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Progress on the phylogeny of caddisflies (Trichoptera)

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Abstract

We present our current phylogenetic hypothesis on the phylogeny of Trichoptera, generated from an analysis of over 7000 nucleotides from 18S and 28S rRNA, EF-1α, COI, and CAD. We corroborate our earlier hypotheses, with results that include a monophyletic Annulipalpia, Integripalpia, Brevitentoria, and Plenitentoria. Monophyly of Psychomyioidea, Pseudoneureclipsidae, and Grumichellinae were confirmed. The "Spicipalpian" families were again found to be paraphyletic, and most closely related to Integripalpia. Ptilocolepidae was not found to be monophyletic, but support for its paraphyly was so weak that we interpret our results as unresolved. We interpret our measures of branch support, and present a collapsed phylogeny that more conservatively represents our current hypothesis. We discuss how these data can eventually be merged into other sources of data, such as COI barcode data and transcriptomes, and suggest that a single huge analysis of all data, with all taxa, is unnecessary if analyses can be phylogenetically subdivided into many separate parts, using transcriptome data to fix the deepest nodes, and allowing faster evolving data to be more appropriately targeted to nodes closer to the tips of the tree.

Key words: Annulipalpia, Integripalpia, Brevitentoria, Plenitentoria, Phylogeny

Introduction

Our research team continues to work toward a comprehensive phylogeny of Trichoptera. Currently, our data come from three diverse sources, each the result of different objectives and each targeted at different levels of divergence. Initial analyses included the standard "toolbox" genes of nuclear ribosomal RNA (rRNA: 18S, 28S) fragments and mitochondrial Cytochrome *c* oxidase subunit I (COI). Subsequently, additional taxa and genes (Elongation factor 1 alpha [EF-1α]) were included in the dataset, resulting in the publication of a number of papers on deep-level Trichoptera phylogenetics (Kjer *et al.* 2001, 2002; Holzenthal *et al.* 2007). The main focus of these studies was to resolve the relationships among the three suborders of Trichoptera - Annulipalpia, Integripalpia, and "Spicipalpia" (the latter included in quotes because its monophyly is seldom recovered). Most recently, we have added another nuclear protein coding gene to the dataset, CPSase II [CAD protein]. Currently, the dataset includes approximately 1000 nucleotides of rRNA data for 1200 taxa. For a subset of 200 of these taxa, the dataset consists of approximately 7000 nucleotides from complete 18S, 28S, EF1a, COI, and CAD data.

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Concurrent with the research directed toward the deepest splits among Trichoptera suborders and families, we have been actively involved with supplying taxa and data to the Trichoptera Barcode of Life initiative [TBOL http://trichopterabol.org/]. The "barcode" data consist of 658 nucleotides of COI that were selected because they are universal, easy to amplify, and possess high variability, even within species (Hebert, *et al.* 2003). Currently, TBOL has COI sequences for over 4,900 Trichoptera species, covering all 49 families. While the COI is ideal for identifying close relatives, it was found to be saturated for deep level Trichoptera phylogenetics Kjer *et al.* (2001).

The third set of data now being generated are transcriptomes from the 1000 Insect Transcriptome Evolution (1KITE) initiative [http://www.1kite.org] (Misof *et al*., 2014). The objective of the 1KITE initiative is to explore insect evolution with orthologous genes assembled from transcriptomes. Transcriptome projects attempt to sequence the majority of the messenger RNA that are transcribed in the organism at the time it is preserved, and the resulting sequences are dominated by protein-coding genes without their introns. The 1KITE initiative is divided into 10 semi-independent subprojects, with one of them focused on Trichoptera. This initiative has modified methods of data collection, assembly, orthology prediction, and analysis that have resulted in an extraordinary coverage of over 1500 orthologous genes across Insecta, most of which are present in nearly all of the taxa (there are relatively few missing data). There are over 20 families sampled for Trichoptera, which span the diversity of the order. These data are not yet public.

These sources of data fit roughly into three levels, each conveniently fitting into the branching nature of phylogeny. At the deepest levels, assessing the relationships among Trichoptera suborders and the early diversification of families, transcriptomes will test our previous hypotheses (*e.g.*, Kjer *et al.* 2001). This analysis will not require extensive taxon sampling (~25 species should be sufficient) to infer the phylogeny among suborders. For the tips of the tree, at the population and species levels, we have the COI barcode data, along with morphology generated in the course of species descriptions and revisions, which will aid in the resolution of relationships among genera, species, and populations. The remaining sequence data (*e.g.*, rRNA, CPSase II, and EF-1α) will provide a bridge between the transcriptomes and the barcodes, and will be used to infer relationships among family-group taxa. This paper will focus on an analysis of these intermediate data, with discussion of how our future work will incorporate the other sources of data.

Diverse data like these, with genomes or transcriptomes for a few taxa, and one or a few genes from many taxa, are not unique to our phylogenetics project. Systematic biology is facing a radical transition from the standard "few genes and morphology," PCR-based approach to phylogenetic analysis, to "next generation" sequencing. Next generation sequencing (Hall 2007), which serves as the key technology in the generation of genomes and transcriptomes, will be as revolutionary as the development of DNA technology was 25 years ago, or the acceptance of cladistics was 40 years ago. The challenge now is to merge these diverse data into a comprehensive Trichoptera phylogeny where a balance must be stuck between using over a million nucleotides from transcriptomes, representing only a few taxa, and using 658 nucleotides of mitochondrial COI from 40,000 individuals. In this paper, we present our current phylogenetic hypothesis, and discuss how we can fit our previous data into this new paradigm.

Materials and methods

Voucher specimens are stored in the University of Minnesota Insect Collection, St. Paul, Minnesota, USA. DNA was extracted from single legs using Qiagen DNeasy kits (Qiagen, Valencia, CA). Standard laboratory techniques were used to extract, amplify and sequence PCR products. PCR reactions for rRNA usually included 800 mM betaine (Sigma Chemical Co.), along with other reagents at standard concentrations. Purified PCR products were sequenced at GeneWiz (Piscataway, New Jersey, U.S.A.).

Ribosomal data were aligned structurally, according to Kjer (1995), and Kjer *et al.* (2007), using the Trichoptera structural model presented by Kjer *et al.* (2001). Molecular data were concatenated into a single Phylip file, and analyzed with RAxML (Stamatakis 2006) using the pseudoreplicate site specific rate model first used by Kjer *et al.* (2001), and described in detail by Kjer and Honeycutt (2007), with five rate classes. We used the following commands for parallel RAxML: -T 4 -# 1000 -m GTRGAMMA -f a -q, which specifies 1000 rapid bootstraps followed by a maximum likelihood tree search.

Branch support was estimated by two measures: standard rapid bootstrap support with RAxML and congruence measures among independent data partitions. The five partitions we used were ribosomal RNA

(combined 18S and 28S), COI, CPSase II, EF-1α, and morphology. The molecular partitions were run independently using RAxML as described for the combined data. The "morphology" partition could be considered as supported in all named taxa, as each was considered to consist of a monophyletic group by some taxonomist at one time. However, we chose a more conservative approach here, taking morphological support from the character matrix of Frania and Wiggins (1997), which was reanalyzed in Kjer *et al.* (2001; Fig. 7b). Lack of support does not always mean that a partition would not support a particular node, because sometimes the lack of support was due to missing data for some taxa.

Results

Results of the phylogenetic analyses are shown in Figs 1–6. Figure 1 is a phylogram intended to show relative branch lengths. Figures 2–5 are expanded versions of Fig. 1. Figure 6 is a summary cladogram of relationships we subjectively find to be credibly supported. Alignments and datasets will be made available on Kjer's with the work of Thomas *et al*. (in prep).

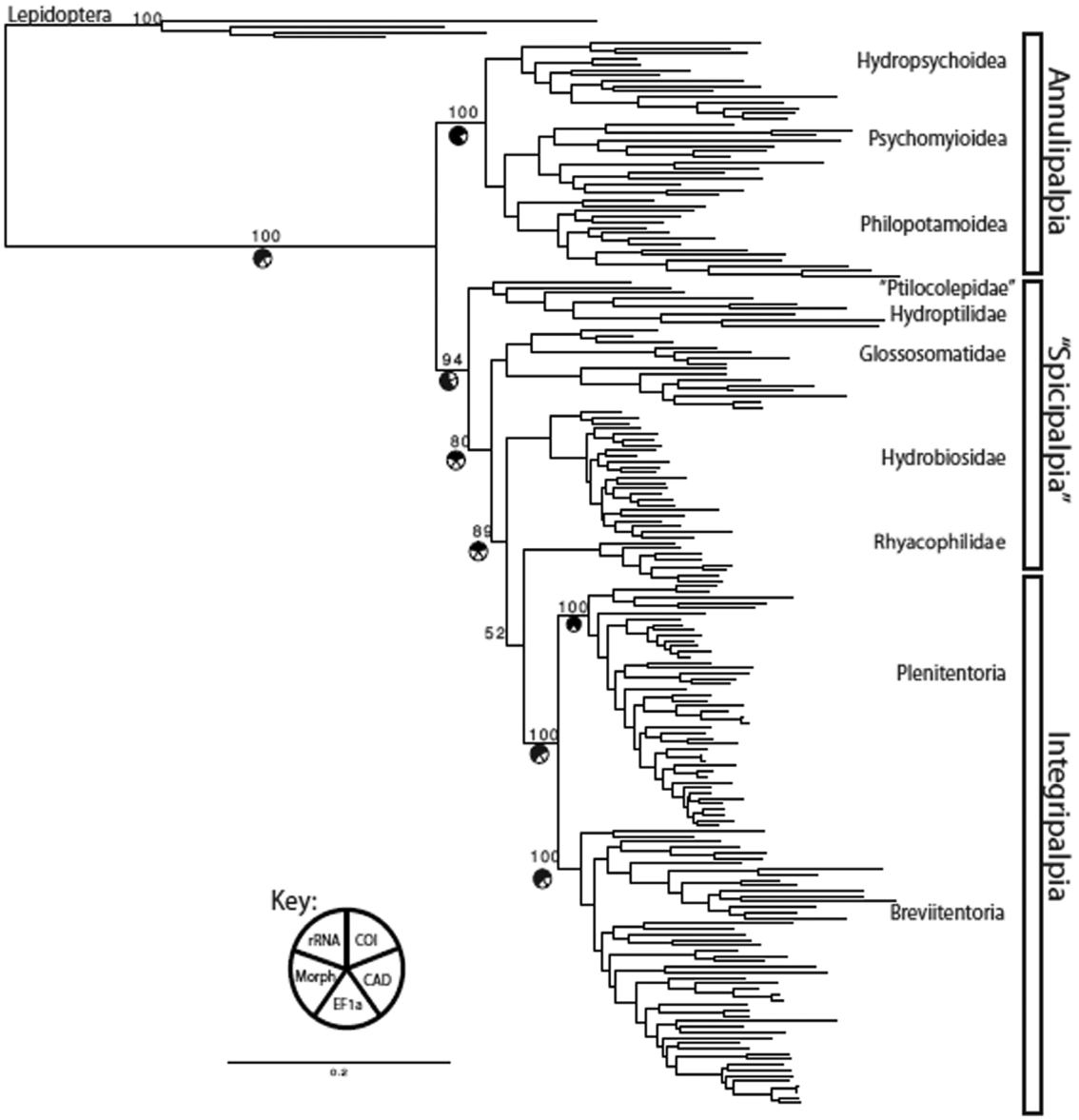

FIGURE 1. Phylogram from a RAxML analysis of the combined DNA data. Numerals at the internodes are bootstrap values. Pie chart indicates which datasets independently confirm each node, shown in black, according to the key. Taxa from this tree are shown in Figs. 2–5.

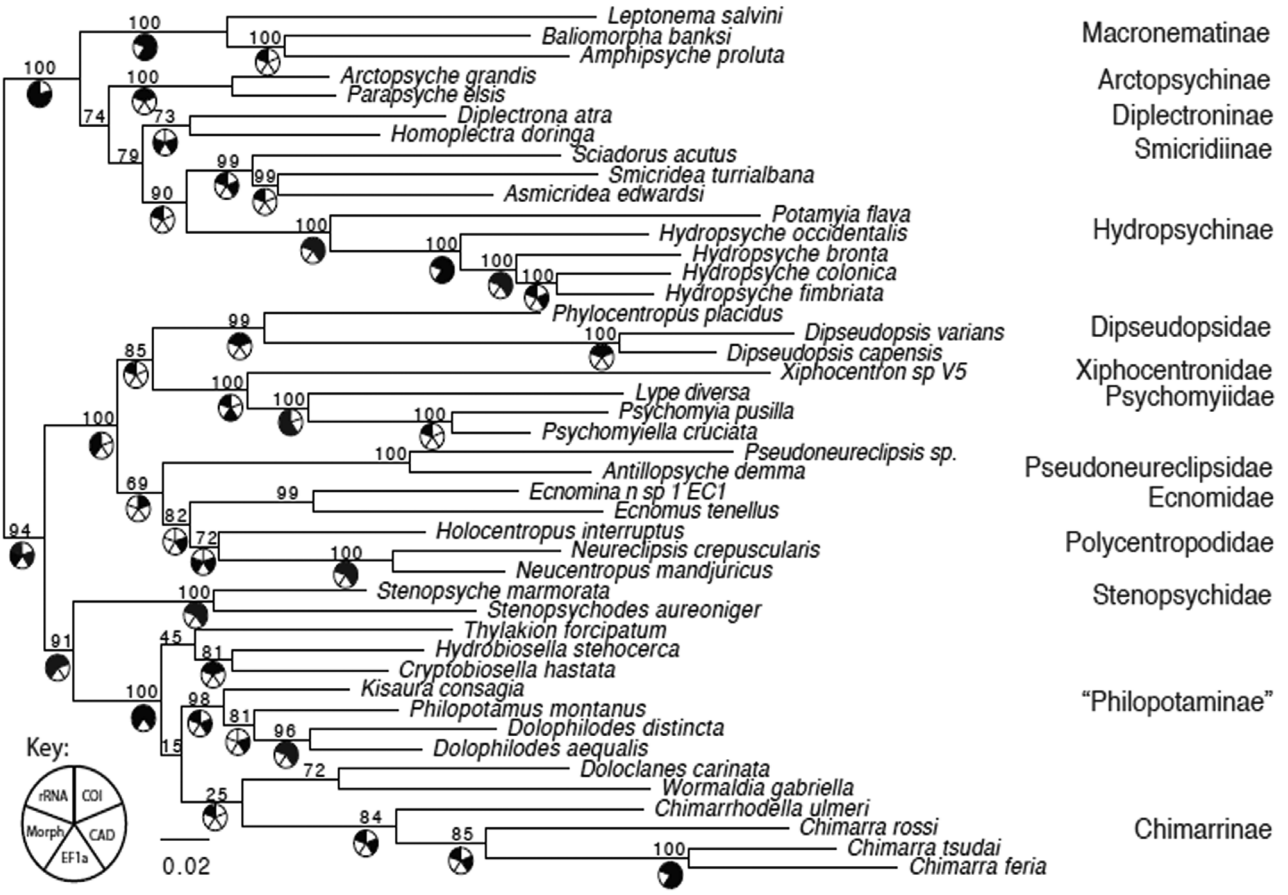

FIGURE 2. Phylogram from a RAxML analysis of the combined DNA data for Annulipalpia. Numerals at the internodes are bootstrap values. Pie chart indicates which datasets independently confirm each node, shown in black, according to the key.

These results are consistent with earlier results (Kjer *et al.* 2001; 2002; Holzenthal *et al.* 2007), with Annulipalpia sister to a paraphyletic grade of "Spicipalpia" associated with a monophyletic Integripalpia, which is divided into Plenitentoria, and Brevitentoria. With over 8000 nucleotides, the current analysis included about 5 times more data than our most recent analysis (Holzenthal *et al*. 2007). For the first time, reasonable bootstrap support (94%) groups "Spicipalpia" with Integripalpia (Fig. 1). The bootstrap support values for relationships among the "spicipalpian" families are also improved in this analysis (80%, 89%, and 52%; Fig. 1).

Within Annulipalpia, support for relationships among family-group taxa is strong. For the first time in our combined analyses, the Hydropsychoidea (=Hydropsychidae) emerged as the sister taxon to all other annulipalpians, with high bootstrap support (94%) (Fig. 2). This clade was also reported by Johanson *et al.* (2012), as well as the morphological analysis presented by Kjer *et al*. (2001). We confirm the establishment of Pseudoneureclipsidae (Chamorro & Holzenthal, 2011). Diplectroninae, Smicridiinae and Hydropsychinae form a clade. Monophyly of Psychomyioidea is confirmed, forming a clade that is sister to Philopotamoidea (Fig. 2.). "Philopotaminae" are weakly supported as paraphyletic.

Spicipalpia was not recovered as monophyletic. The monophyly of Ptilocolepidae was not supported by this analysis (Fig. 3), but the node that renders them paraphyletic was so weakly supported (34%, Fig. 3) that we consider it to be unresolved (Fig. 6). We were able to sequence about 400 nucleotides from the enigmatic genus *Fansipangana*, and in a separate analysis to be published elsewhere (data not shown), this genus clustered with the Rhyacophilidae. *Fansipangana* was suggested by Mey (1996) to lack many of the synapomorphies of the rest of Trichoptera, and was therefore, a taxon of special interest. Within Plenitentoria (Fig. 4), if all bootstrap values below 50% are considered to be as likely random as real, only the monophyly of Plenitentoria itself is supported, along with a few of its families (Fig. 6). Similarly unresolved are relationships among Brevitentoria families (Fig. 5). Although monophyly of Brevitentoria is strongly supported (99%, Fig. 5), there is virtually no support for any groups within the infraorder, except for the

monophyly of most brevitentorian families. We confirm the monophyly of Grumichellinae, which was elevated to subfamily by Malm & Johanson (2011).

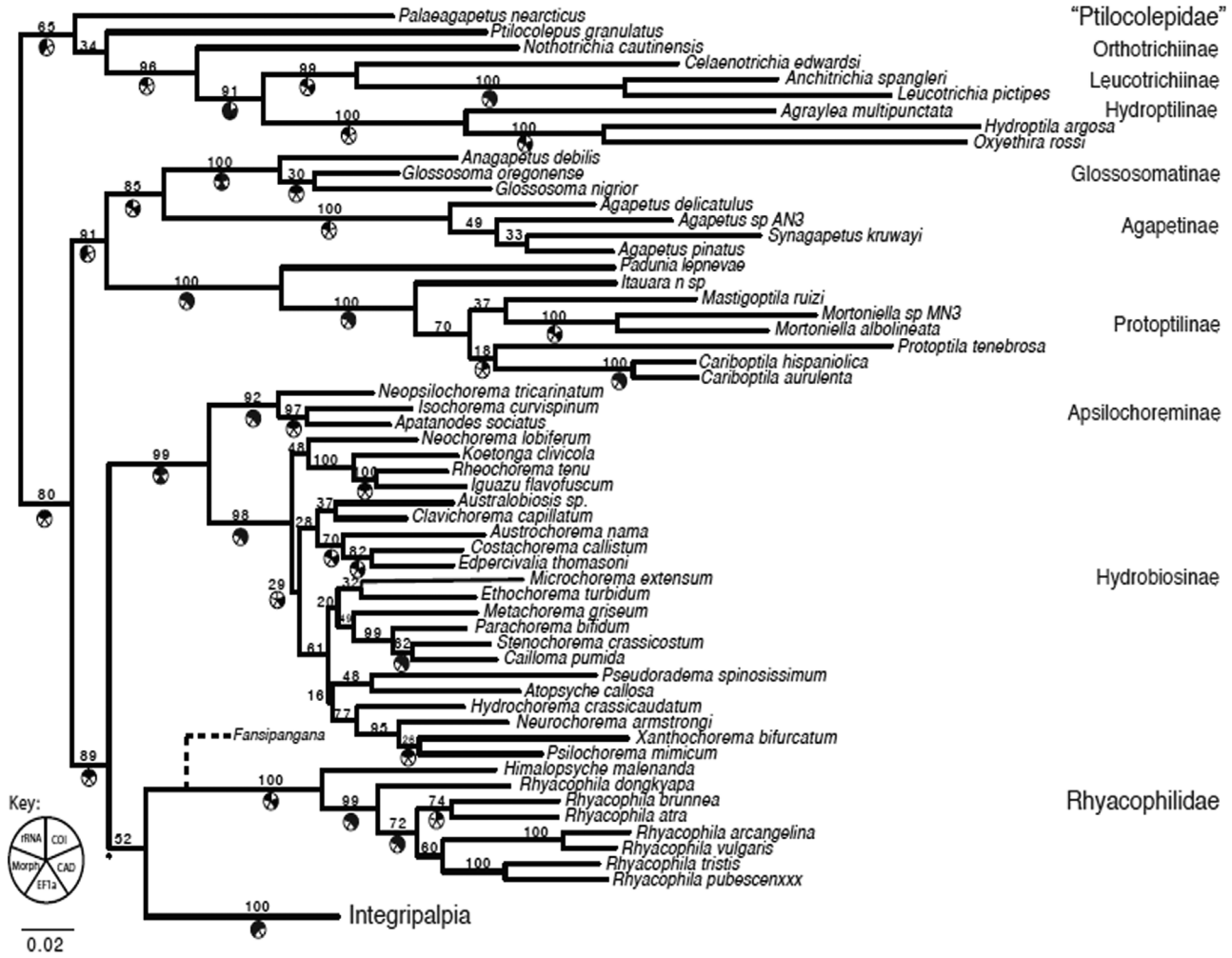

FIGURE 3. Phylogram from a RAxML analysis of the combined DNA data for "spicipalpian families." Numerals at the internodes are bootstrap values. Pie chart indicates which datasets independently confirm each node, shown in black, according to the key.

Discussion

The current study represents the largest dataset assembled to date to address Trichoptera phylogenetics. Its analysis supports results of previous analyses, with a few new findings within Annulipalpia. However, the addition of all these new data (*e.g.*, complete 18S, complete 28S, and CAD) did not resolve relationships among most integripalpian families. We have tripled the number of taxa and increased the number of nucleotide characters by 10-fold since our first work (Kjer *et al.* 2001), but are left with continued weak support for the relative placement of "spicipalpian" and integripalpian families. These genes were selected to resolve the deepest nodes in Trichoptera, and are ideal for Jurassic divergences or older (Kjer *et al.* 2001).

We prefer to remain cautious about our placement of the "spicipalpian" families for three reasons. First, bootstrap values should never be confused with "truth," or confidence intervals. Although the bootstrap result supports "Spicipalpia" with Integripalpia, it does not indicate whether or not the data are biased (bias may come from a wide variety of sources, such as poor models, nucleotide compositional non-stationarity, or substitution rate heterogeneity, to name a few). Second, Malm, Johansen and Walberg performed an extensive analysis of a different dataset (overlapping only with the CPSase II and the COI), and found a different result with respect to "Spicipalpia" (Malm *et al*., 2013). Third, analyses of the transcriptome data from 1KITE,

(Misof *et al.*, 2014) consisting of 1.7 million nucleotides and 5 taxa (species from Rhyacophilidae, Hydroptilidae, Hydropsychidae, Philopotamidae, and Limnephilidae) contradict both this paper and Malm *et al*. (2013). However, in a preliminary analysis (not shown) when we add the data from Malm *et al*. (2013) to the data presented here, our results do not change.

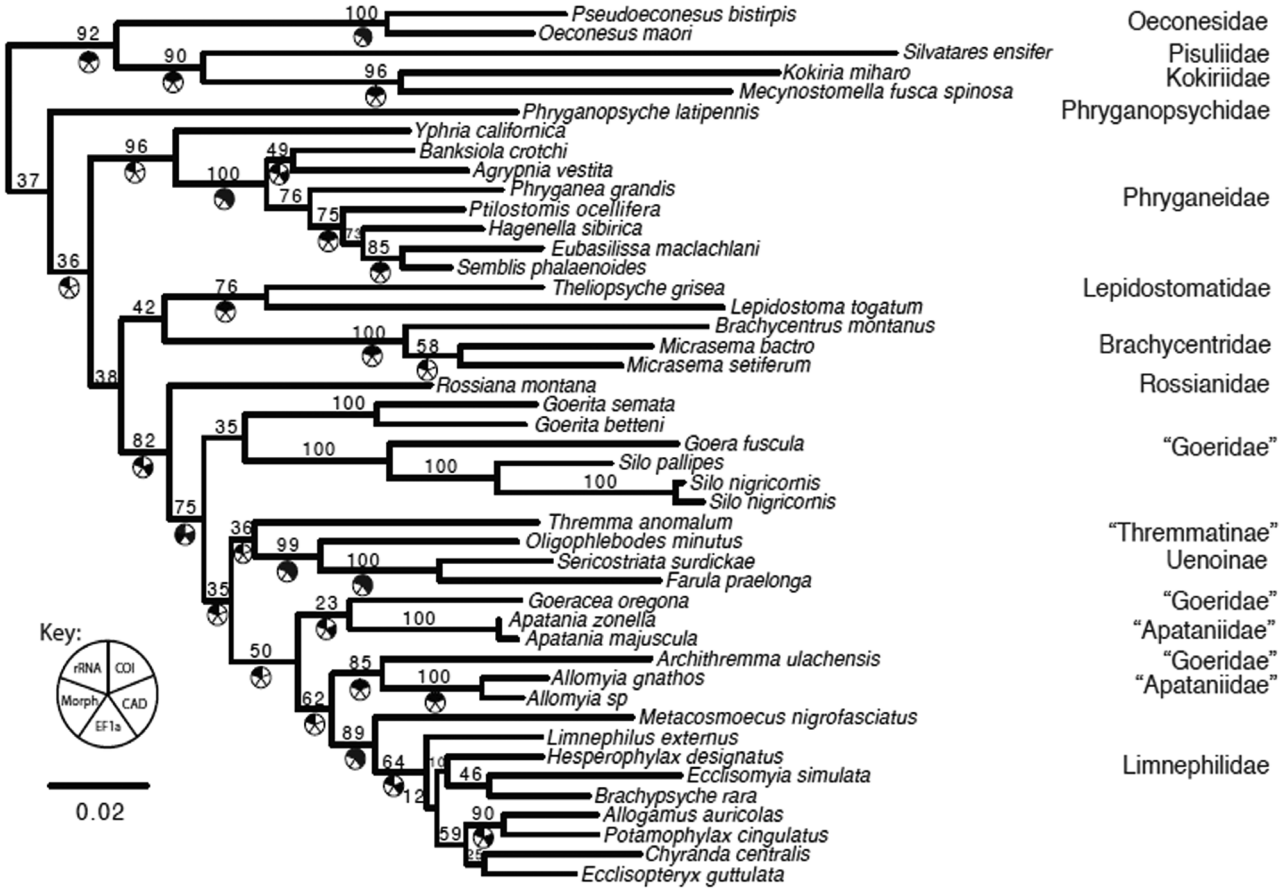

FIGURE 4. Phylogram from a RAxML analysis of the combined DNA data for Plenitentoria. Numerals at the internodes are bootstrap values.

Placing the "spicipalpians" is difficult, as is evidenced by the wide variety of previous phylogenetic hypotheses (*e.g*., Ross 1967; Weaver 1984; Wiggins & Wichard 1989; Ivanov 2002). The phylogram presented in Fig. 1 shows a very long internode leading to Trichoptera, followed by relatively short internodes separating groups within Trichoptera. Unlike Lepidoptera, in which 3 suborders of mandibulate moths still exist, there does not appear to be an extant "proto-trichopteran" with which to root the Trichoptera tree internally. According to this phylogram, extant Trichoptera appear to have radiated rapidly, and presumed extinctions of ancestral groups make this combination of branch lengths among the most difficult to resolve (Whitfield & Kjer 2008). Even from a morphological point of view, it can be more difficult to find homology when groups like Lepidoptera and Trichoptera possess such extreme differences in life history and habitat.

We recommend here that bootstrap values below 75% should be considered to represent weak support, and bootstrap values below 50% should be interpreted to indicate completely stochastic and unresolved relationships. Of course, neither of these values should be considered as hard cut-offs (for example, there is virtually no difference between 49% and 50%, and we could equally justify 77% as representing "credible" support.) We are relatively confident with the nodes in the phylogeny that possess a combination of high bootstrap support and corroboration from multiple independent data sources. Figure 6 is our attempt to publish the phylogeny we believe is supported by the data, and would prefer that it be taken as our 2012 hypothesis, rather than the more resolved trees shown in Figs 1–5. Note that in Figure 6, we include the spicipalpian families within a newly defined Integripalpia, as depicted by Holzenthal *et al*., 2011. Deciding which nodes are supported by the data, and which nodes are simply a result of stochastic processes is a subjective exercise, with no clearly accepted boundaries.

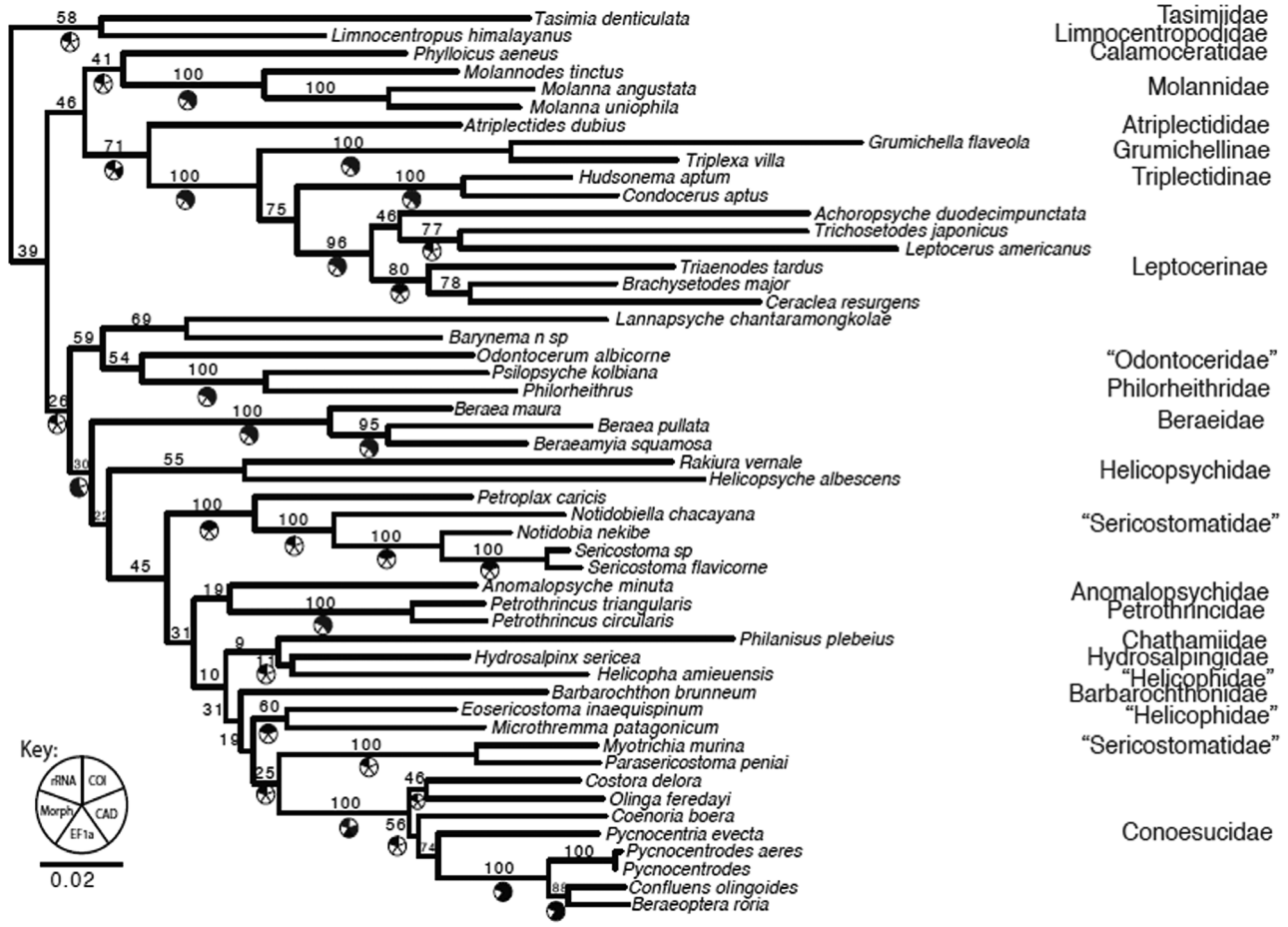

FIGURE 5. Phylogram from a RAxML analysis of the combined DNA data for Brevitentoria. Numerals at the internodes are bootstrap values.

Our future research will be based on combining these intermediate data with both barcodes and transcriptomes. The barcode data will be used to resolve the tips of the tree (*i.e*., relationships among genera, species, populations, as discussed in Frandsen *et al*., this volume). By using a rationale of defining nodes that are supported by some defined criterion, we intend to fill out the tips of the Trichoptera tree with barcode data. For example, if we are confident that Macronematinae are monophyletic (100% bootstrap support, 4 independent data sources) then we can run an analysis of the barcode data for only the macronematines, rooted with other hydropsychids. There are COI barcodes for over 1000 macronematines, representing 16 genera and 179 species in BOLD. Dozens of separate analyses, targeted toward the tips of the tree throughout the order will provide valuable hypotheses for tens of thousands of individual specimens.

At deeper levels we will need to rely on the transcriptome data from 1KITE. However, the 1KITE taxon sampling is not comprehensive, leaving 13 of 49 families with no transcriptome data. Transcriptomes are difficult to obtain because they rely on the preservation and sequencing of the messenger RNA transcripts, and mRNA is, by nature, ephemeral. Special techniques must be used to preserve taxa for transcriptome data (see Frandsen & Thomson, this volume), and we do not yet have some taxa preserved. An alternative approach was published by Lemmon *et al.* (2012), using a technique called "anchored hybrid enrichment" (AHE). Anchored hybrid enrichment uses available genomes or transcriptomes to design probes that target a specified set of loci. These loci can be selected to be compatible with transcriptome data so that taxa that were not preserved for transcriptome work can be included in a combined analysis that includes data from both sources. We have DNA from all of the families of Trichoptera that we do not yet have preserved for transcriptome work, and this material is suitable for AHE. We currently have hundreds of genes from representatives of almost all Trichoptera families, awaiting analysis.

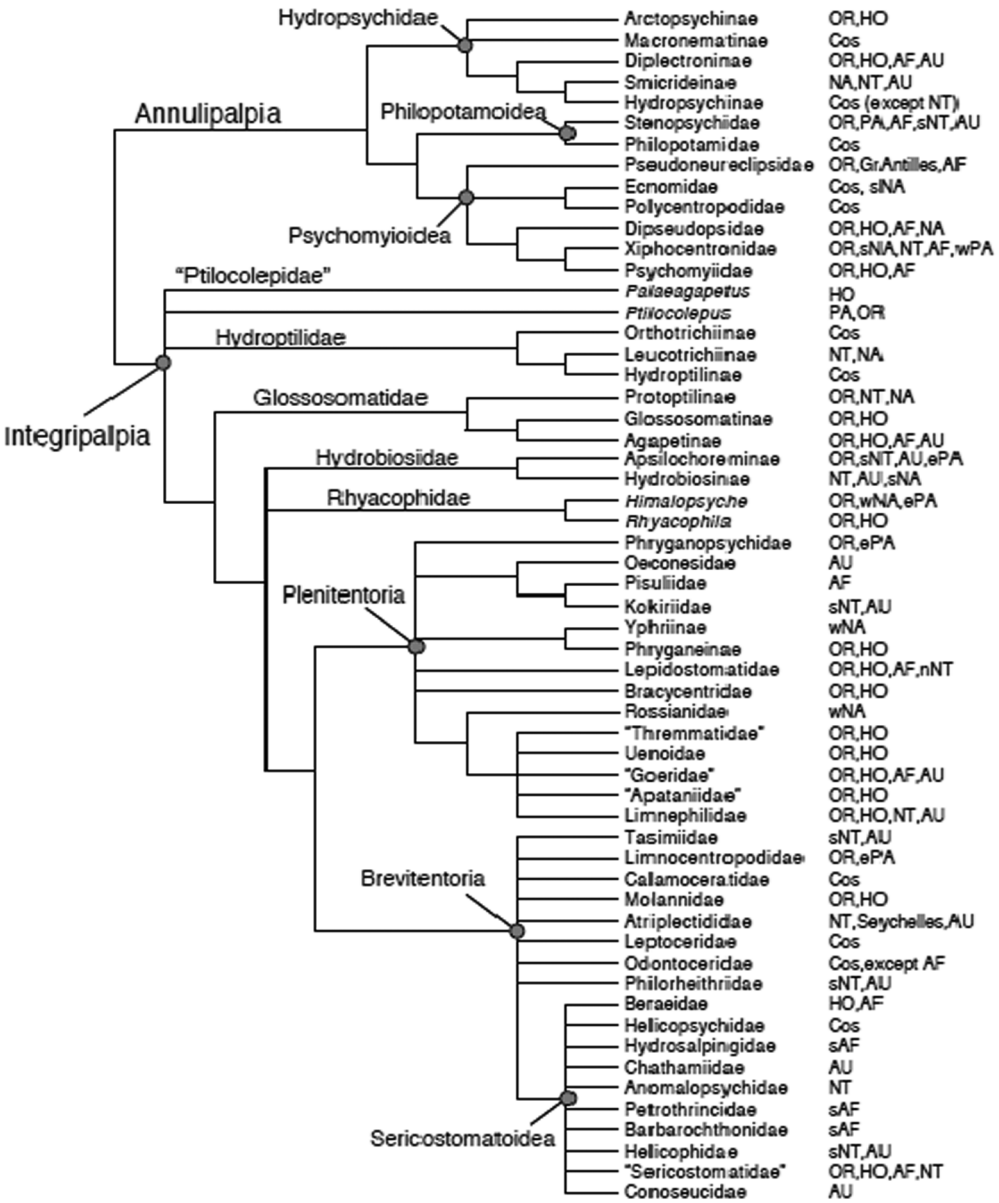

FIGURE 6. Cladogram of results we subjectively consider to be supported by these analyses. The criterion used for defining a node as "supported" was subjectively assigned as having either a 75% or higher bootstrap value or support from three of the five datasets. Abbreviations for biogeographic regions: AF = Afrotropical, AU = Australasian, Cos = cosmopolitan, ePA = eastern Palearctic, GrAntilles = Greater Antilles, HO = Holarctic, NA = Nearctic, NT = Neotropical, OR = Oriental, PA = Palearctic, nNT = northern Neotropical, Seychelles = Seychelle Islands, sNA = southern Nearctic, sNT = southern Neotropical, wNA = western Nearctic, wPA = western Palearctic.

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