



Nelson, C.H. 2008. Hierarchical relationships of North American states and provinces: An area cladistic analysis based on the distribution of stoneflies (Insecta: Plecoptera). *Illiesia*, 4(18):176-204. Available online: <http://www2.pms-lj.si/illiesia/Illiesia04-18.pdf>

## HIERARCHICAL RELATIONSHIPS OF NORTH AMERICAN STATES AND PROVINCES: AN AREA CLADISTIC ANALYSIS BASED ON THE DISTRIBUTION OF STONEFLIES (INSECTA: PLECOPTERA)

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### ABSTRACT

The distribution pattern of 67 genera, 507 species and 2 subspecies of North American Plecoptera is examined using a variant of Parsimony Analysis of Endemicity (PAE), Cladistic Analysis of Distributions and Endemisms (CADE), to assess hierarchical relationships of 85 large political units belonging to Canada, the USA and Mexico. Consensus area cladograms generated from the 146 minimum-length area cladograms revealed three main assemblages of area clades: The states of northwestern Mexico (Chihuahua, Sonora, Baja California) together with the states and provinces of the western USA and Canada (Nunavut, Manitoba, Saskatchewan, Northwest Territories, Arizona, South Dakota, Nevada, New Mexico, Colorado, Utah, Wyoming, Alaska, Yukon, Montana, Idaho, Alberta, British Columbia, California, Oregon, Washington); the states and provinces of the eastern USA and Canada (Rhode Island, New Hampshire, Vermont, Newfoundland, Labrador, Prince Edward Island, Nebraska, North Dakota, Texas, Louisiana, Florida, Mississippi, Alabama, Georgia, South Carolina, North Carolina, Tennessee, District of Columbia, New Jersey, Delaware, Iowa, Minnesota, Wisconsin, Michigan, Ontario, Quebec, Nova Scotia, New Brunswick, Massachusetts, Connecticut, Maine, New York, Pennsylvania, Maryland, Virginia, West Virginia, Kansas, Oklahoma, Arkansas, Missouri, Ohio, Kentucky, Indiana, Illinois); and the remaining states of Mexico (Sinaloa, Tabasco, San Luis Potosi, Puebla, Tamaulipas, Nuevo Leon, Nayarit, Michoacan, Morelos, Distrito Federal, Mexico, Jalisco, Durango, Coahuila, Chiapas, Vera Cruz, Oaxaca, Guerrero). The major clades of the consensus area cladograms may be reflecting historical phenomena as these can be correlated with geologic events that either fragmented or joined principal North American land areas in the late Jurassic (clade 67), early and mid-Cretaceous, and Miocene (clades 2 and 24). Low values for the consistency (CI), retention (RI) and rescaled consistency (RC) indices of the 146 minimum-length area cladograms very likely reflect one or some combination of (1) the extinction of taxa; (2) the influence of random distribution of taxa; (3) the high number as well as the artificial nature of the geographic area units; or (4) incomplete information concerning the distribution of North American Plecoptera genera and species. The hierarchical patterns of this PAE/CADE analysis will need to be corroborated by species phylogenies of North American Plecoptera when they become available.

**Keywords:** Parsimony Analysis of Endemicity, PAE, Cladistic Analysis of Distributions and Endemisms, CADE, distribution, Plecoptera, states, provinces, territories, North America

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### INTRODUCTION

Comprehensive analyses on the biogeography of

North American Plecoptera have been confined to studies by Hynes (1988) and Stewart & Stark (1988,

2002). These workers concluded that there were at least three basic groupings of the North American stonefly fauna: Eastern Boreal, Western Boreal, and Austral. Moreover, they considered that these groupings are compatible with fragmentation and merging of geographic areas associated with plate tectonics. The goal of this study is to add to these findings by determining North American area relationships using taxonomic and distributional data of plecopteran species.

A number of methodological approaches have been employed to analyze the distributions of organisms. Morrone (2005) organized these in a taxonomy of methods that are initially divided into two classes. The first consist of dispersalist approaches that use dispersal from previously identified centers of origin or ancestral areas to explain distribution of organisms. The second include vicariance approaches. These consist of the methods of panbiogeography, which first construct a track of distribution between related organisms and then look for congruence between tracks of unrelated organisms, and cladistic biogeography, which construct relationships between the geographic areas a group of organisms inhabit by employing the phylogeny of that group.

There appears to be agreement among those workers who use vicariance approaches that it would be preferable to apply the comparative phylogenetic approach of cladistic biogeographic methods to resolve the problem of the historical biogeography of a group of organisms (Cracraft 1991; Luna-Vega et al. 1999; Morrone & Escalante 2002; Porzecanski & Cracraft 2005). When North American Plecoptera species are considered, only three such studies have been undertaken: Nelson's (1988) analysis of the species of Pteronarcyidae using a reduced area cladogram incorporating broad geographic regions, Stark & Nelson's (1994) analysis of the species of *Yoraperla* in the Peltoperlidae using Brooks Parsimony Analysis on Asian and western North American mountain chains, and Nelson's (2004) study of the *Capnia californica* species group using a comparative phylogenetic analysis to assess zoogeographic affinities between six western states and northwestern Mexico.

Although Terry & Whiting (In Preparation), using morphological and molecular evidence derived from

species representatives of a large number of Plecoptera genera, have generated a cladistic hypothesis on family and generic relationships within the order, the state of knowledge regarding the phylogeny of species within each North American genus remains largely incomplete. Therefore, a useful first-step to assess geographic area relationships in North America would be to apply a method that relies less heavily on phylogenetic information. Based on the assumption that shared distribution patterns of a biota reflect an underlying common historical explanation, this study employs a panbiogeographic method that applies a variant of the Parsimony Analysis of Endemicity (PAE) approach termed Cladistic Analysis of Distributions and Endemisms (CADE) (Cracraft 1991; Porzecanski & Cracraft 2005). This method uses parsimony to construct a cladogram depicting the hierarchical pattern of relationships between geographic areas based on distributional data of taxa. Geographic areas that have been used in PAE analyses include artificially determined units such as quadrants of varying sizes and natural units such as islands, oceans, continents, ecoregions or biogeographic regions. In this study states, provinces, territories and federal districts of Canada, the USA, and Mexico were used as the area units. The use of PAE or CADE in biogeographic studies has been criticized by Brooks and van Veller (2003), but has been defended by Porzecanski & Cracraft (2005) and Vazquez-Miranda et al. (2007).

## MATERIAL AND METHODS

The basic requirements of CADE (Cracraft 1991; Porzecanski & Cracraft 2005) are:

1. predetermined areas of endemism;
2. a sufficiently large sample of taxa to adequately reflect the region's biota;
3. incorporation of hierarchical information into the data matrix by coding the distribution of subspecies, species, and genera;
4. parsimony analysis of the data matrix to produce a cladogram showing the relationship between the endemic areas.

A total of 85 states, provinces, territories and federal districts from which stoneflies have been reported from Mexico, Canada, and the USA were

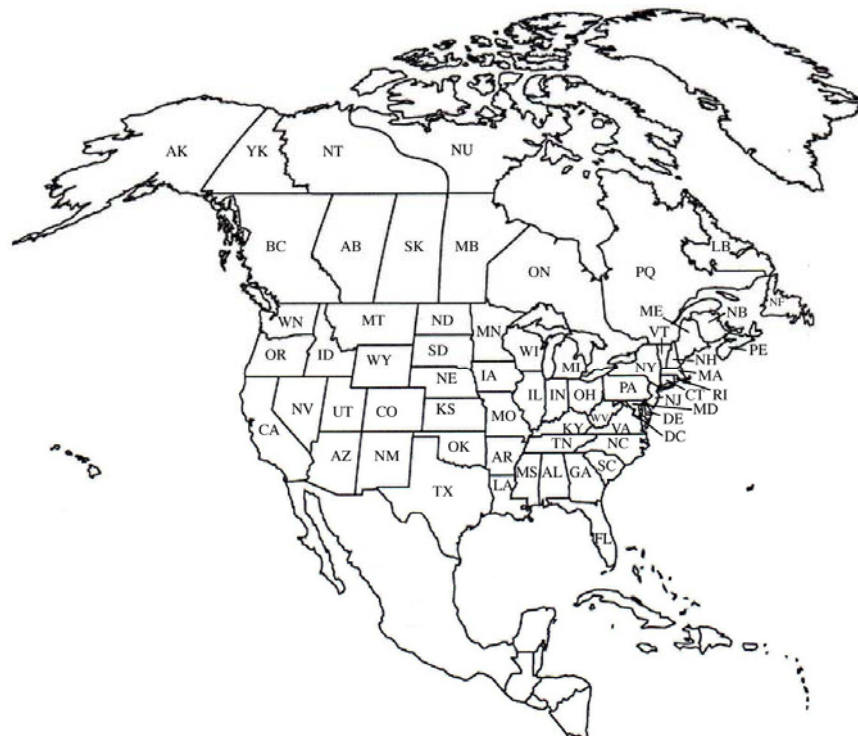


Figure 1. Provinces, territories, states and one federal district representing endemic areas in Canada and the USA that report the presence of stoneflies. Canada: AB (Alberta), BC (British Columbia), LB (Labrador), MB (Manitoba), NB (New Brunswick), NE (Newfoundland), NS (Nova Scotia), NT (Northwest Territories), NU (Nunavut), ON (Ontario), PE (Prince Edward Island), PQ (Quebec), SK (Saskatchewan), YK (Yukon). USA: AL (Alabama), AK (Alaska), AR (Arkansas), AZ (Arizona), CA (California), CO (Colorado), CT (Connecticut), DC (District of Columbia), DE (Delaware), FL (Florida), GA (Georgia), IA (Iowa), ID (Idaho), IL (Illinois), IN (Indiana), KS (Kansas), KY (Kentucky), LA (Louisiana), MA (Massachusetts), MD (Maryland), ME (Maine), MI (Michigan), MN (Minnesota), MO (Missouri), MS (Mississippi), MT (Montana), NC (North Carolina), ND (North Dakota), NE (Nebraska), NH (New Hampshire), NJ (New Jersey), NM (New Mexico), NV (Nevada), NY (New York), OH (Ohio), OK (Oklahoma), OR (Oregon), PA (Pennsylvania), RI (Rhode Island), SC (South Carolina), SD (South Dakota), TN (Tennessee), TX (Texas), UT (Utah), VA (Virginia), VT (Vermont), WN (Washington), WI (Wisconsin), WV (West Virginia), WY (Wyoming).

considered to represent possible areas of endemism and were used in this analysis (Figs. 1, 2). To assist in the discernment of relationships between these North American area units, they were treated as belonging to a monophyletic entity despite published evidence of a number of taxon relationships between the Eastern Palearctic and Western Nearctic, the Eastern Palearctic and Eastern Nearctic and the Western Palearctic and Eastern Nearctic. Since states, provinces, territories and federal districts are political or artificial area units rather than natural area units, it can be argued that these are not the endemic areas

required by CADE. Nihei (2006), for example, has criticized the use of non-natural area units in PAE as they may distort area relationships. Nonetheless, endemism is difficult to define. Crisci et al. (2003) list five definitions for this concept and observe that defining endemism in biogeography is analogous to the attempt of defining the species concept in systematic biology. A second justification for using states, provinces, territories and federal districts is that, although some Plecoptera species have a widespread distribution (Stewart & Stark 2002), most members of this order have limited



Fig. 2. States and federal district representing endemic areas in Mexico that report the presence of stoneflies. BJ (Baja California), CH (Chihuahua), CI (Coahuila), CP (Chiapas), DF (Distrito Federal), DG (Durango), GU (Guerero), JA (Jalisco), MC (Michoacan), MR (Morelos), MX (Mexico), NA (Nayarit), NL (Nuevo Leon), OX (Oaxaca), PU (Puebla), SI (Sinaloa), SL (San Luis Potosi), SO (Sonora), TA (Tamaulipas), TB (Tabasco), VZ (Vera Cruz).

dispersal abilities (Ross & Ricker 1971, Stark & Gaufin 1976; Hynes 1988; Sargent et al. 1991; Stewart & Stark 2002) and are likely to be contained within a few political area units. In this study 176 or 26% of the 688 Plecoptera taxa whose distribution were examined are confined to one state, province, or territory. An additional 86 taxa or 12% are restricted to two states, provinces, or territories. Lastly, states, provinces, territories and federal districts are the most frequently cited geographic area units for North America Plecoptera distribution (Stark et al. 1986; Stark et al. 2008; Stewart & Stark 2002; Stewart & Oswood 2006). Nonetheless, ongoing efforts to compile a database of North American stonefly distribution records at the county level (Kondratieff & Baumann 2000) should be able to provide more detailed information for future analyses.

A terminal area consisting of all 0's (absences) was also included and is used to root the tree (Cracraft 1991; Porzecanski & Cracraft 2005). The terminal area is, thus, a hypothetical outgroup and coding it in this manner assumes that the absence of taxa is the plesiomorphic condition and that the sharing of taxa between two or more areas is the

apomorphic condition. A hypothetical outgroup is used since, as Rosen (1988) noted, there is no convincing means of identifying a 'primitive' area. Moreover, coding the outgroup with 1's would suggest that area relationships should be recognized by the shared loss of taxa or extinction.

The taxa employed in this study included 67 genera, 507 species and 2 subspecies occurring in the USA, Canada, and Mexico (Appendix 1). Incorporating both genera and species was done to amplify the historical 'signal' present in the data set (Porzecanski & Cracraft 2005; Vazquez-Miranda et al. 2007). Species or genera autapomorphic for a single state or province were excluded as they were not informative with respect to grouping the taxa of this study (Bryant 1995). CADE also provides for the incorporation of the distribution of subspecies. While this latter category is not widely employed in Plecoptera, the one instance in North American Plecoptera, *Cultus decisus decisus* and *C. decisus isolatus*, is included. The main sources of information for the distribution of Plecoptera taxa in Canada, the USA, and Mexico were Stark & Kondratieff (2004), Stewart & Oswood (2006) and Stark et al. (2008).

Presence or absence of a taxon in a political area unit was coded as 1 or 0 respectively.

Parsimony analysis of the data matrix was undertaken using PAUP\* (version 4.0b10, Swofford 2002). The heuristic search option was used in lieu of exact approaches such as the branch-and-bound and exhaustive searches. The latter are computationally intractable with large-sized data sets. However, use of the former does not guarantee the identification of the minimum-length area cladogram(s). The heuristic search option was performed using 100 replicates, 100 random addition sequence replicates, random step-wise addition, tree-bisection and reconnection branch swapping, collapse of zero length branches, Multrees option in effect, deepest descent option not in effect. Clade support was assessed using bootstrap frequencies (Felsenstein 1985). Bootstrap branch values were determined in PAUP\* from using the heuristic search option above. Strict Consensus and Majority Rule Consensus area cladograms were constructed when more than one equally parsimonious cladogram resulted. MacClade 4.0 (Maddison & Maddison 2000) was used to trace character transformations for specific clades on the resulting Majority Rule Consensus area cladogram.

## RESULTS

The heuristic approach of PAUP\* identified 146 area cladograms with a length of 2267 steps. These area cladograms have a consistency index (CI) of 0.2532, a retention index (RI) of 0.6704, a rescaled consistency index (RC) of 0.1698, and a homoplasy index (HI) of 0.7468. The Strict Consensus area cladogram (Fig. 3) exhibits three basal clades of states, provinces and territories but political entities from Mexico are largely unresolved. The Majority Rule Consensus area cladogram (Fig. 4) shows clades found in 50% of the 146 most parsimonious trees. It identifies the same three basal clades found in the Strict Consensus area cladogram, but exhibits greater resolution with respect to the areas from Mexico.

The more highly resolved Majority Rule Consensus area cladogram is the basis of the following discussion of relationships between the political area units comprising Canada, the USA, and Mexico. The three basal clusters of the Majority Rule Consensus area cladogram are identified as clades 2, 24, and 67 (Fig. 4). These clades, however, lack

bootstrap support at the 50 % confidence level.

Basal clade 2 is characterized by the distribution of the genus *Capnia* (Appendix 2). Within this clade subordinate clade 3 comprised of the 20 states, provinces, and territories of the western USA and Canada appears as the sister group of subordinate clade 22 comprised of the 3 states of northwestern Mexico. Although subordinate clade 3 does not receive bootstrap support, 14 of its subordinate clades are supported (Fig. 3). Subordinate clade 22, however, receives support as a monophyletic group (Fig. 3). Plecoptera species and genera whose distribution represents unambiguous changes for subordinate clades 3 and 22 and subordinate clades included within them (4 through 21 and 23 respectively) are listed in Appendix 2. In subordinate clade 3 five subordinate clades exhibit a pattern consisting of a pair of geographically adjacent political area units: 16 (Oregon, Washington), 17 (Idaho, Montana), 18 (Yukon, Alaska), 19 (Colorado, New Mexico), and 21 (Saskatchewan, Manitoba). In subordinate clade 22 the two states comprising subordinate clade 23 (Sonora, Chihuahua) are geographically adjacent political area units.

Basal clade 24 is characterized by the distribution of the genus *Allocapnia* (Appendix 2) and includes 43 states, provinces, and territories of the eastern USA and Canada as well as the federal district of the USA. Plecoptera species and genera whose distributions represent unambiguous changes for the subordinate clades within basal clade 24 (25 through 66) are listed in Appendix 2. This clade is largely grouped into three major subordinate clades 28, 36 and 63 (Fig. 4). Major subordinate clade 28 includes the states of the southeastern USA and most of its subordinate clades (30 through 35) receive bootstrap support (Fig. 3). In clade 28 the six states comprising subordinate clade 31 (Mississippi, Alabama, Georgia, South Carolina, North Carolina, Tennessee) exhibit a nesting of geographically adjacent political area units that extend in an arc from west to east. Major subordinate clade 36 includes the central and northeastern political area units of the USA and Canada. However, it does not receive bootstrap support. Subordinate clade 36 largely comprised two subordinate clades 40 and 47 (Fig. 4). The former includes states from the central USA and it and its subordinate clades (41 through 46) receive bootstrap



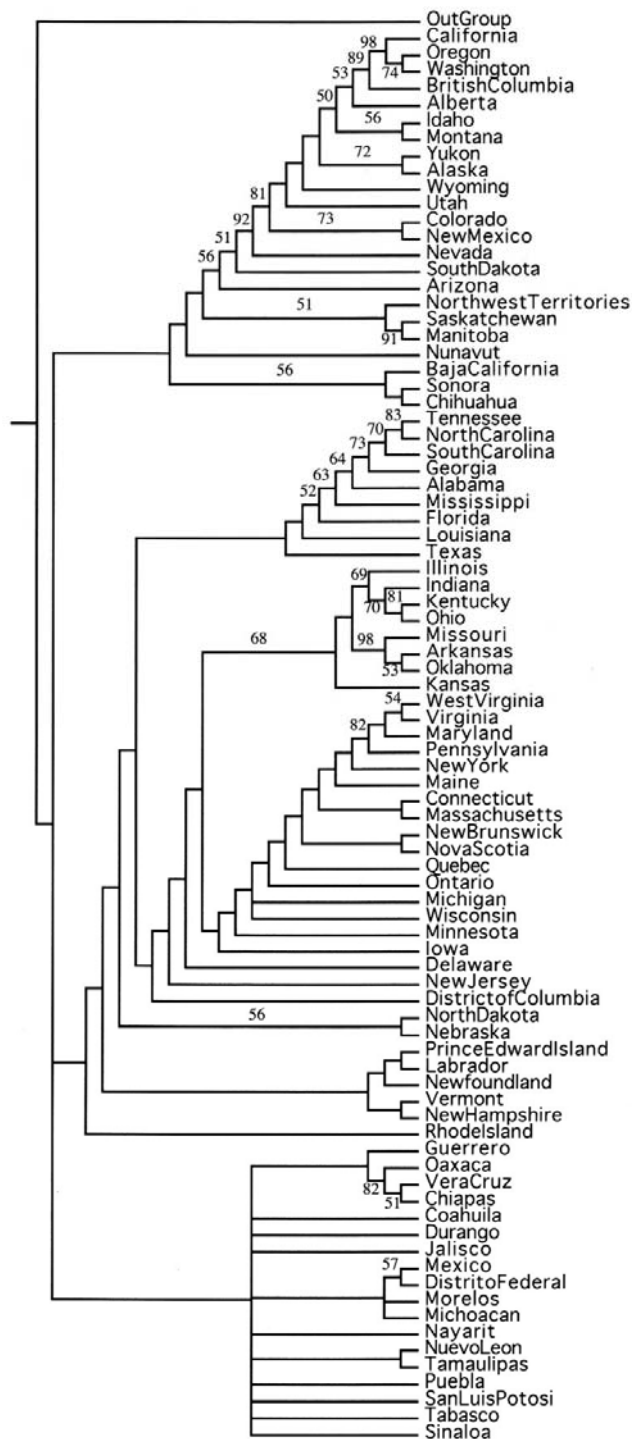


Fig. 3. Strict Consensus area cladogram of the 146 most parsimonious area cladograms of states, provinces, territories, and federal districts of Canada, USA, and Mexico based on Plecoptera distributional data. Numbers above the branch indicate bootstrap values above 50%, otherwise less than 50%.

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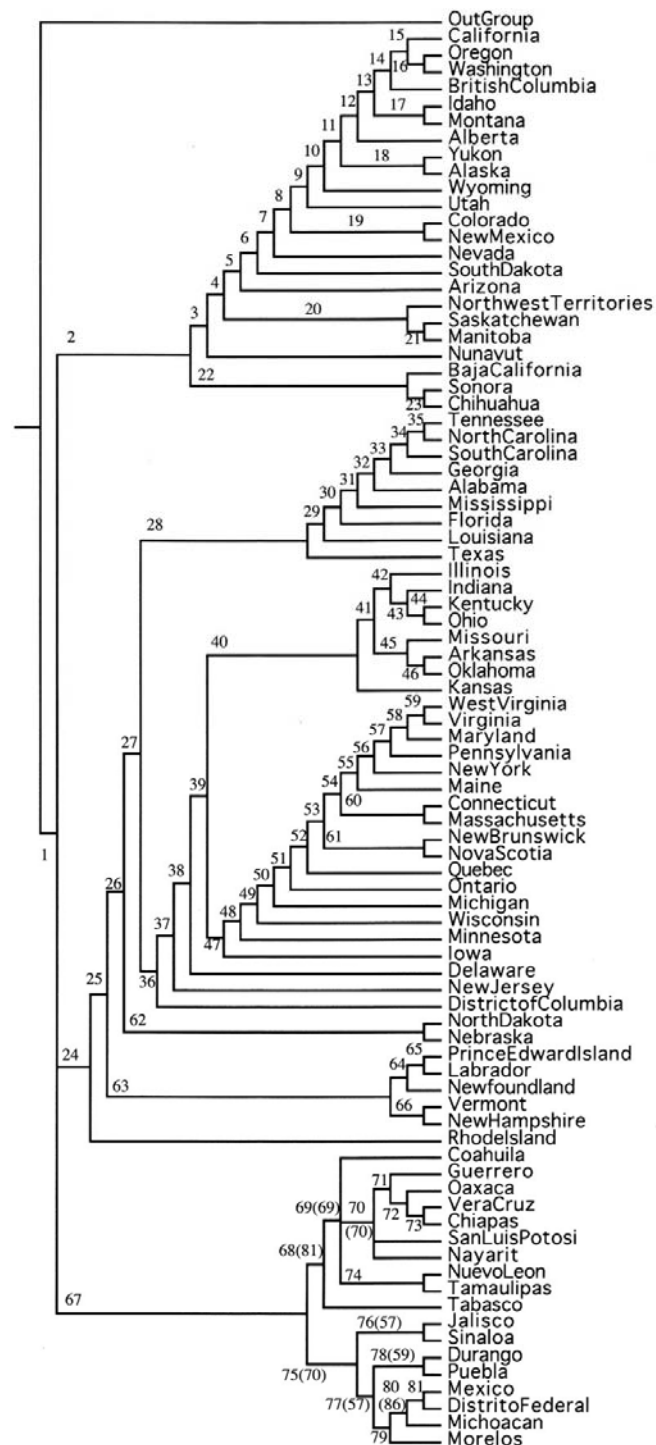


Fig. 4. Majority Rule Consensus area cladogram of the 146 most parsimonious area cladograms of states, provinces, territories, and federal districts of Canada, USA, and Mexico based on Plecoptera distributional data. Numbers identify clades discussed in text. Percentage of a particular clade appearing among the 146 most parsimonious area cladograms indicated within parentheses, otherwise 100%.

support (Fig. 3). States that comprise two of the subordinate clades of clade 40, 42 (Illinois, Indiana, Kentucky, Ohio) and 45 (Missouri, Arkansas, Oklahoma), each exhibit a nesting of geographically adjacent political area units. Subordinate clade 47 includes political area units in central and Atlantic Canada and the northeast, upper south Atlantic and upper Midwest USA. This clade did not receive bootstrap support and only two of its subordinate clades, 57 and 59, are supported. The latter clades are included within subordinate clade 56. The five states comprising this clade (New York, Pennsylvania, Maryland, Virginia, West Virginia) exhibit a nesting of geographically adjacent political area units that extends linearly from north to south. Two additional clades within subordinate clade 47, 60 (Connecticut, Massachusetts) and 61 (New Brunswick, Nova Scotia), each consist of a pair of geographically adjacent political area units. Major subordinate clade 63 of basal clade 24 includes two provinces from Atlantic Canada (Prince Edward Island, Newfoundland and Labrador) and two geographically adjacent New England states (New Hampshire, Vermont). This clade and its subordinate clades did not receive support as monophyletic groupings.

Basal clade 67 is characterized by the distribution of the genus *Anacroneuria* (Appendix 2) and is comprised of 17 states and the federal district of Mexico (Fig. 4). Plecoptera species and genera whose distributions represent unambiguous changes for the subordinate clades within 67 (68 through 81) are listed in Appendix 2. The two subordinate sister clades, 68 and 75, that originate within clade 67 are not present on the Strict Consensus area cladogram but are present on 81% and 70% of the minimum-length trees respectively. Subordinate clade 68 includes the states of eastern and southern Mexico. States comprising one of its subordinate clades, 71 (Guerrero, Oaxaca, Vera Cruz, and Chiapas), show a nesting of geographically adjacent political area units that extends north to south. Another subordinate clade, 74, includes two states (Nuevo Leon, Tamaulipas) that are geographically adjacent political area units. Subordinate clade 75 includes the political units from west-central Mexico. In this clade the state and federal district (Mexico, Distrito Federal) comprising subordinate clade 81 are geographically

adjacent political area units.

## DISCUSSION

The three major area clades of the consensus area cladograms agree with the previous observations of Hynes (1988) and Stewart & Stark (1988, 2002) concerning the grouping of North American stonefly fauna into western boreal (clade 2), eastern boreal (clade 24) and austral (clade 67) areas. Within clade 2, the relationship between subordinate clades 22 (the three states of northwestern Mexico) and 3 (the political units of the western USA and Canada) agrees with the study of Sargent et al. (1991) regarding the zoogeographic affinities of northwestern Mexico. The pattern of grouping in clade 2 agrees with the Rocky Mountains and Sierra-Cascade-Coast Ranges centers of endemism noted by Stewart & Stark (2002). Clade 7 and its subordinate clades are comprised of political area units that include sections of one or both of these mountain systems or are hypothesized to have faunal affinities with these systems (Stewart & Oswood 2006).

A single Appalachian-Ozark center of endemism reported by Stewart & Stark (2002) may correspond to clade 24. However, political area units containing sections of one or both of these mountain systems are distributed among subordinate clades in clade 24 that also include political area units lacking sections of these systems. Major subordinate clades in clade 24 suggest a relationship between states located in the southeastern USA (clade 28, Fig. 4), states located in the central USA (clade 40, Fig. 4), and states and provinces located in central and Atlantic Canada as well as northeast, upper south Atlantic and upper Midwest USA (clades 47 and 63, Fig. 4).

The political area units comprising subordinate clades 68 and 75 of clade 67 indicate a historical relationship between the states from the eastern and southern areas of Mexico and a historical relationship between the states of the west-central area of Mexico respectively.

The three basal clusters of clades found in the consensus area cladograms are compatible with vicariance events associated with plate tectonics. The split of the boreal area into the western and eastern regions of the USA and Canada (Fig. 4, clades 2 and 24) is in agreement with either the late Cretaceous mid-continental seaway that divided the Nearctic



(Allen 1983, Nelson 1988) or the later Miocene orogenies of the Rockies and Sierra Nevada in the west along with the isostatic uplift of the Appalachians in the east or both.

It is not evident what intercontinental vicariant events are responsible for subsequent branching within clades 2 and 24. In general, the relatively recent Pleistocene geological events (Ross & Ricker 1971, Hynes 1988, Sargent et al. 1991, Stewart & Stark 1988, 2002) are thought to have been important. Pleistocene ice at its maximum covered Canada and parts of the northern USA and is considered to have forced Plecoptera into refugia located in the southeastern USA, western USA, and Alaska. As the ice subsided taxa dispersed from these refugia. However, the great age of the primary divisions of the North American Plecoptera implies that the later diversification within clades 2 and 24 had an earlier history than the Pleistocene. The Miocene uplift of the Rockies and Sierra Nevada along with the secondary uplift of the Appalachians by fragmenting formerly continuous habitats and creating new ones could, through parapatric and allopatric speciation, be responsible for the hierarchical patterns seen within these subordinate clades.

Clade 67, the austral clade, is characterized by the Perlidae genus *Anacroneuria* that invaded this area from the Neotropic during the Pliocene (Stark & Gaufin 1976, Hynes 1988, Stewart & Stark 1988, 2002) when North America and South America were re-united by the newly re-established Isthmus of Panama. *Anacroneuria*, however, originated much earlier than this date. Stark & Gaufin (1976) hypothesize that starting in the early Cretaceous, prior to the breakup of Gondwanaland, ancestral progenitors of this genus dispersed from Europe or from Asia via Africa to South America. Subsequently this group became extinct in Africa.

Another possibility is faunal interchange between North and South America prior to the break-up of Pangaea in the late Jurassic. This vicariance event has instead been taken by Zwick (2000) to correspond to the fragmentation of the order itself into two suborders - one representing a northern faunal assemblage and the other a southern faunal assemblage. This would imply a later vicariant separation was responsible for the origin of the Neotropic *Anacroneuria*. However, based on an

examination of fossil stoneflies, Sinitshenkova (1997) reported that separate northern and southern hemisphere groupings of the order actually date from the late Permian. Although this earlier date would make the late Jurassic vicariant event compatible with the separation of an ancestral *Anacroneuria* lineage from a sister Nearctic lineage, the incomplete fossil data and the lack of information on phylogenetic relationships does not allow for any definitive conclusion.

The low CI, RI, and RC values exhibited by the 146 minimum-length area cladograms as well as the lack of bootstrap support of many of the clades (Fig. 3) are indicative of numerous reversals and parallelisms (Schuh 2000). Biogeographically, these have been interpreted to represent the influence of extinction and random long-distance dispersal respectively (Craw et al. 1999) and suggests that these two phenomena may have impacted the distribution of North American Plecoptera genera and species. Extinction of taxa, as reflected by shared-absences of genera and species, was exhibited by 27 of the 69 clades (Appendix 2) of the Majority Rule Consensus area cladogram (Fig. 4). These ranged from 3.8-100% of the unambiguous taxon changes for each of these clades with a mean of 34.9%. Eight clades, 11, 15, 18, 53, 58, 60, 61 and 81, are characterized by having shared-absences constitute a majority of the observed unambiguous changes (Appendix 2). The extent of how greatly extinction and random long-distance dispersal might have distorted any historical signal embedded in the distribution data of Plecoptera is difficult to assess at this time. As distribution data in the same political area units also exist for Ephemeroptera (Randolph, 2002) and Odonata (Mauffray & Beckenbach 2005a, 2005b), two aquatic groups with origins phylogenetically older than Plecoptera, one approach would be to undertake a PAE/CADE analysis of the distribution of these groups similar to that done for stoneflies. Coincident hierarchical patterns exhibited by these groups with that resulting from this analysis would be indicative of common underlying historical causes while their absence would imply the importance of extinction and random long-distance dispersal. However, unlike Plecoptera, which is generally restricted to lotic habitats, Ephemeroptera and Odonata occupy both lotic and lentic habitats

and this may increase the influence of extinction and random long-distance dispersal on the distribution patterns of their taxa.

The high level of homoplasy on the minimum-length area cladograms may also reflect both the large number of area units and their artificial nature. Morrone & Escalante (2002) employing PAE analysis involving the distribution of Mexican terrestrial animals found that the number of steps decreased and the number of synapomorphies increased on their resulting area cladograms when the total number of the geographic area units decreased while simultaneously the area of the individual units increased as well as became more natural. PAE/CADE studies on North American Plecoptera distributional data associated with ecoregions or biogeographic provinces would be desirable, but accurate distributional data based on these area units are not available in a published database. Such information is crucial, however, and will have to be gathered by digitization of specimen data presently housed in a number of museum, university and personal collections before more finely grained PAE/CADE analyses can be expected.

It is also possible, despite the efforts of many workers, that the low level of shared taxa for many clades of the minimum-length area cladograms may represent an artifact of incomplete information on the distribution of North American stonefly genera and species. Accumulating essential additional stonefly distributional data from stream ecosystems in Canada, the USA and Mexico would address this concern as well as possibly clarify unresolved area relationships depicted on the Majority Rule Consensus area cladogram of this study (Fig. 4).

Ultimately corroboration of this PAE/CADE analysis will need to be determined by using as yet unpublished resolved phylogenies of species comprising North American stonefly genera. Several genera each with over thirty described species could provide a basis for generating useful biogeographical hypotheses - *Allocapnia*, *Capnia*, *Alloperla*, *Sweltsa*, and *Isoperla*. Congruence between results obtained from these analyses with that provided by this study would be a further indication that the latter correctly captured the historical signal in existing stonefly distributional data concerning hierarchical relationships of North American large political area

units.

## ACKNOWLEDGMENTS

I thank C. Riley Nelson and R. Edward DeWalt for insightful observations and useful suggestions concerning the manuscript. I also thank Mark Schorr and Joey Shaw for making relevant comments on an earlier version of the manuscript.

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Received 3 April, Accepted 29 April, Published 18 December 2008

**Appendix 1**

Data matrix for the 574 Plecoptera taxa and genera employed as characters for 85 Canadian, United States and Mexican provinces. Presence of taxa indicated by one, absence by zero. An outgroup (OG) consisting of all zeros is included in the matrix. Area acronyms as noted for Figures 1 and 2.

Taxa/Area	CO	CA	CT	DC	DE	FL	GA	IA	IL	IN	KS	KY	LA	MA	MD	ME	MI	MN	MO	MS	NB	NC	ND	NE	NH	NJ	NM	NV	NY	OH	OK	OR	PA	PE	RI	SC	SD	TN	TX	UT	VA	VT	WA	WI	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	AK	BT	CH	CT	DC	GU	IA	MC	MR	NA	NT	NO	ON	PE	PU	RS	ST	TA	VA	WV	WY	A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## Appendix 2

List of unambiguous species and genera changes for the clades noted in Figure 4. \* indicates reversals.

Clade	Unambiguous species and genera changes
2	Genus <i>Capnia</i>
3	<i>Claassenia sabulosa</i> , Genus <i>Isogenoides</i> , <i>I. colubrinus</i>
4	Genus <i>Pteronarcys</i> , genus <i>Pteronarcella</i> , <i>P. badia</i> , genus <i>Amphinemura</i> , genus <i>Suwallia</i> , genus <i>Isoperla</i>
5	<i>Eucapnopsis brevicauda</i> , <i>Amphinemura banksi</i> , <i>Malenka coloradensis</i> , genus <i>Sweltsa</i> , <i>S. coloradensis</i> , genus <i>Triznaka</i> , <i>T. pintada</i> , genus <i>Hesperoperla</i> , <i>H. pacifica</i> , <i>Isogenoides elongatus</i>
6	<i>Capnia confusa</i> , <i>C. gracilaria</i> , genus <i>Utacapnia</i> , <i>U. lemoniana</i> , genus <i>Prostoia</i> , <i>P. besametsa</i> , genus <i>Zapada</i> , <i>Z. cinctipes</i> , <i>Sweltsa borealis</i> , <i>Isoperla quinquepunctata</i>
7	<i>Capnia uintahi</i> , <i>Capnura wanica</i> , <i>Malenka californica</i> , genus <i>Podmosta</i> , <i>P. delicatula</i> , <i>Zapada frigida</i> , <i>Z. haysi</i> , <i>Z. oregonensis</i> , <i>Doddusia occidentalis</i> , <i>Taenionema pallidum</i> , <i>T. uninta</i> , genus <i>Alloperla</i> , <i>A. severa</i> , <i>Plumaperla diversa</i> , <i>Swelta fidelis</i> , <i>Isoperla pinta</i> , genus <i>Megarcys</i> , <i>M. signata</i> , genus <i>Diura</i> , <i>D. knowltoni</i>
8	<i>Pteronarcys californica</i> , <i>Capnia coloradensis</i> , <i>C. vernalis</i> , <i>Isocapnia crinata</i> , <i>I. vedderensis</i> , genus <i>Mesocapnia</i> , <i>Utacapnia logana</i> , <i>U. poda</i> , genus <i>Perlomyia</i> , <i>P. utahensis</i> , <i>Malenka flexura</i> , <i>Taenionema pacificum</i> , <i>Suwallia starki</i> , <i>Sweltsa lamba</i> , <i>Isoperla mormona</i> , <i>I. phalerata</i> , genus <i>Cultus</i> , <i>C. aestivalis</i> , genus <i>Kogotus</i> , <i>K. modestus</i>
9	<i>Capnia petila</i> , <i>Isocapnia grandis</i>
10	<i>Pteronarcys dorsata</i> , <i>Capnia uintahi</i> *, <i>Isocapnia integra</i> , genus <i>Pomoleuctra</i> , <i>P. purcellana</i> , genus <i>Nemoura</i> , <i>N. arctica</i> , <i>Alloperla medvedea</i> , <i>A. serrata</i> , <i>Sweltsa revelstoka</i> , <i>Isoperla fusca</i> , <i>Arcynopteryx compacta</i> , <i>Kogotus nonus</i>
11	<i>Capnura wanica</i> *, <i>Mesocapnia oenone</i> , <i>Utacapnia columbiana</i> , <i>U. lemoniana</i> *, <i>U. logana</i> *, <i>U. poda</i> *, <i>Amphinemura banksi</i> *, <i>Malenka coloradensis</i> *, <i>Taenionema uinta</i> *, <i>Suwallia forcipata</i> *, <i>Sweltsa lamba</i> *, <i>Triznaka pintada</i> *, genus <i>Kathroperla</i> , <i>K. perdita</i> , <i>Isoperla phalerata</i> *
12	Genus <i>Bolshecapnia</i> , <i>B. milami</i> , <i>Capnia sextuberculata</i> , genus <i>Megaleuctra</i> , <i>Sweltsa albertensis</i> , <i>Calineuria californica</i> , <i>Megarcys watertoni</i> , genus <i>Setoena</i> , <i>S. bradleyi</i>
13	<i>Despaxia augusta</i> , genus <i>Soyedina</i> , <i>Sweltsa occidens</i> , <i>Cascadoperla trictura</i> , <i>Megarcys subtruncata</i> , <i>Skwala curvata</i> , <i>Cultus pilatus</i> , <i>C. tostonus</i>

## Appendix 2

### Continued

Clade	Unambiguous species and genera changes
14	<i>Capnia elongata</i> , <i>C. excavata</i> , <i>C. melia</i> , <i>C. promota</i> , <i>Isocapnia abbreviata</i> , <i>Isocapnia crinita</i> *, <i>I. integra</i> *, <i>I. spenceri</i> , <i>Mesocapnia projecta</i> , <i>Malenka cornuta</i> , <i>Soyedina producta</i> , <i>Taenionema kincaidii</i> , <i>Alloperla fraterna</i> , genus <i>Haploperla</i> , <i>H. chilnualna</i> , <i>Sweltsa exquisita</i> , <i>S. pacifica</i> , <i>Yoraperla mariana</i> , <i>Y. siletz</i> , <i>Doroneuria baumannii</i> , <i>Frisonia picticeps</i> , <i>Setvena tibialis</i> , <i>Osobenus yakimae</i>
15	<i>Pteronarcella regularis</i> , <i>Pteronarcys dorsata</i> *, <i>Bolshecapnia milami</i> *, <i>Bolshecapnia spenceri</i> *, <i>Capnia coloradensis</i> *, <i>C. vernalis</i> *, <i>Mesocapnia porrecta</i> , genus <i>Paracapnia</i> , genus <i>Amphinemura</i> *, <i>Alloperla medveda</i> *, <i>Triznaka pintada</i> , genus <i>Utaperla</i> *, <i>U. sopladora</i> *, genus <i>Soliperla</i> , <i>Yoraperla nigrisoma</i> , <i>Doroneuria theodora</i> *, <i>Calliperla luctuosa</i> , <i>Isoperla bifurcata</i> , <i>I. longiseta</i> *, <i>I. marmorata</i> , <i>Arcynopteryx compacta</i> *, <i>Megarcys signata</i> *, <i>M. watertoni</i> *, <i>Setvena bradleyi</i> *, <i>Cultus aestivalis</i> *, <i>Kogotus modestus</i> *, <i>Rickera sorpta</i>
16	<i>Capnia licina</i> , <i>Capnura elevata</i> , <i>C. venosa</i> , <i>Isocapnia palousa</i> , <i>I. rickeri</i> , <i>Paracapnia ensicala</i> , <i>Utacapnia imbera</i> , <i>Megaleuctra complicata</i> , <i>M. kincaidi</i> , <i>Malenka bifurcata</i> , <i>M. perplexa</i> , <i>M. tina</i> , genus <i>Nemoura</i> *, <i>Podmosta obscura</i> , <i>Taenionema jewetti</i> , <i>T. oregonense</i> , <i>Sweltsa adamantea</i> , <i>Isoperla gravitans</i> , <i>I. rainiera</i> , <i>I. tilasqua</i> , <i>Isogenoides colubrinus</i> *
17	<i>Capnura venosa</i> , <i>Amphinemura banksi</i> , <i>Malenka tina</i> , genus <i>Nemoura</i> *, <i>Soyedina potteri</i> , <i>Sweltsa lamba</i> , <i>Soliperla salish</i> , genus <i>Pictetiella</i> , <i>P. expansa</i>
18	<i>Capnia elongata</i> , <i>C. nearctica</i> , <i>C. pileata</i> , <i>Capnura vernalis</i> *, <i>Mesocapnia variabilis</i> , genus <i>Perlomyia</i> *, <i>P. utahensis</i> *, <i>Amphinemura linda</i> , genus <i>Malenka</i> *, <i>M. californica</i> *, <i>M. flexura</i> *, <i>Nemoura rickeri</i> , <i>Podmosta weberi</i> , <i>Taenionema kincaidii</i> , genus <i>Taeniopteryx</i> *, <i>Alaskaperla ovibovus</i> , <i>Isoperla decolorata</i> , <i>I. fulva</i> *, <i>I. pinta</i> *, <i>I. quinquepunctata</i> *, <i>Diura bicaudata</i> , <i>Isogenoides elongatus</i> *
19	Genus <i>Bolshecapnia</i> , <i>B. milami</i> , <i>Capnia decepta</i> , <i>Capnura fibula</i> , <i>Taeniopteryx parvula</i> , <i>Alloperla pilosa</i> , <i>Sweltsa hondo</i> , genus <i>Perlesta</i> , <i>P. decipiens</i> , <i>Isoperla jewetti</i> , <i>Isogenoides zionensis</i>
20	<i>Pteronarcys dorsata</i> , <i>Amphinemura linda</i> , genus <i>Nemoura</i> , <i>Shipsa rotunda</i> , <i>Isoperla decolorata</i>
21	<i>Capnia confusa</i> , <i>C. gracilaria</i> , genus <i>Paracapnia</i> , <i>P. angulata</i> , <i>Malenka californica</i> , <i>Nemoura rickeri</i> , genus <i>Oemopteryx</i> , <i>O. fosketti</i> , genus <i>Taeniopteryx</i> , <i>T. nivalis</i> , genus <i>Acroneuria</i> , <i>A. abnormis</i> , <i>A. lycorias</i> , genus <i>Paragnetina</i> , <i>P. media</i> , <i>Isoperla bilineata</i> , <i>I. marlynia</i> , <i>I. transmarina</i> , <i>Isogenoides frontalis</i>
22	<i>Capnia decepta</i> , genus <i>Mesocapnia</i> , <i>M. frisoni</i>
23	Genus <i>Anacroneuria</i>
24	Genus <i>Allocapnia</i>
25	Genus <i>Isoperla</i>

## Appendix 2

### Continued

Clade	Unambiguous species and genera changes
26	Genus <i>Perlesta</i>
27	<i>Allocapnia granulata</i> , <i>Acroneuria arenosa</i> , genus <i>Perlinella</i> , <i>P. drymo</i> , genus <i>Paragnetina</i>
28	<i>Taeniopteryx burksi</i> , <i>T. lita</i> , <i>T. lonicera</i> , <i>Acroneuria evoluta</i> , genus <i>Neoperla</i> , <i>N. carlsoni</i> , <i>N. clymene</i>
29	Genus <i>Pteronarcys</i> , <i>P. dorsata</i> , genus <i>Leuctra</i> , <i>Acroneuria abnormis</i> , <i>Perlinella ephyre</i> , genus <i>Agnetina</i> , <i>A. annulipes</i> , <i>Paragnetina kansensis</i> , genus <i>Helopicus</i> , <i>H. bogaloosa</i>
30	<i>Nemocapnia carolina</i> , <i>Leuctra cottaquilla</i> , <i>L. ferruginea</i> , <i>Amphinemura nigritta</i> , genus <i>Haploperla</i> , <i>Attaneuria ruralis</i> , <i>Eccoptura xanthenes</i> , <i>Perlinella zwicki</i> , <i>Clioperla clio</i> , <i>Isoperla dicala</i>
31	<i>Allocapnia aurora</i> , <i>A. mystica</i> , <i>A. rickeri</i> , <i>Leuctra tenuis</i> , <i>Amphinemura delosa</i> , genus <i>Prostoia</i> , <i>P. completa</i> , <i>Shipsa rotunda</i> , genus <i>Strophopteryx</i> , <i>S. fasciata</i> , <i>Taeniopteryx maura</i> , genus <i>Alloperla</i> , <i>Acroneuria carolinensis</i> , <i>Neoperla occipitalis</i> , genus <i>Diploperla</i> , <i>D. duplicata</i>
32	<i>Pteronarcys biloba</i> , <i>Allocapnia recta</i> , <i>Leuctra biloba</i> , <i>L. moha</i> , <i>Alloperla atlantica</i> , <i>A. usa</i> , genus <i>Sweltsa</i> , <i>Tallaperla laurie</i> , <i>T. maria</i> , <i>Acroneuria filicis</i> , genus <i>Beloneuria</i> , <i>Agnetina flavescens</i>
33	<i>Pteronarcys scotti</i> , <i>Allocapnia granulata*</i> , <i>A. wrayi</i> , <i>Leuctra cottaquilla*</i> , <i>Amphinemura appalachia</i> , <i>A. wui</i> , <i>Alloperla chloris</i> , <i>A. nanina</i> , <i>A. petasata</i> , <i>Sweltsa lateralis</i> , <i>Tallaperla anna</i> , <i>T. cornelia</i> , <i>Veihoperla ada</i> , <i>Beloneuria stewarti</i> , <i>Paragnetina immarginata</i> , <i>Isoperla holochlora</i> , genus <i>Remenus</i> , genus <i>Malerikus</i> , <i>M. hastatus</i> , genus <i>Yugus</i> , <i>Y. arinus</i>
34	<i>Leuctra alexanderi</i> , <i>Leuctra sibleyi</i> , genus <i>Megaleuctra</i> , <i>M. williamsae</i> , <i>Strophopteryx appalachia</i> , <i>Perlesta frisoni</i> , <i>P. nelsoni</i> , <i>Paragnetina ichusa</i> , <i>Isoperla distincta</i> , <i>I. orata</i> , <i>I. similis</i> , <i>Remenus bilobatus</i> , genus <i>Hydroperla</i> , genus <i>Isogenoides</i> , <i>I. varians</i> , <i>Oconoperla innubila</i>
35	<i>Allocapnia fumosa</i> , <i>A. nivicola</i> , <i>A. stannardi</i> , genus <i>Paracapnia</i> , <i>P. angulata</i> , <i>Leuctra carolinensis</i> , <i>L. moha*</i> , <i>L. nephophila</i> , genus <i>Paranemoura</i> , <i>P. perfecta</i> , genus <i>Soydina</i> , <i>S. carolinensis</i> , genus <i>Zapada</i> , <i>Z. chila</i> , genus <i>Oemopteryx</i> , <i>O. contorta</i> , <i>Strophopteryx limata</i> , genus <i>Taenionema</i> , <i>T. atlanticum</i> , <i>Alloperla neglecta</i> , <i>Rasvona terna</i> , <i>Tallaperla elisa</i> , <i>Acroneuria frisoni</i> , <i>A. lycorias</i> , <i>Isoperla lata</i> , <i>Cultus verticalis</i>
36	<i>Allocapnia nivicola</i> , <i>A. rickeri</i> , genus <i>Haploperla</i> , <i>H. brevis</i>
37	Genus <i>Paracapnia</i> , genus <i>Leuctra</i> , <i>L. tenuis</i> , <i>Isoperla transmarina</i>
38	Genus <i>Prostoia</i> , <i>P. completa</i> , genus <i>Strophopteryx</i> , <i>S. fasciata</i> , <i>Taeniopteryx burksi</i> , <i>Acroneuria abnormis</i> , <i>Paragnetina media</i> , <i>Clioperla clio</i>

## Appendix 2

### Continued

Clade	Unambiguous species and genera changes
39	Genus <i>Pteronarcys</i> , <i>P. pictetii</i> , <i>Allocapnia nivicola</i> *, <i>A. vivipara</i> , <i>Amphinemura delosa</i> , <i>Acroneuria arenosa</i> *, <i>Attaneuria ruralis</i> , <i>Isoperla bilineata</i> , <i>I. longiseta</i> , genus <i>Isogenoides</i> , <i>I. varians</i>
40	Genus <i>Zealeuctra</i> , <i>Z. claasseni</i> , <i>Taeniopteryx metequi</i> , <i>Acroneuria evoluta</i> , <i>A. frisoni</i> , <i>Paragnetina kansensis</i> , <i>Isoperla mohri</i> , <i>I. transmarina</i> *, genus <i>Helopicus</i> , genus <i>Hydroperla</i> , <i>H. crosbyi</i> , <i>H. fugitans</i>
41	<i>Allocapnia mystica</i> , <i>Paracapnia angulata</i> , <i>Amphinemura nigritta</i> , <i>Taeniopteryx parvula</i> , genus <i>Alloperla</i> , <i>A. caudata</i> , <i>Acroneuria filicis</i> , <i>A. internata</i> , <i>A. perplexa</i> , <i>Perlesta decipiens</i> , <i>Neoperla catharae</i> , <i>Agnentina flavescens</i> , <i>Isoperla burksi</i>
42	<i>Allocapnia forbesi</i> , <i>A. illinoensis</i> , <i>A. nivicola</i> , <i>A. recta</i> , <i>A. smithi</i> , <i>Leuctra alta</i> , <i>L. rickeri</i> , <i>L. sibleyi</i> , <i>Zealeuctra fraxina</i> , <i>Amphinemura varshava</i> , <i>Soyedina vallicularia</i> , <i>Perlesta napacola</i> , <i>Neoperla clymene</i> , <i>N. occipitalis</i> , <i>N. stewarti</i> , <i>I. nana</i>
43	<i>Pteronarcys dorsata</i> , <i>Allocapnia indianae</i> , <i>A. ohioensis</i> , genus <i>Ostrocerca</i> , <i>O. truncata</i> , <i>Prostoia similis</i> , <i>Taeniopteryx maura</i> , genus <i>Sweltsa</i> , <i>S. onkos</i> , <i>Perlesta adena</i> , <i>Neoperla gaufini</i> , <i>Isoperla longiseta</i> *, <i>I. mohri</i> *, genus <i>Diploperla</i> , <i>D. robusta</i>
44	<i>Allocapnia frisoni</i> , <i>A. pygmaea</i> , <i>A. zola</i> , genus <i>Taenionema</i> , <i>T. atlanticum</i> , <i>Alloperla caudata</i> *, <i>A. chloris</i> , <i>A. ideii</i> , <i>A. imbecilla</i> , <i>A. usa</i> , genus <i>Peltoperla</i> , <i>P. arcuata</i> , <i>Acroneuria carolinensis</i> , <i>A. lycorias</i> , <i>Eccoptura xanthenes</i> , <i>Perlesta nitida</i> , <i>Agnentina capitata</i> , <i>Paragnetina kansensis</i> *, <i>Isoperla orata</i> , genus <i>Hydroperla</i> *, <i>H. crosbyi</i> *, <i>H. fugitans</i> *, genus <i>Isogenoides</i> *, <i>I. varians</i> *, genus <i>Malirekus</i> , <i>M. hastatus</i>
45	<i>Allocapnia mohri</i> , <i>A. sandersoni</i> , <i>Strophopteryx arkansae</i> , <i>S. cucullata</i> , <i>Acroneuria abnormis</i> *, <i>Perlesta browni</i> , <i>P. fusca</i> , <i>Neoperla choctaw</i> , <i>N. falayah</i> , <i>N. osage</i> , <i>Isoperla ouachita</i> , <i>I. signata</i> , genus <i>Isogenoides</i> *, <i>I. varians</i> *
46	<i>Allocapnia malverna</i> , <i>A. peltoides</i> , <i>Zealeuctra cherokee</i> , <i>Taeniopteryx maura</i> , <i>Perlesta baumanni</i> , <i>I. bilineata</i> *, <i>I. couchatta</i> , <i>I. longiseta</i>
47	<i>Allocapnia pygmaea</i> , <i>Shipsa rotunda</i> , <i>Acroneuria lycorias</i> , <i>Agnentina capitata</i> , <i>Isoperla richardsoni</i> , <i>I. signata</i> , <i>I. slossonae</i>
48	<i>Pteronarcys dorsata</i> , <i>Allocapnia illinoensis</i> , <i>A. minima</i> , genus <i>Capnia</i> , <i>C. vernalis</i> , <i>Paracapnia opis</i> , <i>Leuctra ferruginea</i> , <i>L. tenella</i> , <i>Prostoia similis</i> , genus <i>Oemopteryx</i> , <i>O. glacialis</i> , <i>Taeniopteryx parvula</i> , <i>Haploperla orpha</i> , <i>Acroneuria internata</i> , <i>Isoperla frisoni</i> , <i>I. lata</i> , <i>Isogenoides frontalis</i> , <i>I. olivaceus</i>
49	Genus <i>Capnura</i> , <i>Capnura manitoba</i> , <i>Paracapnia angulata</i> , <i>Isoperla cotta</i> , <i>I. longiseta</i> *, <i>I. nana</i>
50	Genus <i>Ostrocerca</i> , <i>O. albidipennis</i> , <i>Alloperla banksi</i> , <i>Attaneuria ruralis</i> *, <i>Isoperla richardsoni</i> *, genus <i>Cultus</i> , genus <i>Helopicus</i>

## Appendix 2

### Continued

Clade	Unambiguous species and genera changes
51	<i>Pteronarcys pictetii</i> *, <i>Leuctra duplicata</i> , <i>Amphinemura nigritta</i> , <i>Ostrocerca complexa</i> , <i>O. truncata</i> , genus <i>Paranemoura</i> , <i>P. perfecta</i> , <i>Alloperla concolor</i> , <i>A. petasata</i> , genus <i>Sweltsa</i> , <i>S. onkos</i> , <i>Acroneuria carolinensis</i> , <i>A. internata</i> *, genus <i>Perlesta</i> *, <i>Perlinella ephyre</i> *, <i>Isoperla montana</i> , <i>Helopicus subvarians</i>
52	<i>Pteronarcys biloba</i> , <i>Allocapnia maria</i> , <i>A. nivicola</i> , <i>Leuctra truncata</i> , <i>Amphinemura wui</i> , genus <i>Taenionema</i> , <i>T. atlanticum</i> , <i>Alloperla chloris</i> , <i>A. voinae</i> , <i>Sweltsa lateralis</i> , <i>S. naica</i> , <i>Paragnetina immarginata</i> , <i>Isoperla holochlora</i> , <i>I. orata</i> , <i>I. similis</i> , <i>Isogenoides hansonii</i>
53	<i>Allocapnia granulata</i> *, <i>Amphinemura delosa</i> *, <i>A. linda</i> *, <i>Oemopteryx glacialis</i> *, <i>Isoperla nana</i> *, <i>Isogenoides olivaceus</i> *
54	<i>Oemopteryx contorta</i> , <i>Taeniopteryx maura</i> , genus <i>Tallaperla</i> , <i>T. maria</i> , genus <i>Perlesta</i> , <i>Perlinella ephyre</i>
55	<i>Pteronarcys comstocki</i> , <i>P. proteus</i> , <i>Bolotoperla rossi</i> , <i>Rasvona terna</i> , genus <i>Utaperla</i> , <i>U. gaspesiana</i> , <i>Neoperla occipitalis</i>
56	<i>Allocapnia curiosa</i> , <i>A. frisoni</i> , <i>A. granulata</i> , <i>A. rickeri</i> , genus <i>Capnura</i> *, <i>C. manitoba</i> *, <i>Alloperla imbecilla</i> , genus <i>Peltoperla</i> , <i>P. arcuata</i> , <i>Attaneuria ruralis</i> , <i>Eccoptura xanthenes</i> , <i>Agnentina flavescens</i> , <i>Isoperla cotta</i> *, genus <i>Remenus</i> , <i>R. bilobatus</i> , genus <i>Malerikus</i> , <i>M. iroquois</i>
57	<i>Allocapnia aurora</i> , <i>A. harperi</i> , <i>A. minima</i> *, <i>A. wrayi</i> , <i>Paracapnia opis</i> *, <i>Leuctra alexanderi</i> , <i>L. carolinensis</i> , genus <i>Megaleuctra</i> , <i>M. flinti</i> , <i>Amphinemura delosa</i> , <i>Soyedina carolinensis</i> , <i>Strophopteryx appalachia</i> , <i>Taeniopteryx metequi</i> , <i>T. ugola</i> , <i>Alloperla aracoma</i> , <i>A. banksi</i> *, <i>A. biserrata</i> , <i>A. usa</i> , <i>A. voinae</i> *, <i>Acroneuria filicis</i> , <i>A. frisoni</i> , genus <i>Hansonoperla</i> , <i>H. appalachia</i> , <i>Perlesta nelsoni</i> , <i>P. taeyisia</i> , <i>Agnentina annulipes</i> , genus <i>Diploperla</i> , <i>D. duplicata</i> , <i>D. robusta</i> , genus <i>Yugus</i> , <i>Y. kirchmeri</i>
58	<i>Leuctra rickeri</i> , genus <i>Nemoura</i> *, <i>N. trispinosa</i> *, <i>Alloperla vostoki</i> *, <i>Sweltsa palearata</i> , <i>Isoperla burksi</i> , <i>I. francesca</i> *
59	<i>Allocapnia loshada</i> , <i>A. mystica</i> , <i>Taeniopteryx lita</i> , <i>T. nivalis</i> *, <i>Alloperla idei</i> , <i>Peltoperla tarteri</i> , <i>Acroneuria internata</i> , <i>A. kirchmeri</i> , <i>Perlesta frisoni</i> , <i>Isoperla montana</i> *, <i>Diploperla kanawholensis</i> , <i>Malerikus iroquois</i> *
60	<i>Pteronarcys dorsata</i> *, genus <i>Nemoura</i> *, <i>N. trispinosa</i> *, <i>Alloperla banksi</i> *, <i>Sweltsa naica</i> *, <i>Perlesta nitida</i> , <i>Isoperla marlynia</i> *
61	<i>Paracapnia angulata</i> *, <i>Ostrocerca truncata</i> *, <i>Prostoia similis</i> *, genus <i>Oemopteryx</i> *, genus <i>Taeniopteryx</i> *, <i>T. burksi</i> *, <i>T. nivalis</i> *, <i>T. parvula</i> *, <i>Acroneuria carolinensis</i> *, genus <i>Helopicus</i> *, <i>H. subvarians</i> *

## Appendix 2

### Continued

Clade	Unambiguous species and genera changes
62	Genus <i>Pteronarcys</i> , <i>P. pictetii</i> , <i>Acroneuria abnormis</i> , <i>Perlesta decipiens</i> , <i>P. xube</i> , <i>Isoperla bilineata</i>
63	Genus <i>Leuctra</i> , genus <i>Taenionema</i> , <i>T. atlanticum</i> , genus <i>Alloperla</i> , genus <i>Sweltsa</i> , <i>S. naica</i> , <i>S. onkos</i>
64	<i>Paracapnia opis</i> , genus <i>Podmosta</i> , <i>P. macdunnoughi</i> , <i>Isoperla transmarina</i>
65	Genus <i>Pteronarcys</i> , genus <i>Allocapnia</i> *, genus <i>Amphinemura</i> , <i>A. nigrutta</i> , genus <i>Nemoura</i> , <i>N. trispinosa</i>
66	<i>Allocapnia maria</i> , <i>A. pygmaea</i> , <i>Leuctra maria</i> , <i>L. variabilis</i> , genus <i>Paranemoura</i> , <i>P. perfecta</i> , genus <i>Haploperla</i> , <i>H. brevis</i> , <i>Rasvena terna</i> , genus <i>Suwallia</i> , <i>S. marginata</i> , <i>Sweltsa lateralis</i> , <i>Isoperla orata</i> , genus <i>Malerikus</i> , <i>M. Iroquois</i>
67	Genus <i>Anacroneuria</i>
72	<i>Anacroneuria aethiops</i> , <i>A. costana</i> , <i>A. quadriloba</i>
73	<i>Anacroneuria ratcliffei</i>
77	Genus <i>Amphinemura</i>
79	<i>Amphinemura mexicana</i>
80	<i>Amphinemura venusta</i>
81	Genus <i>Anacroneuria</i>