Revisionary Synopsis of the Baetidae (Ephemeroptera) of North and Middle America

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ABSTRACT

Considerable nomenclatural revision of the North and Middle American Baetidae has resulted from comprehensive research aimed at formulating a phylogenetic classification. The 17 Nearctic species in Pseudocloeon not previously assigned to Acentrella or Apobaetis are newly placed in Baetis or Barbaetis. Cloeon in the area is restricted to C. cognatum, while two species previously in Cloeon are placed in Centroptilum and nine in Procloeon, a genus considered for the first time in the Nearctic. Definitions of Centroptilum and Procloeon are modified, both now incorporate species with hindwings and species without hindwings, and 19 species are transferred from Centroptilum to Procloeon. Pseudocentroptilum s. auctt. in North America is synonymized with Procloeon. Neocloeon is recognized as a synonym of Centroptilum s. str. and removed from synonymy with Cloeon. Dactylobaetis is placed in synonymy with Cameloebaetidius, and all species, including those from South America, are newly combined. Two species of Baetis are transferred to Acerpenna, and two to Fallceon. A checklist includes 154 currently recognized species among 19 genera in the area, and incorporates 21 new species synonyms and 57 new combinations. The names Baetis armillatus and Baetis cinctus are substituted for Pseudocloeon parvulum and Pseudocloeon cingulatum, respectively, which otherwise attain homonymic status. Regional distributions for each species and abbreviated synonymies since 1976 are annotated to the checklist. Brief discussions of each genus include information on species diagnosis, revisionary bases, status, and needs. A guide to all nomenclatural changes and added taxa since 1976 provides the bibliographic sources of all such information and serves as a ready index to name equivalencies resulting from extensive recent and present revisions.

INTRODUCTION

Since the last comprehensive listing of North and Central American mayflies (Edmunds et al., 1976), numerous changes in the classification of the Baetidae have been made. Unfortunately, for those systematists who work with baetids on an infrequent basis and for nonsystematists, such as stream biologists, who must identify baetids, these nomenclatural
changes may be a source of frustration. The revisions, however, have been sorely needed in this difficult family of mayflies, as was dramatically indicated by Edmunds’ et al. (1976:155) reference to, “the absurdity of the present classification.”

This paper is written for two purposes. The first is to present additional systematic changes required in the classification of the baetids, particularly reflecting several new generic concepts. The second purpose is to provide workers with a complete guide and necessary references to the recent and present revisions and the current nomenclature of the North and Middle American baetids.

The primary bases of such revisions are recently published studies and additional detailed data to be published elsewhere (Waltz and McCafferty, manuscripts). Our considerable attention to the analysis of larvae from around the world has provided us with valuable and often extensive character sets for deciphering phylogenetic relationships. Phylogeny, deduced by cladistic methodology (Ross, 1974), is paramount in our scheme, since we seek a phylogenetic classification (sensu Hennig, 1966; Wiley, 1981) of the family. Type specimens have been examined for all world genera for which types are available. When determining the application of existent generic names, comparative material other than types was used as available, but only if it was clearly consistent with type characterization.

We find it interesting that Traver’s (1937) statements regarding the future of world Baetidae classification have proven to be quite prophetic. She predicted that a large number of new genera would be found in Baetidae and that they would become obvious only when both the larva and adults of the various species became known.

One result of our research that has broad implications for the classification of the baetids given herein has been the verification of several workers’ beliefs (e.g., Spieth, 1933; Day, 1955; Edmunds et al., 1976) that hindwings may have been lost independently many times within different baetid lineages. We have found that many of the past groupings of baetids based on the presence or absence of hindwings, or pads, are unnatural and not consistent with a phylogenetic classification. Thus, for example, recognition of Cloeon from Centropilum, or Pseudocloeon from Baetis based on the absence of hindwings is not followed. In fact, we have found these four groupings, as they have been known, to be polyphyletic and to have contained elements of at least 11 different nominal world genera, seven of which involve North and Middle American species. The deception caused by using the presence or absence of hindwings as a generic delineator is underscored by the fact that at least three species of Baetidae in the Western Hemisphere have been found to have males with hindwings and females without hindwings (Edmunds et al., 1976; McCafferty and Provonsha, unpublished).

A second result of our research that has direct implications for the classification of world baetids is the discovery of an important synapomorphy shared by Baetis and its closest allies (the Baetis complex of Waltz and McCafferty, 1987d). This is the presence of the villopore on the femora (a new name for the ventral femoral patch sensu Waltz and McCafferty, 1987c) of the larvae. The genus Baetis, as historically composed, was not a holophyletic taxon, and certain Nearctic species placed in it lack the apotypic villopore and thus represent other lineages (Waltz and McCafferty, 1987c). The villopore can be variously developed, being conspicuous in some genera, while appearing almost rudimentary in others. Close scrutiny is therefore called for when examining the ultrastructure.

The holophyletic Baetis complex is primarily Holarctic with more derived lineages extending into the Oriental and Afrotropical regions, but thus far it is unknown from the Neotropics.

A third result of our research has implications for species level taxonomy. We and others
(e.g., Berner and Pescador, 1988) have been of the opinion that the historical reliance on color patterns for establishing species in baetids results in narrow typological concepts and the over-estimation of numbers of species. Experimental data (McCafferty and Pereira, 1984) and field data (Kondratieff and Voshell, 1984) from other families of mayflies support this conclusion. Slight variations in color patterns of adults and/or larvae appear to be easily acquired in many baetid populations as either spatial or phenological gradients. We thus maintain that significant morphological differentiation in at least one of the life stages are most likely to typify species of baetids.

We have not yet resolved all of the species level synonymies that potentially exist in the classification of the North and Middle American fauna. For example, our examination of many collections of baetids from the Western Hemisphere indicates that the number of populations with distinct larval morphology does not correspond to the much larger number of species names based on adult typological concepts in certain genera, such as *Camelo-baetidius* and *Procloeon*. Therefore, it is likely that more synonymies will be required when larval-adult associations become available. Since many of the species of *Baetodes* are weakly differentiated as larvae and unknown as adults, we also anticipate some synonymies in that genus. We have, however, been able to elucidate many necessary synonyms herein for such genera as *Callibaetis*.

We are cognizant that from a purely utilitarian point of view, presentation of a more modern classification and nomenclature results in a rather immediate need for updated taxonomic keys. This paper therefore will be followed by a revised and illustrated key to the Holarctic genera of *Baetidae* (Waltz and McCafferty, in manuscript).

**FORMAT**

We provide an alphabetical checklist of all currently recognized genera and species of *Baetidae* occurring in North and Middle America (= Central America plus the Greater Antilles). New combinations, new synonymies, and new names resulting from our research are defined within the checklist. In the case of new combinations, the previous genus is indicated parenthetically under the new binomial. Also annotated to the checklist is an abbreviated, alphabetical (not chronological) synonymy bracketed under pertinent species. This indicates any nomenclatural history since the classification and listing of baetids of North and Central America that appeared in Edmunds’ *et al.* (1976) generally used book.

Distributions are also annotated to the checklist by way of regional distributions that appear abbreviated after each species name. These regions in North and Middle America are depicted in Figure 1, but require some additional explanation as follows.

The Mesoamerican Region (MA) as used herein includes the Greater Antilles of the West Indies, Central America, and southern Mexico south of the Tropic of Cancer.

The Southwestern Region (SW) is bounded on the south by the Tropic of Cancer and in the west by the Pacific Ocean. It is bounded on the North by a line extending from the northern borders of Oklahoma, New Mexico, and Arizona west to the Pacific Ocean at Monterey Bay, California, with a slight northward deviation to incorporate the Mojave Desert region of southwestern Utah. The eastern boundary is a line along eastern portions of Oklahoma and Texas, so that the more arid region of these states are included but areas such as the Big Thicket of Texas and the Oklahoma Ozarks, which contain faunal elements more typical of eastern areas (e.g., McCafferty and Provonsha, 1978, unpublished), are excluded.

The Northwestern Region (NW) adjoins the Southwestern Region and shares the common
boundary described above. The northern boundary is a line represented by the northern borders of British Columbia, Alberta and Saskatchewan (60 degrees north latitude). The western boundary is the Pacific Ocean. The eastern boundary is a line running along the eastern border of Saskatchewan and roughly connecting the eastern border of Colorado, so that both the Black Hills of South Dakota and the Sand Hills of the panhandle of Nebraska, which mainly contain western mayfly faunal elements (McCafferty 1990; McCafferty and Provonsha, unpublished), are included.

The Northeastern Region (NE) shares the eastern boundary of the Northwestern Region described above. The southern boundary begins at the northern border of Oklahoma, extends northward into Missouri, so as to exclude the Missouri Ozarks, then across the southern tip of Illinois, following the Ohio River and ending along the southern borders of Pennsylvania and New Jersey at the Atlantic coast. The northern boundary is the 60th parallel north latitude at the northern border of Manitoba west of Hudson Bay; however, east of Hudson Bay, all of Quebec and Newfoundland are included.

The Southeastern Region (SE) is bounded on the east and the south by the Atlantic Ocean and the Gulf of Mexico, respectively. Its northern and western borders are shared with the Northeastern Region and the Southwestern Region, respectively, as described above.

The Far North Region (FN) includes Alaska and Canada west of Hudson Bay and north of Hudson Straight. It is bounded on the South by the line demarcating 60 degrees parallel north latitude west of Hudson Bay. East of Hudson Bay, the region includes only Baffin Island, north of mainland Quebec.

These regions are based on our current knowledge of natural distributions of mayflies and represent our attempt to delineate general faunistic tendencies typical of mayflies. In other words, in most cases, if a species occurs in one part of one of our regions, it is highly probable that it may occur in other parts as well. There are, of course, species that are highly restricted ecologically and are not ubiquitous throughout a region, (e.g., big river species discussed by McCafferty et al., 1990). Such patterns are not necessarily ever expressed by broad geographical regions. In some instances, two or more of our regions are strongly linked by common physiographic components, particularly mountain ranges. Thus, montane species are often common to the Northwestern and Southwestern Regions, to the Southwestern and Mesoamerican Regions, and to the Northeastern and Southeastern Regions because of the north-south continuities of montane habitats.

Following the annotated checklist, we have provided a short discussion of each genus. We have attempted to indicate the best available sources of species keys or diagnoses for both larvae and adults. Various general remarks are also given for each genus as appropriate, and these may include additional information on nomenclatural history, diagnostic habitats, systematic status, and future research needs. While the grounds for generic revisions are summarized herein, they are based on the referenced published research of Waltz and McCafferty or more detailed research results to be published elsewhere (Waltz and McCafferty, manuscripts). Rationales for new species synonymies are given herein as necessary.

Following the discussion we provide a guide to all of the name changes and new taxa that have been added since the classification of Baetidae in North and Central America as it appeared in Edmunds et al. (1976). That book serves as a useful baseline because it was the last major reference work for the geographic area of coverage.

Genera and species names are listed alphabetically and include any names found listed in Edmunds et al. (1976) but that since, including herein, have been recombined with different genera, synonymized, substituted, or corrected in orthography. When generic concepts have
Fig. 1. Geographic regions of North and Middle America used for citing baetid species distributions.
changed, the current equivalencies are run alphabetically under the name exactly as it appeared in 1976. Under each previous species name, any names that have applied since 1976 are chronologically listed. Thus the single- or last-listed new name is the current name. The bibliographic sources of genus and species changes are referenced parenthetically after the change notation. If the change has been given in this paper, it is referenced simply as: (herein).

New taxa are incorporated into the alphabetical guide. These names (differentiated by an asterisk) reflect any newly discovered mayflies described since 1976. The bibliographic source for each new taxon appears after its name. A few new taxa are included not because they were described since 1976, but because they are from the Greater Antilles and were not included in Edmunds et al. (1976). These are noted as: (geographic addition herein). If any of the new taxa have undergone taxonomic revision since their description, new names are listed below them as they were for other names that have been changed, as described above.

Use of the guide along with the checklist will give any user a complete cross index to any recent nomenclatural changes and will make revisionary results tractable for nonspecialists.

ANNOTATED CHECKLIST

Acentrella Bengtsson, 1912

Acentrella ampla Traver, 1932 -NE,SE-

[=Baetis amplus (Traver)]

Acentrella carolina (Banks), 1924 -FN,NE,NW,SE-

[=Pseudocloeon carolina (Banks)]

Acentrella insignificans (McDunnough), 1926 -FN,NW,SW-

[=Baetis insignificans McDunnough]

Acentrella lapponica Bengtsson, 1912 -FN-

[=Baetis lapponicus (Bengtsson)]

Acentrella turbida (McDunnough), 1924 -NW-

[=Pseudocloeon turbidum McDunnough]

Acerpenna Waltz and McCafferty, 1987

Acerpenna akataleptos (McDunnough), 1926, n. comb. -NW-

(formerly in Baetis)

Acerpenna harti (McDunnough), 1924, n. comb. -NE-

(formerly in Baetis)

Acerpenna macdunnoughi (Ide), 1937 -NE,SE-

[=Baetis macdunnoughi Ide]

Acerpenna pygmaea (Hagen), 1861 -NE,SE-

[=Baetis pygmaeus (Hagen); =Baetis spiethi Berner]

Apobaetis Day, 1955

Apobaetis etowah (Traver), 1935 -SE-

[=Pseudocloeon etowah Traver]

Apobaetis indeprensus Day, 1955 -NE,NW-
**Baetis** Leach, 1815

*Baetis adonis* Traver, 1935 -SW-

*Baetis alachua* (Berner), 1940, **n. comb.** -SE-

(formerly in *Pseudocloeon*)

*Baetis alius* Day, 1954 -NW-

*Baetis armillatus* McCafferty and Waltz, **n. name** -NE,NW,SE-

(formerly *Pseudocloeon parvulum* McDunnough 1932:210, a secondary homonym, not *Baetis parvulum* Crass, 1947)

*Baetis bicaudatus* Dodds, 1923 -FN,NW,SW-

*Baetis bimaculatus* (Berner), 1946, **n. comb.** -SE-

(formerly in *Pseudocloeon*)

*Baetis brunneicolor* McDunnough, 1925 -NE,SE-

[=*Baetis anachris* Burks, 1953; =*Baetis hiemalis* Leonard, 1950; =*Baetis phyllis* Burks, 1953]

*Baetis caelestis* Allen and Murvosh, 1983 -SW-

[=*Baetis* sp. A Morihara and McCafferty, 1979]

*Baetis caurinus* Edmunds and Allen, 1957 -NW-

*Baetis cinctutus* McCafferty and Waltz, **n. name** -NE-

(formerly *Pseudocloeon cingulatum* McDunnough 1931:85, a secondary homonym, not *Baetis cingulatus* Stephens, 1835; not *Baetis cingulatus* McDunnough 1925:216, a homonym and junior synonym of *Baetis flavistriga* McDunnough)

*Baetis dardanus* McDunnough, 1923 -NW-

[=*Baetis elachistis* Burks, 1953]

*Baetis diablis* Day, 1954 -NW-

*Baetis dubius* (Walsh), 1862, **n. comb.** -NE,SE-

(formerly in *Pseudocloeon*)

[=*Pseudocloeon chlorops* (McDunnough), 1923, **n. syn.**]

*Baetis elliotti* (Daggy), 1945, **n. comb.** -NE-

(formerly in *Pseudocloeon*)

[=*Pseudocloeon ida* (Daggy), 1945, **n. syn.**]

*Baetis ephippiatus* Traver, 1935 -NE,SE-

*Baetis flavistriga* McDunnough, 1921 -NE,SE-

[=*Baetis levitans* McDunnough, 1925; =*Baetis nanus* McDunnough, 1923; =*Baetis phoebus* McDunnough, 1923; =*Baetis quebecensis* Hubbard, 1974]

*Baetis foemina* McDunnough, 1936 -FN-

*Baetis frondalis* McDunnough, 1925 -NE,SE-

[=*Baetis australis* Traver, 1932; =*Baetis baeticatus* Burks, 1953]

*Baetis futile* (McDunnough), 1931, **n. comb.** -NW-

(formerly in *Pseudocloeon*)

*Baetis hudsonicus* Ide, 1937 -FN-

*Baetis intercalaris* McDunnough, 1921 -NE,SE-

*Baetis longipalpus* Morihara and McCafferty, 1979 -NE,SE-

*Baetis macani bundyae* Lehmkühl, 1973 -FN-

[=*Baetis bundyae* Lehmkühl]

*Baetis magnus* McCafferty and Waltz, 1986 -NW,SW-

[=*Baetis* sp. B Morihara and McCafferty, 1979; =*Baetis libos* Allen and Murvosh, 1987, **n. syn.**]
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Baetis moffati Dodds, 1923 -NW-
Baetis notos Allen and Murvosh, 1987 -SW-
  [=Baetis sp. C Morihara and McCafferty, 1979]
Baetis ochris Burks, 1953 -NE-
Baetis palisadi Mayo, 1952 -NW-
Baetis parallelus Banks, 1924 -NW-
Baetis persecutus McDunnough, 1939 -NW-
Baetis piscatoris Traver, 1935 -NW-
Baetis pluto McDunnough, 1925 -NE,SE-
Baetis posticatus (Say), 1824 -NE-
Baetis propinquus (Walsh), 1863 -NE,SE-
Baetis punctiventris (McDunnough), 1923, n. comb. -NE,NW,SE-
  (formerly in Pseudocloeon)
  [=Pseudocloeon anoka Daggy, 1945, n. syn.; =Pseudocloeon edmundsi Jensen, 1969,
   n. syn.; =Pseudocloeon myrsum Burks, 1953, n. syn.]
Baetis rubrolaterale (McDunnough), 1931, n. comb. -NW-
  (formerly in Pseudocloeon)
Baetis rusticans McDunnough, 1925 -NE-
Baetis sinusosus Navas, 1924 -MA-
Baetis sulfurosus Day, 1954 -NW-
Baetis thermophilos McDunnough, 1926 -NW-
Baetis tricaudatus Dodds, 1923 -NE,NW,SE,SW-
  [=Baetis incertans McDunnough, 1925; =Baetis intermedius Dodds, 1923; =Baetis
   jesmondensis McDunnough, 1938; =Baetis sonora Allen and Murvosh, 1987, n. syn.;
   =Baetis vagans McDunnough, 1925]
Baetis veteris (McDunnough), 1924, n. comb. -NE-
  (formerly in Pseudocloeon)
Baetis virile (McDunnough), 1923, n. comb. -NE-
  (formerly in Pseudocloeon)

Baetodes Needham and Murphy, 1924
Baetodes adjustus Cohen and Allen, 1972 -MA-
Baetodes arizonensis Koss, 1972 -SW-
Baetodes caritus Cohen and Allen, 1972 -MA-
  [=Baetodes veracrusensis Mayo, 1972]
Baetodes deficiens Cohen and Allen, 1972 -MA-
  [=Baetodes bellus Mayo, 1972]
Baetodes edmundsi Koss, 1972 -SW-
Baetodes fortinensis Mayo, 1972 -MA-
Baetodes fuscipes Cohen and Allen, 1972 -MA-
  [=Baetodes furvus Mayo, 1973]
Baetodes inermis Cohen and Allen, 1972 -MA,SW-
Baetodes longus Mayo, 1973 -MA-
Baetodes noventus Cohen and Allen, 1972 -MA-
Baetodes obesus Mayo, 1972 -MA-
Baetodes pallidus Cohen and Allen, 1972 -MA-
Baetodes pictus Cohen and Allen, 1972 -MA-
Baetodes tritus Cohen and Allen, 1972 -MA,SW-
Baetodes velmae Cohen and Allen, 1978 -MA-

Barbaetis Waltz and McCafferty, 1985
Barbaetis benfieldi Kennedy, 1985 -SE-
Barbaetis cestus (Provonsha and McCafferty), 1982, n. comb. -NE-
(formerly in Pseudocloeon)

Callibaetis Eaton, 1881
Callibaetis americanus Banks, 1900 -NW,SW-
Callibaetis californicus Banks, 1900 -NW,SW-
Callibaetis centralis Peters, 1959 -NE-
Callibaetis completa Banks, 1924 -MA-
Callibaetis ferrugineus (Walsh), 1862 -NE-
Callibaetis floridanus Banks, 1900 -SE-
Callibaetis fluctuans (Walsh), 1862 -NE-
[=Callibaetis traverae Upholt, 1937, n. syn.]
Callibaetis montanus Eaton, 1885 -MA-
Callibaetis pallidus Banks, 1900 -NW-
[=Callibaetis semicostatus Banks, 1914, n. syn.]
Callibaetis paulinus (Navas), 1924 -MA-
Callibaetis pictus Eaton, 1871 -MA,NW,SW-
[=Callibaetis doddsi Traver, 1935, n. syn.; =Callibaetis pacificus Seeman, 1927, n. syn.; =Callibaetis signatus Banks, 1918, n. syn.]
Callibaetis pretiosus Banks, 1914 -SE-
Callibaetis skokianus Needham, 1903 -NE-
[=Callibaetis brevicostatus Daggy, 1945, n. syn.]
Callibaetis undatus (Pictet), 1845 -MA-

Camelobaetidius Demoulin, 1966
[=Dactylobaetis Traver and Edmunds, 1968, n. syn.]
Camelobaetidius arriaga (Traver and Edmunds), 1968, n. comb. -MA-
(formerly in Dactylobaetis)
Camelobaetidius cepheus (Traver and Edmunds), 1968, n. comb. -NW,SW-
(formerly in Dactylobaetis)
Camelobaetidius chiapas (Traver and Edmunds), 1968, n. comb. -MA-
(formerly in Dactylobaetis)
Camelobaetidius jenseni (Traver and Edmunds), 1968, n. comb. -MA-
(formerly in Dactylobaetis)
Camelobaetidius mexicanus (Traver and Edmunds), 1968, n. comb. -NE,SW-
(formerly in Dactylobaetis)
Camelobaetidius musseri (Traver and Edmunds), 1968, n. comb. -MA-
(formerly in Dactylobaetis)
Camelobaetidius navis (Allen and Chao), 1978, n. comb. -SW-
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Camelobaetidius salinus (Allen and Chao), 1978, **n. comb.** -SW-
(formerly in *Dactylobaetis*)

Camelobaetidius sinaloa (Allen and Murvosh), 1987, **n. comb.** -SW-
(formerly in *Dactylobaetis*)

Camelobaetidius trivialis (Allen and Chao), 1978, **n. comb.** -SW-
(formerly in *Dactylobaetis*)

Camelobaetidius warreni (Traver and Edmunds), 1968, **n. comb.** -SW-
(formerly in *Dactylobaetis*)

Camelobaetidius zenobia (Traver and Edmunds), 1968, **n. comb.** -MA-
(formerly in *Dactylobaetis*)

Centroptilum Eaton, 1869
[=Neocloeon Traver, 1932, **n. syn.**, placed as synonym of *Cloeon* Leach, 1815, by Edmunds et al. (1976)]

Centroptilum alamance (Traver), 1932, **n. comb.** -NE,SE-
(formerly in *Cloeon sensu* Edmunds et al., 1976)

Centroptilum bifurcatum McDunnough, 1924 -NW-

Centroptilum selanderatorum Edmunds, 1954 -NW-

Centroptilum semirufum McDunnough, 1926 -NE-

Centroptilum triangulifer (McDunnough), 1931, **n. comb.** -NE,SE-
(formerly in *Cloeon*)

Centroptilum victoriae McDunnough, 1938 -NE-

Cloeodes Traver, 1938

Cloeodes consignatus Traver, 1938 -MA-

Cloeodes excogitatus Waltz and McCafferty, 1987 -SW-

Cloeodes macrolamellus Waltz and McCafferty, 1987 -SW-

Cloeodes maculipes Traver, 1938 -MA-

Cloeodes peninsulus Waltz and McCafferty, 1987 -SW-

Cloeon Leach, 1815

Cloeon cognatum Stephens, 1835 -NE-
[=*Cloeon dipterum* (Linnaeus), 1761, misidentification of Nearctic material]

Diphetor Waltz and McCafferty, 1987

Diphetor devinctus (Traver), 1935 -NW-
[=*Baetis devinctus* Traver]

Diphetor hageni (Eaton), 1885 -NE,NW-
[=*Baetis hageni* Eaton; =*Baetis parvus* Dodds, 1923]

Fallceon Waltz and McCafferty, 1987

Fallceon garcianus (Traver), 1938, **n. comb.** -MA-
(formerly in *Baetis*)

Fallceon poeyi (Eaton), 1885, **n. comb.** -MA-
(formerly in *Baetis*, transferred from *Centroptilum* by Edmunds, 1974)

Fallceon quilleri (Dodds), 1923 -NE,NW,SE,SW-
[=*Baetis buenoi* Allen, 1985; =*Fallceon buenoi* (Allen), **n. syn.**; =*Baetis hyblis* Allen
and Murvosh, 1983; =Fallceon byblis (Allen and Murvosh), n. syn.; =Baetis cleptis Burks, 1953; =Baetis eatoni Kimmins, 1934; =Fallceon eatoni (Kimmins), n. syn.; =Baetis endymion Traver, 1935; =Baetis erebus Traver, 1935; =Baetis leeche Burks, 1954]

**Guajirolus** Flowers, 1985

*Guajirolus ektrapeloglossa* Flowers, 1985 -MA-

**Heterocloeon** McDunnough, 1925

*Heterocloeon berner* (Müller-Liebenau), 1974 -SE-

*Heterocloeon curiosum* (McDunnough), 1923 -NE, SE-

*Heterocloeon frivolus* (McDunnough), 1925 -NE, SE-

[=Baetis frivolus McDunnough]

*Heterocloeon petersi* (Muller-Liebenau), 1974 -SE-

**Moribaetis** Waltz and McCafferty, 1985

*Moribaetis macaferti* Waltz, 1985 -MA-

*Moribaetis maculipennis* (Flowers), 1979 -MA-

[=Baetis maculipennis Flowers]

*Moribaetis salvini* (Eaton), 1885 -MA-

[=Baetis salvini Eaton]

**Paracloeodes** Day, 1955

*Paracloeodes minutus* (Daggy), 1945 -NE, NW, SE-

[=Paracloeodes abditus Day, 1955, n. syn.]

*Paracloeodes portoricensis* (Traver), 1938 -MA-

**Procloeon** Bengtsson, 1915

*Procloeon album* (McDunnough), 1926, n. comb. -NE, SE-

(formerly in *Centroptilum*)

*Procloeon asperatum* (Traver), 1935, n. comb. -SW-

(formerly in *Centroptilum*)

*Procloeon bellum* (McDunnough), 1924, n. comb. -NE-

(formerly in *Centroptilum*)

*Procloeon caliginosum* (McDunnough), 1925, n. comb. -NE-

(formerly in *Centroptilum*)

*Procloeon conturbatum* (McDunnough), 1929, n. comb. -NW-

(formerly in *Centroptilum*)

*Procloeon convexum* (Ide), 1930, n. comb. -NE-

(formerly in *Centroptilum*)

*Procloeon elsa* (Traver), 1935, n. comb. -NW-

(formerly in *Centroptilum*)

*Procloeon fragile* (McDunnough), 1923, n. comb. -NE-

(formerly in *Centroptilum*)

*Procloeon hobbsi* (Berner), 1946, n. comb. -SE-

(formerly in *Centroptilum*)

*Procloeon implicatum* (McDunnough), 1924, n. comb. -NW-

(formerly in *Cloeon*)
**Procloeon inanum** (McDunnough), 1924, **n. comb.** -NW- (formerly in Cloeon)

**Procloeon ingens** (McDunnough), 1923, **n. comb.** -NW- (formerly in Cloeon)

**Procloeon insignificans** (McDunnough), 1925, **n. comb.** -NE- (formerly in Cloeon)

**Procloeon intermediale** (McDunnough), 1931, **n. comb.** -NE- (formerly in Centroptilum)

**Procloeon mendax** (Walsh), 1862, **n. comb.** -NE- (formerly in Cloeon)

**Procloeon minor** (McDunnough), 1926, **n. comb.** -NE- (formerly in Cloeon)

**Procloeon oreophilum** (Edmunds), 1954, **n. comb.** -NW- (formerly in Centroptilum)

**Procloeon ozburni** (McDunnough), 1924, **n. comb.** -NE- (formerly in Centroptilum)

**Procloeon pennulatum** (Eaton), 1885, **n. comb.** -NW- (formerly in *Pseudocentroptilum*

[=Centroptilum infrequens McDunnough, 1924]

**Procloeon quaesitum** (McDunnough), 1931, **n. comb.** -NW- (formerly in Centroptilum)

**Procloeon rivulare** (Traver), 1935, **n. comb.** -NE- (formerly in Centroptilum)

**Procloeon rubropictum** (McDunnough), 1923, **n. comb.** -NE- (formerly in Cloeon)

**Procloeon rufostrigatum** (McDunnough), 1924, **n. comb.** -NE- (formerly in Centroptilum)

**Procloeon simile** (McDunnough), 1924, **n. comb.** -NE- (formerly in Centroptilum)

**Procloeon simplex** (McDunnough), 1925, **n. comb.** -NE- (formerly in Cloeon)

**Procloeon venosum** (Traver), 1935, **n. comb.** -SW- (formerly in Centroptilum)

**Procloeon vicinum** (Hagen), 1861, **n. comb.** -SE- (formerly in Cloeon)

**Procloeon viridocularis** (Berner), 1940, **n. comb.** -SE- (formerly in Centroptilum)

**Procloeon walshi** (McDunnough), 1929, **n. comb.** -NE- (formerly in Centroptilum)

**Pseudocentroptiloides** Jacob, 1986

*Pseudocentroptiloides usa* Waltz and McCafferty, 1989 -NE-
DISCUSSION

Acentrella Bengtsson


Remarks.— The genus Acentrella is mainly a northern boreal group with some proclivity for circumpolar species distributions. There has been some difference of opinion regarding its taxonomic status. Muller-Liebenau (1981, 1982) and Waltz and McCafferty (1987a,d) recognized Acentrella as a distinct monophyletic group related to Baetis. Novikova and Kluge (1987) have regarded it as a synonym of Baetis.

Acerpenna Waltz and McCafferty


Remarks.— Larvae of this distinctive genus are easily distinguished by the apically pointed gills of abdominal segment seven. Species were previously considered in Baetis; however, Acerpenna is not part of the Baetis complex because larvae lack the villopore of the femora (Waltz and McCafferty, 1987c). Acerpenna macdunnoughi and A. pygmaea are common stream species throughout much of eastern North America. McCafferty and Morihara (1979) discovered that A. macdunnoughi was facultatively parthenogenetic, being parthenogenetic in northern populations at the fringe of its range, but with males common in southern populations.

Apobaetis Day


Remarks.— Male adults of Apobaetis are unique in the Nearctic realm by being the only known two-winged baetid mayflies with paired marginal intercalaries in the forewings and a prominent penes plate. The larva of A. etowah is unknown.

Baetis Leach

Species identification.— Larvae: Morihara and McCafferty (1979a,b), Soluk (1981). Adults: Traver (1935), considering synonymies in Morihara and McCafferty (1979a); (as Pseudocloeon in part): Traver (1935), Daggy (1945), Burks (1953).

Remarks.— Numerous specific names that had been applied to North American Baetis were necessarily synonymized by Morihara and McCafferty (1979a) (see Guide below). Waltz and McCafferty (1987c) removed certain species from Baetis because, in addition to being distinct in other characteristics, they importantly lacked a villopore on the larval femora and therefore were not thought to have shared an immediate common ancestor with other Baetis spp. Several Middle American species that previously would have been assignable to Baetis are more appropriately placed in other genera, such as Moribaetis and Falcceon (Waltz and McCafferty, 1985b, 1987c).

Many Nearctic species previously considered in Pseudocloeon s. auctt. have been placed in Baetis (see Checklist above). In fact, all Nearctic species previously assigned to Pseudocloeon have been reassigned to other Nearctic genera (see Guide below). The
transfers and synonymies are based on extensive revisionary studies, including Waltz and McCafferty (1985a, 1986, 1987a,d,e). Type materials representing all specific names that have been associated with _Pseudocloeon_ in North America have been examined. South American species described as _Pseudocloeon_ are not congeneric with the type species but await generic reassignment until their status is more thoroughly studied (see also Waltz and McCafferty, 1987a; Flowers, 1987). Recombinations of Neotropical species could include _Apobaetis, Baetis, Baetodes, Cloeodes, Paracloeodes_ and possibly other.

_Baetis_, as constituted, now contains species with hindwings and species without hindwings. In addition to these variations, however, McCafferty and Provonsha (unpublished) have discovered an undescribed species of _Baetis_ from Indiana in which the males possess hindwings but the females do not. Such a phenomenon in Baetidae was first noted by Edmunds et al. (1976).

Morihara and McCafferty (1979a) suggested several species groups within North American Baetidae, a system somewhat modified from that formulated for European species by Müller-Liebenau (1970). These groups will require reevaluation in light of revisionary work since that time. The lapponicus group is basically equivalent to _Acentrella_; the rhodani, vernus, fuscatus, and propinquus groups are essentially still valid concepts; and the muticus group equals _Diphetor_ at least in part. Novikova and Kluge (1987) evidently would prefer to recognize some of these groupings or parts of them as subgenera of _Baetis_.

Flannagan and Flannagan (1982) listed all Manitoba species that had been known as _Pseudocloeon_ under the name _Baetis_, presumably on the basis of a suggestion by Keffermüller (1980) that _Pseudocloeon_ was entirely equivalent to _Baetis_. However, a formal synonymy was not made by Keffermüller, and no formal recombinations of names had been made at that time. Also, it should be kept in mind that we have thus far found that species previously classified in _Pseudocloeon_ belong variously to _Acentrella, Apobaetis, and Barbaetis_, as well as _Baetis_ (see Guide below). In addition, Edmunds (1974) found one species of Nearctic _Pseudocloeon_ to belong to _Paracloeodes_.

**Baetodes** Needham and Murphy


*Remarks.*— The ventrally oriented gills and outspread legs of the larvae of _Baetodes_ make them very distinctive among the Baetidae. Adults can be difficult to identify. However, Flowers (1987) described newly associated adults of three species and provided a revised generic diagnosis for the adult stage. The genus is undoubtedly of Neotropical origin, but with many Central and South American species. Species level revisionary research is required.

**Barbaetis** Waltz and McCafferty


*Remarks.*— The striking color pattern of the larvae, including the prominent dark band of the abdomen and cerci, provides a useful field character in distinguishing species of this genus from other Nearctic species (see whole larval figure of Provonsha and McCafferty, 1982). Larvae of this specialized Nearctic genus are found in medium sized to large rivers, usually in association with erosional zones and a pea gravel type of substrate (Provonsha and McCafferty, 1982; Waltz et al., 1985). Their color pattern may be an adaptation for living
in such habitats, possibly providing them with some cryptic protection from predators. The adult of *B. benfieldi* is unknown.

**Callibaetis** Eaton

*Species identification.*— Larvae: No reliable key to the larvae is available. Adults: Traver (1935) must be used tentatively, and considering synonymies given herein.

*Remarks.*— Species of this Western Hemisphere genus can be difficult to identify in either the larval or adult stage. Although color patterns of the wings of *Callibaetis* adults are often striking, they are not particularly good specific characters, being somewhat variable and highly prone to sexual dimorphism. Numerous species synonymies are given herein. We anticipate that even more synonyms will be discovered as more material becomes available for study. Comparative study of the species concepts applied in this genus indicate that many of the previously proposed species merely represent different geographic populations, either with some color variation or with no perceptible variation.

The genus *Callibaetis* is very distinctive among the Baetidae. Some workers (e.g., Riek, 1973; Gillies, 1990) would place it in a separate subfamily Callibaetinae, and Landa and Soldan (1985) considered the genus in a subfamily Cloeoninae. We prefer not to follow any subfamilial classification until more cladistic data on major baetid lineages become available.

**Camelobaetidius** Demoulin

*Species identification.*— Larvae (as *Dactylobaetis*): Traver and Edmunds (1968), Allen and Chao (1978). Adults (as *Dactylobaetis*): Traver and Edmunds (1968).

*Remarks.*— The definitive work on this genus was given by Traver and Edmunds (1968) under their generic name, *Dactylobaetis*. Demoulin (1966), however, while being aware of the comprehensive study being conducted by Traver and Edmunds, proposed the name *Camelobaetidius* for a single South American species (*C. leentvaari* Demoulin). We have examined the types of both *Camelobaetidius* and *Dactylobaetis* and must conclude that not only is there insufficient characterization for maintaining the two names, but also they represent an unnatural classification in that *Dactylobaetis* would be paraphyletic. Therefore, we recognize *Camelobaetidius* Demoulin [Type species: *Camelobaetidius leentvaari* Demoulin 1966:9, by original designation] as the senior subjective synonym of *Dactylobaetis* Traver and Edmunds [Type species: *Dactylobaetis warreni* Traver and Edmunds 1968:630, by original designation] and have formally transferred all North and Middle American species in the checklist above. South American species are formally transferred as follows: *Camelobaetidius anubis* (Traver and Edmunds) **n. comb.**, *C. cayumba* (Traver and Edmunds) **n. comb.**, *C. penai* (Traver and Edmunds) **n. comb.**, *C. phaedrus* (Traver and Edmunds) **n. comb.**, and *C. serapis* (Traver and Edmunds) **n. comb.**.

While larvae of this genus are easily distinguished from all other known baetid genera by the uniquely spatulate form of the claws, our preliminary studies of larval and adult characterization within the genus suggest that several specific synonymies will be required. The Northeast Region distribution indicated in the checklist as part of the range of *C. mexicanus* may appear to be an anomaly based on the otherwise entirely western distribution of the genus. Actually, however, *C. mexicanus* is known only from western Kansas in the Northeast Region (Liechti, 1982).
**Centroptilum** Eaton

*Species identification.*— Larvae: No reliable key to the larvae of Nearctic species is available, see instead descriptions of Traver (1935) (including *Neocloeon*), Burks (1953), Bergman and Hilsenhoff (1978b), and Lowen and Flannagan (1990a,b,c). Adults (including *Neocloeon*): Traver (1935).

*Remarks.*— As newly defined herein, species of *Centroptilum* may possess hindwings (hindwing pads present in the larval stage) or may completely lack hindwings (hindwing pads absent in the larval stage). The genus *Centroptilum* is restricted to include those species with adult males possessing a prominent medial spine between the forceps bases and an elongated terminal segment of the forceps. Lowen and Flannagan (1990c) have also recognized some such characteristics for *Centroptilum*. The world distribution of true *Centroptilum* cannot be ascertained until further studies of materials from other regions, are conducted. *Centroptilum* of the Afrotropics, which is essentially equivalent to Gillies recent *Afroptilum* (Gillies, 1999a) appears to be polyphyletic.

Larvae of *Centroptilum s. str.*, as pointed out by several earlier authors (Kazlauskas, 1972; Jacob, 1973; Keffermuller and Sowa, 1984), are unique among the more broadly included species of *Centroptilum s. I.* because of the presence of strongly expanded, apically truncated (slightly excavate medially) terminal segments of the labial palps. Several Nearctic larvae possess lateral spines on abdominal segments 8-9, which are not present in all species of the genus. We do not regard the presence or absence of such lateral spines as generic criteria. A more detailed discussion of the basis for the revision of *Centroptilum* will be published elsewhere (Waltz and McCafferty, in manuscript).

We have designated *Neocloeon* Traver [Type species: *Neocloeon alamance* Traver, by original designation] as a junior subjective synonym of *Centroptilum* Eaton. Comparisons of *Neocloeon* with *C. luteolum* clearly indicate the synonymy. The previous inclusion of *Neocloeon* as a junior synonym of *Cloeon* (Edmunds et al., 1976) is apparently based on the absence of hindwings. *Neocloeon*, however, is very distinct from the type species of *Cloeon*, *C. dipterum*.

We are aware that some larvae that we have assigned to *Procloeon* Bengtsson come close to our definition of *Centroptilum* larvae. Nevertheless, these larvae are associated with adults lacking the distinctive medial spine between the forceps bases of the male genitalia. Critical review of more larval-adult associations, such as that being provided by the rearings of Lowen and Flannagan (1990c), may result in refinements of the basic generic scheme that we propose. Our restriction of the concept of *Centroptilum* is based on the examination of types and comparisons with the Nearctic species and related world genera (see also discussions of *Cloeon* and *Procloeon*).

*Centroptilum* larvae, as here restricted, are typically found in slow or quiet waters (e.g., Sweeney and Vannote, 1984) often with silty or sandy bottoms. The small, cold-water, meandering brooks found in beaver pond meadows in the Upper Peninsula of Michigan represent a common type of habitat for *Centroptilum* (McCafferty, unpublished).

**Cloeodes** Traver

Remarks.— As larvae, species of Cloeodes may be distinguished in the field by a Centroptilum-like appearance, and on closer inspection, by their short edentate claws, simple gills, distinct bands of setae on the tibiae, and ventral abdominal setal tufts (high magnification may be required). Species of Cloeodes may possess hindwings, or hindwings may be absent. Waltz and McCafferty (1987b) gave a generic description of the adult stage; however, several species remain to be described as adults.

This dominantly Western Hemisphere genus is undoubtedly Neotropical in origin, with its most northern known distribution being Oak Creek Canyon in northern Arizona (Waltz and McCafferty, 1987a). Apparently some new species of Cloeodes have recently been discovered in Cuba by N. Kluge of Leningrad (Kluge, pers. comm.).

Cloeon Leach

Species identification.— Larvae and adults: Sowa (1975).
Remarks.— Only one species of Cloeon is present in North and Middle America. Previous keys written for Nearctic Cloeon actually are applicable to species of Procloeon and Centroptilum (see Guide below). The first verifiable records of Cloeon s. str. in the Nearctic were reported by Burks (1953) and Traver (1962). Flowers (1978) updated the Nearctic nomenclature based upon Sowa (1975). Our own review of several collections of C. cognatum compared with European material confirmed the uniqueness of this species in the Nearctic fauna.

Although our restriction of the genus Cloeon in the Nearctic may be regarded by some as severe, it is the only defensible conclusion we can make based on our examination of extensive collections of adults and larvae of pertinent species in North America and comparisons with the adults and larvae of the type species of Cloeon, C. dipterum from Europe (Waltz and McCafferty, unpublished). We concur with Edmunds et al. (1976) that in the Nearctic Cloeon s. auctt. and Centroptilum s. auctt. make up a cohesive unit. The majority of these species, however, belong neither to Cloeon s. str. nor to Centroptilum s. str. but rather are assignable to Procloeon Bengtsson (see Guide below).

Diphetor Waltz and McCafferty

Remarks.— This genus, which may eventually prove to be Holarctic, is distinguished in the larval stage by the loss of gills 1 and in the adults by unique wing venation. Diphetor is not a member of the Baetis complex because it lacks the larval femoral villopore. Because of this and on the basis of other characteristics, its species were removed from Baetis by Waltz and McCafferty (1987c). Waltz and McCafferty (unpublished) have studied the undescribed larva of D. devinctus, which presently keys to D. hageni in Morihara and McCafferty (1979a).

Bergman and Hilsenhoff (1978c) experimentally showed D. hageni to be obligate parthenogenetic, as had been suggested by the field observations of Ide (1930, 1937). At least California populations of D. devinctus are sexually reproductive (Traver, 1935).

Fallceon Waltz and McCafferty

Species identification.— Larvae (as Baetis): Morihara and McCafferty (1979a). Adults
SYNOPSIS OF BAETIDAE

(as Baetis): Traver (1935), considering synonymies in Morihara and McCafferty (1979a).

Remarks.—The Western Hemisphere genus *Fallceon* is distinguishable in the larval stage by numerous characteristics, including the absence of a femoral villopore; adults are easily told from other Western Hemisphere genera by the their characteristic hindwings (Waltz and McCafferty, 1987c). A review of large series of Nearctic *Fallceon* larvae has indicated the presence of some consistent patterns of morphological variation. Some of these variants may ultimately require recognition as distinct species, but this cannot be determined definitively without larval-adult reared associations becoming available.

To avoid confusion that might arise in the future in trivial name formation when combining with *Fallceon*, it should be noted that the generic nomen was an arbitrary combination of letters designated as masculine in gender. Thus, the genus is not neuter as might be construed when referring to some other neuter names in Baetidae, such as Choeon or *Heterocloeon*, which have similar three-letter endings.

**Guajirolus** Flowers


Remarks.—Larvae of this Neotropical genus are easily recognized on the basis of the distinctive mouthparts. Although this genus is noted as a new taxon since 1976 in the following Guide, it actually has been known since Roback (1966) referred to a Peruvian population of it as Genus 3 nr Pseudocloeon. Flowers (1985) later found it in Panama and gave it a formal name. Additional species of this genus are pending description (Waltz and McCafferty, in manuscript).

**Heterocloeon** McDunnough


Remarks.—McCafferty and Provonsha (1975) revalidated this Nearctic genus, affirmed its distinctiveness, and showed that the name Rheobaetis was synonymous with *Heterocloeon*. Larvae of the genus are typically found in medium sized, clean-water streams with heterogeneous substrates.

**Moribaetis** Waltz and McCafferty

*Species identification.*—Larvae and Adults: Waltz and McCafferty (1985b).

Remarks.—This genus appears to be restricted to tropical areas in the Western Hemisphere. The large size of the larvae, unusual claw structure (similar only to Baetodes), and unique mouthpart structure provide useful identification characters for this genus. Among other places, larvae have been collected out of the water in the splash zone along the edge of small waterfalls of some high elevation streams in Costa Rica (Waltz and McCafferty, 1985b, McCafferty, unpublished).

**Paracloeodes** Day

*Species identification.*—Larvae and adults: Day (1955).

Remarks.—The placement of *Paracloeodes abditus* Day as a junior subjective synonym of *P. minutus* (Daggy) is based on an examination and comparison of the type series associated with the two names as well as comparisons with other available collections of *Paracloeodes*
larvae and adults from North America.

The genus is apparently indigenous to the Western Hemisphere. Kondratieff and Harris (1986) provided the only data-verified record of Paracloeodes for the Southeast Region, although those workers were unable to assign a species name. In the Northeast Region, we have found it as far east as Lafayette, Indiana, where we have collected large populations of P. minutus larvae along the edges of the Wabash River in summer.

**Procloeon** Bengtsson

*Species identification.*— Larvae: No reliable keys to species are presently available, see instead descriptions under Centroptilum and Cloeon of Traver (1935) and Burks (1953). Adults (as Centroptilum or Cloeon): Traver (1935).

*Remarks.*— The genus *Procloeon* is widespread in the Palearctic, Afrotropical, and Oriental realms, and is herein reported as well represented in the Nearctic realm. It is distinct from both *Cloeon* and Centroptilum in the larval and adult stage. We have found that the majority of species previously placed in Centroptilum and Cloeon in the Nearctic to be congeneric with the type of *Procloeon*, *P. bifidum* (see Guide below). Furthermore, these species are not assignable to *Pseudocentroptilum* Bogocescu, as would be suggested by the recent work of Keffermüller and Sowa (1984). In fact, the genus *Pseudocentroptilum* is doubtfully distinct from *Procloeon*, although several world species have recently been assigned to it, primarily to recognize their distinct separation from the type of Centroptilum, C. luteolum and its cognates. The comprehensive morphological bases for our revision will be published elsewhere (Waltz and McCafferty, in manuscript).

There may be some problems in clearly diagnosing certain western North American larvae to either Centroptilum or Procloeon. As more larvae are associated with their respective adults, as being provided by Lowen and Flannagan (1990c), we anticipate this problem will be rectified and probably require a refinement of the presently relatively strict definition of the *Procloeon*.

**Pseudocentroptiloides** Jacob


*Remarks.*— As larvae, this genus is relatively easy to identify in field samples by the extremely elongated claws, Centroptilum-like external morphology, and distinctive labium. The genus demonstrates a Laurasian type of distribution pattern, being known from the Holarctic and Oriental realms (Waltz and McCafferty, 1989). We suspect that it may eventually be found to be represented by more than one species in the Western Hemisphere.

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A GUIDE TO NAME CHANGES AND ADDED TAXA (*) SINCE 1976

*Baetis* Leach, 1815

= *Acentrella* Bengtsson, 1912, in part (Waltz and McCafferty, 1987d); = *Acerpenna* Waltz and McCafferty, 1987, in part (Waltz and McCafferty, 1987c); = *Baetis* Leach, 1815, in part, (herein); = *Diphetor* Waltz and McCafferty, 1987, in part (Waltz and McCafferty, 1987c); = *Fallceon* Waltz and McCafferty, 1987, in part (Waltz and McCafferty, 1987c); = *Heterocloeon* McDunnough, 1925, in part (Morihara and McCafferty, 1979c); = *Moribaetis* Waltz and McCafferty, 1985, in part (Waltz and McCaff-
ferty, 1985b)
Baetis akataleptos McDunnough, 1926
   = Acerpenna akataleptos (McDunnough) (herein)
Baetis amplus (Traver), 1932
   = Acentrella ampla Traver (Waltz and McCafferty, 1987d, as originally described)
Baetis anachris Burks, 1953
   = Baetis brunneicolor McDunnough, 1925 (Morihara and McCafferty, 1979a)
Baetis australis Traver, 1932
   = Baetis frondalis McDunnough, 1925 (Morihara and McCafferty, 1979a)
Baetis baeticatus Burks, 1953
   = Baetis frondalis McDunnough, 1925 (Bergman and Hilsenhoff, 1978a)
*Baetis buenoi Allen, 1985
   = Fallceon buenoi (Allen) (Waltz and McCafferty, 1987c)
   = Fallceon quilleri (Dodds), 1923 (herein)
Baetis bundyae Lehmkuhl, 1973
   = Baetis macani bundyae Lehmkuhl (Morihara and McCafferty, 1979d)
*Baetis byblis Allen and Murvosh, 1983
   = Fallceon byblis (Allen and Murvosh) (Waltz and McCafferty, 1987c)
   = Fallceon quilleri (Dodds), 1923 (herein)
*Baetis caelestis Allen and Murvosh (1983)
Baetis cleptis Burks, 1953
   = Baetis quilleri Dodds, 1923 (Morihara and McCafferty, 1979a)
   = Fallceon quilleri (Dodds) (Waltz and McCafferty, 1987c)
Baetis dardanus McDunnough, 1923 (revalidation by Morihara and McCafferty, 1979b)
Baetis devinctus Traver, 1935
   = Diphetor devinctus (Traver) (Waltz and McCafferty, 1979c)
Baetis eatoni Kimmins, 1934
   = Fallceon eatoni (Kimmins) (Waltz and McCafferty, 1987c)
   = Fallceon quilleri (Dodds), 1923 (herein)
Baetis elachistis Burks, 1953
   = Baetis dardanus McDunnough, 1923 (Morihara and McCafferty, 1979b)
Baetis endymion Traver, 1935
   = Baetis quilleri Dodds, 1923 (Morihara and McCafferty, 1979a)
   = Fallceon quilleri (Dodds) (Waltz and McCafferty, 1987c)
Baetis erebus Traver, 1935
   = Baetis quilleri Dodds, 1923 (Morihara and McCafferty, 1979a)
   = Fallceon quilleri (Dodds) (Waltz and McCafferty, 1987c)
Baetis frivolus McDunnough, 1925
   = Heterocloeon frivolum (McDunnough) (Morihara and McCafferty, 1979c)
*Baetis garcianus (Traver), 1938 (geographic addition herein)
   = Fallceon garcianus (Traver) (herein).
Baetis hageni Eaton, 1885
   = Diphetor hageni (Eaton) (Waltz and McCafferty, 1987c)
Baetis harti McDunnough, 1924
   = Acerpenna harti (McDunnough) (herein)
Baetis hiemalis Leonard, 1950
Baetis brunneicolor McDunnough, 1925 (Morihara and McCafferty, 1979a)

Baetis incertans McDunnough, 1925
= Baetis vagans McDunnough, 1925 (Bergman and Hilsenhoff, 1978a)
= Baetis tricaudatus Dodds, 1923 (Morihara and McCafferty, 1979a)

Baetis insignicans McDunnough, 1926
= Acentrella insignificans (McDunnough)(Waltz and McCafferty 1982d)

Baetis intermedius Dodds, 1923
= Baetis tricaudatus Dodds, 1923 (Morihara and McCafferty, 1979a)

Baetis jesmondensis McDunnough, 1938
= Baetis tricaudatus Dodds, 1923 (Waltz and McCafferty, 1990)

Baetis lapponicus (Bengtsson), 1912
= Acentrella lapponica Bengtsson (Muller-Liebenau, 1981, as originally described)

Baetis leechi Day, 1954
= Baetis quilleri Dodds, 1923 (Morihara and McCafferty, 1979a)
= Fallceon quilleri (Dodds) (Waltz and McCafferty, 1987c)

Baetis levitans McDunnough, 1925
= Baetis flavistraga McDunnough, 1921 (Morihara and McCafferty, 1979a)

*Baetis libos Allen and Murvosh 1987
= Baetis magnus McCafferty and Waltz, 1986 (herein)

*Baetis longipalpus Morihara and McCafferty 1979b

Baetis macdunnoughi Ide, 1937
= Acrpenna macdunnoughi (Ide) (Waltz and McCafferty, 1987c)

*Baetis maculipennis Flowers, 1979
= Moribaetis maculipennis (Flowers) (Waltz and McCafferty, 1985b)

*Baetis magnus McCafferty and Waltz, 1986

Baetis nanus McDunnough, 1923
= Baetis flavistriga McDunnough, 1921 (Morihara and McCafferty, 1979a)

*Baetis notos Allen and Murvosh 1987

Baetis pallidulus McDunnough, 1924
= Baetis flavistregia McDunnough, 1921 (Morihara and McCafferty, 1979a)

Baetis parvus Dodds, 1923
= Baetis hageni Eaton, 1885 (Morihara and McCafferty, 1979a)
= Diphetor hageni (Eaton) (Waltz and McCafferty, 1987c)

Baetis phoebus McDunnough, 1923
= Baetis pallidulus McDunnough, 1924 (Bergman and Hilsenhoff, 1978a)
= Baetis flavistriga McDunnough, 1921 (Morihara and McCafferty, 1979a)

Baetis phyllis Burks, 1953
= Baetis brunneicolor McDunnough, 1925 (Morihara and McCafferty, 1979a)

*Baetis poyei (Eaton), 1885

Baetis pygmaeus (Hagen), 1861
= Acrpenna pygmaea (Hagen) (Waltz and McCafferty, 1987c)

Baetis quebecensis McDunnough [sic]
= Baetis phoebus McDunnough, 1923 (Bergman and Hilsenhoff, 1978a)
= Baetis quebecensis Hubbard, 1974 (new name for Baetis cingulatus McDunnough, 1925) (incorrectly ascribed to McDunnough by Edmunds et al., 1976) (Morihara and McCafferty, 1979a)
SYNOPSIS OF BAETIDAE

= Baetis flavistriga McDunnough, 1921 (Morihara and McCafferty, 1979a)
Baetis quillleri Dodds, 1923
= Fallceon quillleri (Dodds) (Waltz and McCafferty, 1987c)
Baetis salvinii Eaton, 1885
= Moribaetis salvini (Eaton) (Waltz and McCafferty, 1985b)
= Baetis tricaudatus Dodds, 1923 (herein)
*Baetis sp. A Morihara and McCafferty, 1979a
= Baetis caelestis Allen and Murvosh, 1983 (McCafferty and Waltz, 1987)
*Baetis sp. B Morihara and McCafferty, 1979a
= Baetis magnus McCafferty and Waltz, 1986 (McCafferty and Waltz, 1986)
*Baetis sp. C Morihara and McCafferty, 1979a
Baetis spiechi Berner, 1940
= Baetis pygmaeus (Hagen), 1861 (Morihara and McCafferty, 1979a)
= Acerpenna pygmaea (Hagen) (Waltz and McCafferty, 1987c)
Baetis spinosus McDunnough, 1925
= Baetis propinquus (Walsh), 1863) (Bergman and Hilsenhoff, 1978a)
Baetis vagans McDunnough, 1925
= Baetis tricaudatus Dodds, 1923 (Morihara and McCafferty, 1979a)
Baetodes bellus Mayo, 1972
= Baetodes deficiens Cohen and Allen, 1972 (Cohen and Allen, 1978)
Baetodes furvus Mayo, 1973
= Baetodes fuscipes Cohen and Allen, 1972 (Cohen and Allen, 1978)
*Baetodes velmae Cohen and Allen 1978 (Cohen and Allen, 1978)
Baetodes veracrusensis Mayo, 1972
= Baetodes caritus Cohen and Allen, 1972 (Cohen and Allen, 1978)
*Barbaetis Waltz and McCafferty, 1985 in Waltz et al. (1985)
*Barbaetis benfieldi Kennedy, 1985 in Waltz et al. (1985)
*Barbaetis cestus (Provonsha and McCafferty), 1982 (Provonsha and McCafferty, 1982)(as Pseudocloeon)
Callibaetis brevicostatus Daggy, 1945
= Callibaetis skokianus Needham, 1903 (herein)
Callibaetis carolus Traver, 1935
= Callibaetis americanus Banks, 1900 (herein)
Callibaetis Coloradensis Banks, 1900
= Callibaetis americanus Banks, 1900 (herein)
*Callibaetis completa Banks, 1924 (geographic addition herein)
Callibaetis doddsii Traver, 1935
= Callibaetis pictus (Eaton), 1871 (herein)
Callibaetis evergreenensis Thew, 1959
= Callibaetis americanus Banks, 1900 (herein)
Callibaetis hebes Upholt, 1936
= Callibaetis americanus Banks, 1900 (herein)
Callibaetis pacificus Seemann, 1927
Callibaetis pictus (Eaton), 1871 (herein)

Callibaetis semicostatus Banks, 1914
   = Callibaetis pallidus Banks, 1900 (herein)

Callibaetis signatus Banks, 1918
   = Callibaetis pictus (Eaton), 1871 (herein)

Callibaetis traverae Upholt, 1937
   = Callibaetis fluctuans (Walsh), 1862 (herein)

Centroptilum Eaton, 1869
   = Centroptilum Eaton, 1869, in part (herein); = Procloeon Bengtsson, 1915, in part (herein)

Centroptilum album McDunnough, 1926
   = Procloeon album (McDunnough) (herein)

Centroptilum asperatum Traver, 1935
   = Procloeon asperatum (Traver) (herein)

Centroptilum bellum McDunnough, 1924
   = Procloeon bellum (McDunnough) (herein)

Centroptilum caliginosum McDunnough, 1925
   = Procloeon caliginosum (McDunnough) (herein)

Centroptilum conturbatum McDunnough, 1929
   = Procloeon conturbatum (McDunnough) (herein)

Centroptilum convexum Ide, 1930
   = Procloeon convexum (Ide) (herein)

Centroptilum elsa Traver, 1935
   = Procloeon elsa (Traver) (herein)

Centroptilum fragile McDunnough, 1923
   = Procloeon fragile (McDunnough) (herein)

Centroptilum hobbsi Berner, 1946
   = Procloeon hobbsi (Berner) (herein)

Centroptilum infrequens McDunnough, 1924
   = Pseudocentroptilum pennulatum (Eaton), 1885 (Lowen and Flannagan 1990b)
   = Procloeon pennulatum (Eaton) (herein)

Centroptilum intermediale McDunnough, 1931
   = Procloeon intermediale (McDunnough) (herein)

Centroptilum oreophilum Edmunds, 1954
   = Procloeon oreophilum (Edmunds) (herein)

Centroptilum ozburni McDunnough, 1924
   = Procloeon ozburni (McDunnough) (herein)

Centroptilum quaesitum McDunnough, 1931
   = Procloeon quaesitum (McDunnough) (herein)

Centroptilum rivulare Traver, 1935
   = Procloeon rivulare (Traver) (herein)

Centroptilum rufostrigatum McDunnough, 1924
   = Procloeon rufostrigatum (McDunnough) (herein)

Centroptilum similie McDunnough, 1924 [sic] in Edmunds et al. (1976)
   = Procloeon similie (McDunnough) (herein)

Centroptilum venosum Traver, 1935
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= Procloeon venosum (Traver) (herein)
Centroptilum viridocularis Berner, 1940
  = Procloeon viridocularis (Berner) (herein)
Centroptilum walshi McDunnough, 1929
  = Procloeon walshi (McDunnough) (herein)

*Cloeodes* Traver, 1938 (Waltz and McCafferty, 1987a)
*Cloeodes consignatus* Traver, 1938 (geographic addition herein)
*Cloeodes exogitatus* Waltz and McCafferty 1987 (Waltz and McCafferty, 1987a)
*Cloeodes macrolamellus* Waltz and McCafferty 1987 (Waltz and McCafferty, 1987a)
*Cloeodes maculipes* Traver, 1938 (geographic addition herein)
*Cloeodes peninsulus* Waltz and McCafferty 1987 (Waltz and McCafferty, 1987a)

Cloeon Leach, 1815
  = Centroptilum Eaton, 1869, in part (herein); = Cloeon Leach, 1815, in part (herein);
  = Procloeon Bengtsson, 1915, in part (herein)
Cloeon alamance (Traver), 1932
  = Centroptilum alamance (Traver) (herein)
Cloeon dipterum (Linnaeus), 1761
  = Cloeon cognatum Stephens, 1835 (in North America) (Flowers, 1978)
Cloeon implicatum McDunnough, 1924
  = Procloeon implicatum (McDunnough) (herein)

Cloeon inanum McDunnough, 1924
  = Procloeon inanum (McDunnough) (herein)

Cloeon ingens McDunnough, 1923
  = Procloeon ingens (McDunnough) (herein)

Cloeon insignificans McDunnough, 1925
  = Procloeon insignificans (McDunnough) (herein)

Cloeon mendax (Walsh), 1862
  = Procloeon mendax (Walsh) (herein)

Cloeon minor McDunnough, 1925
  = Procloeon minor (McDunnough) (herein)

Cloeon rubropictum McDunnough, 1923
  = Procloeon rubropictum (McDunnough) (herein)

Cloeon simplex McDunnough, 1925
  = Procloeon simplex (McDunnough) (herein)

Cloeon triangulifer McDunnough
  = Centroptilum triangulifer (McDunnough) (herein)

Cloeon vincinum (Hagen), 1861
  = Procloeon vincinum (Hagen) (herein)

Dactylobaetis Traver and Edmunds, 1968
  = Camelobaetidius Demoulin, 1966 (herein)

Dactylobaetis arriga Traver and Edmunds, 1968
  = Camelobaetidius arriga (Traver and Edmunds) (herein)

Dactylobaetis cepheus Traver and Edmunds, 1968
  = Camelobaetidius cepheus (Traver and Edmunds) (herein)
Dactylobaetis chiapus Traver and Edmunds, 1968
  = Camelobaetidius chiapus (Traver and Edmunds) (herein)
Dactylobaetis jenseni Traver and Edmunds, 1968
  = Camelobaetidius jenseni (Traver and Edmunds) (herein)
Dactylobaetis mexicanus Traver and Edmunds, 1968
  = Camelobaetidius mexicanus (Traver and Edmunds) (herein)
Dactylobaetis musseri Traver and Edmunds, 1968
  = Camelobaetidius musseri (Traver and Edmunds) (herein)
* Dactylobaetis navis Allen and Chao, 1978
  = Camelobaetidius navis (Allen and Chao) (herein)
* Dactylobaetis salinus Allen and Chao, 1978
  = Camelobaetidius salinus (Allen and Chao) (herein)
* Dactylobaetis sinaloa Allen and Chao, 1978
  = Camelobaetidius sinaloa (Allen and Chao) (herein)
* Dactylobaetis trivialis Allen and Chao, 1978
  = Camelobaetidius trivialis (Allen and Chao) (herein)
Dactylobaetis warreni Traver and Edmunds, 1968
  = Camelobaetidius warreni (Traver and Edmunds) (herein)
Dactylobaetis zenobia Traver and Edmunds, 1968
  = Camelobaetidius zenobia (Traver and Edmunds) (herein)

Fallceon buenoi (Allen), 1985 (Waltz and McCafferty, 1987c)
  = Fallceon quilleri (Dodds), 1923 (herein)
Fallceon byblis (Allen and Murvosh), 1983 (Waltz and McCafferty, 1987c)
  = Fallceon quilleri (Dodds), 1923 (herein)
* Fallceon garcianus (Traver), 1938 (geographic addition herein)
* Fallceon poeyi (Eaton), 1885 (geographic addition herein)

* Genus Incertae Allen and Murvosh, 1983
  = Cloeodes peninsulus Waltz and McCafferty, 1987 (Waltz and McCafferty, 1987a)

* Guajirolis Flowers, 1985
* Guajirolis ektrapeloglossa Flowers, 1985
* Moribaetis Waltz and McCafferty, 1985
* Moribaetis macaferti Waltz, 1985 in Waltz and McCafferty (1985b)
* Moribaetis maculipennis (Flowers), 1979 (Waltz and McCafferty, 1985b)

Neocloeon Traver, 1932
  = Centroptilum Eaton, 1869, s. str. (herein)

* Paracloeodes portoricensis Traver, 1938 (geographic addition herein)
Paracloeodes abditus Day, 1955
  = Paracloeodes minutus (Daggy), 1945 (herein)

Pseudocloeon Klapalek, 1905
  = Acentrella Bengtsson, 1912, in part (Waltz and McCafferty, 1987d); Apobaetis Day,
1955, in part (Waltz and McCafferty, 1986); = *Baetis* Leach, 1815, in part (herein);
= *Barbaetis* Waltz and McCafferty, 1985, in part (herein)

*Pseudocloeon* alachua Berner, 1940
= *Baetis* alachua (Berner) (herein)

*Pseudocloeon* anoka Daggy, 1945
= *Baetis* punctiventris (McDunnough), 1923 (herein)

*Pseudocloeon* bimaculatum Berner, 1946
= *Baetis* bimaculatus (Berner) (herein)

*Pseudocloeon* carolina (Banks), 1924
= *Acentrella* carolina (Banks) (Waltz and McCafferty, 1987d)

*Pseudocloeon* chlorops (McDunnough), 1923
= *Baetis* dubius (Walsh), 1862 (herein)

*Pseudocloeon* cingulatum McDunnough, 1931
= *Baetis* cinctatus McCafferty and Waltz (herein)

*Pseudocloeon* edmundsi Jensen, 1969
= *Baetis* punctiventris (McDunnough), 1923 (herein)

*Pseudocloeon* elliottii Daggy, 1945
= *Baetis* elliottii (Daggy) (herein)

*Pseudocloeon* etowah Traver, 1935
= *Apoebaetis* etowah (Traver) (Waltz and McCafferty, 1986)

*Pseudocloeon* futile McDunnough, 1931
= *Baetis* futile (McDunnough) (herein)

*Pseudocloeon* ida Daggy, 1945
= *Baetis* elliottii (Daggy), 1945 (herein)

*Pseudocloeon* myrsum Burks, 1953
= *Baetis* punctiventris (McDunnough), 1923 (herein)

*Pseudocloeon* parvulum McDunnough, 1932
= *Baetis* armillatus Waltz and McCafferty (herein)

*Pseudocloeon* punctiventris McDunnough, 1923
= *Baetis* punctiventris (McDunnough) (herein)

*Pseudocloeon* rubrolaterale McDunnough, 1931
= *Baetis* rubrolaterale (McDunnough) (herein)

*Pseudocloeon* turbidum McDunnough, 1924
= *Acentrella* turbida (McDunnough) (Waltz and McCafferty, 1987d)

*Pseudocloeon* veteris McDunnough, 1924
= *Baetis* veteris (McDunnough) (herein)

*Pseudocloeon* virile McDunnough, 1923
= *Baetis* virile (McDunnough) (herein)

*Pseudocentroptiloides* Jacob, 1986 (Waltz and McCafferty, 1989)

*Pseudocentroptiloides usa* Waltz and McCafferty, 1989

*Pseudocentroptilum* pennulatum (Eaton), 1885 (Lowen and Flannagan, 1990b)
= *Procloeon* pennulatum (Eaton) (herein)
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LITERATURE CITED


