	N/A	0	1	N/A
	16		N/A	N/A	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
	17		N/A	N/A	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	N/A	1	1	1	0	0	1	1	1	1	0
	18		N/A	N/A	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	19		0	1	0	0	0	0	0	0	0	N/A	0	N/A	N/A	N/A	0	0	0	N/A	1	0	1	N/A	0	0	0	0	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A
	20		0	N/A	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	1	N/A	0	N/A	1	0	0	0	0	1	N/A	1	1	1	1	0	1
	21		0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	1	1	0	N/A	0	0	0	0	0	0
	22		0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	2	0	0	0	2	0	0	0	0	1	1	2	1	2	1	0	2
	23		0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	1
	24		0	1	1	1	1	1	0	1	1	N/A	1	N/A	0	0	0	1	1	N/A	1	0	1	0	0	1	1	0	0	N/A	N/A	0	N/A	0	1	N/A
	25		0	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	1	N/A	2	0	0	0	N/A	N/A	2	N/A	0	N/A	0	0	N/A	N/A	0	0	1	2	0	2	0	N/A	. 2
	26		0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	27		N/A	N/A	N/A	0	N/A	1	0	0	0	1	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	2	1	1	1	1	1	0	1
	28		N/A	N/A	N/A	1	N/A	1	1	0	1	1	0	2	2	2	1	0	0	2	0	2	0	2	0	2	1	1	2	2	2	1	2	2	0	2
	29		0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0
	30		0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	1	1	0	1
_	31		0	0	1	1	1	0	1	0	1	1	0	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1
_	32		0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	33		0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	34		0	0	1	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1

TABLE 2. Matrix of character states of 32 species of Brachycercinae, using *Caenis youngi* Roemhild and *Callistellina panda* Sun and McCafferty as outgroups when possible (N/A = not applicable).

Character number	Character state	Species	Caenis youngi	Callistellina panda	acutalis	berneri	bishopi	capnicus	cayo	choctaw	cibola	colombianus	coushatta	cree	etowah	fox	harrisella	japonica	lacustris	lilliei	maculatus	mahakam	miccosukee	minutus	nasutus	needhami	nitidus	ojibwe	peruanicus	petersorum	pomeiok	prudens	serpentis	tuberculatus	tubulatus	winnebago
	35		0	0	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1	2	1	1	1	2	1	0	1	1	1	2	2	1	2	1	1	2
	36		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	37		0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	1
	38		0	0	0	1	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	1	1	N/A	N/A	N/A	N/A	N/A	1	N/A	N/A
	39		0	1	0	1	0	0	1	0	1	1	0	2	2	2	2	0	0	2	0	1	0	2	0	0	1	1	2	1	2	2	2	2	0	2
	40		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	41		0	0	1	1	0	0	0	0	1	1	1	2	2	2	1	0	0	2	1	1	0	2	0	1	1	1	2	1	2	1	2	1	0	2
	42		0	0	1	1	0	0	1	0	0	0	0	2	2	2	1	0	0	2	0	1	0	2	0	0	1	1	2	1	2	1	2	1	0	2
	43		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
	44		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0
	45		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
	46		0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	47		0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	48		0	1	0	2	1	1	1	2	1	1	2	1	1	1	2	2	2	1	1	0	1	1	2	1	2	2	1	N/A	0	1	1	1	2	1
	49		0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	50		0	1	1	1	1	1	1	1	1	2	1	3	2	2	1	1	1	3	1	1	1	2	1	0	1	1	2	3	3	2	2	2	1	3
	51		0	0	1	2	0	1	2	2	1	2	1	1	2	1	2	2	2	1	2	1	2	1	2	1	2	2	2	N/A	1	2	1	1	2	1
	52		0	0	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1	2	1	1	1	2	1	1	1	1	2	2	2	2	2	2		2
	53		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
	54		0	0	1	1	0	0	0	0	0	1	0	2	2	2	1	0	0	2	0	1	0	2	0	2 1	1	1	2	2	2	2	2	2	0	2
	55		0	0	1	1	0	0	0	0	0	1	0	2	2	2 1	1	0	0	2	0	1	0	2 1	0	1	1	1	2	2	2	2	2	2	0	2
	57		0	0	0	1	0	0	0	0	0	0	0	2	2	1	1	0	0	3 2	0	0	0	1 2	0	0	1	1	1	2	2	1	2	1	0	2
	58		0	0	0	1 2	0	0	2	1	1	3	1	2	∠ ۲	2	1	0	1	∠ 3	1	3	1	∠ 3	1	1	1 2	1 2	1	2	2	1	2	1	0	2
	59		0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	1	N/A	1	1	0	1	0	1
	60		0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	2	0	1	0	1	0	1	1	1	0	N/A	2	1	1	1	0	2
-	61		0	0	0	1	0	0	1	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	2	1	1	1	N/A	1	1	1	1	1	1
-	62		0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
\vdash	63		0	0	2	3	2	2	2	2	1	1	3	0	1	1	0	1	3	0	2	1	3	0	2	0	1	2	1	2	0	0	1	1	0	1
	64		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	65		0	0	1	1	1	1	1	1	1	1	1	3	3	2	1	1	1	3	1	1	1	2	1	1	1	1	1	N/A	3	1	3	1	1	3
F	66		0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
	67		0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	68		0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0

Character number	Character state	Species	Caenis youngi	Callistellina panda	acutalis	berneri	bishopi	capnicus	cayo	choctaw	cibola	colombianus	coushatta	cree	etowah	fox	harrisella	japonica	lacustris	lilliei	maculatus	mahakam	miccosukee	minutus	nasutus	needhami	nitidus	ojibwe	peruanicus	petersorum	pomeiok	prudens	serpentis	tuberculatus	tubulatus	winnebago
	69		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1
	70		0	0	0	0	0	0	1	0	1	1	0	2	2	1	0	0	0	2	0	2	0	0	0	0	0	0	1	1	2	0	2	0	0	2
	71		0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
	72		0	0	1	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2
	73		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	0
	74		0	0	1	2	2	1	1	1	1	2	1	1	1	1	2	1	1	1	2	1	1	2	1	1	2	2	2	1	0	1	1	1	1	1
	75		0	0	0	0	0	0	3	0	3	3	0	3	3	3	0	0	0	2	0	3	0	1	0	0	0	0	1	1	1	0	3	0	0	1
	76		0	0	0	0	0	0	1	0	1	2	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	0	1	0	0	1
	77		0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0
	78		0	0	1	2	4	2	4	1	4	4	3	4	4	4	2	1	2	4	3	4	2	4	1	1	3	2	4	2	4	2	4	1	1	4
	79		0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
	80		0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
	01		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	1	0	0
	92		0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0		0	0
	84		0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
	85		0	0	1	1	1	1	0	0	1	1	0	0	0	0	1	1	0	0	1	1	1	1	0	1	1	1	0	0	0	1	0	1	1	0
	86		0	0	1	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
	87		0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1
	88		0	1	0	0	1	0	1	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	1	0	0	1
	89		0	N/A	1	1	0	2	1	0	1	1	1	1	1	1	1	1	1	1	1	0	2	1	1	1	1	1	2	N/A	N/A	1	1	1	0	N/A
	90		0	1	N/A	N/A	0	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A	N/A	N/A	N/A	N/A	N/A	N/A	1	1	N/A	N/A	N/A	0	1
	91		0	0	0	0	0	2	3	2	1	3	2	3	3	3	0	2	2	3	1	3	2	3	1	0	0	0	3	0	0	1	3	1	2	0
	92		0	N/A	1	0	1	0	N/A	0	0	0	0	0	0	0	0	0	0	0	0	N/A	0	0	0	0	0	0	0	N/A	N/A	0	0	0	0	N/A
	93		0	0	0	0	0	0	1	0	2	2	0	2	2	2	0	0	0	2	0	2	0	2	0	0	0	0	2	2	2	2	2	2	0	2
	94		1	1	1	0	1	0	0	0	N/A	N/A	0	N/A	N/A	N/A	0	0	0	N/A	0	N/A	0	N/A	0	0	0	0	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A
	95		1	0	0	0	0	0	0	0	N/A	N/A	0	N/A	N/A	N/A	0	0	0	N/A	0	N/A	0	N/A	0	0	0	0	N/A	N/A	N/A	N/A	N/A	N/A	0	N/A
	96		0	0	1	0	1	1	N/A	1	N/A	N/A	1	N/A	N/A	N/A	0	1	1	N/A	1	N/A	1	N/A	1	1	0	0	N/A	N/A	N/A	N/A	N/A	N/A	1	N/A
	97		0		0	1		1		1	1	1	1	1	1	1	1	1	1	1	1		1	1	1		1	1	1			1	1	1	1	1
	98		0					1		1		1	1	1	1	1	1	1	1	1	1		1	1	1			1			1	0	1			1
	99		N/A					0		1		N/A	0	0	N/A	N/A	0	0	0	N/A	0		N/A	N/A	0			0			N/A	N/A	N/A			N/A
	100)	N/A					0		N/A		2	0	0	2	1	0	0	0	1	0		1	2	0			0			2	N/A	1			2
	101	1	N/A					0		0		0	0	0	0	0	1	0	0	0	0		0	0	0			1			0	N/A	0			0
	102	2	0					0		0		0	1	0	0	0	0	0	0	0	1		1	0	1			0			0	0	0			0

TABLE 3. Revised hierarchical phylogenetic classification of Brachycercinae genera and species.

Tribe Caenoculini

Genus Caenoculis Caenoculis acutalis Caenoculis bishopi Caenoculis nhahoensis

Tribe Sparbarini

Genus Sparbarus

Sparbarus europaeus Sparbarus capnicus Sparbarus gilliesi Sparbarus tubulatus Sparbarus japonicus Sparbarus corniger Sparbarus kabyliensis Sparbarus nasutus Sparbarus nasutus Sparbarus choctaw Sparbarus lacustris Sparbarus coushatta Sparbarus miccosukee Sparbarus maculates

Tribe Insulibrachini

Genus Insulibrachys Insulibrachys needhami

Tribe Brachycercini

Genus Brachycercus Brachycercus harrisella Brachycercus ojibwe Brachycercus nitidus Brachycercus berneri

Tribe Latineosini

Genus Oriobrachys Oriobrachys mahakam

Genus Latineosus Latineosus colombianus Latineosus cibola Latineosus cayo

Tribe Cercobrachini

Genus Susperatus Susperatus tuberculatus Susperatus prudens Susperatus tonkawa

Genus Alloretochus Alloretochus peruanicus

Genus Cercobrachys

Cercobrachys minutus Cercobrachys fox Cercobrachys etowah Cercobrachys serpentis Cercobrachys cree Cercobrachys lilliei Cercobrachys petersorum Cercobrachys winnebago Cercobrachys pomeiok



FIGURES 1–4. Caenis youngi, larva.

- 1. Body plan (dorsolateral view).
- 2. Foreleg.
- 3. Hindleg.
- 4. Operculate gill.



FIGURES 5–10. Caenis youngi, larva.

- 5. Labrum.
- 6. Angulate mandible.
- 7. Planate mandible.
- 8. Hypopharynx.
- 9. Maxilla.
- 10. Labium.





- 11. Head.
- 12. Pronotum.
- 13. Thoracic sterna.
- 14. Abdominal terga 2–6 (left half).





- 15. Operculate gill (ventral).
- 16. Ventral microtrichia row of operculate gill.
- 17. Abdominal terga 7 and 8.
- 18. Egg.



FIGURES 19-23. Brachycercinae, larval characters.

- 19. Sparbarus nasutus body plan (dorsolateral view).
- 20. Left foreleg model in live position.
- 21. Left hindleg model in live position.
- 22. Example of left foreleg drawing in this study (Cercobrachys winnebago).
- 23. Example of left hindleg drawing in this study (Cercobrachys winnebago).



FIGURE 24. Caenoculis acutalis, larva, habitus.





- 25. Labrum.
- 26. Angulate mandible.
- 27. Planate mandible.
- 28. Hypopharynx.
- 29. Maxilla.
- 30. Labium.



FIGURES 31–37. Caenoculis acutalis, larva.

- 31. Head and pronotum (lateral view, without mouthparts).
- 32. Antenna.
- 33. Foreleg.
- 34. Hindleg.
- 35. Abdominal segments 1–3 (lateral).
- 36. Posterior margin of sternum 9.
- 37. Operculate gill.



FIGURES 38–41. Caenoculis acutalis, larva.

- 38. Operculate gill (ventral).
- 39. Ventral microtrichia row of operculate gill.
- 40. Genitalia dissected from mature larva (ventral).
- 41. Forceps dissected from mature larva (ventral).



FIGURES 42–46. Caenoculis bishopi, larva.

- 42. Habitus.
- 43. Toadstool-shaped setae on wingpad.
- 44. Head and pronotum (dorsolateral view).
- 45. Abdominal segments 1–2 (lateral).
- 46. Operculate gill.



FIGURES 47–53. Caenoculis bishopi, larva.

- 47. Labrum.
- 48. Maxilla.
- 49. Labial palp.
- 50. Foreleg.
- 51. Hindleg.
- 52. Posterolateral projections (dorsal view).
- 53. Sternum 9.



FIGURES 54-60. Caenoculis nhahoensis, larva (from Soldán 1986).

- 54. Antenna.
- 55. Labrum.
- 56. Angulate mandible.
- 57. Maxillary palp.
- 58. Labial palp segments 2–3.
- 59. Midleg.
- 60. Operculate gill.


FIGURES 61–67. Sparbarus capnicus, larva.

- 61. Habitus.
- 62. Head capsule (lateral view).
- 63. Antenna.
- 64. Labrum.
- 65. Hypopharynx.
- 66. Maxilla.
- 67. Labial palp.



FIGURES 68–73. Sparbarus capnicus, larva.

- 68. Pronotum (left half, dorsolateral view).
- 69. Foreleg.
- 70. Hindleg.
- 71. Posterolateral projections 2-8 (ventrolateral view).
- 72. Posterior margin of sternum 9 (ventral).
- 73. Operculate gill.



FIGURES 74–77. Sparbarus capnicus, male adult.

- 74. Habitus.
- 75. Foreleg.
- 76. Forewing.
- 77. Genitalia (ventral).





FIGURES 78–84. Sparbarus choctaw, larva.

- 78. Habitus.
- 79. Head and pronotum (dorsolateral view).
- 80. Antenna.
- 81. Labrum.
- 82. Hypopharynx.
- 83. Maxilla.
- 84. Labial palp.





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- 85. Larva, head and pronotum.
- 86. Larva, head (lateral view).
- 87. Larva, antenna.
- 88. Larva, labrum.
- 89. Larva, maxilla.
- 90. Larva, abdomen.
- 91. Larva, posterolateral projections (lateral view).
- 92. Adult, head.
- 93. Adult, head (lateral view).

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FIGURES 94–100. Sparbarus coushatta, larva.

- 94. Habitus.
- 95. Head and pronotum (dorsolateral view).
- 96. Antenna.
- 97. Labrum.
- 98. Hypopharynx.
- 99. Maxilla.
- 100. Labial palp.



FIGURES 101–107. Sparbarus europaeus, larva and adult (from Kluge 1991).

- 101, 102. Larva, head and pronotum.
- 103. Larva, maxilla.
- 104. Larva, posterolateral projections (lateral view).
- 105. Larva, Operculate gill.
- 106. Adult, head.
- 107. Adult, male genitalia.



FIGURES 108–115. Sparbarus gilliesi, larva (from Soldán and Landa 1991).

- 108. Antennal scape and pedicel.
- 109. Labrum.
- 110. Mandibular incisors.
- 111. Hypopharynx.
- 112. Maxillary palp segment 2.
- 113. Labial palp segment 2.
- 114. Foreclaw.
- 115. Operculate gill.



FIGURES 116–122. Sparbarus japonicus, larva.

- 116. Habitus.
- 117. Head and pronotum (dorsolateral view).
- 118. Antenna.
- 119. Labrum.
- 120. Hypopharynx.
- 121. Maxilla.
- 122. Labial palp.



FIGURES 123–126. Sparbarus japonicus, male adult.

- 123. Habitus.
- 124. Foreleg.
- 125. Forewing.
- 126. Genitalia (ventral).



FIGURES 127–136. Sparbarus kabyliensis, larva (from Soldán 1986).

- 127. Antennal scape and pedicel.
- 128. Labrum.
- 129. Angulate mandible.
- 130. Hypopharynx.
- 131. Maxillary palp.
- 132. Labial palp segment 2.
- 133. Midleg.
- 134. Claw.
- 135. Posterolateral projections (dorsal view).
- 136. Operculate gill.



FIGURES 137–140. Sparbarus lacustris, larva.

- 137. Habitus of larva from Iowa.
- 138. Habitus of larva from Texas.
- 139. Head and pronotum (dorsolateral view).
- 140. Thoracic sterna (ventrolateral view).



FIGURES 141–146. Sparbarus lacustris, larva.

- 141. Labrum.
- 142. Angulate mandible.
- 143. Planate mandible.
- 144. Hypopharynx.
- 145. Maxilla.
- 146. Labium.



FIGURES 147–150. Sparbarus lacustris, larva.

- 147. Antenna.
- 148. Foreleg.
- 149. Hindleg.
- 150. Operculate gill.



FIGURES 151–154. Sparbarus lacustris, larva and male adult.

- 151. Larva, ventral microtrichia row of operculate gill.
- 152. Male adult, habitus.
- 153. Male adult, hindfemur.
- 154. Male adult, genitalia (ventral).







- 155. Habitus.
- 156. Head and pronotum (dorsolateral view).
- 157. Antenna.
- 158. Labrum.
- 159. Hypopharynx.
- 160. Maxilla.
- 161. Labial palp.



FIGURES 162–165. Sparbarus maculatus, male adult.

- 162. Head.
- 163. Antenna.
- 164. Abdominal terga.
- 165. Genitalia (ventral).



FIGURES 166–173. Sparbarus miccosukee, larva.

- 166. Habitus.
- 167. Head and pronotum (dorsolateral view).
- 168. Antenna.
- 169. Labrum.
- 170. Hypopharynx.
- 171. Maxilla.
- 172. Labial palp.
- 173. Mid- and hindfemur.





FIGURES 174–178. Sparbarus nasutus, larva.

- 174. Habitus.
- 175. Head.
- 176. Head and pronotum (dorsolateral view).
- 177. Pronotum.
- 178. Hindclaw.



FIGURES 179–186. Sparbarus nasutus, larva.

- 179. Antenna.
- 180. Labrum.
- 181. Hypopharynx.
- 182. Maxilla.
- 183. Labial palp.
- 184. Foreleg.
- 185. Hindleg.
- 186. Operculate gill.



FIGURES 187–190. Sparbarus nasutus, larva and male adult.

- 187. Larva, posterolateral projections 2-7.
- 188. Larva, posterior margin of sternum 9 (ventral).
- 189. Male adult, abdominal terga.
- 190. Male adult, genitalia (ventral).





FIGURES 191–197. Sparbarus tubulatus, larva.

- 191. Habitus.
- 192. Head (dorsolateral view).
- 193. Antenna.
- 194. Labrum.
- 195. Hypopharynx.
- 196. Maxilla.
- 197. Labial palp.







- 198. Habitus.
- 199. Anterior margin of head (ventral).
- 200. Head and prothorax (lateral view, mouthparts removed).
- 201. Ventral microtrichia row of operculate gill.



FIGURES 202–207. Insulibrachys needhami, larva.

- 202. Labrum.
- 203. Angulate mandible.
- 204. Planate mandible.
- 205. Hypopharynx.
- 206. Maxilla.
- 207. Labium.



FIGURES 208–213. Insulibrachys needhami, larva.

- 208. Antenna.
- 209. Foreleg.
- 210. Hindleg.
- 211. Posterolateral projections 3-9 (ventrolateral view).
- 212. Posterior margin of sternum 9 (ventral).
- 213. Operculate gill.





- 214. Habitus.
- 215. Head and pronotum (dorsolateral view).
- 216. Thoracic sterna (lateral view).
- 217. Process on abdominal tergum 2 and posterolateral projection 3.
- 218. Posterolateral projections 2-8.



FIGURES 219–225. Brachycercus berneri, larva.

- 219. Antennal scape and pedicel.
- 220. Labrum.
- 221. Hypopharynx.
- 222. Maxilla.
- 223. Foreleg.
- 224. Hindleg.
- 225. Operculate gill.



FIGURES 226–229. Brachycercus harrisella, larva.

- 226. Habitus.
- 227. Head and pronotum (dorsolateral view).
- 228. Thoracic sterna (lateral view).
- 229. Posterolateral projections 2-9.



FIGURES 230–235. Brachycercus harrisella, larva.

- 230. Labrum.
- 231. Angulate mandible.
- 232. Planate mandible.
- 233. Hypopharynx.
- 234. Maxilla.
- 235. Labium.



FIGURES 236–240. Brachycercus harrisella, larva and male adult.

- 236. Larva, antennal scape and pedicel.
- 237. Larva, foreleg.
- 238. Larva, hindleg.
- 239. Larva, operculate gill.
- 240. Male adult, forewing.



FIGURES 241–244. Brachycercus harrisella, male adult.

- 241. Habitus.
- 242. Head and thorax (ventrolateral view).
- 243. Vestiges of posterolateral projections 3-8.
- 244. Genitalia (ventral).



FIGURES 245–247. Brachycercus nitidus, larva.

- 245. Habitus.
- 246. Head and pronotum (dorsolateral view).
- 247. Thoracic sterna (lateral view).



FIGURES 248–254. Brachycercus nitidus, larva.

- 248. Antennal scape and pedicel.
- 249. Labrum.
- 250. Hypopharynx.251. Maxilla.
- 252. Foreleg.
- 253. Hindleg.
- 254. Operculate gill.



FIGURES 255–257. Brachycercus nitidus, larva and female adult.

- 255. Larva, process on abdominal tergum 2 anterior to base of operculate gill.
- 256. Larva, ventral microtrichia row of operculate gill.
- 257. Female adult, habitus.





- 258. Habitus.
- 259. Head (anterior view).
- 260. Head and pronotum (dorsolateral view).
- 261. Thoracic sterna (lateral view).



FIGURES 262–268. Brachycercus ojibwe, larva.

- 262. Antennal scape and pedicel.
- 263. Labrum.
- 264. Hypopharynx.
- 265. Maxilla.
- 266. Foreleg.
- 267. Hindleg.
- 268. Operculate gill.


FIGURES 269–272. Oriobrachys mahakam, larva.

- 269. Habitus.
- 270. Head and pro- and mesothorax (dorsolateral view, mouthparts removed).
- 271. Caudal filaments.
- 272. Posterolateral corner of operculate gill (ventral).



FIGURES 273–278. Oriobrachys mahakam, larva.

- 273. Labrum.
- 274. Angulate mandible.
- 275. Planate mandible.
- 276. Hypopharynx.
- 277. Maxilla.
- 278. Labium.



FIGURES 279–284. Oriobrachys mahakam, larva.

- 279. Antenna.
- 280. Foreleg.
- 281. Hindleg.
- 282. Posterolateral projections (dorsal view).
- 283. Posterolateral projections and operculate gill (lateral view).
- 284. Operculate gill.





- 285. Habitus.
- 286. Head and pronotum (dorsolateral view).
- 287. Antenna.
- 288. Foreleg.
- 289. Hindleg.
- 290. Posterolateral projections (dorsal view).
- 291. Operculate gill.





- 292. Labrum.
- 293. Angulate mandible.
- 294. Planate mandible.
- 295. Hypopharynx.
- 296. Maxilla.
- 297. Labium.





- 298. Habitus.
- 299. Head and pronotum (dorsolateral view).
- 300. Setae on dorsal operculate gill.
- 301. Posterolateral corner of operculate gill (ventral).



FIGURES 302–307. Latineosus cibola, larva.

- 302. Labrum.
- 303. Angulate mandible.
- 304. Planate mandible.
- 305. Hypopharynx.
- 306. Maxilla.
- 307. Labium.





- 308. Antenna.
- 309. Foreleg.
- 310. Hindleg.
- 311. Posterolateral projections (dorsal view).
- 312. Operculate gill.



FIGURES 313–320. Latineosus colombianus, larva.

- 313. Habitus.
- 314. Head and pronotum (dorsolateral view).
- 315. Antenna.
- 316. Foreleg.
- 317. Hindleg.
- 318. Posterolateral projections (dorsal view).
- 319. Posterolateral projections (lateral view).
- 320. Operculate gill.



FIGURES 321–326. Latineosus colombianus, larva.

- 321. Labrum.
- 322. Angulate mandible.
- 323. Planate mandible.
- 324. Hypopharynx.
- 325. Maxilla.
- 326. Labium.



FIGURES 327–330. Susperatus prudens, larva.

- 327. Habitus.
- 328. Head and pronotum (dorsolateral view).
- 329. Thoracic sterna (lateral view).
- 330. Abdominal sterna (lateral view).



FIGURES 331–336. Susperatus prudens, larva.

- 331. Labrum.
- 332. Angulate mandible.
- 333. Planate mandible.
- 334. Hypopharynx.
- 335. Maxilla.
- 336. Labium.



FIGURES 337–340. Susperatus prudens, larva.

- 337. Antenna.
- 338. Foreleg.
- 339. Hindleg.
- 340. Operculate gill.



FIGURES 341–346. Susperatus prudens, larva.

- 341. Head.
- 342. Pronotum.
- 343. Thoracic sterna.
- 344. Hindclaw.
- 345. Posterolateral projections 3-7.
- 346. Lateral region of operculate gill (ventral).





FIGURES 347–352. Susperatus prudens, male adult.

- 347. Habitus.
- 348. Antenna.
- 349. Head and pronotum (lateral view).
- 350. Foreleg.
- 351. Forewing.
- 352. Genitalia (ventral).



FIGURES 353–358. Susperatus tonkawa, male adult.

- 353. Habitus.
- 354. Antenna.
- 355. Head and pronotum (lateral view).
- 356. Foreleg.
- 357. Forewing.
- 358. Genitalia (ventral).



FIGURES 359–362. Susperatus tuberculatus, larva.

- 359. Habitus.
- 360. Head and pronotum (dorsolateral view).
- 361. Thoracic sterna (lateral view).
- 362. Abdominal sterna (lateral view).



FIGURES 363–368. Susperatus tuberculatus, larva.

- 363. Labrum.
- 364. Angulate mandible.
- 365. Planate mandible.
- 366. Hypopharynx.
- 367. Maxilla.
- 368. Labium.



FIGURES 369–372. Susperatus tuberculatus, larva.

- 369. Antenna.
- 370. Foreleg.
- 371. Hindleg.
- 372. Operculate gill.





- 373. Habitus.
- 374. Head and pronotum (dorsolateral view).
- 375. Posterolateral projections.



FIGURES 376–381. Alloretochus peruanicus, larva.

- 376. Labrum.
- 377. Angulate mandible.
- 378. Planate mandible.
- 379. Hypopharynx.
- 380. Maxilla.
- 381. Labium.



FIGURES 382–387. Alloretochus peruanicus, larva and male adult.

- 382. Larva, antenna.
- 383. Larva, foreleg.
- 384. Larva, hindleg.
- 385. Larva, operculate gill.
- 386. Male adult, abdominal segments 5-7 (lateral view) (from Molineri and Goitia 2006).
- 387. Male adult, genitalia (from Molineri and Goitia 2006).



FIGURES 388–393. Cercobrachys cree, larva.

- 388. Habitus.
- 389. Antenna.
- 390. Foreleg.
- 391. Hindleg.
- 392. Sternum 9.
- 393. Caudal filaments.



FIGURES 394–399. Cercobrachys cree, larva.

- 394. Labrum.
- 395. Angulate mandible.
- 396. Planate mandible.
- 397. Hypopharynx.
- 398. Maxilla.
- 399. Labium.





- 400. Head.
- 401. Pronotum.
- 402. Hindclaw.
- 403. Posterolateral projections 3-6.
- 404. Abdominal terga 7–10.
- 405. Operculate gill.



FIGURES 406–409. Cercobrachys cree, male adult.

- 406. Habitus.
- 407. Forewing.
- 408. Metathorax and abdominal segment 1 (lateral view).
- 409. Genitalia (ventral).



FIGURES 410–417. Cercobrachys etowah, larva.

- 410. Habitus.
- 411. Antenna.
- 412. Foreleg.
- 413. Hindleg.
- 414. Posterolateral projections 3–6 (dorsal view).
- 415. Posterolateral projections 3-6 (ventrolateral view).
- 416. Posterior margin of sternum 9.
- 417. Operculate gill.



FIGURES 418–423. Cercobrachys etowah, larva.

- 418. Labrum.
- 419. Angulate mandible.
- 420. Planate mandible.
- 421. Hypopharynx.
- 422. Maxilla.
- 423. Labium.



FIGURES 424-429. Cercobrachys etowah, larva and male adult.

- 424. Larva, head.
- 425. Larva, pronotum.
- 426. Larva, hindclaw.
- 427. Larva, abdominal terga 7-8.
- 428. Larva, operculate gill (ventral).
- 429. Male adult, forceps (ventral).



FIGURES 430-438. Cercobrachys etowah, male adult.

- 430. Habitus.
- 431. Head (anterior view).
- 432. Head and thorax (ventral view).
- 433. Thorax (lateral view).
- 434. Foreleg.
- 435. Forewing.
- 436. Vestiges of posterolateral projections 4-6.
- 437. Tergum 10.
- 438. Genitalia (ventral).



FIGURES 439–444. Cercobrachys fox, larva.

- 439. Habitus.
- 440. Antenna.
- 441. Foreleg.
- 442. Hindleg.
- 443. Posterior margin of sternum 9.
- 444. Operculate gill.



FIGURES 445–450. Cercobrachys fox, larva.

- 445. Labrum.
- 446. Angulate mandible.
- 447. Planate mandible.
- 448. Hypopharynx.
- 449. Maxilla.
- 450. Labium.



FIGURES 451–455. Cercobrachys fox, larva.

- 451. Head.
- 452. Pronotum.
- 453. Hindclaw.
- 454. Posterolateral projections 3-6.
- 455. Apex of posterolateral projection 6.



FIGURES 456–458. Cercobrachys fox, male subimago and female adult.

- 456. Male subimago, habitus.
- 457. Male subimago, genitalia (ventral).
- 458. Female adult (ventral view).



FIGURES 459–463. Cercobrachys lilliei, larva.

- 459. Habitus.
- 460. Antenna.
- 461. Foreleg.
- 462. Hindleg.
- 463. Operculate gill.



FIGURES 464–469. Cercobrachys lilliei, larva.

- 464. Labrum.
- 465. Angulate mandible.
- 466. Planate mandible.
- 467. Hypopharynx.
- 468. Maxilla.
- 469. Labium.


FIGURES 470–474. Cercobrachys lilliei, larva.

- 470. Head.
- 471. Pronotum.
- 472. Hindclaw.
- 473. Posterolateral projections 3-6.
- 474. Abdominal terga 7-9.



FIGURES 475-481. Cercobrachys minutus, larva.

- 475. Habitus.
- 476. Head (dorsolateral view).
- 477. Antenna.
- 478. Foreleg.
- 479. Hindleg.
- 480. Posterolateral projections
- 481. Operculate gill.



FIGURES 482–487. Cercobrachys minutus, larva.

- 482. Labrum.
- 483. Angulate mandible.
- 484. Planate mandible.
- 485. Hypopharynx.
- 486. Maxilla.
- 487. Labium.



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FIGURES 488-491. Cercobrachys minutus, male adult.

- 488. Habitus.
- 489. Antenna.
- 490. Foreleg.
- 491. Genitalia (ventral).



FIGURES 492–497. Cercobrachys petersorum, larva.

- 492. Head (from Soldán 1986).
- 493. Habitus.
- 494. Antenna.
- 495. Foreleg.
- 496. Posterolateral projections and operculate gill (lateral view).
- 497. Operculate gill.



FIGURES 498–503. Cercobrachys petersorum, larva.

- 498. Labrum.
- 499. Angulate mandible.
- 500. Planate mandible.
- 501. Hypopharynx.
- 502. Maxilla.
- 503. Labium.



FIGURES 504–509. Cercobrachys pomeiok, larva.

- 504. Habitus.
- 505. Antenna.
- 506. Foreleg.
- 507. Hindleg.
- 508. Posterolateral projections
- 509. Operculate gill.



FIGURES 510–515. Cercobrachys pomeiok, larva.

- 510. Labrum.
- 511. Angulate mandible.
- 512. Planate mandible.
- 513. Hypopharynx.
- 514. Maxilla.
- 515. Labium.



FIGURES 516–520. Cercobrachys serpentis, larva.

- 516. Habitus.
- 517. Antenna.
- 518. Foreleg.
- 519. Hindleg.
- 520. Operculate gill.



FIGURES 521–526. Cercobrachys serpentis, larva.

- 521. Labrum.
- 522. Angulate mandible.
- 523. Planate mandible.
- 524. Hypopharynx.
- 525. Maxilla.
- 526. Labium.





- 527. Head.
- 528. Head (dorsolateral view, mouthparts removed).
- 529. Pronotum.
- 530. Hindclaw.
- 531. Posterolateral projections 3-6.
- 532. Abdominal terga 7-10.



FIGURES 533–537. Cercobrachys winnebago, larva.

- 533. Habitus.
- 534. Antenna.
- 535. Foreleg.
- 536. Hindleg.
- 537. Operculate gill.



FIGURES 538–543. Cercobrachys winnebago, larva.

- 538. Labrum.
- 539. Angulate mandible.
- 540. Planate mandible.
- 541. Hypopharynx.
- 542. Maxilla.
- 543. Labium.



FIGURES 544–550. Cercobrachys winnebago, larva.

- 544. Head.
- 545. Pronotum.
- 546. Thoracic sterna (ventrolateral view).
- 547. Hindclaw.
- 548. Posterolateral projections 3-6.
- 549. Abdominal terga 7-10.
- 550. Abdominal sterna (ventral).





- 551. Male, habitus.
- 552. Male, head and pronotum (lateral view).
- 553. Male, genitalia (ventral).
- 554. Female (ventral view).



FIGURES 555-560. Brachycercus and Sparbarus, egg.

- 555. B. harrisella.
- 556. B. harrisella (cross section).
- 557. B. ojibwe.
- 558. S. lacustris.
- 559. S. lacustris (cross section).
- 560. S. choctaw.



FIGURES 561–565. Sparbarus, egg.

- 561. S. coushatta.
- 562. S. japonicus.
- 563. S. maculatus.
- 564. S. miccosukee.
- 565. S. nasutus.



FIGURES 566–570. Latineosus, Susperatus, and Cercobrachys, egg.

- 566. L. colombianus.
- 567. S. prudens.
- 568. S. tonkawa.
- 569. C. etowah.
- 570. C. fox.





- 571. C. cree.
- 572. C. lilliei.
- 573. C. serpentis.
- 574. C. pomeiok.
- 575. C. winnebago.



FIGURES 576–581. Sparbarus and Cercobrachys, egg (575–579 from Kluge 1991).

- 576. S. capnicus.
- 577. S. corniger.
- 578. S. europaeus.
- 579. S. europaeus (rear end view).
- 580. C. minutus.
- 581. C. minutus (rear end view).



FIGURE 582. A 50% majority-rule consensus tree of 32 Maximum Parsimony trees obtained in PAUP* for 32 Brachycercinae species based on 103 morphological characters (Caeninae species *Caenis youngi* and *Callistellina panda* serve as outgroups). Numbers above branches are frequencies of the occurrence that are greater than 50%. Numbers below branches are bootstrap values that are greater than 50%. Bootstrap values are only shown for clades present in the majority-rule consensus tree.



FIGURE 583. Hypothesized evolutionary relationships among Brachycercinae genera. Numbers represent characters. Parenthetical numbers represent character states encoded in Table 1. Single asterisk indicates convergences. Double asterisk indicates reversions occurring in apotypic lineages. Character states were traced in MacClade with Resolving Options set to ACCTRAN (Characteristics that were traced differently if using DELTRAN mode are shaded).



FIGURE 584. Hypothesized phylogeny of all known Brachycercinae species and their worldwide distribution. Species with dashed line were deduced from other relationship trends. EP = eastern Palearctic, WP = western Palearctic (east or west of Ural Mtns), EN = eastern Nearctic, WN = western Nearctic (east or west of Mississippi River), HO = widespread Holarctic, O = Oriental (southeast Asia), NT = Neotropical (Central and South America and Caribbean area).