1990

Southeastern caddisfly fauna: origins and affinities

Steven W. Hamilton

John C. Morse

Follow this and additional works at: https://tigerprints.clemson.edu/bio_pubs

Recommended Citation

Please use publisher's recommended citation.

This Article is brought to you for free and open access by the Biological Sciences at TigerPrints. It has been accepted for inclusion in Publications by an authorized administrator of TigerPrints. For more information, please contact kokeefe@clemson.edu.

SOUTHEASTERN CADDISFLY FAUNA: ORIGINS AND AFFINITIES

STEVEN W. HAMILTON
The Center for Field Biology
Austin Peay State University
Clarksville, Tennessee 37044

JOHN C. MORSE
Department of Entomology
Clemson University
Clemson, South Carolina 29634

ABSTRACT

About 40% of the 1369 Nearctic caddisfly species occur in the southeastern portion of North America, with 12% being endemic to it. Using techniques of cladistic historical biogeography, generalized tracks were found among Trichoptera species that link the Southeast with areas outside of the continent and with areas elsewhere in the Nearctic Region. A few tracks are known internally among the major southeastern areas of endemism, but none are sufficiently well corroborated to be considered generalized. Intercontinentally, the most recent generalized tracks are with the Eastern Palearctic, Neotropical, and Western Palearctic areas of endemism. At least 16 species occur exclusively in both the southeastern part of the Nearctic Region and the Neotropical Region, suggesting a greater modern bio-continuity between these areas than with other intercontinental regions. Within North America, the Southeast is most properly considered a subset of the Eastern Nearctic area of endemism or, on a more refined scale, as a mosaic of at least three areas of endemism. The biota of the Southeastern Coastal Plain, especially, probably has experienced many episodes of cosmopolitanism and vicariance through time.

RESUMEN

Aproximadamente el 40% de las especies Neárticas de frigáneas ocurren en la porción sudeste de Norte América, el 12% siendo endémicas. Usando las técnicas de biogeografía histórica cladística, se encontraron trazas generales entre especies de Tricópteros que conectan el sudeste con áreas fuera del continente y con áreas de otros lugares de la región Neártica. Algunas trazas se conocen internamente entre las principales áreas de endemismo en el sudeste, pero ninguna está suficientemente corroborada para considerarla generalizada. Intercontinentalmente, las trazas generalizadas más reciente se encuentran en las áreas de endemismo Paleártico del Este, Neotropical, y Paleártico del Oeste. Por lo menos 16 especies ocurren exclusivamente en ambas la parte sudeste de la Región Neártica y en la Región Neotropical, lo que sugiere una bio-continuidad mayor entre estas áreas, que con otras regiones intercontinentales. Dentro de Norte América, el sudeste es el más propiamente considerado como un grupo de la región Neártica del Este del endemismo, o en una escala más refinada, como un mosaico de por lo menos tres áreas de endemismo. La biota de la Llanura Costera del Sudeste, probablemente ha experimentado muchos episodio de cosmopolitismo y vicarismo a través del tiempo.

The caddisflies, or Trichoptera, are a monophyletic group of holometabolous insects generally considered to be the sister group of the moths, or Lepidoptera. Their eggs, larvae, and pupae develop almost exclusively in freshwater environments, most abun-

dantly in ponds, lakes, creeks, and rivers, but also in small snowmelt pools, seeps, springs, and even ocean surf. About a half dozen species worldwide have terrestrial, or virtually terrestrial larvae. In freshwater habitats, eggs usually are found in gelatinous-matrix masses attached to stable surfaces, either terrestrial or aquatic; larvae may be found burrowing in the hyporheic zone beneath the aquatic substrate, clinging to stones or other solid materials, climbing vegetation, sprawling on the stream or pond bottom, or swimming; pupae typically are buried in the hyporheic zone beneath the aquatic substrate or attached to stable benthic materials (Wiggins, 1984, 1987).

In North America, there are about 1369 caddisfly species (Table 1) in 149 genera in 22 families. A total of 544 of these species, or about 40%, occur in the southeastern United States (as defined in the Introduction to this symposium), 168 of them exclusively (about 12% of all Nearctic species). Among families with more than 100 North American species, Hydroptilidae, Hydropsychidae, and Leptoceridae are disproportionately well represented in the Southeast (137, 84, and 76 species, representing 59%, 55%, and 67% of their respective families) and also show high percentages of endemism (25%, 13%, and 19%, respectively). Limnephilidae and Rhyacophilidae are poorly represented (29 and 25 species, 10% and 20%, respectively), with low percentages of endemism (2% and 5%, respectively).

These data and the caddisfly distributions that follow are based on our working checklist of Nearctic Trichoptera, which is too extensive to present here (currently nearly 250 manuscript pages). The most recently published Nearctic checklist was provided by Ross (1944); the *Trichopterorum Catalogus* (Fischer, 1960-1973) gave distribu-

TABLE 1. NORTH AMERICAN TRICHOPTERA SPECIES PRESENT OR ENDEMIC IN THE SOUTHEASTERN UNITED STATES, WITH FAMILIES RANKED BY NUMBER OF SPECIES PRESENT IN THOSE STATES.

Family	Total spp. in N. Amer.	Total spp. in SE states/ percent of N. Amer. spp.	Endemic spp. in SE states/ percent of N. Amer. spp.
Hydroptilidae	231	137/59%	57/25%
Hydropsychidae	154	84/55%	20/13%
Leptoceridae	113	76/67%	21/19%
Polycentropodidae	76	41/54%	10/13%
Lepidostomatidae	66	31/47%	13/20%
Limnephilidae	293	29/10%	5/ 2%
Glossosomatidae	77	26/34%	9/12%
Rhyacophilidae	126	25/20%	6/ 5%
Brachycentridae	36	19/53%	4/11%
Philopotamidae	47	19/40%	5/11%
Uenoidae	47	13/28%	6/13%
Sericostomatidae	14	11/79%	7/50%
Phryganeidae	28	9/32%	0/ 0%
Odontoceridae	13	8/62%	2/15%
Molannidae	8	5/63%	0/ 0%
Psychomyiidae	18	4/22%	1/ 6%
Helicopsychidae	8	3/38%	1/13%
Beraeidae	3	2/67%	1/33%
Calamoceratidae	5	2/40%	0/ 0%
Ecnomidae	1	0/ 0%	0/ 0%
Hydrobiosidae	3	0/ 0%	0/ 0%
Xiphocentronidae	2	0/ 0%	0/ 0%
TOTAL/MEAN %	1,369	544/40%	168/12%

tions for all world species through 1960; and subsequent records were made available in scattered publications. G. B. Wiggins and O. S. Flint, Jr., (pers. com.) are preparing an updated North American caddisfly species checklist for publication.

HISTORICAL BIOGEOGRAPHY TECHNIQUES AND DEFINITIONS

To use cladistic methods in historical biogeography (e.g., Nelson & Platnick, 1981, Allen, 1984, Humphries & Parenti, 1986), one first identifies areas of endemism by congruence of limits of distribution for many different taxa. These can be identified on any of several scales, from the six principal intercontinental biogeographical regions for terrestrial organisms (Sclater, 1858) to intracontinental biomes and communities (Andrewartha & Birch, 1954). One then examines the phylogenies of these taxa to discover their interrelated patterns of historical relationships. Phylogenetic patterns among taxa in a minimum of three different areas of endemism suggest patterns of historical relationship among those areas. Two areas of endemism that are more closely related to each other than to any other such area are said to be connected by a "track." Several congruent tracks constitute a "generalized track" whose probability of occurrence by chance alone is very small, suggesting a common cause.

Areas of Endemism: Intercontinentally, Sclater's (1858) six biogeographic regions have merit as areas of endemism for caddisflies (Ross, 1956, 1967). In addition, the Palearctic Region appears to have eastern and western areas of endemism (Levanidova, 1982, Malicky, 1983). Concerning large-scale areas of endemism in North America, caddisflies generally occur either east of the Rocky Mountains or in and west of the Rocky Mountains (Ross, 1956, Allen, 1984).

As mentioned in the Introduction to this symposium, the three major areas of endemism occurring within "the Southeast" are the Eastern Highlands, the Interior Highlands, and the Southeastern Coastal Plain (Introduction, Fig. 1). Obviously, although much or most of each of these areas of endemism lies within "the Southeast," each also extends beyond its arbitrary political borders. Substantial evidence for the southeastern Nearctic areas of endemism based on the caddisflies has been presented for the Eastern Highlands by Etnier & Schuster (1979), Unzicker et al (1982), Harris (1986), Lago & Harris (1987), and Morse et al (1989); for the Interior Highlands by Unzicker et al (1970) and Bowles & Mathis (1989); and for the Southeastern Coastal Plain by Blickle (1962), Morse et al (1980), Unzicker et al (1982), Harris et al (1982a, 1982b, 1984), Holzenthal et al (1982), Lago et al (1982), Harris (1986), and Lago & Harris (1987). These include at least 104 species endemic for the Eastern Highlands, 13 species endemic for the Interior Highlands, and 89 species endemic for the Southeastern Coastal Plain.

Tracks and Associations: Few cladistic analyses have been made for the Trichoptera either on a worldwide scale or for the Nearctic species. Therefore, evidence for "tracks," as discussed above, is limited and of various levels of usefulness. For us to infer the phylogenies of each of the caddisfly taxa cited below in order to substantiate "tracks" is beyond the scope of this work. Therefore, in addition to tracks, we cite three classes of data which provide evidence for recent and historical associations (panbiogeographic "tracks" of Croizat, 1958). The relative generality of an association, as determined by the number of taxa supporting it, provides evidence inversely for the effectiveness of recent and historical ecological barriers between the areas of endemism; i.e., the more general the association, the less effective has been the ecological barrier either recently or at some time in the past. Unlike track analysis, analysis of associations provides no evidence for their relative recency.

A track is recognizable by two sister lineages (either distinct species or monophyletic species groups) in different areas of endemism; in the minimum three-taxon statement, a sister lineage of these two lineages ideally occurs in a third area of endemism (Nelson & Platnick, 1981, Humphries & Parenti, 1986). Redundancy (two or more successive

clades distributed in the same area of endemism) is resolved by reduction. Absence of one or more areas in a given cladogram is recognized by congruence of other cladograms that include those areas. Ambiguity from apparently widespread taxa inhabiting two or more areas of endemism may result, for example, from dispersal or from failure to speciate in response to an ecological vicariance event; these are resolved by admitting that some of the components of the cladogram are false (Nelson & Platnick, 1981, Nelson, 1982, Humphries & Parenti, 1986). The result of a track analysis is the discovery that two areas of endemism are more closely (= recently) related to each other than either is to a third area.

A Class A Association is recognizable by the distribution of one modern species in two particular areas of endemism. A Class A Association represents a situation in which these areas have become areas of endemism for many other species, but for which the cited species has not responded with allopatric speciation. Some possible reasons that it has not responded are either (a) because of homeostasis in that species following ecological vicariance separating an original area of endemism into two such areas, (b) because the ecological requirements of the cited species are sufficiently broad that, for it, no ecological vicariance has occurred, or (c) because the distribution represents a recent dispersal of the species across an ecological barrier, a dispersal too recent to have allowed allopatric speciation to occur.

A Class B Association is one for which a monophyletic or presumably monophyletic superspecific taxon is distributed in only two areas of endemism. In such cases, there may actually be one or more tracks or Class A Associations. Phylogenetic analysis within the taxon would reveal these, but such analysis is outside the scope of this discussion.

A Class C Association is one for which a monophyletic or presumably monophyletic superspecific taxon is distributed in three or more areas of endemism; the sister taxon occurs ideally in some other area of endemism. In such cases, an actual track between any two of these particular areas of endemism *may* occur, but has not yet been demonstrated. With such a more nearly cosmopolitan distribution and with such poor phylogenetic evidence, it can be said only that the probability of a track occurring between any two of these particular areas of endemism is greater than between any other, uninhabited areas.

EASTERN NORTH AMERICAN TRACKS

Tracks are evident for the following southeastern caddisfly taxa between Australian (AUS), Eastern North American (ENA), Eastern Palearctic (EPL), Ethiopian (ETH), Neotropical (NTR), Oriental (ORL), Western North American (WNA), and Western Palearctic (WPL) areas of endemism. Phylogeny is indicated by internested parentheses in which terminal sister taxa or areas are separated with a "+" and, in area cladograms, areas of endemism occupied by a widely distributed taxon are separated by a comma. For example, in cladogram 1, the species *alagma* and *brevis* and *neph* and *protonepha* and *tarsipunctata* share one or more homologues (= synapomorphies) not shared with any other taxa and thus are grouped as a single lineage; *major* shares with them one or more additional homologues; species of the *spinosa* Group share with all six of the above one or more additional homologues uniquely; the cladogram of the areas of endemism that each species inhabit is organized completely congruently with the taxon cladogram. In cladogram 2, *ancylus* and *kamonis* are sister species which together form a single lineage; *flava* and *forcipata* are independent lineages for which no homologues are known by which to resolve the trichotomy with the *ancylus* + *kamonis* lineage. Also in cladogram 2, the redundancy of the original area cladogram is reduced in a refined area cladogram.

1. *Ceraclea* (*Athripsodina*) (((*alagma* + *brevis* + *nepha* + *protonepha* + *tarsipunctata*) + *major spinosa* Group) (Morse, 1974; Yang & Morse, 1988) = ((ENA + ORL) ETH).
2. *Ceraclea* (*Athripsodina*) ((*ancytus* + *kamonis*) and/or *flava* and/or *forcipata*) (Morse, 1974; Yang Morse, 1988) = ((ENA + EPL) and/or ENA and/or ORL) = ((ENA + EPL) ORL).
3. *Ceraclea* (*Athripsodina*) ((*diluta* + *perplexa*) (*annulicornis* Group (*riparia* Group + *marginata* Group))) (Morse, 1974, 1975) = ((ENA + WPL) (ENA, WNA, EPL, WPL ((WPL, EPL, ORL) + (EPL, ORL)))) = ((ENA + WPL) (ENA, WNA (WPL + EPL, ORL))).
4. *Ceraclea* (*Athripsodina*) ((*tarsipunctata* Group + *spinosa* Group) rest of Subgenus *Athripsodina*) (Morse, 1974) = ((ENA + ETH) ENA, EPL, ORL, WNA, WPL) = ((ENA + ETH) EPL, ORL, WNA, WPL).
5. *Ceraclea* ((Subgenus *Ceraclea* + Subgenus *Pseudoleptocerus*) Subgenus *Athripsodina*) (Morse, 1974, 1975, 1978) = ((ENA, EPL, WNA, WPL + ETH) ENA, EPL, ORL, WNA, WPL) = ((ENA, EPL, WNA, WPL + ETH) ORL).
6. *Dolophilodes* (*D.*) ((*distinctus* + *similis*) (*indica* + *japonica* + *orientalis*)) (Ross, 1956; Levanidova, 1982) = ((ENA + EPL) ORL, EPL, ORL) = ((ENA + EPL) ORL).
7. *Glossosoma* (*Eomystra*) (((*nigrior* + *dulkeji*) *lividum*) and/or (*ussuricum* + *inops*) and/or (*intermedium* + *verdonia*)) (Ross, 1956) = (((ENA + EPL) ENA) and/or (EPL + EPL) and/or (ENA, EPL, WNA, WPL + WNA)) = ((ENA + EPL) (WPL + WNA)).
8. *Micrasema* (((*rusticum* and/or *moestum* and/or (*rickeri* (*minimum* + *setiferum*))) rest of *rusticum* Group) *baitinum*) (Chapin, 1978) = (((ENA and/or WPL and/or (ENA (WPL + WPL))) ENA) ORL) = ((ENA + WPL) ORL).
9. *Mystacides* ((*sepulchralis* + *bifida*) *alafimbriata*) (Yamamoto & Ross, 1966) = ((ENA + EPL) WNA).
10. *Oxyethira* (*Argyrobothrus*) ((*zeronia* (*velocipes* + *flagellata*)) Subgenus *Dampftrichia*) (Kelley, 1982, 1984) = ((ENA (ETH + ETH)) AUS, ENA, NTR, ORL, WNA) = ((ENA + ETH) AUS, NTR, ORL, WNA).
11. *Oxyethira* (*Dactylotrichia*) ((*kingi* + rest of Subgenus *Dactylotrichia*) Subgenus *Loxotrichia*) (Kelley, 1982, 1984; Holzenthal & Kelley, 1983) = ((ENA + NTR) ENA, NTR, WNA) = ((ENA + NTR) WNA).
12. *Oxyethira* (*Dampftrichia*) (((*florida* + *simulatrix*) *aculea*) *ulmeri*) (*incana* + *galekoluma*) (Kelley, 1982) = (((ENA + NTR) NTR) NTR) (AUS + ORL)) = ((ENA + NTR) (AUS + ORL)).
13. *Oxyethira* (*Dampftrichia*) (((*verna* + *circaverna*) (*discaelata* + *campesina*)) *pallida* Subgroup) (Kelley, 1982, 1983, 1984) = (((ENA + NTR) (NTR + NTR)) ENA, NTR, WNA, Hawaii) = ((ENA + NTR) WNA, Hawaii).
14. *Oxyethira* (*Holarctotrichia*) (((*elerobi* (*archaica* + *iglesiassi*)) rest of Subgenus

- Holarctotrichia*) Subgenera *Argyrobothrus*, *Dampftrichia*, *Mesotrichia*, *Oxytrichia*, *Tanytrichia*, *Dactylotrichia*, and *Loxotrichia*) (Kelley, 1982, 1984) = (((ENA (WPL + WPL)) ENA, WPL) AUS, ENA, ETH, NTR, ORL, WNA) = ((ENA + WPL) AUS, ETH, NTR, ORL, WNA).
15. *Oxyethira* (*Oxytrichia*) ((*sininsigne* + *maryae*) (*unispina* (*dualis* (*leonensis* + *glasa*)))) (Kelley, 1982, 1983) = ((ENA + NTR) (NTR (ENA, WNA (ENA + ENA, NTR)))) = ((ENA + NTR) (WNA (ENA + NTR))).
 16. *Phylocentropus* ((*auriceps* + *spiniger*) *orientalis*) (Ross, 1965) = ((ENA + WPL) ORL).
 17. *Polycentropus* ((*confusus* Group + *nigriceps* Group) (*arizonensis* Group + *gertschi* Group)) (Hamilton, 1986, 1988) = ((ENA + NTR) (NTR + WNA)).
 18. *Rhyacophila* ((*glaberrima* + *stigmatica* Group) (*vagrita* Group + *montana* Group)) (Ross, 1956; Schmid, 1970) = ((ENA + WPL) (WNA + ENA)).
 19. *Rhyacophila* ((*torva* (*nigrocephala* Group)) rest of *divaricata* Branch) (Schmid, 1970) = ((ENA (EPL + ORL)) ORL, WNA, EPL) = ((ENA (EPL + ORL)) WNA).
 20. ((*Theliopsyche* + *Martynomyia*) and/or *Crunoecia* and/or *Archaeocrunoecia* and/or *Maniconeurodes*) (Weaver, 1983) = ((ENA + WPL) and/or WPL, EPL and/or WPL and/or WPL) = ((ENA + WPL) EPL).
 21. *Wormaldia* (*Doloclanes*) ((*mohri* + *kisoensis*) *montana*) (Ross, 1956) = ((ENA + EPL) ORL).
 22. *Wormaldia* (W.) ((*moesta* + *chinensis* + *relicta*) *gabriella*) (Ross, 1956) = ((ENA + EPL + ORL) WNA).

EASTERN NORTH AMERICAN ASSOCIATIONS

Associations are evident for the following southeastern Trichoptera taxa between the Eastern North American (ENA) and the Western Palearctic (WPL) areas of endemism:

Class A Associations, ENA + WPL:

None.

Class B Associations, ENA + WPL:

Ironoquia.

Class C Associations, ENA + WPL + one or more other areas:

Agapetus, *Agraylea*, *Agrypnia*, *Apatania*, *Beraea*, *Brachycentrus* (B.), *Ceratomyche*, *Cheumatopsyche*, *Chimarra*, *Culoptila*, *Diplectrona*, *Dolophilodes*, *Goera*, *Glossosoma*, *Helicopsyche*, *Heteroplectron*, *Hydatophylax*, *Hydropsyche*, *Hydroptila*, *Lepidostoma*, *Leptocerus*, *Limnephilus*, *Lype*, *Molanna*, *Mystacides*, *Neureclipsis*, *Oecetis*, *Orthotrichia*, *Palaeagapetus*, *Parapsyche*, *Phryganea*, *Polycentropus*, *Protoptila*, *Psychomyia*, *Rhyacophila*, *Setodes*, *Stactobiella*, *Triaenodes*, *Wormaldia*, *Ylodes*.

Associations are evident for the following southeastern Trichoptera taxa between the Eastern North American (ENA) and the Eastern Palearctic (EPL) areas of endemism:

Class A Associations, ENA + EPL:

None.

Class B Associations, ENA + EPL:

Potamyia.

Class C Associations, ENA + EPL + one or more other areas:

Agapetus, *Agrypnia*, *Anisocentropus*, *Apatania*, *Arctopsyche*, *Beraea*, *Brachycentrus* (B.), *Brachycentrus* (*Sphinctogaster*), *Ceratopsyche*, *Cheumatopsyche*, *Chimarra*, *Diplectrona*, *Goera*, *Helicopsyche*, *Hydatophylax*, *Hydropsyche*, *Hydroptila*, *Lepidostoma*, *Limnephilus*, *Macrostemum*, *Micrasema*, *Molanna*, *Neophylax*, *Neureclipsis*, *Nyctiophylax*, *Oecetis*, *Oxyethira*, *Palaeagapetus*, *Parapsyche*, *Phryganea*, *Phylocentropus*, *Polycentropus*, *Pseudostenophylax*, *Psychomyia*, *Rhyacophila*, *Setodes*, *Stactobiella*, *Triaenodes*, *Ylodes*.

Associations are evident for the following southeastern caddisfly taxa between the Eastern North American (ENA) and the Neotropical (NTR) areas of endemism:

Class A Associations, ENA + NTR:

Cernotina calcea, *Cheumatopsyche lasia*, *Cyrnellus marginalis*, *Hydroptila angusta*, *Mayatrichia ayama*, *Nectopsyche spiloma*, *Nectopsyche pvida*, *Neotrichia vibrans*, *Ochrotrichia tarsalis*, *Oecetis cinerascens*, *Orthotrichia aegerfasciella*, *Oxyethira* (*Loxotrichia*) *azteca*, *Oxyethira* (*Oxytrichia*) *glasa*, *Oxyethira* (*Loxotrichia*) *janella*, *Oxyethira* (*Dampftrichia*) *maya*, *Triaenodes mephitis*.

Class B Associations, ENA + NTR:

Cernotina, *Cyrnellus*.

Class C Associations, ENA + NTR + one or more other areas:

Anisocentropus, *Chimarra*, *Culoptila*, *Dolophilodes*, *Helicopsyche*, *Hydroptila*, *Leucotrichia*, *Macrostemum*, *Nectopsyche*, *Neotrichia*, *Nyctiophylax*, *Ochrotrichia*, *Oecetis*, *Protophila*, *Triaenodes*, *Wormaldia*.

Associations are evident for the following southeastern caddisfly taxa between the Eastern North American (ENA) and the Oriental (ORL) areas of endemism:

Class A Associations, ENA + ORL:

None.

Class B Associations, ENA + ORL:

Psilotreta.

Class C Associations, ENA + ORL + one or more other areas:

Agapetus, *Anisocentropus*, *Apatania*, *Arctopsyche*, *Ceraclea*, *Ceratopsyche*, *Cheumatopsyche*, *Dolophilodes*, *Goera*, *Glossosoma*, *Helicopsyche*, *Hydropsyche*, *Hydroptila*, *Leptocerus*, *Lype*, *Macrostemum*, *Molanna*, *Mystacides*, *Nyctiophylax*, *Oecetis*, *Orthotrichia*, *Oxyethira*, *Paduniella*, *Parapsyche*, *Phryganea*, *Phylocentropus*, *Polycentropus*, *Pseudostenophylax*, *Setodes*, *Triaenodes*.

Associations are evident for the following southeastern caddisfly taxa between the Eastern North American (ENA) and the Ethiopian (ETH) areas of endemism:

Class A Associations, ENA + ETH:

None.

Class B Associations, ENA + ETH:

None.

Class C Associations, ENA + ETH + one or more other areas:

Anisocentropus, *Cheumatopsyche*, *Chimarra*, *Dolophilodes*, *Helicopsyche*, *Hydropsyche*, *Hydroptila*, *Leptocerus*, *Lype*, *Macrostemum*, *Nyctiophylax*, *Oecetis*, *Orthotrichia*, *Paduniella*, *Polycentropus*, *Triaenodes*, *Wormaldia*.

Associations are evident for the following southeastern caddisfly taxa between the Eastern North American (ENA) and the Australian (AUS) areas of endemism:

Class A Associations, ENA + AUS:

None.

Class B Associations, ENA + AUS:

None.

Class C Associations, ENA + AUS + one or more other areas:

Anisocentropus, *Cheumatopsyche*, *Chimarra*, *Diplectrona*, *Dolophilodes*, *Helicopsyche*, *Hydropsyche*, *Hydroptila*, *Leptocerus*, *Macrostemum*, *Nyctiophylax*, *Oecetis*, *Oxyethira*, *Triaenodes*.

SOUTHEASTERN NORTH AMERICAN TRACKS

Tracks are evident for the following caddisfly taxa between the Southeastern North American (SE), other parts of the Eastern North American (ENA), and the Western North American (WNA) areas of endemism:

23. *Arctopsyche (irrorata (grandis + inermis))* (Schmid, 1968) =
 (SE (ENA, WNA + WNA)) =
 (SE (ENA + WNA)).
24. *Brachycentrus (Sphinctogaster) (((etowahensis (numerosus + solomoni)) (apalachia + spinae) lateralis* Subgroup) (Flint, 1984) =
 (((SE (ENA + ENA)) (ENA + SE)) ENA, WNA) =
 ((SE + ENA) WNA).
25. *Cheumatopsyche (((gyra + vannotei) etrona) gracilis)* (Gordon, 1974) =
 (((SE + ENA) ENA) ENA, WNA) =
 ((SE + ENA) WNA).
26. *Cheumatopsyche ((rossi (logani + smithi)) pettiti)* (Gordon, 1974) =
 ((SE (WNA + WNA)) ENA + WNA) =
 ((SE + WNA) ENA).
27. *Lepidostoma (Mormomyia) ((((((excavatum + sommermanae) libum) (vernale* Group + *mittelli* Group)) serratum Group) griseum Group) Subgenus *Nosopus*) (Weaver, 1983) =
 ((((((SE + ENA) ENA) (ENA + SE)) ENA, SE) ENA, SE) ENA, NTR, WNA) =
 ((SE + ENA) NTR, WNA).
28. *Lepidostoma (Mormomyia) (((((((flinti + glenni) vernale) sackeni) mittelli* Group) *libum* Group) serratum Group) griseum Group) Subgenus *Nosopus*) (Weaver, 1983) =
 (((((((SE + SE) ENA) ENA) SE) ENA, SE) ENA, SE) ENA, SE) ENA, NTR, WNA) =
 ((SE + ENA) NTR, WNA).
29. *Oxyethira (Holarctotrichia) (((setosa + dunbartonensis) forcipata) obtatus michiganensis)* (Kelley, 1982) =
 (((SE + SE) ENA) ENA) ENA, WNA) =
 ((SE + ENA) WNA).
30. *Oxyethira (O.) (((novasota + grisea) (coercens + rivicola) lumosa) (allagashensis (frici + simplex)))* (Kelley, 1985) =
 (((SE + ENA) (ENA + ENA)) SE) (ENA (WPL + WPL))) =
 ((SE + ENA) (ENA + WPL)).
31. *Oxyethira (Oxytrichia) ((abacatia + anabola) aeola)* (Kelley, 1982) =
 ((SE + ENA) WNA).
32. *Parapsyche ((cardis + elsis) (((apicalis + almota) spinata) extensa) turbinata)* (Schmid, 1968) =
 ((SE + WNA) (((ENA + WNA) WNA) WNA) WNA)) =
 ((SE + WNA) ENA).
33. *Rhyacophila (((amicis + melita) atrata) (pellisa + valuma))* (Ross, 1956) =
 (((SE + ENA) ENA) (WNA + WNA)) =
 ((SE + ENA) WNA); or
Rhyacophila ((amicis + melita) ((atrata + colona) (pellisa + valuma)))
 (Schmid, 1970) =
 ((SE + ENA) ((ENA + WNA) (ENA + WNA))) =
 ((SE + ENA) (ENA + WNA)).
34. *Rhyacophila ((montana (milnei + vagrita)) glaberrima)* (Schmid, 1970) =

- ((SE (WNA + WNA)) ENA) =
 ((SE + WNA) ENA).
 35. *Theliopsyche* (((((epilonis + parva) melas) grisea) corona) Genus *Martynomyia*
 (Weaver, 1983) =
 (((((SE + ENA) ENA) ENA) SE) WPL) =
 ((SE + ENA) WPL).
 36. *Wormaldia* (W.) ((thyria + hamata) (shawnee + strota) and/or occidea) (Ross
 1956) =
 ((SE + WNA) (ENA + ENA) and/or WNA) =
 ((SE + WNA) ENA).

SOUTHEASTERN NORTH AMERICAN ASSOCIATIONS

Associations are evident for the following southeastern caddisfly taxa with the rest of Eastern North America:

Class A Associations, SE + ENA:

317 species.

Class B Associations, SE + ENA:

Agarodes, *Goerita*, *Oligostomis*, *Oxyethira grisea* Group (Kelley, 1985), *Platycentropus*, *Pycnopsyche*, *Theliopsyche*.

Class C Associations, SE + ENA + one or more other areas:

Agapetus, *Agraylea*, *Agrypnia*, *Anisocentropus*, *Apatania*, *Arctopsyche*, *Banksiola*, *Beraea*, *Ceraclea*, *Ceratopsyche*, *Cernotina*, *Chimarra*, *Culoptila*, *Cyrnellus*, *Diplectrona*, *Dolophilodes*, *Goera*, *Glossosoma*, *Helicopsyche*, *Hesperophylax*, *Heteroplectron*, *Hydatophylax*, *Hydropsyche*, *Hydroptila*, *Ironoquia*, *Leptocerus*, *Leucotrichia*, *Limnephilus*, *Lype*, *Macrostemum*, *Mayatrichia*, *Molanna*, *Mystacides*, *Nectopsyche*, *Neophylax*, *Neotrichia*, *Neureclipsis*, *Nyctiophylax*, *Ochrotrichia*, *Oecetis*, *Orthotrichia*, *Parapsyche*, *Phryganea*, *Phylocentropus*, *Polycentropus*, *Protophila*, *Pseudostenophylax*, *Psilotreta*, *Psychomyia*, *Ptilostomis*, *Setodes*, *Stactobiella*, *Triaenodes*, *Wormaldia*.

Associations are evident for the following caddisfly taxa between Southeastern North America (SE) and the Western North American (WNA) area of endemism:

Class A Associations, SE + WNA:

Culoptila thoracica, *Dolophilodes sisko*.

Class B Associations, SE + WNA:

None.

Class C Associations, SE + WNA + one or more other areas:

Agapetus, *Agraylea*, *Agrypnia*, *Apatania*, *Banksiola*, *Brachycentrus* (*Sphinctogaster*), *Ceraclea*, *Ceratopsyche*, *Chimarra*, *Diplectrona*, *Goera*, *Glossosoma*, *Helicopsyche*, *Hesperophylax*, *Heteroplectron*, *Homoplectra*, *Hydatophylax*, *Hydropsyche*, *Hydroptila*, *Lepidostoma*, *Leucotrichia*, *Limnephilus*, *Macrostemum*, *Mayatrichia*, *Molanna*, *Mystacides*, *Nectopsyche*, *Neophylax*, *Neotrichia*, *Neureclipsis*, *Nyctiophylax*, *Ochrotrichia*, *Oecetis*, *Orthotrichia*, *Paleagapetus*, *Phryganea*, *Polycentropus*, *Protophila*, *Pseudostenophylax*, *Psychomyia*, *Ptilostomis*, *Triaenodes*.

INTRA-SOUTHEASTERN NORTH AMERICAN TRACKS

The number of shared species and genera among the three areas of endemism in the Southeast is so great (very many Class A, B, and C Associations) that relative relationships actually are masked. The number of Tracks is smaller, mostly because of the few phylogenetic analyses that have been accomplished to date. Despite this selective nature of the evidence, the following Tracks are noteworthy. Tracks for at least the following

caddisfly taxa have been inferred between the Southeastern Interior Highlands (SIH), Southern Eastern Highlands (SEH), and Coastal Plain (SCP) areas of endemism as indicated:

((SIH + SCP) sister area):

37. *Micrasema* ((*ozarkana* + n. sp.) *wataga*) (Chapin, 1978; Chapin & Morse, in prep.) = ((SIH + SCP) ENA).

38. *Setodes* (((*oxapius* + *dixiensis*) (*incertus* + *stehri*)) *arenatus*) (Holzenthal, 1982) = (((SIH + SCP) (ENA + SEH)) SCP).

((SIH + SEH) sister area):

39. *Helicopsyche* ((*limnella* + *paralimnella*) and/or *borealis* and/or *mexicana*) (Morse et al, 1989) = ((SIH + SEH) and/or ENA, NTR, WNA and/or WNA, NTR) = ((SIH + SEH) ENA, NTR, WNA).

40. *Rhyacophila* (((*kiamichi* + *ledra*) *fenestra*) *teddyi*) *carolina*) *castanea* Group) (Ross, 1956; Schmid, 1970) = (((SIH + ENA) ENA) SEH) ENA) ORL) = ((SIH + ENA) SEH) ORL).

((SCP + SEH) sister area):

41. *Agarodes* ((*alabamensis* + *tetron*) *griseus*) Ross & Scott, 1974; Harris, 1987) = ((SCP + SEH) ENA).

CONCLUSIONS

The intercontinental tracks suggest that the eastern North American caddisflies evolved with close relations in several different regions, most recently in the Neotropical (cladograms 11, 12, 13, 15, and 17) and East Palearctic (cladograms 2, 6, 7, 9, 19, 21, and 22) regions. As might be expected, the Neotropical + Eastern North American fauna generally had its most recent relatives in Western North America (Allen, 1984, Noonan, 1986). Some of the Eastern Palearctic + Eastern North American fauna also had its most recent relatives at least partly in Western North America (cladograms 7, 9, and 19), but some of this fauna (cladograms 2, 6, 21, and 22) had its most recent relatives in the Oriental Region. The Western Palearctic relationships are also relatively recent (cladograms 3, 8, 14, 16, 18, and 20), typically preceded by ancestors also living in one or more of each of the world's biogeographic regions. Lineages whose extant species suggest ancestral distributions involving Eastern North America and the Ethiopian Region (cladograms 4, 5, and 10) or the Oriental Region (cladogram 1) are less common, and provide insufficient evidence for discovering distributions of their historical antecedents, implying that the relationships are much more ancient than for the previous three regions.

The Southeastern species mostly evolved from widespread Eastern North American ancestors (cladograms 24, 25, 27, 28, 29, 30, 31, 33, and 35), preceded by older transcontinental populations or populations also living in the Neotropical or Western Palearctic regions. There are several examples, however, of apparent evolution directly from more widespread North American ancestors (cladograms 23, 26, 32, 34, and 36).

The less rigorously analyzed associations for Eastern North America with Western Palearctic, Eastern Palearctic, and Neotropical Biogeographic regions are supported nearly equally by the evidence from caddisflies. The major difference is that there are at least 16 Class A Associations of southeastern species presently living in Eastern North America and the Neotropical Region and none known in both Eastern North America and Europe or Asia. This suggests to us that the biogeographic relationships

of Eastern North America have been well established historically with these other three regions, but that either the Atlantic and Pacific oceanic barriers have been more effective in facilitating allopatric speciation than has the arid North American Southwest and/or the relationship with the Neotropical Region has been more recent. The large number of unresolved Class C Associations among these areas of endemism suggests that there is yet much historical biogeographic evidence to be gleaned from future phylogenetic studies.

Within the Nearctic Biogeographic Region, there are many species endemic to the Southeast (168 spp.), but nearly twice as many more (317 spp.) are shared with Eastern North America outside the Southeast. Clearly, if the Southeast is to be treated as an area of endemism, it can only be considered a sub-area of Eastern North America.

The number of caddisfly associations between the Southeast and Eastern North America also is much greater than between the Southeast and Western North America, especially for Class A Associations (317 spp. versus 2 spp.). The number of Class B and C Associations between the Southeast and Western North America (0 genn. and 42 genn., respectively) is comparable to those between Eastern North America and Europe (1 gen. and 40 genn., respectively) or Asia (1 gen. and 40 genn., respectively) or the Neotropics (2 genn. and 16 genn., respectively). This fact seems to corroborate the hypothesis that Eastern and Western North American areas of endemism are as distinctive as are these other areas.

Although the number of endemic caddisfly species in the southeastern areas of endemism is large, especially for the Eastern Highlands and the Coastal Plain, the number of cladograms that have been published for these species is small, such that the number of tracks presently known among them is insufficient to consider any intra-southeastern track generalized. It is interesting, however, that many of the Coastal Plain endemics are more closely related to species further north, such as the Class B Association for *Neureclipsis melco* Ross (Polycentropodidae) with the other five species of the genus in North America. Very few species have sister lineages that are also Coastal Plain endemics, although a few examples exist, such as sister species *Cheumatopsyche morsei* Gordon and *C. virginica* Denning (Hydropsychidae; Gordon, 1974). We thus infer that the endemic Southeastern Coastal Plain caddisfly fauna had multiple origins, perhaps the result of numerous peripheral isolations of ancestral taxa resulting from fluctuating climates and possibly associated sea level oscillations.

Flint and Harp (1990) offered a similar explanation for the origin of several members of the *Lepidostoma modestum* Group. Four of the species are widespread from the Northeast to the southern Appalachians while four other members are more restricted: *L. compressum* Etnier and Way and *L. modestum* (Banks) in the Cumberland Plateau and Appalachian Mountains, *L. weaveri* Harris in the upper Coastal Plain of Alabama, and *L. ozarkensis* Flint and Harp in the Ozarks of the Interior Highlands. The first three are sister species according to Weaver (1983), the latter is the sister species of the widely distributed northeastern *L. ontario* Ross (Flint & Harp 1990). These authors suggested that the southeastern species may represent "relictual distributions resulting from expanding and contracting ranges related to earlier advances and retreats of the main range of the species group." For this reason, although the Southeastern Coastal Plain is an area of endemism for many species, the causes for this endemism must be viewed as multiple and complex, and determination of the timing of vicariance events will be very difficult to correlate geologically, ecologically, and faunistically.

ACKNOWLEDGMENTS

We are grateful to R. N. Vineyard (Royal Ontario Museum) for translating important parts of the volume by Levanidova (1982).

REFERENCES CITED

- ALLEN, R. T. 1984. Distribution patterns among arthropods of the North Temperate Deciduous Forest Biota. *Ann. Missouri Bot. Garden* 70: 616-628.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution abundance of animals. University of Chicago Press, Chicago. 782 pp.
- BLICKLE, R. L. 1962. Hydroptilidae (Trichoptera) of Florida. *Florida Entomol.* 45(3): 153-155.
- BOWLES, D. E., AND M. L. MATHIS. 1989. Caddisflies (Insects: Trichoptera) of mountainous regions in Arkansas, with new state records for the order. *J. Kansas Entomol. Soc.* 62(2): 234-244.
- CHAPIN, J. W. 1978. Systematics of Nearctic *Micrasema* (Trichoptera: Brachycentridae). Ph.D. dissertation, Clemson University. 136 pp.
- CROIZAT, L. 1958. Panbiogeography. Published by the author, Caracas.
- ETNIER, D. A., AND G. A. SCHUSTER. 1979. An annotated list of Trichoptera (caddisflies) of Tennessee. *J. Tennessee Acad. Sci.* 54(1): 15-22.
- FISCHER, F. C. J. 1960-1973. Trichopterorum Catalogus. Volumes 1-15, index. Nederlandse Entomologische Vereniging, Amsterdam.
- FLINT, O. S., JR. 1984. The genus *Brachycentrus* in North America, with a proposed phylogeny of the genera of Brachycentridae (Trichoptera). *Smithsonian Contrib. Zool.* 398. iv + 58 pp.
- FLINT, O. S., JR., AND P. A. HARP. 1990. *Lepidostoma* (*Nosopus*) *ozarkense* (Trichoptera: Lepidostomatidae), a new species from Arkansas. *Entomol. News* 101(2): 81-87.
- GORDON, A. E. 1974. A synopsis and phylogenetic outline of the Nearctic members of *Cheumatopsyche*. *Proc. Acad. Nat. Sci. Philadelphia* 126(9): 117-160.
- HAMILTON, S. W. 1986. Systematics and biogeography of the New World *Polycentropus* sensu stricto (Trichoptera: Polycentropodidae). Ph.D. dissertation, Clemson University. 257 pp.
- HAMILTON, S. W. 1988. Historical biogeography of two groups of Caribbean *Polycentropus* (Trichoptera: Polycentropodidae), pp. 153-182 in J. K. Liebherr [ed.], *Zoogeography of West Indian Insects*, Cornell University Press, Ithaca, New York. 285 pp.
- HARRIS, S. C. 1986. Hydroptilidae (Trichoptera) of Alabama with descriptions of three new species. *J. Kansas Entomol. Soc.* 59(4): 609-619.
- HARRIS, S. C. 1987. A new species of *Agarodes* (Trichoptera: Sericostomatidae) from southeastern United States. *Proc. Biol. Soc. Washington* 89(1): 74-76.
- HARRIS, S. C., P. K. LAGO, AND J. F. SCHEIRING. 1982a. An annotated list of Trichoptera of several streams on Eglin Air Force Base, Florida. *Entomol. News* 93(3): 79-84.
- HARRIS, S. C., P. K. LAGO, AND R. W. HOLZENTHAL. 1982b. An annotated checklist of the caddisflies (Trichoptera) of Mississippi and southeastern Louisiana. Part II: Rhyacophiloidea. *Proc. Entomol. Soc. Washington* 84(3): 509-512.
- HARRIS, S. C., P. K. LAGO, AND P. E. O'NEIL. 1984. Trichoptera of the Cahaba River system in Alabama. *Entomol. News* 95(3): 103-112.
- HOLZENTHAL, R. W. 1982. The caddisfly genus *Setodes* in North America (Trichoptera: Leptoceridae). *J. Kansas Entomol. Soc.* 55(2): 253-271.
- HOLZENTHAL, R. W., S. C. HARRIS, AND P. K. LAGO. 1982. An annotated checklist of the caddisflies (Trichoptera) of Mississippi and southeastern Louisiana. Part III: Limnephiloidea and conclusions. *Proc. Entomol. Soc. Washington* 84(3): 513-520.
- HOLZENTHAL, R. W., AND R. W. KELLEY. 1983. New micro-caddisflies from the southeastern United States (Trichoptera: Hydroptilidae). *Florida Entomol.* 66(4): 465-472.
- HUMPHRIES, C. J., AND L. R. PARENTI. 1986. Cladistic biogeography. *Oxford Monographs on Biogeography* No. 2, Oxford Science Publications. 98 pp.
- KELLEY, R. W. 1982. The micro-caddisfly genus *Oxyethira* (Trichoptera: Hydro-

- ptilidae): Morphology, biogeography, evolution and classification. Ph.D. dissertation, Clemson University. 432 pp.
- KELLEY, R. W. 1983. New Neotropical species of *Oxyethira* (Trichoptera: Hydroptilidae). Proc. Entomol. Soc. Washington 85(1): 41-54.
- KELLEY, R. W. 1984. Phylogeny, morphology, and classification of the micro-caddisfly genus *Oxyethira* Eaton (Trichoptera: Hydroptilidae). Trans. Amer. Entomol. Soc. 110: 435-463.
- KELLEY, R. W. 1985. Revision of the micro-caddisfly genus *Oxyethira* (Trichoptera: Hydroptilidae). Part II: Subgenus *Oxyethira*. Trans. Amer. Entomol. Soc. 111: 223-253.
- LAGO, P. K., R. W. HOLZENTHAL, AND S. C. HARRIS. 1982. An annotated checklist of the caddisflies (Trichoptera) of Mississippi and southeastern Louisiana. Part I: Introduction and Hydropsychoidea. Proc. Entomol. Soc. Washington 84(3): 495-508.
- LAGO, P. K., AND S. C. HARRIS. 1987. An annotated list of the Curvipalpia (Trichoptera) of Alabama. Entomol. News 98(5): 255-262.
- LEVANIDOVA, I. M. 1982. Aquatic insects of the mountain region of Far Eastern U.S.S.R.: Faunistics, ecology, and zoogeography of Ephemeroptera, Plecoptera, and Trichoptera. Akademia Nauk CCCP, Leningrad. 214 pp. [in Russian]
- MALICKY, H. 1983. Atlas of European Trichoptera. Series Entomologica 24, Dr. W. Junk Publishers, The Hague. 298 pp.
- MORSE, J. C. 1974. The classification, evolution, and past dispersals of the caddisfly genus *Ceraclea* (Trichoptera, Leptoceridae). Ph.D. dissertation, University of Georgia. 186 pp.
- MORSE, J. C. 1975. A phylogeny and revision of the caddisfly genus *Ceraclea* (Trichoptera: Leptoceridae). Contrib. Amer. Entomol. Inst. 11(2): 1-97.
- MORSE, J. C. 1978. Evolution of the caddisfly genus *Ceraclea* in Africa: implications for the age of Leptoceridae (Trichoptera), pp. 199-206 in M. I. Crichton [ed.], Proceedings of the second international symposium on Trichoptera, University of Reading, England 25-29 July 1977. Dr. W. Junk by Publishers, The Hague. 359 pp.
- MORSE, J. C., J. W. CHAPIN, D. D. HERLONG, AND R. S. HARVEY. 1980. Aquatic insects of Upper Three Runs Creek, Savannah River Plant, South Carolina. Part I: Orders other than Diptera. J. Georgia Entomol. Soc. 15(1): 73-101.
- MORSE, J. C., S. W. HAMILTON, AND K. M. HOFFMAN. 1989. Aquatic insects of Lake Jocassee catchment in North and South Carolina, with descriptions of four new species of caddisflies (Trichoptera). J. Elisha Mitchell Sci. Soc. 105(1): 14-33.
- NELSON, G. 1982. Cladistique et biogeographie. Compte Rendus de la Société de Biogeographie 58: 75-94.
- NELSON, G., AND N. PLATNICK. 1981. Systematics and biogeography: cladistics and vicariance. Columbia University Press, New York. 567 pp.
- NOONAN, G. R. 1986. Distribution of insects in the Northern Hemisphere: Continental drift and epicontinental seas. Bull. Entomol. Soc. Amer. 32(2): 80-84.
- ROSS, H. H. 1944. The caddis flies, or Trichoptera, of Illinois. Bull. Illinois Natural History Survey 23: 1-326.
- ROSS, H. H. 1956. Evolution and classification of the mountain caddisflies. University of Illinois Press, Urbana, Illinois. 213 pp.
- ROSS, H. H. 1965. The evolutionary history of *Phylocentropus* (Trichoptera: Psychomyiidae). J. Kansas Entomol. Soc. 38(4): 398-400.
- ROSS, H. H. 1967. The evolution and past dispersal of the Trichoptera. Ann. Rev. Entomol. 12: 169-207.
- ROSS, H. H., AND D. C. SCOTT. 1974. A review of the caddisfly genus *Agarodes*, with descriptions of new species (Trichoptera: Sericostomatidae). J. Georgia Entomol. Soc. 9: 147-155.
- SCHMID, F. 1968. La famille des Arctopsychides (Trichoptera). Mémoires de la Société Entomologique du Québec 1: 1-84.
- SCHMID, F. 1970. Le genre *Rhyacophila* et la famille des Rhyacophilidae (Trichoptera). Mémoires de la Société Entomologique du Canada 66: 1-230, pls. I-LII.

- SCLATER, P. L. 1858. On the general geographical distribution of the members of the class Aves. J. Linnean Soc. London, Zoology 2: 130-145.
- UNZICKER, J. D., L. AGGUS, AND L. O. WARREN. 1970. A preliminary list of the Arkansas Trichoptera. J. Georgia Entomol. Soc. 5(3): 167-174.
- UNZICKER, J. D., V. H. RESH, AND J. C. MORSE. 1982. Trichoptera, pp. 9.1-9.138, in A. R. Brigham, W. U. Brigham, and A. Gniska [eds.], Aquatic Insects and Oligochaetes of North and South Carolina. Midwest Aquatic Enterprises, Mahomet, Illinois. 837 pp.
- WEAVER, J. S., III. 1983. The evolution and classification of Trichoptera, with a revision of the Lepidostomatidae and a North American synopsis of this family. Ph.D. dissertation, Clemson University. 411 pp.
- WIGGINS, G. B. 1984. Trichoptera. Chapter 16, pp. 271-311 in R. W. Merritt and K. W. Cummins [eds.], An Introduction to the Aquatic Insects of North America, Second edition. Kendall/Hunt Publishing Company, Dubuque, Iowa. 722 pp.
- WIGGINS, G. B. 1987. Order Trichoptera, Chapter 25, pp. 253-287 in F. W. Stehr [ed.], Immature Insects. Kendall/Hunt Publishing Company, Dubuque, Iowa. 754 pp.
- YAMAMOTO, T., AND H. H. ROSS. 1966. A phylogenetic outline of the caddisfly genus *Mystacides* (Trichoptera: Leptoceridae). Canadian Entomol. 98(6): 627-632.
- YANG, L., AND J. C. MORSE. 1988. *Ceraclea* of the People's Republic of China (Trichoptera: Leptoceridae). Contrib. Amer. Entomol. Inst. 23(4): 1-69.