
Phylogeny of caddisflies (Insecta, Trichoptera)

KARL M. KJER, ROGER J. BLAHNIK & RALPH W. HOLZENTHAL

Accepted: 29 July 2001

Kjer, K. M., Blahnik, R. J. & Holzenthal, R. W. (2002). Phylogeny of caddisflies (Insecta, Trichoptera). — *Zoologica Scripta*, 31, 83–91.

Trichoptera are holometabolous insects with aquatic larvae that, together with the Lepidoptera, comprise the Amphiesmenoptera. Previous phylogenetic hypotheses and progress on our ongoing data collection are summarized. Fragments of the large and small subunit nuclear ribosomal RNAs (D1, D3, V4–5), the nuclear elongation factor 1 alpha gene and a fragment of mitochondrial cytochrome oxidase 1 (COI) were sequenced, and molecular data were combined with previously published morphological data. Equally and differentially weighted parsimony analyses were conducted in order to present a phylogeny of Trichoptera, including 43 of 45 families. Our phylogeny closely resembles that proposed by Herbert Ross with respect to the relationships among suborders, with a monophyletic Annulipalpia at the base of the tree, and a clade consisting of Spicipalpia plus a monophyletic Integripalpia. The monophyly of Spicipalpia is weakly supported in the combined equally weighted analysis, and Spicipalpia is paraphyletic in the differentially weighted analysis. Within Integripalpia, our phylogeny recovered monophyletic Plententoria, Brevitentoria and Sericostomatoidea. Leptoceroidea was unresolved in the equally weighted analysis and monophyletic in the differentially weighted analysis. Within Annulipalpia, we recovered a basal but paraphyletic Philopotamoidea and a monophyletic Hydropsychoidea.

Karl M. Kjer and Roger J. Blahnik, Department of Entomology, 91 Lipman Drive, Blake Hall, Rutgers University, Cook College, New Brunswick, NJ 08901, USA. E-mail: kjer@aesop.rutgers.edu
Ralph W. Holzenthal and Roger J. Blahnik (current address), Department of Entomology, 219 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108, USA. E-mail: bolze001@tc.umn.edu; blahn003@tc.umn.edu

Introduction

Trichoptera is an order of holometabolous insects with aquatic immature stages that are integral components of almost all freshwater communities (Resh & Rosenberg 1984). With a fauna of some 10 000 described extant species, distributed among 45 families (Morse 1997a), the order is diverse in terms of the microhabitats and trophic niches occupied by the species (Mackay & Wiggins 1979).

We collected sequence data and re-evaluated a morphological dataset from Frania & Wiggins (1997). In this study, we present our progress in the ongoing data collection for the estimation of phylogenetic relationships within Trichoptera. We have recently presented an analysis of 89 taxa with rRNA data, and a combined analysis including 59 taxa (Kjer *et al.* 2001). Here, we present a combined parsimony analysis of 117–120 taxa, adding 28 taxa and four integripalpian families that were absent from our previous work.

Within Trichoptera, it is now accepted that the order contains two monophyletic suborders, Annulipalpia and Integripalpia, with a third suborder, Spicipalpia, whose monophyly is equivocal. Annulipalpian larvae make fixed retreats, while

integripalpian larvae make portable tube cases. Spicipalpian larvae include ‘free-living’ predators (Rhyacophilidae and Hydrobiosidae), ‘purse-case makers’ (Hydroptilidae) and ‘saddle-’ or ‘tortoise-case makers’ (Glossosomatidae). The Annulipalpia and Spicipalpia are primarily lotic, while the Integripalpia occur in both lotic and lentic habitats (Wiggins 1996).

Ross (1956, 1964, 1967) provided the first modern phylogenetic hypotheses of subordinal and superfamily relationships (Fig. 1A). Recently, alternative morphologically based phylogenies have been proposed challenging Ross’ view (Weaver 1983, 1984, 1992a,b; Weaver & Morse 1986; Wiggins & Wichard 1989; Wiggins 1992; Frania & Wiggins 1997; Ivanov 1997; summarized by Morse 1997b). To date, at least five very different hypotheses of the relationships among the components of the three suborders have been proposed or suggested (Fig. 1A–E). Hypotheses differ in the placement and monophyly of Spicipalpia and its included families. Phylogenies challenging traditional classifications have also been proposed for family relationships within suborders (Fig. 2; see Morse 1997b for a review).

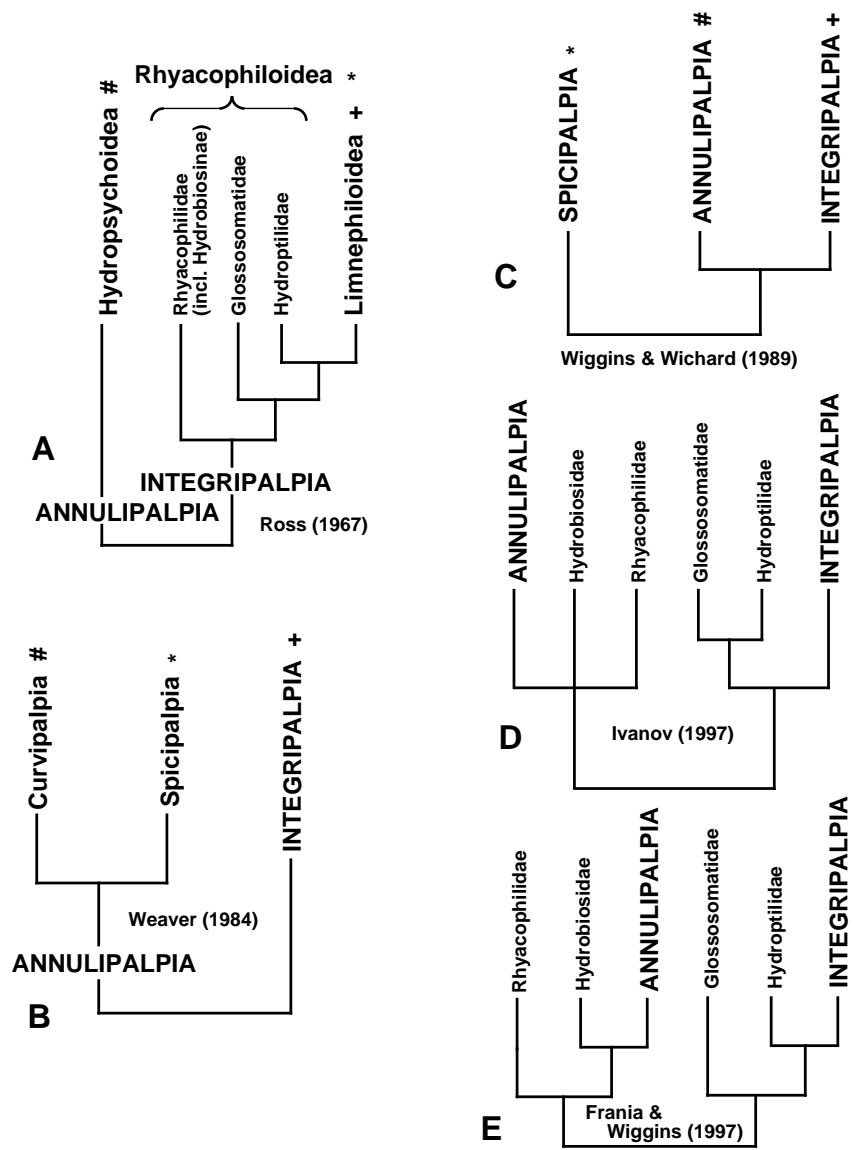


Fig. 1 Five contemporary hypotheses of subordinal relationships of the Trichoptera. Equivalent taxonomic units are indicated by like symbols (e.g. Ross' Hydropsychoidea = Weaver's Curvipalpia = Wiggins & Wichard's Annulipalpia). —A. From Ross (1967). —B. From Weaver (1984). —C. From Wiggins & Wichard (1989), based on pupation only (Wiggins 1992). —D. From Ivanov (1997). —E. A strict consensus of five trees from Frania & Wiggins (1997; figs 24 and 25). Spicipalpia as used here includes the families Rhyacophilidae, Hydrobiosidae, Glossosomatidae and Hydroptilidae.

While the analysis of morphological characters has been extensive, consensus over relationships among suborders is at an impasse. However, apart from our work, only one of the published studies has used automated searches for most parsimonious trees (Frانيا & Wiggins 1997) and none has included molecular data. Additional data, rigorously analysed, will provide a fresh perspective to help stabilize caddisfly classification.

Materials and methods

Laboratory protocols

The methods have been completely described by Kjer *et al.* (2001). DNA was extracted with sodium dodecyl sulphate, proteinase-K and phenol–chloroform as described by Hillis

& Davis (1986). Polymerase chain reaction-amplified DNA was separated on a 1.5% low melting point agarose gel (NuSieve 3 : 1, FMC Bioproducts), and sequenced on an ABI 377 automated sequencer using manufacturer's recommendations (Applied Biosystems), in a reduced volume reaction.

Our dataset includes outgroup representatives from Diptera, Mecoptera and Siphonaptera, as well as representatives of every lepidopteran suborder. Ingroup taxa include all trichopteran families except two: Antipodoeciidae (Sericostomatoidea) and Rossianidae (Limnephiloidea). Due to space limitations, we do not present here a table that includes taxonomic affiliation and voucher information. This table is available upon request from Karl M. Kjer. Complete current taxonomic information is maintained in the 'Trichoptera

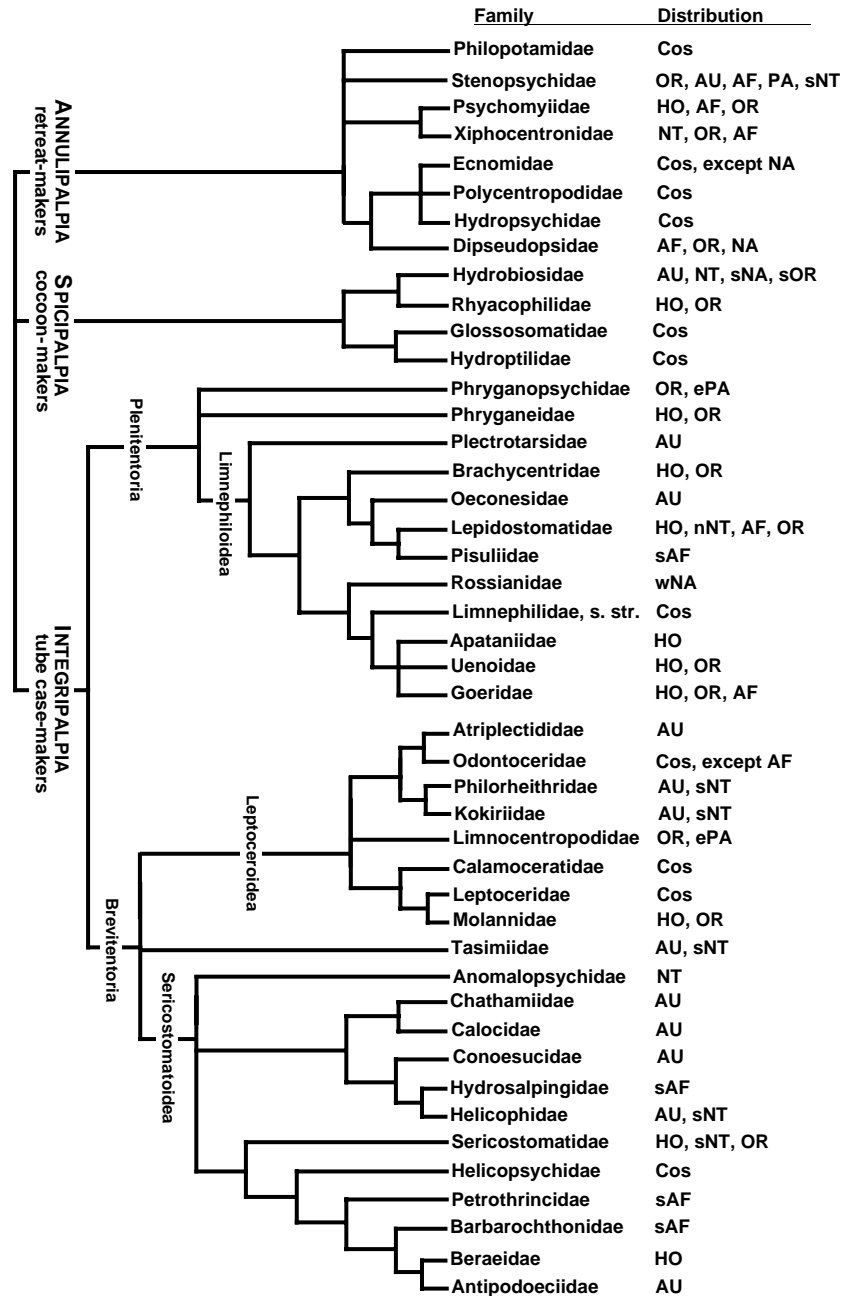


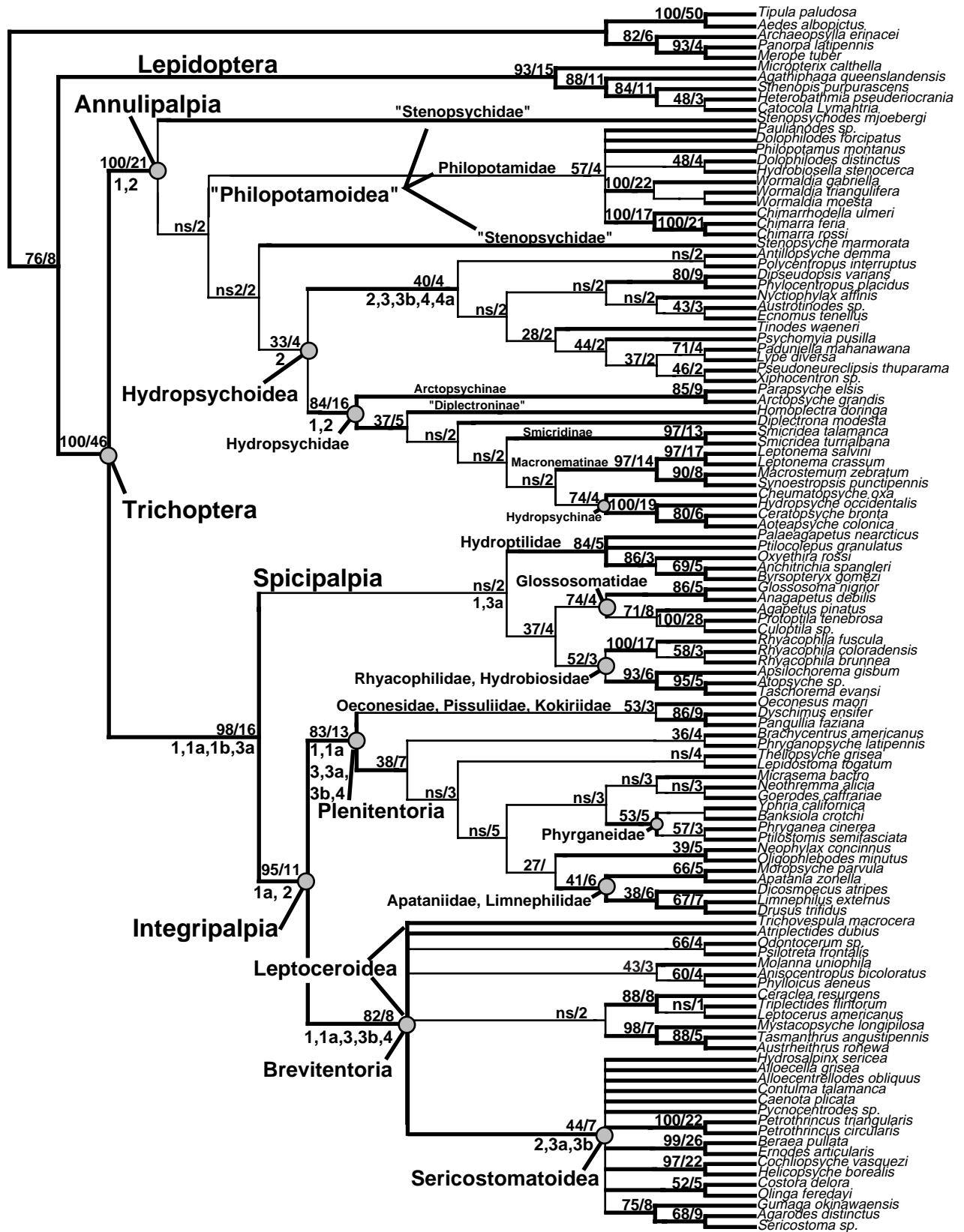
Fig. 2 Composite phylogeny of family group taxa of Trichoptera and general global distribution. Relationships based on Weaver (1983, 1984), Weaver & Malicky (1994) for families of Annulipalpia; Weaver (1983, 1984) for families of Spicipalpia; Gall (1994, 1997) for families of Plenitentoria; Weaver (1983), Weaver & Morse (1986) for families of Leptoceroidea; and de Moor (1993) for families of Sericostomatoidea. AU, Australasian; cos, cosmopolitan; AF, Afrotropical; HO, Holarctic; NA, Nearctic; NT, Neotropical; OR, Oriental; PA, Palearctic; e, eastern; n, northern; s, southern; w, western.

World Checklist' <http://entweb.clemson.edu/database/trichopt/> (Morse 1997a).

Some taxa were not included in our analysis of branch support because data were missing from two or more of our molecular fragments. These taxa were: *Limnacentropus*, *Plectrotarsus*, *Goera*, *Philanisus* and *Barbarochthon*. When measuring nodal support through bootstrapping or decay index, adding taxa for which much of the data are missing results in a potentially large decrease in resolution and support, because the missing data permit the taxa to 'float' relatively freely

throughout the tree. Therefore, a separate differentially weighted parsimony analysis was conducted that included these taxa, representing five families, in order to place them as best as we could at this time.

We sequenced the first and third variable regions of the large subunit nuclear rRNA (D1, 334 nucleotides (nts); D3, 233 nts), the fourth through the fifth variable regions of the small subunit nuclear rRNA (V4-5, 511 nts) and a fragment of the mitochondrial COI gene (441 nts) for most taxa. COI was sequenced to provide additional resolution within



suborders. Initially, we began sequencing nearly the entire elongation factor 1 alpha gene (EF-1 α , 1098 nts) to obtain a second conservative marker (using either its nucleotides or its amino acids), independent of the RNA genes. However, preliminary analysis showed that the third codon positions of the EF-1 α sequence varied to saturation (excessive homoplasy), while few amino acids varied at all. Therefore, further sequencing of EF-1 α was abandoned, but sequencing of most of the annulipalpi and spicopalpi taxa had already been completed for this gene at the time of our preliminary analysis, and EF-1 α amino acids are included here.

The alignment of the COI gene was trivial because it was length invariant, except for a single missing codon in Dipseudopsidae. The EF-1 α gene lacked introns, and did not vary in length. The rRNA was aligned manually with reference to secondary structure, as described by Kjer (1995). Alignments followed secondary structure models of Gutell *et al.* (1994). Regions that could not be aligned were excluded from the analysis, based on criteria described by Kjer (1997). Further discussion on the alignment and character coding is given in Kjer *et al.* (2001).

Informative insertions and/or deletions were evaluated separately by successive outgroup comparison, and divided into one of three classes: (1) insertions; (2) deletions; (3) 'indels'. Ingroup insertions were identified and 'ancestrally missing' nucleotides were coded with an asterisk and defined in the 'symbols' option in PAUP. Deletions in the ingroup were defined as missing data. When we could not categorize a region as either an insertion or a deletion by outgroup comparison, we defined the region as an 'indel.' Indel regions of variable length were coded by giving each unique combination of nucleotides a symbol, similar to the method of Lutzoni *et al.* (2000).

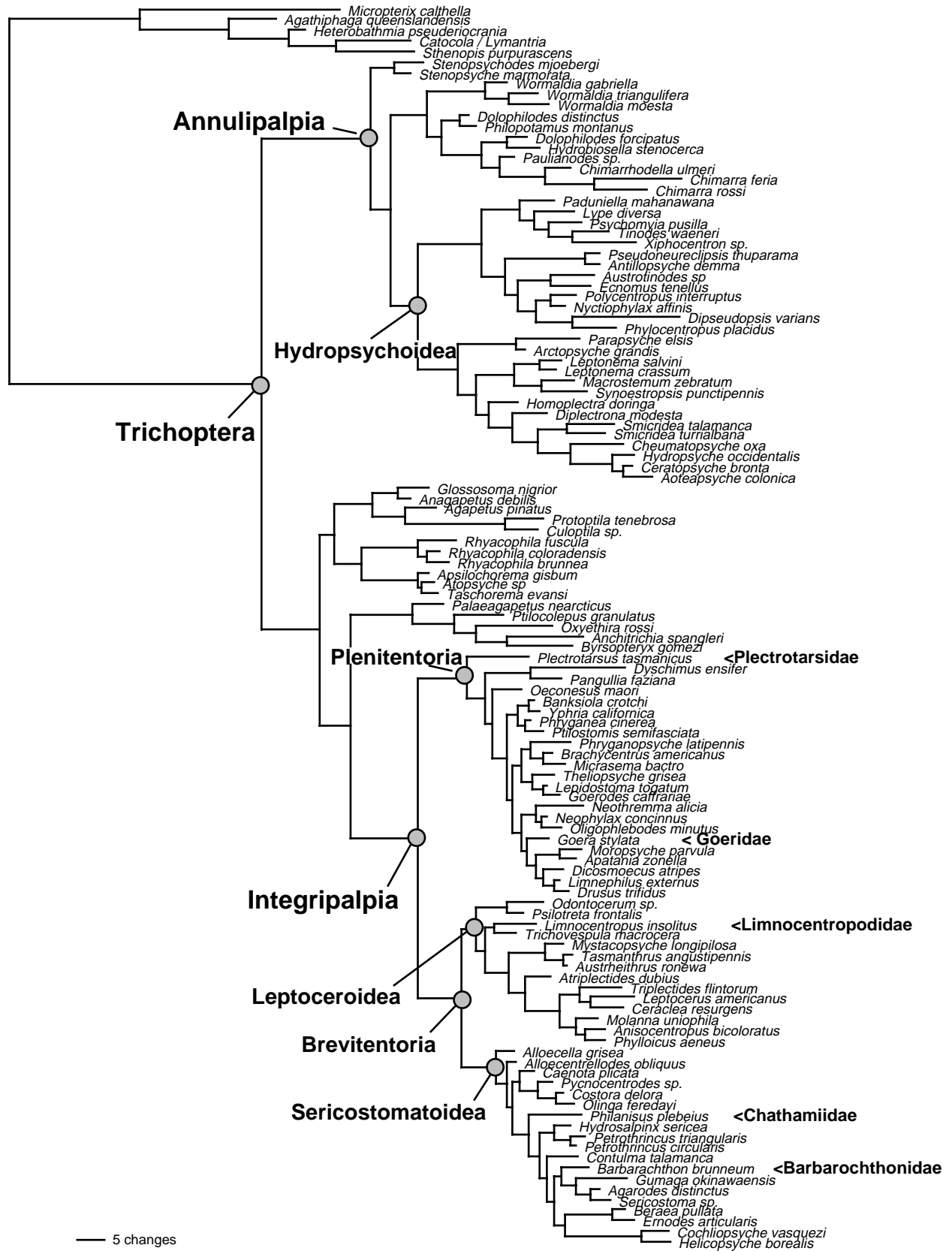
Phylogenetic analysis was performed via equally weighted parsimony using PAUP 4 (Swofford 1999). Heuristic searches were implemented, with 1000 replicates of random taxa additions. Support at each node in the cladogram was analysed according to the decay index (Bremer 1988; Donoghue *et al.* 1992) and non-parametric bootstrapping (Felsenstein 1985).

We also performed a differentially weighted parsimony analysis to place five taxa that were missing sequence data from at least two of the molecular gene fragments. The weighting

scheme was accomplished by conducting 100 separate bootstrap analyses of the combined data, each including only a single pseudoreplicate, and saving each of these 100 trees. The 100 PAUP bootstrap treefiles were saved to a file. Also added to this treefile were trees from analyses of the combined data that had been constrained to the proposals (Fig. 1) of Ross (1967), Weaver (1984), Wiggins & Wichard (1989) and Ivanov (1997). Finally, we added trees to the treefile that had been constrained to topologies from all our previous partitioned rRNA, EF-1 α and COI analyses. The pooled treefile contained some 500 trees that covered every recent hypothesis of relationships among the suborders, as well as trees from the analysis of 100 pseudoreplicated combined datasets (the bootstrap trees). We then reweighted the data according to the rescaled consistency index, using the 'best fit' option in PAUP to all starting trees. It was not our goal to find the optimum tree in creating this pooled set of trees, but rather to cast a wide net and evaluate a large variety of non-random trees, any one of which may have been accurate at some nodes and inaccurate at others, and then to use this wide set of trees to estimate site-specific substitution rates. This result was a weighting scheme superficially similar to successive weighting (Farris 1969), except that it has the advantage that the large number of diverse but potentially accurate starting trees break the circularity that can result from calculating weights from a single initial resolved tree. We devised this scheme because rRNA datasets are characterized by a high degree of among-site rate variation, and we do not feel that other weighting schemes (i.e. stem-loop weighting, transversion parsimony and successive weighting) adequately define hypervariable sites. We justify this scheme with the observation that hypervariable characters would always be measured to be hypervariable, irrespective of any reasonable tree they are fit upon, while conservative characters, when evaluated with the 'best fit' option, will likely be weighted according to (or close to) the true number of changes on at least one of the many starting trees.

The morphological data used in our analysis were as presented by Frania & Wiggins (1997) except that, while Frania and Wiggins assigned plesiomorphic states to outgroup taxa, even when no homologue existed in the outgroup, we coded these characters in our dataset as '?' rather than '0'. Another

Fig. 3 Strict consensus of 24 trees from the combined parsimony analysis of 117 taxa. Tree length = 8637. Quotation marks indicate taxa shown as non-monophyletic in this analysis. Numerals above the internodes are bootstrap values/decay indices. Bootstrap values below 50% are calculated as the highest percentage also compatible with the 50% majority rule. Numerals below selected (basal ingroup) internodes refer to support by separate analysis of independent datasets (not shown); 1, parsimony analysis of rRNA nucleotides; 1a, maximum likelihood analysis of rRNA nucleotides; 1b, parsimony analysis of gap characters from rRNA; 2, morphology (Frانيا & Wiggins 1997); 3, EF-1 α maximum likelihood analysis of nucleotides; 3a, parsimony analysis of EF-1 α amino acids; 3b, LogDet minimum evolution analysis of EF-1 α nucleotides (Lockhart *et al.* 1994); 4, parsimony analysis of COI nucleotides; 4b, parsimony analysis of COI amino acids. Heavier lines indicate nodes subjectively considered to be well supported, with a decay index of five or above, a bootstrap value of 80% or more or independent corroboration from multiple datasets. 'ns', not supported in the bootstrap analysis.



difference was that, in our analysis, the morphological characters were considered to be unordered.

The combined data included taxa for which the majority of sequences were complete. Characters in this combined analysis included D1, D3, V4–5 rRNA, EF-1 α amino acids, COI nucleotides and morphology. The dataset is available in a NEXUS format from the TREEBASE website (herbaria.harvard.edu/treebase). Data were equally weighted and unordered in the 117-taxon analysis, and differentially weighted in the 120-taxon analysis. EF-1 α amino acids were included instead of nucleotides because all measures of signal showed these data to be saturated.

Results

We preceded our analysis with an evaluation of appropriate dataset combinations, and we concluded that the EF-1 α nucleotide data should be excluded from a combined analysis. The EF-1 α nucleotides did not show significant left skew in the distribution of tree lengths from randomly selected five-taxon (maximally divergent) data subsets according to the *g*1 statistic of Hillis & Huelsenbeck (1992). EF-1 α nucleotides did not increase in mean uncorrected pairwise distances from nodes representing the suborders through Amphiesmenoptera and then to Mecoptera. A chi-squared test showed that nucleotide composition for individual taxa, when compared to mean values, did not deviate significantly from expected values for either the RNA data or COI data, but did differ significantly for the EF-1 α sequences. These differences remained when the outgroup was eliminated and when each of the suborders was examined individually. This result cast further suspicion on the EF-1 α nucleotides, and therefore, due to all these analyses, the EF-1 α nucleotides were excluded from the combined analysis, preferring instead to use the EF-1 α amino acids.

Our phylogenetic hypothesis from the combined analysis (excluding COI amino acids and EF-1 α nucleotides) is shown in Fig. 3. The tree depicted in Fig. 3 is a strict consensus of 24 trees from a combined analysis (tree length = 8637 steps). In order to place five additional families for which significant data were missing, and also in order to present a more resolved tree, we present the results of our weighted parsimony analysis in Fig. 4.

Discussion

Figures 3 and 4 show a similar hypothesis of basal relationships, with differences confined to the more apical branches. All of the differences involve weakly supported branches. It

is prudent to be sceptical of conflicting nodes between the two trees, and to carefully examine the support presented by both bootstrap and decay index and the corroboration from multiple datasets. For the time being, we would prefer the ‘Kjer, Blahnik and Holzenthal hypothesis’ to be a consensus of Figs 3 and 4.

We conclude that Annulipalpia is the most basal suborder, with Spicipalpia and Integripalpia forming a clade. Although the monophyly of Spicipalpia is not consistently supported, it does emerge from the analyses as a possibility; equally weighted data support it (Fig. 3), as did the parsimony analysis of the RNA data from our previously presented 89-taxon dataset, and the analysis of EF-1 α amino acids (not shown). In Fig. 3, Spicipalpia is monophyletic, with a decay index of 1. With such weak support, we cannot exclude various paraphyletic alternatives with any confidence. If Spicipalpia is monophyletic, then equally parsimonious solutions exist for the evolution of various key innovations, including cocoon-making and case-making behaviours. Both Annulipalpia and Integripalpia are found to be monophyletic, with relatively high measures of support, as well as support from multiple independent datasets (Fig. 3). It is clear that characters shared between Annulipalpia and Integripalpia cannot be invoked to have a common origin, except with the possibility that the character state was primitive for the order and lost in the Spicipalpia. Shared primitive characters would be harder to reconcile if Spicipalpia is paraphyletic. Therefore, in terms of discussing key behavioural attributes within Trichoptera, we are faced with a problem: the most unstable part of our tree concerns how the Spicipalpia are related to one another, and it is this group that shows the behavioural modifications and intermediates of greatest interest. Any discussion of these behaviours should be performed with the realization that the presentation of a resolved tree does not mean that other suboptimal alternatives are not nearly equally feasible.

Within Annulipalpia, it is most conservative to consider a quadratotomy: Stenopsychidae, Philopotamidae, Hydropsychidae and a clade consisting of all other annulipalpien families (Fig. 3). While Fig. 3 shows a monophyletic Hydropsychoidea, support measured by bootstrap and decay index is weak. The differentially weighted analysis also supports monophyly of the Hydropsychoidea, and a basal but paraphyletic Philopotamoidea (Philopotamidae and Stenopsychidae) within Annulipalpia. The node defining the Hydropsychoidea corresponds to a loss of ocelli. Six of the families that were not recovered as monophyletic in the equally weighted analysis were recovered as monophyletic in the differentially

Fig. 4 Phylogram from the differentially weighted parsimony analysis of the combined data. Arrows mark the additional families, absent from the 117-taxon dataset shown in Fig. 3. Note that in order to better present the internodes within the ingroup in this phylogram, outgroup taxa from Siphonaptera, Mecoptera and Diptera were the same as in Fig. 3, but are not shown here.

weighted analysis. Within the Integripalpia, we find strong support from multiple datasets for the division of the group into two infraorders, Plenitentoria and Brevitentoria, essentially as it has been divided, with the exception that *Pangullia* (Kokiriidae) is now placed in the Plenitentoria. The monophyly of Leptoceroidea is supported only in the differentially weighted analysis (Fig. 4). We are particularly cautious against overconfidence in the resolution within Plenitentoria; many nodes presented in Fig. 3 had extremely low decay indices (≤ 2), and were not recovered in the bootstrap analysis or the differentially weighted analysis (Fig. 4).

Future studies

This work was designed to determine the relationships among suborders. The dataset was dominated by relatively conservative rRNA fragments, which were aligned across four panorpoid insect orders. Because the study was designed to answer the most basal higher level phylogenetic questions, we are less confident with the resolution within suborders and superfamilies. By focusing on more basal nodes and using a universal alignment, there were few characters to inform us about relationships within more recent clades. For example, within the Plenitentoria, the 1078 nucleotide rRNA dataset had only 30 parsimony informative characters. By focusing on clades recovered in this analysis, we can now target faster evolving genes, and realign the data to include many more positions that can be aligned within lower taxa but not across Panorpida. Currently, we are in the process of adding sequence data from the entire 28S gene for a subset of annulipalpi taxa, and adding the D2 region of the large subunit rRNA and a larger portion of the COI gene to evaluate relationships among Plenitentoria and Sericostomatoidea. Aysha Prather and Susan Weller are collecting morphological and additional molecular data in a study of the Leptoceroidea. Other studies of the relationships among some of the larger families will follow.

Acknowledgements

We are especially grateful to Dr Oliver S. Flint, Jr. (Smithsonian Institution, Washington DC, USA), Dr Alice Wells (Australian Biological Resources Study, Canberra, Australia), Dr Arturs Neboiss (Museum of Victoria, Abbotsford, Victoria, Australia), Dr Ferdy de Moor (Albany Museum, Grahamstown, South Africa), Dr Yoshitaka Kamimura (Tokyo Metropolitan University, Japan), Dr Andrew Nimmo (University of Alberta, Edmonton, Canada) and James Bower for specimens used in this study. Lepidopteran DNA samples were provided by Dr Tim Friedlander and Dr David Wagner (University of Connecticut, Storrs, CT, USA). Thanks are due to Catherine Duckett (University of Puerto Rico), Jack Sites Jr. (Brigham Young University, Provo, UT, USA), Mike May and John LaPolla (Rutgers University, NJ, USA) and

Susan Weller (University of Minnesota, MN, USA) for helpful comments on the manuscript. Thanks are also due to Michael Whiting (Brigham Young University, Provo, UT, USA) for organizing the symposium session at the 2000 International Entomology Congress, on which this paper was based. This work was supported by NSF grants, DEB 9632879 (KMK, RWH), DEB 9191091 (Jack Sites Jr) and DEB 9974081 (Catherine Duckett, KMK), and the New Jersey Agricultural Experiment Station.

References

- Bremer, K. (1988). The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution*, 42, 795–803.
- Donoghue, M. J., Olmstead, R. G., Smith, J. F. & Palmer, J. D. (1992). Phylogenetic relationships of Dipsacales based on rbcL sequences. *Annals of the Missouri Botanical Garden*, 79, 333–345.
- Farris, J. S. (1969). A successive approximations approach to character weighting. *Systematic Zoology*, 18, 374–385.
- Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783–791.
- Francia, H. E. & Wiggins, G. B. (1997). Analysis of morphological and behavioral evidence for the phylogeny and higher classification of Trichoptera (Insecta). *Royal Ontario Museum, Life Sciences Contributions*, 160, 1–67.
- Gall, W. K. (1994). Phylogenetic studies in the Limnephiloidea, with a revision of the world genera of Goeridae (Trichoptera). PhD Thesis. Toronto: University of Toronto.
- Gall, W. K. (1997). Biogeographic and ecologic relationships in the Plenitentoria (Trichoptera). In: R. W. Holzenthal & O. S. Flint, Jr (Eds) *Proceedings of the 8th International Symposium on Trichoptera* (pp. 109–116). Columbus, OH: Ohio Biological Survey.
- Gutell, R. R., Larsen, N. & Woese, C. R. (1994). Lessons from an evolving rRNA: 16S and 23S rRNA structures from a comparative perspective. *Microbiological Reviews*, 58, 10–26.
- Hillis, D. M. & Davis, S. K. (1986). Evolution of ribosomal DNA: fifty million years of recorded history in the frog genus *Rana*. *Evolution*, 40, 1275–1288.
- Hillis, D. M. & Huelsenbeck, J. (1992). Signal, noise and reliability in molecular phylogenetic analysis. *Journal of Heredity*, 83, 189–195.
- Ivanov, V. D. (1997). Rhyacophiloidea, a paraphyletic taxon. In: R. W. Holzenthal & O. S. Flint, Jr (Eds) *Proceedings of the 8th International Symposium on Trichoptera* (pp. 189–193). Columbus, OH: Ohio Biological Survey.
- Kjer, K. M. (1995). Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from the frogs. *Molecular Phylogenetics and Evolution*, 4, 314–330.
- Kjer, K. M. (1997). An alignment template for amphibian 12S rRNA, domain III: conserved primary and secondary structural motifs. *Journal of Herpetology*, 31, 599–604.
- Kjer, K. M., Blahnik, R. J. & Holzenthal, R. W. (2001). Phylogeny of Trichoptera (Caddisflies): characterization of signal and noise within multiple datasets. *Systematic Biology*, 50(6).
- Lockhart, P. J., Steel, M. A., Hendy, M. D. & Penny, D. (1994). Recovering evolutionary trees under a more realistic model of sequence evolution. *Molecular Biology and Evolution*, 11, 605–612.
- Lutzoni, F., Wagner, P. & Reeb, V. (2000). Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses using

- unequivocal coding and optimal character-state weighting. *Systematic Biology*, 49, 628–651.
- Mackay, R. J. & Wiggins, G. B. (1979). Ecological diversity in the Trichoptera. *Annual Review of Entomology*, 24, 185–208.
- de Moor, F. C. (1993). A cladistic analysis of character states in twelve families here considered as belonging to the Sericostomatoidea. In: Scott, K. M. F. (1993). Three recently erected Trichoptera families from South Africa, the Hydrosalpingidae, Petrothrincidae and Barbarochthonidae (Integripalpia: Sericostomatoidea) (pp. 347–352). *Annals of the Cape Provincial Museums, Natural History*, 18, 293–354.
- Morse, J. C. (1997a). Checklist of world Trichoptera. In: R. W. Holzenthal & O. S. Flint, Jr (Eds) *Proceedings of the 8th International Symposium on Trichoptera* (pp. 339–342). Columbus, OH: Ohio Biological Survey.
- Morse, J. C. (1997b). Phylogeny of Trichoptera. *Annual Review of Entomology*, 42, 427–450.
- Resh, V. H. & Rosenberg, D. M. (Eds) (1984). *The Ecology of Aquatic Insects*. New York: Praeger.
- Ross, H. H. (1956). *Evolution and Classification of the Mountain Caddisflies*. Urbana, IL: University of Illinois Press.
- Ross, H. H. (1964). Evolution of caddis worm cases and nets. *American Zoologist*, 4, 209–220.
- Ross, H. H. (1967). The evolution and past dispersal of the Trichoptera. *Annual Review of Entomology*, 12, 169–206.
- Swofford, D. L. (1999). *PAUP* — Phylogenetic Analysis Using Parsimony and Other Methods, Version 4 [Computer Software]*. Sunderland, MA: Sinauer.
- 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. PhD Thesis. Clemson, SC: Clemson University.
- Weaver, J. S. III (1984). The evolution and classification of Trichoptera, Part 1: the groundplan of Trichoptera. In: J. C. Morse (Ed.) *Proceedings of the 4th International Symposium on Trichoptera* (pp. 413–419). The Hague: Junk.
- Weaver, J. S. III (1992a). Remarks on the evolution of Trichoptera: a critique of Wiggins and Wichard's classification. *Cladistics*, 8, 171–180.
- Weaver, J. S. III (1992b). Further remarks on the evolution of Trichoptera: a reply to Wiggins. *Cladistics*, 8, 187–190.
- Weaver, J. S. III & Malicky, H. (1994). The genus *Dipseudopsis* Walker from Asia (Trichoptera: Dipseudopsidae). *Tijdschrift voor Entomologie*, 137, 95–142.
- Weaver, J. W. III & Morse, J. C. (1986). Evolution of feeding and case-making behavior in Trichoptera. *Journal of the North American Benthological Society*, 5, 150–158.
- Wiggins, G. B. (1992). Comments on the phylogeny of pupation behavior in Trichoptera: a response to Weaver. *Cladistics*, 8, 181–185.
- Wiggins, G. B. (1996). *Larvae of the North American Caddisfly Genera (Trichoptera)*, 2nd edn. Toronto: University of Toronto Press.
- Wiggins, G. B. & Wichard, W. (1989). Phylogeny of pupation in Trichoptera, with proposals on the origin and higher classification of the order. *Journal of the North American Benthological Society*, 8, 260–276.

