



Results from Prior NSF Support

CARPENTER, J. M.: DEB-9870232: "Collaborative research: Multi-taxa inventory of threatened conservation areas in Vietnam" (Co-PIs: E. Sterling, D. Harder). **Publications:** Bain and Truong (2001a, b, 2002a, b, c, d, e); Bain et al. (in press); Carpenter (2001, in press); Carpenter and Starr (2000); Chou et al. (2001); Eames (2002); Engel (2000); Grimaldi and Blagoderov (2001); Lathrop et al. (1998); Liu et al. (2000); Lunde and Musser (in press); Lunde et al. (submitted); Nguyen and Carpenter (2002); Sterling et al. (2001); Vogel et al. (submitted); Wang and Yin (2001). AMNH has developed the Vietnam Research and Conservation site: (http://research.amnh.org/biodiversity/vietnamresearch/viet_main.html). **Training:** seven Vietnamese staff and students in Hanoi, a two day seminar for guards, foresters and supervisory staff at the Vu Quang Nature Reserve, eight preparators and 10 student interns.

ENGEL, M.: KAN29503 - Kansas NSF EPSCoR: "Hymenoptera in Cretaceous ambers and Mesozoic diversification of the order." **Publications:** Engel (in press a, b).

HERATY, J.: BSR-9978150: "Classification of Aphelinidae and Trichogrammatidae (Insecta: Hymenoptera: Chalcidoidea)," PEET grant aimed at training students in systematics of Chalcidoidea. Four Ph.D. students are currently studying Aphelinidae (*Aphytis* and *Aberus*) and Trichogrammatidae (*Ufens* and *Paracentrobia*). As well as revisionary studies, molecular studies are in progress on Aphelininae, Trichogrammatidae and higher level placement of the Azotinae within Chalcidoidea. **Publications:** Burks and Heraty (2002); Burks and Pinto (2002); Gates (in press); Kim (in press). Website for project <http://cache.ucr.edu/~heraty/index.html>. **Training:** seven graduate students and five undergraduates.

DEB0108245: "Systematics of Eucharitidae (Hymenoptera: Chalcidoidea)." Grant is for molecular systematics of the family Eucharitidae. We have sequenced 103 species in 34 genera of Eucharitidae and 15 species in 8 genera of Perilampidae for 18S and 28S-D2&D3, and we are just starting on COI and EF-1a. **Publications:** Heraty (2002, in press). **Training:** one new MSc student and two undergraduates.

SHARKEY, M.: DEB 9972024: "Insect Survey of a Megadiverse Country: Colombia" (Co-PI: B. V. Brown). **Publications:** Brown (2001, 2002); Hansson (2002); Deans and Huben (2003); Fernandez (2000); Freytag and Sharkey (in press); Gonzalez et al. (2002); Kung and Brown (2001); Martinez (in press); Martins and Galileo (2002 a, b); Saaksjarvi et al. (in press); Smith (2003 a, b); Smith-Pardo (2003); Triapitsyn and Berezovskiy (2001); Whitfield et al. (in press a, b). PI has developed a website for the survey that contains interactive keys, descriptions of the sites, label databases, and a specimen/species database with thousands of species entries (www.uky.edu/~mjshar0). **Training:** some of the Hispanic graduate students mentored through the project in Colombia and the USA are E. Amat, M. Garcia, D. Arias, T. Arias, C. Sarmiento, and D. Campos.

OBJECTIVES

1. A large-scale phylogenetic analysis of Hymenoptera, a taxon that encompasses approximately 10% of the species diversity of life (see Grissell 1999), with over 115,000 described species, and many more undescribed. Recent estimates for the total number of species range from 0.3 to 2.5 million (Gaston 1991; Gauld and Gaston 1995; Stork 1996). There are 89 extant families currently recognized, with another 24 extinct (see supplemental documentation). This will entail the analysis of several thousand terminals, including fossils, more than 500 morphological characters, and five molecular markers (two nuclear 18S, 28S,

- and three mitochondrial COI, 16S, 12S).
2. A high quality, well-documented, vouchered, database of observations and taxa that will be the basis for the morphological and molecular character scores. We will use Winclada and Morphbank (www.morphbank.net) to support image links to taxa (virtual taxon vouchers) and characters (virtual character-state vouchers) in a user-friendly manner, and the export and import of standardized data structures through both XML and SQL protocols. These images will be made available on project website (www.uky.edu/~mjshar0) using software linking them directly to cladograms (a demonstration utilizing Winclada with Vespidae may be seen at www.diversityoflife.org). Sequences and alignments will be deposited in GenBank, in TreeBase, and on the project web site.
 3. We will standardize the limits of higher taxa and the terms used for morphological characters which are currently highly variable among different subgroups of Hymenoptera. Ours will not be the last study of hymenopteran phylogeny and these standards will greatly simplify the use of our data for future investigations of the phylogeny and comparative biology of any group of Hymenoptera.
 4. A well-supported, reliably dated phylogenetic hypothesis for relationships among the early clades of the Hymenoptera. This will involve phylogenetic analyses at the family level for the entire order, and additionally robust hypotheses at the subfamily level for the Aculeata, Chalcidoidea and Ichneumonoidea, the largest and most diverse clades. The hypotheses will be based on molecular and morphological data for extant forms and morphological data for fossil forms and will be derived using a variety of methods, including parsimony and statistical methods (Bayesian inference). The results of the analyses will be made available on the Diversity-of-Life and Tree-Of-Life web sites, as well as on the project web site.
 5. Timing of key splitting events in the early radiation of the Hymenoptera based on this new phylogenetic hypothesis. The focus will be on hymenopteran life history changes with major impact on other components of terrestrial ecosystems: the history of primary pollen feeding and herbivory on different host plant clades, the origin of insect parasitism, the origins of endoparasitism, the origins of egg, larval, pupal, and adult parasitism, hyperparasitism, gregarious parasitism, secondary phytophagy, polydnavirus associations, and shifts among different host clades!
 6. A major "value-added" objective is an interactive, web-based key to the families of Hymenoptera using the morphological characters employed in the phylogenetic analysis and non-cladistic characters that will be added.

Why A Collaborative Effort?

The objectives are considerable and could only be accomplished by a large team of international collaborating experts and support staff. The advantages of working as one large team are many, and a survey of the current literature demonstrates this. There have been few recent attempts to treat the entire Hymenoptera at the family level. The outstanding exception to this is Rasnitsyn's (1988) analysis, but this was not cladistic. Ronquist et al. (1999) modified Rasnitsyn's treatment such that all characters could be coded into a matrix, but as Sharkey and Roy (2002) pointed out; many of their character codings are flawed and in some cases based on erroneous assumptions of monophyly at the family level. The Chalcidoidea, 19 families, are treated as a single terminal taxon, and thus relationships within one of the single largest groups of Hymenoptera were not even considered. The reason that Rasnitsyn's (1988) study has not been significantly improved upon over the past 15 years is that the undertaking is simply too daunting. The NSF ATOL initiative presents an opportunity to tackle this challenge using a large number of mutually consistent approaches across all subtaxa. Numerous (34) investigators with expertise in different taxa and different character systems are united in this proposal. They will share characters, exchange specimens and review one another's choice of characters and coding decisions such that the whole will be much stronger than any individual study could be.

Currently there is a great deal of instability both in the limits of taxa within the Hymenoptera and in basic morphological terminology. For example, Symphyta is still considered a suborder despite the fact that it is clearly paraphyletic. Evanioidea and Proctotrupoidea have varied membership, and there are many family taxa with the same problem. In the case of morphology, we have three different systems of wing nomenclature and even more systems for genitalic features. We have assembled leading hymenopteran systematists from varied parts of the world with a wide range of knowledge in a spectrum that covers both molecular and morphological

expertise with all major subtaxa. Although we do not expect to solve all taxonomic and morphological nomenclatorial problems we do know that we will produce consistent results. Our results will set precedents for methodological approaches to large data sets, quality control in the construction of large phylogenetic data matrices and provide a framework that will be of use in all future systematic studies of Hymenoptera.

Selection of personnel: We have selected the personnel for this proposal to represent strength in hymenopteran phylogenetics, both in respect to morphological and molecular data, and also in theory and software development for large data set analysis (Carpenter, Heraty, and Ronquist). The team has also been selected on the basis of representation of the major clades within Hymenoptera, as well as fossils (Engel, Rasnitsyn). The PIs and senior personnel include taxonomic specialists in Aculeata (Brothers, Carpenter), Chalcidoidea (Heraty), Cynipoidea (Ronquist), Ichneumonoidea (Sharkey), Proctotrupeoidea (Ronquist and Sharkey) and Symphyta (Schulmeister, Vilhelmsen), providing broad expert coverage. This coverage is further broadened by participants in the specialist group workshops (see below).

HISTORY OF PHYLOGENETIC RESEARCH

The Hymenoptera are traditionally divided into two suborders, the Symphyta (sawflies) and the Apocrita, with the latter subdivided into the Parasitica (parasitoids) and Aculeata (stinging wasps, bees, and ants). With the application of cladistic principles, the Symphyta were found to be paraphyletic, with the Orussidae considered as the sister group to the apocritan wasps (*Vespina sensu Rasnitsyn 1988*). Hymenoptera are divided into 20 superfamilies and 89 families with several families unplaced (e.g. Goulet and Huber 1993; see supplementary documentation). Phylogenetic research on the order as a whole began with a series of papers by Rasnitsyn (1969, 1980, 1988) and Königsman (1976, 1977, 1978a, 1978b). Rasnitsyn's research was not cladistic, but very thorough and original. Königsman's research was mostly comprised of morphological characters taken from the literature, and though ostensibly cladistic, the data were analyzed intuitively with little resolution obtained at the superfamily level.

Since then a series of papers have investigated character systems across the Hymenoptera or in large clades of the Hymenoptera. A series of thoracic characters including muscle attachments and appendage articulations were developed by Gibson (1985, 1986b, 1999), Johnson (1988), Whitfield et al. (1989), Heraty et al. (1994, 1997) and Vilhelmsen (2000a, b, c). Darling (1988) investigated the labrum across the order; Vilhelmsen (1996, 1997a, 1997b, 1999, 2000 a, b, c) examined the preoral cavity, head capsule, antennal bases, occipital region, thoraco-abdominal boundary, prothorax, and the ovipositor respectively. Quicke et al. (1992, 1994, 1999b) studied ovipositor morphology (see also Vilhelmsen 2000c), Basibuyuk and Quicke (1999a) antennal cleaners and grooming behavior, Basibuyuk and Quicke (1997) wing structures (see also Sharkey and Roy 2002), Basibuyuk and Quicke (1999b) antennae and Basibuyuk et al. (2000) the orbiculae. Schulmeister (2003) recently published on the plantulae. Other studies have concentrated on phylogenetic relationships or character systems in restricted superfamilies or grades: Ronquist (1995, 1999), Liljeblad (2002), Liljeblad and Ronquist (1998) Cynipoidea; Gibson et al. (1999), Heraty et al. (1997), Heraty and Schauff (1998), Heraty and Quicke (in press), Chalcidoidea; Vilhelmsen (1997b, 2001), Jervis and Vilhelmsen (2000), Schulmeister et al. (2002), Schulmeister (in press a,b,c), Symphyta; Austin and Field (1997), Platygastroidea; Brothers (1975, 1999), Brothers and Carpenter (1993), Aculeata; Carpenter (1986, 1999), Chrysidoidea; Sharkey and Wahl (1992), Quicke et al. (1999a, c), Belshaw et al. (1998), Ichneumonoidea. Whitfield (1992a) is unique in having tried to synthesize data from various data sets for the Apocrita. Unfortunately, because terminals are mismatched across the data sets, he used ad hoc methods to produce a consensus tree of sorts.

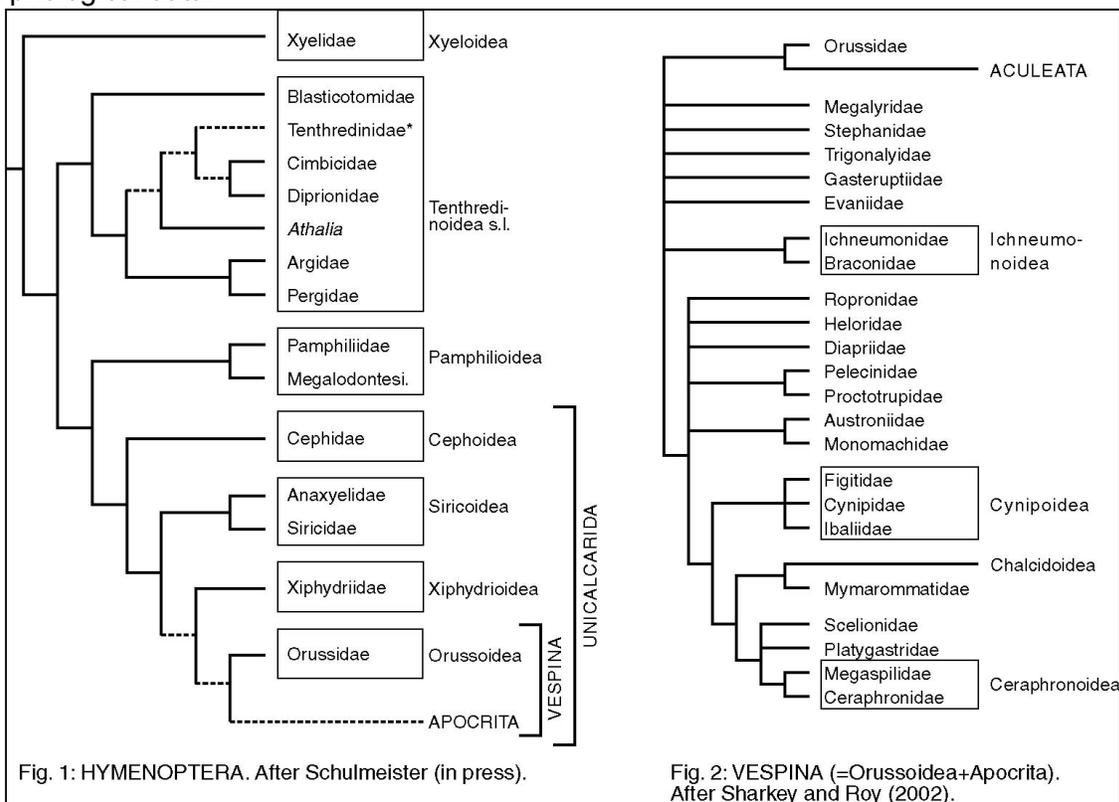
Until recently, Rasnitsyn's 1988 data have been the starting point for phylogenetic studies of the Hymenoptera at the family level. Four years ago a group led by Ronquist (Ronquist et al., 1999), which included Rasnitsyn, revisited the 1988 data, and coded it into a numerical cladistic analysis matrix. This data set has been used in the combined molecular/morphological analyses of the higher-level relationships of the Hymenoptera as a whole (Carpenter and Wheeler, 1999) and Apocrita (Dowton and Austin, 2001).

The Ronquist et al. (1999) morphological data represent Rasnitsyn's (1988) interpretations of many character systems, but in many cases these are not cladistic in nature. Also, the matrix was designed for representing fossil information, and many character definitions are not ideal

for recent taxa. The characters were coded for hypothesized ground-plan taxa instead of exemplars and many characters, particularly those published after 1988, were not included. Sharkey and Roy (2002) looked critically at the characters of the matrix that pertain to wings (37 of the 169 characters). They edited these but did not correct other morphological characters, which in many cases need to be reconsidered.

CURRENT STATUS

Recently published analyses of the Symphyta by Vilhelmsen (2001), Schulmeister et al. (2002) and Schulmeister (in press b) illustrate that the phylogeny of the basal lineages of Hymenoptera are reasonably well resolved at the superfamily level (Fig. 1, from Schulmeister in press b), though some problematic areas remain. In contrast, Sharkey and Roy's (2002) reanalysis of the Ronquist et al. (1999) data set (recoded wing characters) is representative of what little is known of apocritan familial phylogenetic relationships (Fig. 2), based on morphological data.



One pervasive problem with published simultaneous analyses of the Hymenoptera is that all focus on one of the three largest groups, reflecting the taxonomic interest of the authors. For example, in Schulmeister et al. (2002) and Schulmeister (in press b) taxonomic sampling is mainly from Symphyta, with no more than 16 apocritan species. Dowton and Austin (2001) focused on the Parasitica, with only three sawfly and six aculeate species, and Carpenter and Wheeler's (1999) analysis was biased towards the Aculeata, with just 17 non-aculeate species. Although Schulmeister (in press b) used a sufficiently large number of outgroup taxa to resolve the relationships of the basal superfamilies, this was not the case for the other simultaneous analyses. At present, there is no consensus whatsoever for the phylogeny within the Apocrita. What is needed now is a supermatrix that includes large taxon samples from all sources, i.e. non-hymenopteran insects, Symphyta, Parasitica, and Aculeata.

Of the 89 families of Hymenoptera presently recognized, 20 are dubiously monophyletic, known to be paraphyletic or even polyphyletic, viz., Agaonidae, Andrenidae, Aphelinidae, Argidae, Aulacidae, Colletidae, Diapriidae, Megaspilidae, Melittidae, Pergidae, Perilampidae, Proctotrupidae, Pteromalidae, Ropronidae, Scelionidae, Tenthredinidae, Tetracampidae, Torymidae, Xyelidae, and Tanaostigmatidae. Pteromalidae (Chalcidoidea) represent one of the

worst problems with more than 700 genera and 33-35 subfamilies, united not by apomorphic features but rather by shared plesiomorphies, making it essentially “a dumping ground for lost chalcidoids” (Gibson et al. 1999). The situation in the Chalcidoidea is by no means unique: for example, the Braconidae (Ichneumonoidea) has its dumping ground as well (Helconinae s.l., Hormiinae s.l.). One solution to this problem has been to divide the family into less inclusive subfamilies (e.g. Achterberg 1993); this solution solves the polyphyly problem but creates paraphyletic taxa instead. Changing classification is obviously not the first step. Even the monophyly of some hymenopteran superfamilies is suspect, i.e. Xyeloidea, Evanioidea, and Proctotrupeoidea, but because our proposed analysis involves numerous terminals within each family we will be able to corroborate or refute the current status of these taxa.

METHODS

We plan to study the phylogenetic relationships of Hymenoptera, employing both morphological and molecular data. Morphological data will be coded and associated through image databases for both characters and taxa. With about 1200 terminals, some thousands of character states (including molecular data) and images, and numerous investigators entering data there will be opportunities for error. We propose to address this problem in two ways, first by working to prevent errors from entering the matrix, and second by incorporating a series of careful checks after initial data entry. These quality control checks are described in the following paragraphs.

Morphological Data

Data Entry: Data will be collected almost exclusively with terminals delimited as exemplar species. Exceptionally we may have to draw on data at a more inclusive taxonomic level. By treating species, coding will be much easier and more accurate because terminals will be readily defined, and monomorphic for the characters scored. Species names may change, but the species taxa themselves do not; they are much easier to track over time than genera or higher taxa whose limits may be poorly defined and radically different over a generation or even a few years. When necessary for particular analyses, composite terminals can be automatically generated with Winclada that combine exemplars into clade representatives, e.g. subfamilies, families, on the basis of exterior classifications, character distributions, or prior trees.

The standardized data entry procedure will be as follows: 1) for each set of entries, a specimen, citation, or other source will be newly entered or selected from an existing database (e.g. Morphbank), and linked through the XML interface of Winclada; 2) All subsequent data entry will be automatically linked to the same source, including individual state scores within polymorphic cells; 3) When the same score is entered from a different citation or specimen, this will create an additional link to that score; 4) All matrices will be decomposable into a standard SQL database such as Microsoft ACCESS (see Nixon et al. 2001), using a facility now in beta form in Winclada. Likewise, data selected from a database will be used to reconstruct matrices.

Character Selection: The first step in our analysis will be a recoding of the Ronquist et al. (1999) data set. Sharkey and Roy (2002) already corrected the wing characters. After editing and recoding by Sharkey, Ronquist, Heraty, and others, Sharkey and Heraty will compile images of all character states and, using Winclada, they will associate these with the new matrix. Instead of the family level terminals, Sharkey will score all characters for two species of Ichneumonoidea and Heraty for two species of Chalcidoidea. Following this, and with the associated images of character states as a guide, two terminals will be scored for each superfamily, the Symphyta and two outgroups will be scored by Schulmeister (postdoctoral fellow in Carpenter's laboratory) and Vilhelmsen; Ronquist the Cynipoidea, Proctotrupeoidea, and Ceraphronoidea; Brothers, Carpenter and Engel the Aculeata; Sharkey the Platygastroidea and remaining small apocritan superfamilies, and Rasnitsyn and Engel will score fossil taxa.

When the matrix is scored for all of these taxa it will be compiled by Sharkey who will then organize an exchange of specimens between the taxonomic group leaders, for the purpose of double-checking the scoring. For example, Sharkey may be sent an aculeate specimen from Carpenter, Heraty might get an ichneumonoid or trigonalid from Sharkey, Schulmeister may get a proctotrupoid from Ronquist, etc. After the exchange, collaborators will run through the small matrix with the specimens provided and check the initial scoring. Besides quality control, the

procedure of exchanging specimens and cross-checking scores will familiarize collaborators with a wider spectrum of Hymenoptera and may result in the discovery of new informative characters. All of this will be completed before our first PI and collaborator meeting in the summer of 2004. At this meeting collaborators will discuss difficulties with characters and protocols. We expect that some character definitions will be refined or perhaps even deleted from the matrix. The product of this entire exercise will be the "base" matrix. After the summer 2004 meeting, participants will be asked to score a large portion of the base matrix (characters to be decided at the meeting) for all of their terminal taxa before the next collaborator meeting in the late spring of 2005. For morphological data we will not rely on published information except in exceptional instances where invasive dissections of extremely rare material would be required.

The meeting of PIs and collaborators in the summer of 2004 will also be used to consider characters to be added to the base matrix. Using the NSF model for reviewing proposals, sets of published or proposed characters will be assigned, by Sharkey, to a major reviewer and at least one minor reviewer. Each major reviewer will lead a discussion at the meeting on the published characters addressing the following questions.

1. Is it a discrete character?
2. What is the cladistic information potential?
3. Is it coded properly? Are state changes logical? Are character states unambiguous so that all collaborators and future investigators will have no trouble in interpretation?
4. Should it be treated as additive or non-additive?
5. Is the character easily observed or is dissection or some other specialized method such as SEM required?

Besides reviewing published characters, the meeting will provide an opportunity for PIs and collaborators to introduce new characters for discussion. The product of this meeting will be a larger standardized morphological matrix.

Sharkey will again be responsible for compiling images for the newly added characters. He will be assisted by Carpenter and Heraty and to a lesser degree all other collaborators. Collaborators will be responsible for scoring two taxa from each superfamily for the new characters. The same process and quality control measures that are in place to build the "base" matrix will be repeated with the expanded matrix which we will refer to here as the "general" matrix for clarification. When we meet again in the spring of 2005, the new characters will be reevaluated before collaborators are assigned to score them for all terminals. Meetings of collaborators are scheduled for each year of the project and the procedures of discussing problems with newly introduced characters, adding new characters for partial coding, cross-checking etc., will be repeated at each meeting. Of course the number of new characters added will be dramatically reduced after the first two years of the project. In the meetings of spring 2005 and January 2006 morphology-based collaborators (see below) will have opportunities to introduce characters as well.

Whenever major additions are made to the matrix preliminary trees will be generated. Sharkey, Carpenter, and perhaps others will map character changes on the resulting trees using the various options of Winclada. This exercise will reveal homoplastic occurrences. Some of these instances of homoplasy will stand out as being unlikely or surprising and the relevant taxa will be reinvestigated. There may also be surprising taxon placements. The characters supporting these placements will be carefully checked for errors.

An effort to put together a mega-matrix for hymenopteran morphological characters, drawing chiefly on published data sets (Basibuyuk and others, www.bio.ic.ac.uk/staff/dlq/morphch.rtf), might be viewed as a good starting point for further work, however the matrix is so problematic that a complete overhaul is required. The matrix builds on that of Ronquist et al. (1999), characters of which we have already criticized. Although it may be a good source for ideas, the posted data are not where we intend to start building our morphological data set.

Character Based Studies: Concurrent with the taxon based studies, Schulmeister will code all taxa for male reproductive characters, a Ph.D. student in Sharkey's lab will code for internal female reproductive characters, and Vilhelmsen will code for internal thoracic characters. As well, various collaborators will be involved with analyzing character systems peculiar to their particular groups, but which may ultimately be added to the general matrix.

Male Genitalia: Until recently, the male reproductive system has been largely ignored for in the of phylogenetic systematics of Hymenoptera. This was due mainly on the complexity of this character system and the unavailability of alcohol-preserved material. Schulmeister (in press c) has recently carried out a large scale phylogenetic study of the male genitalia in Hymenoptera, examining all symphytan families and some apocritan representatives. She found 85 characters informative for the basal lineages alone, which demonstrates the amount of phylogenetic information contained in the male reproductive system. When more apocritan taxa are included in the study, it is expected that more characters will be revealed.

Female Reproductive System: The graduate student in Sharkey's lab, co-supervised by Packer, will be investigating the wealth of characters associated with the female reproductive system, especially the ovipositor complex. This is a complicated system with a potential for more than 50 characters and 150 character states (Oeser 1961; Quicke et al. 1992, 1994, 1999b; Rasnitsyn 1968; Le Ralec et al. 1996; Heraty and Quicke in press) and we think it better to have one expert survey all taxa rather than to train all collaborators to dissect ovipositors and recognize homologies. Packer has already published a broad survey of apoid ovipositors (Packer in press) and we will extend many of the characters across the Hymenoptera as well as collecting other ovipositor characters from the literature. In addition to contributing important characters to the analysis, the evolution of the ovipositor system is expected to be highly correlated with major shifts in behavior and this will complement our general investigation of the evolution of hymenopteran natural history (Objective 5, above).

Thoracic Characters: The thoracic (mesosoma) region is the most morphologically complex body region in Hymenoptera and as such has high potential for providing informative characters for phylogenetic analysis. This has been amply demonstrated by recent studies of selected parts of the thoracic skeletomusculature for Hymenoptera as a whole (e.g. Gibson 1985, Heraty et al. 1994) or subsamples thereof (e.g. Heraty et al. 1997 on Chalcidoidea; Vilhelmsen 2000a, b on Symphyta). In the recent morphology-based phylogenetic analysis of the basal hymenopteran lineages by Vilhelmsen (2001), characters from the thorax/mesosomal region and its associated appendages (excluding wings) comprised more than half (120 out of 236) of the characters included. Vilhelmsen will investigate the skeletomusculature of a selected sample of Hymenoptera with representatives from all superfamilies, with the greatest emphasis on the non-Aculeate Apocrita. Due to the time-consuming investigations (e.g. dissections, serial sectioning) involved in this work, it is not feasible to score all of these characters for all the exemplars included. However, the detailed investigations are likely to reveal a number of new, more accessible characters that will be communicated to the research group to be scored for the entire taxon sample.

As it is doubtful that any of these character-based collaborators will be able to dissect and score all of the expected 1200+ terminal taxa, the taxon based collaborators will therefore only supply specimens of the critical taxa of their group. For example, Sharkey and others will be looking into the phylogeny of the Ichneumonidea in some detail, but character-based collaborators will only be sent a sampling of specimens representing basal lineages with a preponderance of plesiomorphic character states. If the character-based collaborator finds informative variation within these taxa two options present themselves, i.e. expand the sampling of the Ichneumonidea within the framework of the grant or leave it as a spin-off project to follow the tenure of the grant. These decisions will be made as information passes back and forth between taxon and morphology-based collaborators on a case-by-case basis.

Morphology of Chalcidoidea: This superfamily represents a large and unique problem within the Hymenoptera. Most species range in size between 2 and 5 mm, with extremes from 0.11 mm to 45 mm (Gibson et al. 1999). Many taxa have undergone parallel reduction, are highly modified, or have undergone considerable convergence in morphological traits. There is a long history of detailed morphological studies in Chalcidoidea (e.g. Bucher 1948, Domenichini 1953, 1954, 1978, Gibson 1986a, b; Darling 1988, Heraty 1989; Heraty et al. 1997; Heraty and Schauf 1998 – 66 papers as reviewed in Gibson et al. 1999), and this overwhelming amount of information requires independent synthesis and reevaluation. For this reason, we are requesting one postdoctoral fellow in Heraty's lab to score a morphological data set for characters that are both standardized for all Hymenoptera and others that are unique for helping to resolve relationships within Chalcidoidea. The postdoctoral fellow will spend time working with collaborators in year 2 in Washington, Ottawa, London and Montpellier to resolve issues surrounding character assignment and coding. All characters and results will be discussed,

modified and reevaluated at chalcidoid “TWiG” and PI meetings.

Molecular Data

Of the potential array of genetic regions used in molecular studies, only a few regions have been used for Hymenoptera or for insects in general (Caterino et al. 2000). The earliest studies of hymenopteran relationships focused almost entirely on 16S (Derr et al. 1992a, b; Dowton and Austin 1994, 1995; Dowton et al. 1998; Kambhampati 2000). The 28S-D2 or D2&D3 expansion region has been used successfully for analyses of relationships within superfamilies, but with varying degrees of success at higher taxonomic levels (Belshaw et al. 1998, 2001; Gauthier et al. 1999; Campbell et al. 2000; Babcock et al. 2000). Combinations of 16S, COI, 28S and 18S-E23 have been used for studies of relationships within Apocrita (Dowton and Austin 1998, 2001; Mardulyn and Whitfield 1999), across basal Hymenopteran superfamilies (Schulmeister et al. 2002), and across Hymenoptera (Carpenter and Wheeler 1999). Especially in the combined gene analyses, the largest single problem in the analysis of relationships across Hymenoptera, surpassing issues of alignment and analytical method, is the lack of adequate taxon sampling (Carpenter and Wheeler 1999, 45 spp.; Dowton and Austin 2001, 87 species; Schulmeister et al. 2002, 39 species). Considering the sheer size of the order, the proportion of taxa sampled is miniscule. In addition to the previously published sequences, available unpublished sequences produced by Carpenter and Wheeler fill in some gaps: representatives of all superfamilies have now been sequenced. The total available now is 571 sequences from 208 taxa (28S-D3 - 119 taxa, 18S - 137, COI - 98, COIext - 109, 16S - 108). From Heraty's lab, there are now also 75 sequences for 18S, 342 sequences for 28S-D2 and 244 of 28S-D3 for Chalcidoidea (186 directly relevant to this study – see Supplementary Documentation), which are not well represented in the sample from Carpenter and Wheeler. The proposed sequencing in this project will provide substantial additional data during the course of this proposal, with the taxon sample to emphasize groups that are poorly represented in the presently available data. We are proposing to sample five gene regions (18S-E23, 28S-D2&D3, COI, 12S and 16S) - both nuclear and mitochondrial markers - across approximately 300 different species of Hymenoptera in each of four labs (AMNH, Kentucky, Riverside, Florida State), for a total of about 1200 species. Additions to Genbank during the course of this proposal will certainly push the total sequence data set to more than 1400 species.

Alignment and character applicability. Alignment of sequence data is likely one of the most contentious issues in systematics today. We recognize that in the five year span of this project, there will likely be novel approaches to alignment, and the PIs have the expertise necessary to address these changes. Alignment of the one mitochondrial gene region (COI) is trivial. COI sequences will be aligned using a simple alignment program (i.e. ClustalX) and then optimized to ensure that all gaps conform to a reading frame. These final alignments will be fixed in all subsequent analyses. Ribosomal genes are more difficult to align. 18S, 12S and 16S are more conserved and can be aligned across all Hymenoptera. 28S is valuable for subfamily and some family level analyses, but variable helices likely will be impossible to align across Hymenoptera. We propose to address this problem by concatenating ambiguous alignments within related groups (Whiting 2001). Ambiguous alignments will be identified using multi-parameter alignment as implemented in SOAP (Loytynoja & Milinkovitch 2001). Regions that cannot be aligned across Hymenoptera will be partitioned into smaller concatenated blocks of data appropriate for estimating relationships within related taxa. For example, ambiguous regions of 28S that can be aligned reasonably within Chalcidoidea will be treated as an independent block of data, with all other Hymenoptera treated as missing. Ambiguously aligned regions will be treated in two ways: 1) Carpenter's group will analyze the data using direct optimization in POY using various gap/extension cost parameters to resolve ambiguous blocks (Wheeler 1996; Gladstein & Wheeler 1997), 2) Heraty and Ronquist will develop fixed alignments using secondary structure models (Gutell et al. 1995; Kjer 1995, 1997). In all cases, clade support will be measured using sensitivity analyses (Schulmeister et al. 2002) based on comparison of results from a variety of alignment techniques (data independent). Groupings that are alignment sensitive will be considered as suspect, even if supported by strong bootstrap, jackknife, or Bremer support under particular models (alignment dependent). The retention of well-supported monophyletic groups (genera or family group taxa) is our basic criterion for the evaluation of resulting trees and helps to sort out bad data (poor sequence or poor character

coding), bad alignments or potential paralogous gene regions. However, we expect that some of even the most well-respected 'intuitive' groups will need to be reevaluated with this new data. In cases of poor homology (alignment) and uneven sampling, parallel problems occur with morphology. Thus, for particular clades there are certain unique suites of morphological characters available that may not be scorable for other clades. Likewise, lack of material could pose a sampling problem similar to that seen in molecular data. These issues are part of the general phenomenon of inapplicability and ambiguity in data matrices (Nixon & Carpenter 1996; Nixon 1996; Kearney 2002). All data will be treated independently (morphology versus molecules) and combined into a total evidence analysis.

Taxon Sampling Strategy

Besides having carefully assessed and coded characters in our data set, we also need quality taxa, and we see several challenges in this regard that can only be solved by increased sampling. The first difficulty is that, for the existing data sets, the terminal taxa are quite heterogeneous. For example, data sets such as those of Ronquist et al (1999) and Sharkey and Roy (2001) are composed of ground plan taxa, whereas sequence data from Dowton and Austin (2001) and others are necessarily exemplar in nature. The morphological data sets from which we hope to glean characters are also a combination of exemplar and ground plan terminals. The terminal mismatch is more severe in that the taxa of some data sets are simply not represented in others. For example the Symphyta are not represented in the Dowton and Austin (2001) data and few apocritan taxa are included in Vilhelmsen's comprehensive morphological data sets. These problems can be solved only by expanding the taxon sampling and by using exemplar species as terminals so that molecular and morphological data are congruent.

Where available, at least three genera will be sampled for each subfamily group spanning suspected basal and divergent lineages (*sensu* Yeates 1995). Where monophyly is not supported, additional representative exemplars will be scored. In cases where subfamilies are monotypic at the generic level, multiple species will be scored. Even for strongly supported groups (*i.e.* well-supported by morphological synapomorphies), we will use multiple terminals as an internal test of the quality of the sequence data (*i.e.* monophyly at the genus, tribal, or subfamily level). In a few rare cases, such as Anaxyelidae (one extant species), our sampling is necessarily limited. Where there is even a remote possibility of paraphyly or polyphyly an even larger sample will be required.

We intend to sample much more thoroughly than previous studies due to the problems of potential para- and polyphyly discussed above, therefore the number of extant terminal taxa studied for morphology will initially be more than 400. The exact number will be determined at the PI and collaborator meetings after weighing the amount of time it will take to score each character with information potential.

Another sampling challenge concerns extinct taxa. Paleontological data are often critical in phylogenetic analyses. By introducing into the analysis unique character combinations, fossils can provide the necessary information for resolving particularly ancient, but highly autapomorphic lineages (*e.g.* Gauthier et al., 1988). Fossils, taken in a phylogenetic context, serve to resolve patterns of descent while also identifying periods of diversification and extinction and their study may uncover the sequence and origin of synapomorphies. Fossils uniquely tie episodes of radiation to novel biological and morphological attributes. The recognition of numerous extinct lineages, *e.g.* Serphitidae, Stigmaphronidae, Paleomelittidae, Falsiformicidae, as well as now extinct diversity within others, highlights the critical importance of applying a paleontological perspective to the reconstruction of Hymenopteran phylogeny.

Of the largest insect orders, Hymenoptera is the best known paleontologically, at least in terms of numbers of described Mesozoic taxa and proportion of families recorded as fossil. Of 79 families considered as valid by Rasnitsyn (2002, Chalcidoidea taken as single entity because of the inferior quality of its fossil record), only six families have no fossil records, a very low figure compared to the other main insect orders (Coleoptera, Lepidoptera, Diptera). Over 3,000 fossil species and at least 900 genera have been described. The Mesozoic is the most important segment of hymenopteran fossil history, in relation to this proposal, for it was the time of family level diversification in the order. The richest and most diverse collection of Mesozoic hymenopterans is housed in the Paleontological Institute, Russian Academy of Sciences (Moscow) and it includes 2,300 individual fossils from more than 60 localities (mainly Asiatic). This collection will be the main source of paleontological information to be used in the present

project, supplemented with the Mesozoic material housed in the American Museum of Natural History (AMNH, mainly the Early Cretaceous fossils from Santana, Brazil), and University of Kansas (KU, mostly Middle Cretaceous Burmese amber), and when appropriate the abundant Cenozoic fossils (particularly the amber inclusion fossils) kept in various available collections (PIN in Moscow, AMNH, KU, National Museum of Natural History). Critical for the fossil material, which cannot readily be exchanged among PI's, will be adequate documentation of taxa and their character combinations. All fossils included in the analyses will be photo-documented. Perhaps as many as 100 fossil taxa will be added to the morphological matrix. These additions to the matrix will also be discussed at the PI meeting in terms of feasibility and taxonomic coverage.

Aculeata, Chalcidoidea, and Ichneumonoidea. These clades are massive and will require special attention. Within Hymenoptera, they are numerically and biologically the largest and most diverse groups. The number of described species in each group is over 20,000 (e.g. Gaston, 1991). Chalcidoidea alone have been estimated to contain more than 400,000 species (Noyes 2000). Morphological analyses across each group using more than a single character system have only been carried out in parts of Aculeata (Chrysidoidea and Vespoidea: Brothers 1975, 1999; Carpenter 1986, 1999; Brothers and Carpenter 1993; Apoidea: Melo 1999), without completely resolving relationships. Major problems facing such analyses include the sheer number of taxa, the extreme diversity of form, and in Chalcidoidea, the tendency towards reduction of the same structures in unrelated taxa. The Ichneumonoidea are divided into only two families but the superfamily could just as easily have been broken into as many families as the Chalcidoidea (19) or Aculeata (28)..

As another example of the current state of these taxa, Campbell et al. (2000) investigated the higher level relationships within Chalcidoidea using 108 species distributed across 23 subfamilies and 16 families using a single gene region (28S-D2). Although monophyly of some important groups (Eulophidae, Trichogrammatidae, Eucharitidae) and most subfamilies was supported, several families that have distinct morphological synapomorphies were polyphyletic (e.g. Chalcididae, Wijesekara 1997; Gibson et al. 1999). Clearly, better morphological sampling, more genes and more taxa are necessary to look at each entire group. Relationships within Ichneumonoidea at the subfamily level are as little known as family level relationships within Chalcidoidea. Results are usually contradictory, and unresolved unless weighting techniques are employed (Quicke and Achterberg 1990, Dowton, et al. 1998, Dowton 1999, Dowton et al. in press., Belshaw et al. 1998).

Relationships among the superfamilies are also controversial. Some recent analyses place the Ichneumonoidea as the sistergroup of the Aculeata, but this far from universal (Fig. 2). Several phylogenetic studies, both morphological and molecular, place Chalcidoidea + Mymarommatoidea as a relatively derived apocritan lineage and sister group to the Platygastroidea and/or Ceraphronoidea (Fig. 2). However, based on transitions of muscle groups, Gibson (1999) placed Mymarommatoidea as a more basal lineage and likely not closely related to Chalcidoidea. Molecular analyses also do not discount an even earlier origin and suggest a sister group relationship with Cynipoidea (Dowton and Austin 2001). Resolution of outgroup relationships and better sampling of character data and taxa are critical for resolving relationships within each of these three groups and placing them within the Hymenoptera with confidence.

Our plan is to sample exemplar taxa across the subfamilies of Aculeata, Chalcidoidea and Ichneumonoidea for both morphology and the five gene regions (18S-E23, 28S-D2&D3, COI, 16S). Some rare subfamilies, e.g. Vaepelinae, may be sampled only for morphology, but, in general, we hope to sample an average of 4 species for each subfamily for both morphology and molecules.

To deal with these three taxa the responsible PIs (Heraty, Carpenter, and Sharkey) have built "Taxonomic Working Groups", TWiGs (to borrow a phrase from D. Janzen). The responsibilities of the TWiG members are the same as those of the PIs but at a less inclusive level. PIs will direct their TWiGs with a management plan similar to that of the overall project with the goal of producing "TWiG" morphological matrices. In the spring of 2005 each of the three TWiGs will assemble independently (see project management). Each member will have been sent the "general" data matrix. Each TWiG member will be assigned published data sets that they will present at the meeting. For example, the ichneumonoid TWiG will survey the

characters in all published data sets dealing with their taxon (e.g. Quicke and Achterberg 1990, Wharton et al. 1992, Whitfield 1992b, 1997, Wahl and Gauld 1998, Downton and Austin 1998, Rahman et al. 1998, Quicke and Belshaw 1999, Quicke et al. 1999c). These characters will be edited and added to the “general” data set to produce a “taxon specific data set”. The new characters that are thought to have information potential at a higher level will be forwarded to Sharkey to be considered for inclusion in the “general” matrix at the next meeting of PIs. All “TWiG” characters will eventually be included in the “general” matrix but only those that are easily scored will have filled cells. Carpenter, Sharkey, and Heraty will be responsible for preparing their “TWiG” matrices and assembling images of character states and taxa. The aculeate, ichneumonoid and chalcidoid taxa will be divided among the members of the respective TWiGs. The protocols for checking data and exchanging specimens are the same as those for production of the “general” matrix.

Outgroups: The Ronquist et al. (1999) and Sharkey and Roy (2002) studies used a synthetic terminal as a root (an all-zero “outgroup”), but we will include real species as outgroups. Vilhelmsen’s (2001) analysis included a coleopteran, a raphidiopteran, a neuropteran, and a psocodean in addition to antliophoran and amphiesmenopteran representatives to cover the main groups within the Holometabola as well as an obvious root in Psocoptera. In order to be able to polarize ovipositor characters, for example, it is actually necessary to include something outside the Holometabola (e.g. the psocodean) since it is the only other holometabolan order with a fully developed appendicular ovipositor apparatus. Schulmeister et al. (2002) have already sequenced most of these outgroup taxa. Schulmeister (in press b) has further expanded the outgroup sample, scoring them for morphology as well as sequencing them; we will use these outgroups

In the supplementary documentation section we present a preliminary list of the genera from which we intend to select our exemplar species. Although many of these specimens are in hand or easy to obtain, others will require collection effort. In the project management plan we outline our collection strategies and the localities selected, these are further justified in some of the budget justifications.

ANALYSIS

In recent years, many DNA sequences have been collected across insects. Sequence data provide relatively easy assessment of homology across broad groups, and provide the potential for large scale phylogenetic analyses using hundreds or thousands of terminal taxa. Yet, even with well-aligned sequence data, analyses of matrices with more than 500 taxa remain challenging. Recently, our ability to undertake parsimony analysis has been dramatically extended through the development of new techniques including the parsimony ratchet (Nixon 1999, now implemented in the program Winclada, Nixon 2002) and tree fusion, sectorial searches, and tree drift (Goloboff 1999, now implemented in the program TNT, Goloboff et al. 2002). These techniques extend parsimony analysis to matrices well in excess of 500 taxa - in fact to thousands of taxa, and to tens of thousands of taxa when techniques for estimating consensus trees such as parsimony jackknifing (Farris et al. 1996) are used. Ongoing development of graphical and database tools for constructing and managing large data sets (supermatrices), and tools for constructing and manipulating supertrees by Nixon are addressing the problems associated with combining data, including issues of fossil inclusion, and large amounts of missing data that often result when morphological and molecular data sets are merged (Kearney 2002).

Tree Searches: For phylogenetic inference we will primarily be using parsimony analysis and Bayesian statistical inference. Both are relatively fast inference methods that can handle combined morphological and molecular data. Parsimony has been established for some years as the method of choice for large data sets. It is a relatively sophisticated optimality approach and its efficiency in analyzing large taxon sets has been dramatically extended recently through the development of the new techniques mentioned above. Bayesian inference using Markov chain Monte Carlo (MCMC) estimation is a more recent addition to the analytical tools of phylogeneticists (see reviews in Huelsenbeck et al. 2001, Holder and Lewis 2003). In contrast to parsimony, this is an explicit parametric statistical approach to phylogenetic inference. The first Bayesian phylogenetics papers demonstrated the techniques on relatively

small problems (e.g., Rannala and Yang 1996). Recently, using a convergence acceleration technique known as Metropolis-coupling, Huelsenbeck et al. (2001) were able to show convergence (the criterion of success in MCMC estimation) of Bayesian phylogenetic inference for problems with up to 357 taxa. Despite the size of these analyses, they complete within days on modern personal computers using current software implementations (e.g. Huelsenbeck and Ronquist, 2001, Ronquist and Huelsenbeck in press). Nobody presently knows the limit of Bayesian MCMC estimation of phylogeny but it seems likely that the method can be extended to deal with problems comprising 1,000 or more taxa in the near future. Furthermore, Bayesian phylogenetic analysis has recently been extended to deal with combined data sets including multiple molecular markers and morphology (Ronquist and Huelsenbeck in press, Nylander et al. submitted). Thus, Bayesian inference of our data should be feasible and it will be fully comparable to parsimony analysis in utilizing both morphological and molecular data.

Alignment and Character Applicability. Alignment of sequence data is likely one of the most contentious issues in systematics today. We recognize that in the five year span of this project, there will likely be novel approaches to alignment, and the PIs have the expertise necessary to address these changes. Alignment of the one mitochondrial gene region (COI) is trivial. COI sequences will be aligned using a simple alignment program (i.e. ClustalX) and then optimized to ensure that all gaps conform to a reading frame. These final alignments will be adjusted in all subsequent analyses. Ribosomal genes are more difficult to align. 18S, 12S and 16S are more conserved and can be aligned across all Hymenoptera. 28S is valuable for subfamily and some family level analyses, but variable helices likely will be impossible to align across Hymenoptera. We propose to address this problem by concatenating ambiguous alignments within related groups (Whiting 2001). Ambiguous alignments will be identified using multi-parameter alignment as implemented in SOAP (Loytynoja & Milinkovitch 2001). Regions that cannot be aligned across Hymenoptera will be partitioned into smaller concatenated blocks of data appropriate for estimating relationships within related taxa. For example, ambiguous regions of 28S that can be aligned reasonably within Chalcidoidea will be treated as an independent block of data, with all other Hymenoptera treated as missing. Ambiguously aligned regions will be treated in two ways: 1) Carpenter's group will analyze the data using direct optimization in POY using various gap/extension cost parameters to resolve ambiguous blocks (Wheeler 1996; Gladstein & Wheeler 1997), 2) Heraty and Ronquist will develop fixed alignments using secondary structure models (Gutell et al. 1995; Kjer 1995, 1997). In all cases, sensitivity analyses (Schulmeister et al. 2002) based on comparison of results from a variety of alignment techniques will be used to measure of clade support (data independent). Taxon associations that are alignment sensitive are suspect, even if supported by strong bootstrap, jackknife, or Bremer support under particular models (alignment dependent). The retention of well-supported monophyletic groups (genera or family group taxa) is our basic criterion for the evaluation of resulting trees and helps to sort out bad data (poor sequence or poor character coding), bad alignments or potential paralogous gene regions. However, we expect that some of even the most well-respected 'intuitive' groups will need to be reevaluated with this new data. In cases of poor homology (alignment) and uneven sampling, parallel problems occur with morphology. Thus, for particular clades there are certain unique suites of morphological characters available that may not be scorable for other clades. Likewise, lack of material could pose a sampling problem similar to that seen in molecular data. These issues are part of the general phenomenon of inapplicability and ambiguity in data matrices (Nixon & Carpenter 1996; Nixon 1996; Kearney 2002). All data will be treated independently (morphology versus molecules) and combined into a total evidence analysis.

Dating. The relatively large effort within this project devoted to scoring of morphological characters of extant and fossil taxa should make it possible to accurately date many of the early splitting events in hymenopteran phylogeny. This will provide a much needed temporal framework for the occurrence of important events in early hymenopteran evolution, such as the origin of insect parasitism. Beyond the increased understanding of the factors underlying the successful radiation of the Hymenoptera, this should produce new insights into past ecological changes, since some of these events undoubtedly had a significant impact on the terrestrial ecosystems at the time.

Untangling rate and time is an inherently difficult problem, whether one uses parsimony

or a parametric statistical approach. Typically, the topology is assumed to be given (known without error) before statistical analysis under relaxed clock models or non-parametric rate smoothing is applied refs. Furthermore, fossils are often used to fix the dates of certain calibration nodes in the phylogeny. Uncertainty in phylogenetic placement and in taxon age is often ignored. Preliminary results of Bayesian phylogenetic analysis of combined recent and fossil data indicate that many hymenopteran impression fossils, which constitute the oldest fossils of the order, are difficult to place exactly in the phylogeny (Ronquist, Vilhelmsen, and Rasnitsyn, unpublished data). However, the fossils do not float around randomly in the phylogeny of extant taxa. Instead, they tend to be placed within certain regions of the tree of extant taxa. It is essential to take this type of uncertainty in the phylogenetic placement of the fossils into account but, even so, fossils should be able to contribute to the dating of splitting events. New releases of the program MrBayes (Ronquist and Huelsenbeck, in press) will combine simultaneous analysis of fossil and recent taxa with dating under relaxed clock models. This will allow us to take uncertainty both in the phylogenetic relationships among recent taxa and in the placement of the fossil taxa into account when dating splitting events. The prospects of analyzing the entire taxon set simultaneously are similar to those discussed above for the phylogenetic analysis itself. If the entire taxon set cannot be addressed in one analysis, we will break it into smaller components and date these separately.

Supermatrix Construction: One of the most difficult issues regarding the construction of large matrices has been a limited number of tools for automating matrix authoring tasks. For both morphology and molecular data, among the most important of these are tools to merge submatrices (Winclada MATRIX MERGE). For morphology, also of importance are tools to view quickly and ergonomically summaries of data scores to detect errors in coding. All of these tools currently exist in the package Winclada (Nixon, 2002; i.e. the TPANEL, CPANEL and DIAGNOSTIC KEY functions, and BULK scoring functions within TPANEL), and have been utilized by various workers. M. W. Allard (pers.comm.) has used Winclada to produce large supermatrices of both mammal and human forensic data, with more than 4,000 terminals, and successfully analyzed these using both NONA (Goloboff, 1993) and TNT (Goloboff et al., 2001).

Simultaneous Analysis: The final morphological matrix will be analyzed in combination with all available molecular sequences in a "total evidence" analysis of hymenopteran phylogeny. The analysis will use standard techniques (Nixon and Carpenter 1996), software already available (Winclada, Nona, TNT), and software that may become available during the tenure of the grant (e.g. MrBayes).

SUMMARY AND FEASIBILITY

The final product of this research will be a major contribution to the phylogeny of Hymenoptera, including extensive morphological data, placement of important fossils, and resulting estimates of ancestral forms and times of divergences for major groups.

The type of analysis proposed here is definitely attainable within the 5-year time frame. Most of the functions for data management, image linkage, data input and verification already exist in varying levels of development in the program Winclada. Refinements and improvements continue to be implemented, based in part on feedback from co-PI Carpenter, who is a beta-tester for this program. Current tree search algorithms, likewise, have already proved successful with large data sets (from 500-4,000 taxa). The program Nona is presently adequate for such an analysis, but as improvements are developed in TNT these will be available, as Carpenter is also a beta-tester for that program. It is entirely likely that other software choices will be available when we are prepared for analysis.

The mega-matrix will be constructed on a community-level basis. To this end, we have obtained the collaboration of 38 hymenopterists including 4 graduate students (see supplementary documentation and attached letters of support). Because of the involvement of a broad array of collaborators outside of the core participants, completion of the matrix is quite feasible. The plan to hold a series of workshops to bring the collaborators together to assemble the matrix facilitates completion within the 5-year time-frame of this proposal.

Expected Results and Dissemination

Publications: Two books are planned. The first will publish the data set and fully

illustrate and document all taxa and character states. This will be accompanied by a compact disk containing the matrix. The second book will contain analyses of the entire data set, and individual chapters on the phylogenies of individual superfamilies. The morphologically based collaborators will also be encouraged to publish in this venue. Other revisionary studies will include, at minimum, (* indicates only partially supported by grant): Sharkey et al. (Phylogeny of the Braconidae); Wahl, Bennett, et. al. (Phylogeny of the of the Ichneumonidae); Carpenter, Brothers, Engel, and Rasnitsyn (Phylogeny of the Aculeata); Schulmeister and Vilhelmsen (Phylogeny of the basal Hymenoptera); Schulmeister et al. (Phylogenetic analysis of the Hymenoptera based on male reproductive characteristics); Sharkey's student et al. (Phylogenetic analysis of the Hymenoptera based on female reproductive characteristics); Vilhelmsen* et al. (Phylogenetic analysis of the Hymenoptera based on thoracic musculature); Sharkey et al. (Phylogeny of the Platygastroidea); Heraty et al. (Phylogeny of the Chalcidoidea); Ronquist et al. (Phylogeny of the Cynipoidea, Phylogeny of the Proctotrupeoidea, Dating Hymenoptera family-level splitting events using extant and fossil evidence); Many collaborators (Natural history characteristics of the Hymenoptera from a phylogenetic perspective); Austin and Dowton* (Phylogeny of the Hymenoptera based on the entire mitochondrial genome); Engel et al. (Geological history of the Hymenoptera, Phylogeny of the Apoidea); and of course: ALL (Phylogeny of the Hymenoptera: Total Evidence).

Electronic Dissemination: Sharkey et al. will produce an illustrated interactive key to the families of Hymenoptera; furthermore, his group will extensively illustrate and add to the glossary of morphological terms already posted on his web site. The database of hymenopteran characters and with associated images will be posted. The latter will include archiving of data sets (specimens, characters, nomenclature, trees, and character-by-taxon matrices). All results will be placed on a website at the University of Kentucky. Sharkey will set up a dedicated server for the project, an appropriate web address will be used and it will be maintained at UK and elsewhere e.g. <http://www.tolweb.org/tree/phylogeny.html>, and www.diversityoflife.org. We will intermittently post character lists and descriptions as the project progresses to solicit input from hymenopterists at large. Because each of our workshops will involve students, postdoctoral associates and outside faculty, the educational impact of our efforts will be significant. After publication of our results the Winclada supermatrix will be accessible to the public. One of the final products to be posted will be the phylogenetic hypothesis(es) in the form of a tree with embedded character state information. Other products on the site will be a synopsis of the proposal, and links to other Hymenoptera sites.

All images for specimens will be associated with the Winclada supermatrix and deposited in the Morphbank website. One of the goals of this project is not only to illustrate characters, but also whole morphologies (habitus) that might be used for additional character information or simply for taxonomic reference. The Cynipoidea files currently on Morphbank will be used as a model for loading image files. Ronquist's group have developed a series of 72 image views that they feel best describe each genus of Cynipoidea for phylogenetic features. For each group similar sets of images will be developed, with additional views using Automontage digital images and illustrations. All images will be arranged in a taxonomic hierarchy and will be fully searchable by image view.

Public workshops and meeting presentations: Collaborators will present at numerous meetings during the course of the investigation and at the International Congress of the Hymenopterists' Society in South Africa in 2006. Sharkey will use the interactive key as a "hands on" teaching tool at several workshops on the identification of hymenopteran families. These are held every second year at the University of Maryland and at irregular intervals elsewhere. We are planning a symposium on hymenopteran phylogeny at the International congress of Entomology, in 2008, the final year of the project.

EDUCATION

Workshops: A series of workshops are planned for TWiG working groups that will incorporate students, postgraduate researchers and a large group of outstanding international collaborators. Workshops are designed to discuss systematic methodology, data management and evaluation of results. All participants will be introduced to a variety of techniques and taxonomic groups, and through interaction, will develop future collaborative research on

Hymenoptera. Students are an important part of these workshops and we expect all participants to present aspect of their ongoing studies. Funds are also budgeted to include graduate students in the workshops from other institutions not specifically tied to this proposal.

Scientific meetings: Students and researchers will be encouraged to present results at national scientific meetings. Project oriented opportunities will include the International Society of Hymenopterists Congress in South Africa and a final symposium at the International Congress of Entomology.

Collaboration: Sharkey has budgeted for students to travel to Heraty' lab for training in sequencing techniques and data alignment. Collaborator Packer will mentor one of Sharkey's graduate students in dissection techniques and character systems associated with the female reproductive system. Heraty's postdoctoral researcher will be working with collaborators at the Canadian National Collection, the Museum of Natural History and the INRA research station in Montpellier for development of appropriate character sets, Workshops will be coupled with local funding opportunities to allow for longer term visits and scientific exchange with international researchers, students and postgraduate researchers. Collaborators, where appropriate, will be invited to serve as external reviewers for student theses, which in part will be supported by workshop funds. The central web site developed for the project will act as a center for the exchange of information between students, postgraduate researchers, and all participants.

Human Resources: Each subproposal, where appropriate, will incorporate students or postdoctoral researchers as integral components of the overall program. Students will be trained in a wide array of approaches, including but not limited to morphology and theoretical systematics. All students will have considerable exposure to advanced analytical techniques and the use of fossils in phylogenetic analysis. We are especially interested in establishing a mentorship program that will assist under represented groups in gaining training that will lead to future careers in systematics, paleontology, biodiversity, and information sciences. UCR is a registered minority institution. Undergraduates will be involved directly in research projects, not limited to menial tasks, and where appropriate, encouraged to attend the planned workshops and courses. The PI participants in this program are actively committed to engaging students in a meaningful way that will not only enhance their understanding of phylogeny, morphology, and paleontology but more importantly establish a network that effectively links concepts in evolutionary biology to an understanding of the diversity of insects through time. We believe that these cross-disciplinary interactions will result in invigoration of these fields with new perspectives and encourage novel approaches for both graduate and undergraduate students involved in these projects.

Examples of student/postdoctoral projects: 1) Schulmeister (postdoctoral associate) will carry out research on the higher phylogeny of Symphyta and outgroups using morphology and molecules, and in collaboration with Carpenter on the supermatrix; 2) a postdoctoral associate in Heraty's lab will focus on relationships of Chalcidoidea using morphology and in collaboration with Heraty on a combined morphological and molecular analysis of chalcidoid phylogeny; 3) a graduate student in Engel's lab will work extensively on all groups of Hymenoptera in connection with the coding of paleontological data throughout the order as well as more detailed work on the Aculeata; 4) graduate students in Sharkey's laboratory will focus on studies of the female reproductive system, wing venation and relationships of the Ichneumonoidea; 5) undergraduates will be assigned specific morphological projects involving, for example, SEM surveys of structures or taxa. All studies will include everything from specimen collection, identification, preparation, coding, and data analysis.

Internet sites: Dissemination of information is a priority of this proposal. The PIs have established sites for NSF funded projects (see Prior Results). Initial information for the public will be available through the project web site at www.uky.edu/~mjshar0, www.diversityoflife.org sites and morphbank.net. These sites will be mirrored at the main project institutions. Research exchange will occur through discussion groups and data matrices made available only to participants, but these will be open to the public at the end of the project. See the "Electronic Dissemination" section for more details.

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