



## A Celebration of Systematics

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#### MOLECULES AND MORPHOLOGY IN EVOLUTION: THE CASE OF SUMATRAN AND BORNEAN ORANGUTANS

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The rapidly increasing volume of molecular data in recent years has made it possible to examine on a wider basis the congruity (or the lack thereof) between morphological and molecular findings. The Hominidae traditionally includes *Homo* and four species of great apes: common chimpanzee, pygmy chimpanzee, gorilla and orangutan. Two subspecies of orangutan, Sumatran and Bornean orangutans, are commonly acknowledged. The Sumatran and the Bornean orangutan are morphologically similar and produce fertile offspring in spite of the fact that the difference between the complete mitochondrial DNA (mtDNA) molecules of the two orangutans is similar or even greater than that between several distinct but closely related mammalian species. Thus, the difference between the two orangutans is much greater than that among the harbour, grey and ringed seals, as well as that between the common and the pigmy chimpanzees. The difference is similar to that between the horse and the donkey, and the fin and blue whales, respectively. The mitochondrial nucleotide difference between the two orangutans is about 75% of that between *Homo* and chimpanzee, whereas their amino acid difference is

greater than that between *Homo* and *Pan*. On the basis of comparisons of complete mtDNAs we have recently proposed that the two orangutans should be recognized as distinct species (Xu and Arnason, 1996). The Sumatran and Bornean orangutans are a prime example of a discord between morphological and molecular evolution and demonstrate the potential error in relying on morphological distinction in the fossil record to date species divergences. Relative to their molecular distinction, the osteomorphological difference between the Sumatran and the Bornean orangutans is very limited. The correct timing of their divergence will therefore remain unrecognized in the palaeontological record.

#### PHYLOGENY OF THE TRIBE AESALINI (COLEOPTERA, LUCANIDAE)

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We made a preliminary study of the phylogeny of the lucanid tribe Aesalini (including the genera *Aesalus*, *Echinoaesalus* and *Lucanobium*) on the basis of adult and larval morphologies. The resultant phylogeny shows that the Aesalini is composed of two major lineages: northern and southern Aesalini lineages. The northern Aesalini lineage is composed of two major

lines: a Palearctic *Aesalus* line (containing *A. scarabaeoides*, *A. ulanoskii* and *A. asiaticus*) and a Chinese *Aesalus* line (containing *A. imanishii* and *A. sichuaenensis*). The southern Aesalini lineage contains two major lines: a Himalayan *Aesalus* and a tropical Aesalini line. The former line consists of the *A. himalayicus* complex and the latter consists of two major groups: a bristly tropical Aesalini group (containing Neotropical *Aesalus* members and the south-east Asian *Echinoaesalus matsuii* complex) and a clumpy Aesalini group (containing Neotropical *Lucanobium squamosum* and the south-east Asian *E. timidus-hidakai* subgroup). Their geographical distribution is also discussed.

#### PHYLOGENETIC ANALYSIS OF TOTAL MITOCHONDRIAL DNA IN BIRDS

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We have attempted to resolve some of the higher order relationships of several groups of birds; specifically, the relationships of Galliformes (grouse, quail, turkeys, etc.) and Anseriformes (ducks, geese, swans) to each other and to other avian orders. It is believed that Galliformes and Anseriformes, which each have primitive morphological characteristics, may be sister taxa forming a clade basal to the rest of neognath birds, although morphological evidence alone has not been successful in resolving relationships among these large groups. To address these relatively neglected areas of avian systematics, we sequenced whole mtDNA for many avian groups and several other reptilian taxa to serve as outgroups. Most molecular phylogenetic studies to date have focused on single genes such as cytochrome b (e.g. Murray et al., 1994), often with inconclusive results due to homoplasy in the small data sets. However, preliminary results suggest that

homoplasy does not overwhelm the phylogenetically informative sites when the entire genome is analysed simultaneously. The resulting hypotheses may serve as the phylogenetic context for the further study of genetic, morphological, and behavioral characteristics of birds.

#### MOLECULAR PHYLOGENETIC RELATIONSHIPS WITHIN *PELARGONIUM* SECTION *PERISTERA* (GERANIACEAE): EVIDENCE FOR LONG-RANGE DISPERSAL

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Most *Pelargonium* sections are confined to South Africa, where section *Peristera* is distributed in South Africa, Madagascar, Australia (including Tasmania and New Zealand) and Tristan da Cunha. *Peristera* accommodates 25–30 predominantly weedy, annual herbs which are characterized by small flowers and fruits. Monophyly of *Peristera* as well as (close) relationships with the Australian species have long been questioned but never tested. Phylogenetic analysis of rDNA ITS and trn L (UAA)–trn F (GAA) chloroplast DNA spacer sequences from species of *Pelargonium* section *Peristera*, together with putative outgroups, suggests paraphyly for the section and a close relationship between the highly disjunct South African and Australian *Peristera*. Representatives of *Pelargonium* sect. *Reniformia*, *Polyactium* and *Isopetalum* (the St. Helena endemic *P. cotyledonis*) appear to be nested within the *Peristera* clade. The close relationship between the South African and Australian *Peristera* is interpreted as being not consistent with mid-Cretaceous vicariance, but caused by long-range dispersal to Australia, probably as recently as the late Pliocene.

## SIMPLIFIED ALIGNMENT OF VARIABLE PROTEIN-CODING DNA SEQUENCES

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The use of suitably variable DNA sequences is a prerequisite for molecular systematic studies. The alignment of these sequences must be carried out in a manner that satisfies criteria of homology. However, extreme levels of sequence variation (caused by large sample sizes or sampling across the extremes of divergence ranges or rapidly diverging or evolving sequences) can make the alignment process a difficult one. While the alignment of variable protein-coding DNA sequences can be simplified by converting them into amino acid sequences, this is not possible for non-coding regions or RNA genes. Examples taken from a range of molecular systematic studies are used to highlight alignment problems in a range of sequence types. In particular, attention is focused on a set of intriguing "special case" sequences: sequences composed of repeat units. A grass-specific insert in the plastid *rpoC2* gene is an example of this category of sequence. Using a data set of over 60 *rpoC2* insert sequences, the effects of various alignment methods are demonstrated.

## ROOTING WITH MULTIPLE OUTGROUPS: CONSENSUS VS PARSIMONY

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When exact and heuristic algorithms of parsimony programs such as Hennig86 and PAUP are used, rooting with multiple outgroup terminals yields ambiguous results concerning the basal outgroup nodes and associated character states. This is the case if the ingroup appears either monophyletic or non-monophyletic. The order of the outgroup terminals listed in the data matrix is responsible for these ambiguities. As a consequence, successive analyses using each outgroup as the prime outgroup should be carried out to obtain all equally parsimonious rooted trees. Although the commonest implicit practice is the choice of one outgroup for selecting and orientating the tree, we propose that the strict consensus tree should be used as the only tree resulting from the overall study, even if, as a consensus, this tree is not the most parsimonious.

## TAXONOMIC STUDIES IN ENTOMOLOGY USING CONVENTIONAL MUSEUM SPECIMENS: WHICH SPECIES CONCEPT TO USE?

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Most systematists, particularly entomologists, form large data sets using museum specimens, from which they derive the characters used to distinguish between and determine the limits of species. The data sets are usually comprised solely of morphological (quantitative and qualitative) characters. Although the aim, particularly in revisionary work, is to use as many characters as possible, morphological characters are usually the most feasible. Biological information for most insect taxa, particularly species, is lacking, and thus impossible to use in a taxonomic study. Biochemical and molecular techniques are expensive, often resulting in the destruction of the insect. The loss of a specimen is not appropriate when the species is represented by very few specimens, which is often the case. Certain insect taxa exhibit extreme sexual dimorphism,

for example Mutillidae (Hymenoptera). Morphologically it is not possible to link the sexes of mutillid wasps as the same species unless caught in copula; thus, males and females are described as separate species. A revision of *Tricholabiodes* (Hymenoptera: Mutillidae) was recently undertaken, using pinned specimens, where the separation of specimens into species was based solely on morphological characters. Biological and biochemical characters (cuticular hydrocarbons) were considered but not included in the final data set. Biological information is only available for three species of *Tricholabiodes* while the results from the cuticular hydrocarbon analysis for species tested were too variable. Based on this evidence, the evolutionary species concept is the most appropriate species concept to use in such taxonomic studies.

#### PHYLOGENETIC ANALYSIS OF SHELL-USING BEHAVIOURS IN THE GENUS *LAMPROLOGUS* (PISCES: CICHLIDAE)

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Cichlid fish (*Lamprologini*) from Lake Tanganyika exhibit a suite of unique behaviour patterns associated with the use of snails' shells for breeding and refugia. The evolution of five behaviour traits is examined in nine species. A cladogram was constructed using 28 independent characters: morphological and meristic features, behaviour, colouration and scale patterns. The five behaviour patterns examined were fitted to this tree. Results suggest that: the genus *Lamprologus* is not monophyletic; shell burying appears to have evolved independently on two occasions; shell excavation has evolved in a different lineage to the "buriers"; horizontal shell burying and shell hiding are plesiomorphic character states; shell movement may have arisen twice within the shell users; and hole-dwelling

species evolved from shell users. Phylogenetic distributions of the five behavioural characters and their evolution are discussed.

#### FRANCOLIN PHYLOGENY REVISITED—SEPARATE VS COMBINED EVIDENCE

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We studied 660 base pairs of the mitochondrial DNA cytochrome b gene for 20 species of francolins representing the eight previously proposed species groups as well as two ungrouped Asiatic species. Our data do not support francolin monophyly but reflect the suggested "quail-francolin/partridge-francolin" dichotomy. The partridge-francolins show a close affinity to quails and Euro-Asian partridges (including *Coturnix*, *Margaroperdix* and *Alectoris*). Within this assemblage the validity of Hall's Vermiculated group is not supported. The quail-francolins includes the Asiatic species and is the relatively older group. The merits of a combination of morphological and molecular evidence are discussed.

#### CONSERVATION GENETICS OF THE LOCALLY EXTINCT EGYPTIAN VULTURE

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Mitochondrial DNA cytochrome b gene sequences of Egyptian vultures (*Neophron percnopterus*) were studied to determine the systematic relationships of extinct

populations of this species from South Africa. Analyses of sequences of 480 base pairs from museum and living specimens from throughout the species' range suggest that South African Egyptian vultures are genetically most similar to those from populations in Namibia and are distinct from populations in East Africa and the northern hemisphere. The implications of these results to conservation and local restoration of this species are discussed.

## LOCOBUG: COMPUTER MODELLING ARTHROPOD WALKING TECHNIQUES

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Computer modelling was employed to investigate the walking techniques of extinct arthropods. LocoBug models a generic arthropod body plan when animated by gait parameters that describe the motion of the walking legs. The feasible phase difference between opposite and successive legs may be determined for each gait by analysing the extent of a "stability polygon" joining the legs that are on the substrate at each instant of the step cycle. LocoBug may calculate the speed of the animal and determine the variation in the number of propulsive legs used during the step cycle. Thus the speed:stability relationship may be determined and the most feasible walking techniques for any (extinct or extant) arthropod body plan analysed. LocoBug can also produce a computer-generated trackway, facilitating comparisons with actual fossil trackways (and allowing behavioural variants to be detected) and enabling the producer of the trackways to be assessed with greater certainty.

LocoBug has been applied to a study of eurypterid (sea scorpion) walking techniques. The majority of eurypterid trackways display an opposite arrangement of tracks which indicates that most used in-phase walking techniques. This contradicts previous reconstructions, based on functional studies, which suggested that they moved their legs out-of-phase (as

in the terrestrial arachnids). An analysis with LocoBug indicates that many eurypterids were capable of using in-phase walking techniques at slow speeds. Therefore, most eurypterids walked like *Limulus* and not like the arachnids, suggesting that they were not primarily adopted for excursions onto land. The consideration of biomechanical and behavioural factors can improve phylogenetic hypotheses (e.g. by investigating the locomotory feasibility of hypothetical ancestors or providing an idea of when ecological transitions (e.g. water to land) were possible. Continued work using computer modelling of the walking techniques of other arthropod groups may illuminate their affinities.

## ESTIMATING BRANCH SUPPORT

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One way of quantifying the support for individual branches in trees generated by parsimony analysis is to examine how many extra steps are necessary to lose the branch in the consensus of near-most-parsimonious trees (sometimes called "Bremer support"). A problem with this support measure is that it is difficult to calculate for large data sets. The problem lies in the difficulties of finding and examining all relevant near-most-parsimonious trees among the astronomical numbers of possible trees. The number of near-most-parsimonious trees that it is necessary to examine in order to calculate high support values soon becomes too large to handle. The alternative "converse constraint" approach, where support is estimated as the extra length of the shortest trees not containing a particular group and which requires a search with the most forceful options in order not to give gross over-estimates, is consequently as time-consuming as the original search for the most-parsimonious trees, and has to be repeated for every single group to be evaluated. A radically different possibility, suggested here, is to abandon the search for near-most-parsimonious trees altogether, and examine a large sample of

random trees instead. If the data support a particular group, the mean length of random trees without the group should be longer than the mean length of trees containing the group. Preliminary calculations (using a program written by J. S. Farris) indicate that this difference in length between random trees without and with a particular group may be useful as an estimate of branch support. The length difference is very quickly calculated; however, it is not directly equivalent to branch support. It is influenced by the size of the group to be evaluated, and by other properties of the data.

## THE PURPOSES, FUNCTIONS AND FORMS OF BIOLOGICAL CLASSIFICATIONS

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The purpose of any biological classification is the facilitation of communication about groups of organisms amongst a wide variety of people through the efficient performance of a few basic functions. These functions are the provision of an indexing system whereby information may be retrieved, a device whereby information may be summarized and a device whereby hypotheses about as-yet-unknown information (whether characteristics or taxa) may be formulated. These three functions are maximized using a non-overlapping and hierarchical system of groups.

Usefulness is enhanced if a classification is repeatable (using the same characters), testable (using different character sets), stable with the consideration of new characters and with the incorporation of new taxa, "natural" in both the epistemological and ontological senses, and practical.

The three basic approaches to higher classification, viz. phenetics, cladistics and phylistics (evolutionary classification), differ in the degrees to which they can fulfil the above characteristics of an ideal classification. When scoring these approaches during various

workshops and postgraduate courses dealing with the principles of biological systematics, the phylistic approach was invariably scored highest (best), closely followed by the cladist approach (the major difference being the perception that a strictly cladistic classification is likely to be less stable with the addition of new taxa).

## THE EVOLUTIONARY SPECIES CONCEPT

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In evolutionary biology, including most systematic studies, the basic unit most often used in treating organismal diversity is the species. Unfortunately, most concepts of "the species" which have been proposed are tied to one or a few criteria, most often involving reproductive processes, and generally formulated in operational terms. As a result, such concepts are not applicable to large numbers of organisms, limiting their usefulness. Nevertheless, most workers use a general concept of "species", and most people have a good feel for what is meant, even when dealing with a diversity of organisms, not all of which would fulfil the criteria accepted by those workers. This reinforces the idea that a single concept of "speciesness" would be very useful.

The search for such a single species concept which is applicable across all living organisms is futile, however, unless one is willing to accept an heuristic rather than an operational concept. The evolutionary species concept, which equates species with independent lineages or groups of lineages which have a unitary origin and fate, is such a concept. It can be applied to all living organisms, but its application is certainly not easy in practice since no particular criteria have to be fulfilled for a group of organisms to be considered to comprise a single species. Instead, a series of falsifiable hypotheses must be formulated, involving a variety of processes or conditions which should be expected to

hold if the group represents part of a distinct lineage. Thus, estimation of species limits under an evolutionary concept is likely to be less clear cut than under other (operational) concepts, but is also likely to agree better with the variety of patterns and processes which are observed in nature. Since science aims to estimate the ontological reality of nature as closely as possible, such a concept is probably as close as we are likely to get to a generally applicable one.

### CLADISTIC BIOGEOGRAPHY AND THE HEIRARCHY OF ENDEMISM: FURTHER IMPLICATIONS OF PARALOGY-FREE SUBTREES

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Cladistic biogeographers associate the nodes of cladograms with the geographical distributions of taxa in order to infer the common histories of areas, and then represent that history in branching diagrams (area cladograms). Taxa that are widespread across areas of endemism are equivocal as evidence of area relationships. Nelson and Ladiges have recently presented a definitive method for cladistic biogeography in which they associate nodes with distributions only for paralogy-free subtrees of a cladogram (i.e. subtrees free of geographical duplication). In this paper I present some further implications of biogeographical paralogy. Considering paralogy-free nodes from all possible cladograms, biogeographically coherent nodes find mutual support often; biogeographically incoherent nodes find less support. We are compelled, then, to interpret the universe of paralogy-free nodes parsimoniously, and to infer area relationships directly. I present three tests of this method and show results of an analysis of endemism in Africa.

### ON CONSENSUS, COLLAPSIBILITY AND CLADE CONCORDANCE

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Consensus in cladistics is reviewed. Consensus trees, which summarize the agreement in grouping among a set of cladograms, are distinguished from compromise trees, which may contain groups that do not appear in all the cladograms being compared. Only a strict, or Nelson, tree is an actual consensus. This distinction has implications for the concept of support for cladograms: only those branches supported under all possible optimizations are unambiguously supported. We refer to such cladograms as strictly supported, in contrast to the semi-strictly (ambiguously) supported cladograms output by various current microcomputer programs for cladistic analysis. Such semi-strictly supported cladograms may be collapsed, however, by a variety of options in various programs. Consideration of collapsibility and optimization on multifurcations leads to some conclusions on the use of consensus. Consensus tree length provides information about character conflict that occurs between, not within, cladograms. We propose the clade concordance index, which employs the consensus tree length to measure inter-cladogram character conflict for all characters among a set of cladograms.

### PARAPHYLETIC SPECIES

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We present evidence, mainly from plants, that many recognized species and subspecies are paraphyletic. Whilst some cladists have argued that species are like other taxa, and should be monophyletic, it is clear that even cladists either implicitly or explicitly recognize non-monophyletic species. Moreover, species concepts such as the phylogenetic species concept and the composite species concept predict non-monophyly of many species. Whenever a monophyletic species is circumscribed, it is possible that a paraphyletic or metaphyletic "residual" species is simultaneously recognized. Furthermore, attempts to place all organisms in a monophyletic taxon at every rank regress to the population level where monophyly is no longer applicable, leaving paraphyletic residuals. These groups of organisms can hardly be ignored, unless one wishes to define them out of existence (as in the monophyletic species concept). It has been argued that paraphyly is only an artefact of the Linnaean system, which requires all organisms to be classified in certain ranks, e.g. species. However, the phenomenon of regress shows that this is incorrect, because paraphyly is inherent in species. The solution to this conundrum is to recognize species as special taxa, which may be monophyletic or paraphyletic. (Higher taxa should always be monophyletic, and can be made so.) This requires the acceptance of a species concept that allows paraphyly, such as the phylogenetic species concept or the composite species concept. The monophyletic species concept, which does not allow paraphyly, is not acceptable. The special nature of species derives from their basal position in the phylogenetic system. Theoretically, the proportion of paraphyletic and metaphyletic species may be 50% or higher. Empirical estimates range from 20 to 50%.

See Crisp, M. D., and Chandler, G. (1996). Paraphyletic species. *Telopea* 6, 813–844.

## ROOTS AND ROOTING

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Rooting is a procedure riddled with questions not yet settled, even though the root determines most of the elements considered relevant in cladistic hypotheses, such as synapomorphy and monophyly. This paper reviews the theoretical and methodological aspects of roots and root assignments. Polarity is seen as a corollary of rooting, not its cause. Thus, polarity determination as applied to individual characters (i.e. decoupled from a more general rooting procedure) is incomplete theoretically and, as a consequence, remains a nebulous procedure in practice. The uncertainty stems from a widespread confusion between optimization and directionality, which are different concepts. The outgroup method of polarization is a way to extend the directionality of one network onto another, and has no bearing on the character-state assignment to nodes, which is a non-directional procedure. Outgroups usually do not specify the exact location of the root, only its general region. Combined analyses of ingroup and multiple outgroups cannot provide a directed result for both assemblages at the same time without violating the initial assumption of separation between in- and outgroups. Rooting can be implemented as a hypothetical ancestor treated as an additional terminal during parsimony calculations, and the procedure called "all-zeros outgroup" is shown to be justifiable in some circumstances. Rooting by ontogenetic sequences is the most consistent way to direct dendrograms.

## A CLADISTIC AND BIOGEOGRAPHICAL ANALYSIS OF *BORONIA* SECTION *VALVATAE* (RUTACEAE)

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*Boronia* is the largest genus of Rutaceae in Australia with c. 130 endemic species. Section *Valvatae*, c. 63 spp, is found in most of the recognized major biogeographical areas of Australia, e.g. the Kimberley region



(N.W.A.), the "Top End" of the Northern Territory, Cape York (northern Queensland), south-eastern Australia, and south-western Western Australia. Each geographical area has endemic species, most restricted ranges, and the group therefore is highly suitable for testing biogeographical hypotheses of area relationships. Previous analyses by Weston et al. (1984, *Aust. J. Bot.* **32**, 187–203) show that the group is monophyletic. A cladistic analysis of a subset of taxa representing all species groups within *Valvatae*, and using the other sections of *Boronia* as outgroups, confirms the results of Weston et al. (1984). *Boronia algida* (S.E. Australia), *B. edwardsii* (S.A.) and *B. alata* (coastal SW W.A.) are basal to a clade containing the remainder of *Valvatae* (inland SW W.A., east coast, N. Australia). Synapomorphies for the SW W.A., east-coast and northern Australian clade are the presence of multangular stellate hairs and valvate sepals. This clade is reanalysed using the basal three species of *Valvatae* as outgroups. In the second analysis the inland SW W.A. taxa are monophyletic and sister to the east-coast and northern Australian taxa. The final analysis of all species uses the inland SW W.A. taxa and the other three basal taxa as outgroups. A hypothetical area cladogram for *Boronia* section *Valvatae* is presented, that is, SW Western Australia first differentiated, followed by the differentiation of the east from the north-west. Within the north-west, the Kimberley region differentiated from the Northern Territory; and within the east, N. Queensland differentiated from S.E. Australia.

## A METHOD FOR GROUPING SPECIES FOR CLADISTIC ANALYSIS

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In cladistic studies the objectives of the investigation should be clearly defined, the data analysed relevant to the goal and the methodology properly described in order to make the study repeatable. Missing data, such as sex-limited characters where only one sex is known

or where only damaged material is available for study, and similar species that differ only in the possession of homoplastic character states cause a proliferation of equally parsimonious trees and polytomies. This hinders the interpretation of the analysis. Such difficulties can be overcome by grouping species. Grouping leads to the loss of some data but, if wisely done, the results of the study could be improved. The description of the methods and recording of the data for each taxon which is eliminated when taxa are grouped will make the research repeatable. When the species are grouped, some characters are represented within the group by more than one state. The state of each character chosen as that for the ground plan should be the one that gives the most parsimonious tree, unless there is other evidence to support preference for a longer tree. To obtain the data matrix that will give the shortest tree, each character that is represented by different states in a species group should be considered independently and the state that gives the most parsimonious tree used.

## PARSIMONY JACKKNIFING AND DATA STRUCTURE

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This presentation covers three aspects of the connection between parsimony jackknifing and hierarchic structure. (1) Trees that include poorly supported groups can create misleading impressions, in turn providing seeming support for objections to phylogenetic systematics, for example those by Colless concerning asymmetry of trees. If those groups are removed, such problems vanish. (2) Various methods (Nei's confidence probabilities, Hillis' skewness, Faith's T-PTP) have been proposed for assessing groups and/or general data structure. All can attribute statistical significance to unsupported groups and/or poorly structured data; parsimony jackknifing provides a practical and effective alternative. (3) As has long been

recognized, ambiguity in data is connected to homoplasy and so can often be reduced by successive weighting which, however, is laborious for large matrices. Parsimony jackknifing offers a way to speed up such calculations greatly.

## COMBINABILITY VS CONGRUENCE

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Recent unreleases of PAUP\* have included a "combinability test" that happens to be Farris et al.'s (*Cladistics* 1994: 315) test for incongruence. This is (*inter alia*) a misinterpretation, since incongruence and non-combinability are not the same thing. The idea of testing for non-combinability seems questionable at best. The total evidence approach is wrong, some maintain, because good statisticians would never combine data from different processes. But, in fact, good statisticians do just that all the time, as examples will show. Further, a wrong conclusion is worse than no conclusion, which is actually a reason to combine incongruent data, and examples will show that, too.

## WHICH WAY FORWARD FOR THE RECOGNITION CONCEPT OF SPECIES?

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It has been suggested that systematists should abandon theory-laden approaches towards defining species and rather apply operational definitions which aid a better understanding of wider evolutionary problems.

However, there is a need to have a fundamental understanding of the distinctive characteristics of speciation. If theory-laden approaches have utility in understanding speciation, then operational approaches need to be compatible with the former. The Recognition Concept (RC) is one such theoretical approach. The strength of the RC is the predictions about the communicatory processes preceding fertilization, making the RC eminently falsifiable. Sufficiently detailed experimental evidence suitable for testing these predictions has not commonly been forthcoming, causing the RC to become stagnant as a scientific theory. In addition it appears that, from a theoretical point of view, modification of the RC is required. First, the fertilization system (FS) is a loose collection of phenomena with the fortuitous consequence of enabling fertilization: the RC is thus vulnerable to the same criticisms leveled at the Biological Species Concept. Redefinitions of the roles of the FS and the specific-mate recognition system (SMRS) are required. Second, mechanisms resulting in stasis of the SMRS and those causing change of the SMRS need to be examined in detail. For the RC to live up to its excellent standing as a scientific theory, these issues need to be addressed through theory as well as through experiment.

## THE ABDUCTION OF CLADISTICS

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The strength of cladistics has often been asserted by regarding minimum-length cladograms as having maximum explanatory power and being consistent with Popperian falsification. This conjunction assumes cladograms are explanatory hypotheses, yet falsification via the introduction of characters or taxa is deductive, which conflates hypothesis formation and testing. This problem is alleviated by showing cladistics to be a form of abductive inference. Abduction

promotes parsimony and consilience, but does not suffer the limitations of enumerative induction. I will show that cladistics conforms to Popper's notion of "conjecture", whereas falsification has been misconstrued: the modification of a topology by character/taxon addition simply reflects change in the premises of an abductive argument. The fate of character weighting and confidence measures such as the bootstrap is assessed in light of these considerations.

### GENETIC VARIATION AMONGST FOUR SPECIES OF THE FAMILY MYCTOPHIDAE

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Myctophids are abundant around the southern African coast and comprise a large proportion of the commercial bycatch of pelagic fishes. Given the uncertain future of currently exploited marine resources, myctophid stocks may eventually be targeted directly. In an effort to be proactive in this regard, the generic structure of four myctophid species populations was investigated using starch-gel electrophoresis. This is the first such study on these fishes from the region and, although it was initiated to test the method, interesting data have arisen which contrast with current taxonomic thinking.

### SELF-DEWEIGHTED OPTIMIZATION: TREE SEARCHES AND CHARACTER STATE RECONSTRUCTIONS UNDER IMPLIED TRANSFORMATION COSTS

### Pablo Goloboff

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A way to assess the cost of character state transformations based on congruence is proposed. Measuring the distortion of different transformations with a convex increasing function of the number of transformations, and choosing those reconstructions which minimize the distortion for all transformations, may provide a better optimality criterion than the lineal functions implemented in currently used methods for optimization. The consequence of optimizing (and selecting) trees on the basis of such a measure is that transformation costs are dynamically determined during the reconstruction. Unlike other methods proposed to solve this problem (TSA, dynamic weighting), the present method is not iterative, avoiding the concern of different final results for different starting points, and it has a more explicit optimality criterion. The computational cost of evaluating trees according to convex increasing functions of state transformations is very high. Algorithms that may lessen those computations are described, and are implemented in an MS-DOS prototype program, which can search for optimal trees using SPR branch-swapping and multiple addition sequences.

### HIGHER CLASSIFICATION OF THE ARANEOMORPH SPIDERS

### Charles Griswold

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The spider infraorder Araneomorphae comprises more than 30,000 described species, with perhaps twice that number to be described. The problem of estimating the phylogeny for such a large group was simplified by choosing two types of exemplars: (1) groundplans optimized after lower level cladistic

studies; and (2) taxa retaining primitive characters. The relationships among and within most major araneomorph clades were examined, including Palaeocribellatae, Neocribellatae, Araneoclada (including Haplogynae and Entelegynae), Eresoidea, Orbiculariae, Lycosoidea, Dictynoidea and Amaurobioidea.

### THE GUINEA-PIG IS NOT A RODENT: ICONOCLASTIC MOLECULAR DATA VS THE REST

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The Guinea-pig has become a topic of contention because of its anomalous phylogeny. Classic concepts of rodent monophyly have been strongly questioned by the authors and others, and now have been supported by significant amounts of new molecular data. Are morphological characters no longer sufficient to define a topology? A brief review of the debate will be presented, together with a summary of the molecular support for current topologies. A paradigm shift to genome comparisons will be discussed.

### THE PHYLOGENY OF EUTHERIANS, MARSUPIALS AND MONOTREMES

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It is commonly acknowledged that the evolutionary relationship among three main mammalian groups,

monotremes, marsupials and eutherians, has been conclusively resolved by means of traditional approaches. An early divergence of the monotremes is generally postulated on the basis of synapomorphic characters shared by marsupials and eutherians. This traditional view is known as the Theria hypothesis. Based on morphological comparisons, only few publications have questioned this relationship in favour of a sister-group relationship between marsupials and monotremes, i.e. the Marsupionta hypothesis. The complete mitochondrial genome (16,896 nucleotides) of the wallaroo (*Macropus robustus*) was sequenced. The concatenated amino acid sequences of twelve protein-coding genes of the mtDNA of the wallaroo and several other mammals were included in a phylogenetic analysis of early mammalian divergences. Consistent with the Marsupionta hypothesis, the analysis joined monotremes and marsupials to the exclusion of eutherians. The analysis significantly rejected the commonly acknowledged Theria hypothesis, according to which Marsupialia and Eutheria are grouped together to the exclusion of Monotremata. Thus, the most ancient divergence among extant mammals is that between Eutheria and the lineage leading to Marsupialia and Monotremata. According to calculations based on amino acid distances the divergence between Eutheria and the Monotremata/Marsupialia took place *c.* 130 MYBP (million years before present). The same approach suggests that Monotremata and Marsupialia diverged *c.* 115 MYBP and that Australian and American marsupials separated *c.* 75 MYBP. The findings show, furthermore, that many, probably most, extant eutherian orders had their origin in the middle to late Cretaceous, 115–65 MYBP.

### MOLECULAR PHYLOGENY OF DUIKER ANTELOPE

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Duikers constitute a distinct tribe within the Bovidae. The Cephalophini is currently regarded as

comprising the monotypic *Sylvicapra*, the Gray duiker (a grassland specialist) and the species *Cephalophus*, which includes all forest duikers. A third genus, *Philanthomba*, is sometimes recognized for the blue and Maxwell's duikers. Phylogenetic information based on seven of the 19 duiker species will be presented. Sequence data from two mitochondrial DNA genes (cytochrome b and 12S rRNA) were analysed separately as well as in combination. The sequence data support the recognition of the blue and Maxwell's duikers as sister taxa. Additionally, the bay and yellow-backed duikers cluster together to the exclusion of the red duiker. Based on morphology, these three species were thought to belong to the same species group. The data suggest that *Cephalophus* is paraphyletic as is evidenced by the clustering of *Sylvicapra* within the *Cephalophus* clade and the grouping of *C. leucogaster* with *Philanthomba*. These relationships indicated by mitochondrial DNA gene sequences are further supported by fluorescence *in situ* hybridization (FISH).

## METHODOLOGICAL PROBLEMS IN GREEN PLANT PHYLOGENY

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Methods for obtaining nucleotide sequence data have become more efficient, and sequence data for green plants are now extensive and rapidly increasing. However, most methods of phylogenetic analysis have not kept pace, and the time needed to analyse the ever-larger data matrices has increased disproportionately. Proposed solutions to this problem have included: (1) using just small samples of available taxa to save time; (2) eliminating third codon sites to make structure more obvious; and (3) eliminating transitions for the same reason. Our examples, drawn from analyses

of a large *rbcl* data set and several subsets, suggest that all these suggestions involve risks. More than 2500 *rbcl* sequences have been obtained from Genbank and through the courtesy of several of our colleagues. The sequences span over a wide taxonomic range including cyanobacteria, green algae, bryophytes, ferns, conifers, cycads, Gnetales, and more than 400 angiosperm families. Several analyses were performed using parsimony jackknifing, using all characters, or 1st and 2nd positions only, or transversions only. Our results show that, for *rbcl*, using all available information gives a better-resolved tree, with more well-supported groups. Removing third positions, or transitions, results in dramatic loss of resolution. A tree based on third positions only is almost as resolved as one based on all positions. Adding taxa generally adds support to the tree and only rarely causes groups to "disappear", whereas too small samples of taxa often give misleading results.

## TESTABILITY AND RESEARCH CYCLES: CONSEQUENCES FOR WEIGHTING

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Cladistics is described in terms of Popperian testability and those research cycles that lead to increases in knowledge of sister-species relationships and character generality. The labels "a priori" and "a posteriori" that are attributed ordinarily to character weighting lose their meaning when cladistics is understood as a research cycle. Further, character weighting can play no direct role in assessing degree of corroboration of cladograms if testability is to retain its refutationist nature. Verificationism can be avoided if weighting is limited to character (re-)analysis, which can lead to informed, "traditional", views of characters as evidence.

## THE MECHANISM OF SPECIATION

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A major biological problem is how the continuous process of evolution produces the morphologically discontinuous groups known as species. Once formed, species tend to remain phenotypically stable for geologically long periods of time, sometimes through such intense climatic changes as glacial cycling. When phenotypic change occurs it tends to be palaeontologically abrupt, again producing phenotypic gaps, but not between successive species. A surprisingly simple mechanism might explain both phenomena. Since, by definition, fit traits replace less fit traits, fit traits tend to become common, while maladaptive traits tend to develop low to very low allelomorph frequencies. Sexual creatures would therefore be expected to prefer mates sporting predominantly common features. This is termed koinophilia. When two polygenic traits initially formed independent, continuously variable, phenotypic clines on a continuous resource gradient, a stochastic computer model of koinophilia invariably caused the *de novo* evolution of distinct morphospecies, separated by prominent phenotypic gaps, involving both traits, under a wide range of selection criteria. Koinophilia reproductively isolated the morphospecies one from the other, suggesting that this might be the crucial first step in the development of other barriers to hybridization. The rapidity with which koinophilia canalized the initial continuum of interbreeding phenotypes into reproductively isolated species, and its subsequent defense of those phenotypes against invasion by unusual or unfamiliar phenotypes, might be a paradigm of evolutionary punctuated equilibria (Koeslag, J. H. (1995). *J. Theor. Biol.* **177**, 401–409).

## SPECIES AS PARAPHYLETIC GROUPS OF INTERNODONS

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For a sensible discussion of species and higher taxa as paraphyletic and monophyletic groups, it is necessary to indicate of what entities these groups consist. Using the composite species concept, for example, a species is simultaneously a polyphyletic group of organisms, a paraphyletic group of internodons, and—if it has no descendent species—a monophyletic group of species. It is fruitful to interpret higher taxa as monophyletic groups of species, since we require them to form a nested hierarchy. In contrast, we require species not to be nested but to be mutually exclusive. Therefore, it is counterproductive to interpret species as monophyletic groups of either organisms, internodons or populations: this would portray descendant species as nested within ancestral species. The unwarranted extension of the demand that higher taxa should be monophyletic groups of species to the demand that species should be monophyletic groups of subspecific entities has led to the denial that ancestral species exist. In the composite species concept, ancestral species do exist, albeit as historical entities rather than as individuals. Provided that we recognize the paraphyletic nature of species, reconstruction methods are not threatened by the existence of ancestral species.

## ASSESSMENT OF INFLORESCENCE CHARACTERS FOR PHYLOGENETIC ANALYSIS IN EPACRIDACEAE

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Characterization of inflorescences was considered in the context of a cladistic analysis aimed at testing the generic boundaries between *Andersonia* and *Sprengelia* (Epacridaceae). *Andersonia* has been divided into two

sections on the basis of flower position—axillary and subtended by two bracteoles, or terminal subtended by a series of “bracts and bracteoles”. However, the current treatment of two species is inconsistent with the precept on which this division is based. The question of the homologies of the structural elements had never been addressed, and assessment of the validity of sub-generic division depended on these homology relationships. In the process of analysis, terms commonly employed in inflorescence description proved inadequate and confusing. Some were found to be used so loosely as to render them almost meaningless. Other common terms are questionable for use in cladistics because of their foundation in theory which runs directly counter to that of phylogenetic analysis. In the case in hand, this necessitated a complete reassessment of inflorescence structure in *Andersonia*. The terminology of Briggs and Johnson (1979), although incomplete, was used, as it represents a starting point for a rigorous terminology. The methods of cladistic analysis imply a rejection of typological methods of inflorescence analysis and suggest it may be necessary for cladistics to part from some of the general terminology used for describing inflorescences.

## SUPPORT, RIBOSOMAL SEQUENCES, AND THE PHYLOGENY OF THE EUKARYOTES

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Large ambiguous data sets may have many most-parsimonious trees, and finding them all may be impossible given current computational limitations. This problem clearly exists when trying to estimate relationships among distantly related organisms such as in studies trying to uncover the phylogeny of all eukaryotes using molecular sequences. Some workers

using the small subunit ribosomal RNA sequences limit their studies of eukaryotic kingdoms to no more than 35 species at a time because of these constraints. We report on using a different approach—parsimony jackknifing. This procedure uses jackknife resampling to search rapidly for shortest trees and avoid arbitrary branch-swapping. The method allowed us to analyse all 440 eukaryotic taxa in the Ribosomal Database (University of Illinois). The results indicate that many phylogenetic proposals based on analysis of the small subunit sequences are poorly supported or contradicted. For example, there is no evidence for a crown group of multicellular eukaryotes or for an intermediate grade of unicellular forms.

## THE PHYLOGENETIC POSITION OF *PRIONIUM* (JUNCACEAE) WITHIN THE ORDER JUNCALES: TESTING INCONGRUENCE

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We investigate the problem of conflicting phylogenetic signal in the Juncales through an examination of the position of *Prionium*. While the genus has always been included in Juncaceae, *rbcL* sequence data indicate that *Prionium* is basal to Cyperaceae plus Juncaceae. Our trees, based on morphological and *rbcL* sequence data, support this position for *Prionium*. There is also conflict in the placement of two juncaeous genera, *Oxychloe* and *Luzula*. In the morphological tree *Oxychloe* is placed within Juncaceae, while in the *rbcL* tree it is within Cyperaceae. *Luzula* is basal to Cyperaceae in the morphological tree, whereas it is unresolved in the *rbcL* tree. Conflict between the two data sets was investigated by determining the frequency retrieval of the conflicting node in a set of 100 morphological bootstrap replicates for the position of the node in the *rbcL* topology and *vice versa*. This method suggests that the conflict associated with *Oxychloe* may be real, whereas that linked to

*Luzula* is due to chance. A jackknife was executed on a combined data set including *Oxychloe* to investigate the effect that *Oxychloe* had on tree parameters. The exclusion of *Oxychloe* had no effect on tree length or retention index (RI). Successive taxa were pruned from the morphological tree using the rbcL character set and similarly for the rbcL tree using the morphological character set. The pruning of *Oxychloe* from both trees decreased the tree length by 46 and 13 steps respectively and increased RI. *Oxychloe* was excluded from the morphological and rbcL data sets and they were combined. In the resulting topology *Prionium* was basal to Cyperaceae plus Juncaceae, while *Luzula* was unresolved. The monophyly of Juncaceae is not corroborated by the morphological tree, the rbcL tree, nor the combined tree. The basal position of *Prionium* is supported by several unique features and it is suggested that *Prionium* should be elevated to family status.

## ALEOCHARINAE CLADISTICS (COLEOPTERA, STAPHYLINIDAE)

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The rove beetles, family Staphylinidae, is a family of insects with seemingly endless numbers of species occupying most terrestrial and arboreal habitats of the world. The largest subfamily, Aleocharinae, is notoriously difficult taxonomically. Relatively few scientists have worked on this group and most of them within only a limited faunal region. Largely because of this, numerous genera have been and still are described, although the monophyly of the existing ones is entirely untested and even the tribal classification remains artificial and chaotic. This was the first attempt to search for expressly monophyletic groups within the subfamily. The main goal was to evaluate the monophyly of the largest aleocharine tribe, Athetini. About 51 tribes and some 650 genera have been included in the

Aleocharinae. In the analysis I used 87 binary characters from 41 genera. Twelve tribes were included in the analysis: Aleocharini, Athetini, Corotocini, Dorylominini, Falagrini, Homalotini, Hoplandrini, Myllaenini, Oxypodini, Termitodiscini, Termitohospitini, and Zyrsini. The genus *Oxypoda* was used as the outgroup. Hennig86, NoNa and Clados were used for obtaining the cladograms and/or studying unambiguous branch support and optimizing characters. Four minimum-length trees of 334 steps (CI=0.26, RI=0.46) were obtained. They differed from each other in minor details in two apical clades. The results suggested that only three tribes were monophyletic, Aleocharini, Homalotini and Corotocini. Three tribes, Oxypodini, Falagrini and Zyrsini, were polyphyletic, and two tribes, Athetini and Hoplandrini, turned out to be paraphyletic. The remaining four tribes, Myllenini, Termitohospitini, Termitodiscini and Dorylominini formed, together with Zyrsini and Hoplandrini, a clade that had its sister group within the tribe Athetini. These preliminary results reinforced the view that the present Aleocharinae classification is largely unnatural. Although far-reaching conclusions must not be made on the basis of this still-limited sampling effort, a few potentially important results deserve to be pointed out. First, the paraphyly of the huge tribe Athetini appears to be fairly well established. Second, the result of all the myrmecophilous and termitophilous Aleocharinae form a monophyletic group that has evolved from Athetini ancestors suggests very interesting evolutionary and biogeographical implications.

## PHYLOGENETIC RELATIONSHIPS OF BARBUS AND PSEUDOBARBUS OF SOUTHERN AFRICA USING KARYOLOGY DATA

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A chromosome study was carried out on 16 species of *Barbus* and six species of *Pseudobarbus* (Pisces: Cyprinidae) from southern Africa. Chromosome number and arm number (NF) were recorded and karyotype morphology described for all species. Chromosome complements of different species indicate at least three ploidy levels, i.e. diploidy (2n), tetraploidy (4n) and hexaploidy (6n). Based on the proportion of uniarms to biarm chromosomes the karyotype morphology of the barbine species can be grouped as having asymmetrical or symmetrical karyotypes. For instance, all four species of the *Barbus anoplus* complex have symmetrical karyotypes characterized by approximately equal numbers of uniarms and biarm chromosomes. The results indicate that karyotype morphology coincides well with the biogeographical temperate and sub-tropical (Zambezi) regions. A phylogenetic tree was constructed using traditional morphological characters and tested against karyological data. The results show that similar ploidy states do not necessarily indicate close relationships between species. This supports a hypothesis of polyphyly of the African barbine cyprinids as well as providing independent karyological support for species/genus complexes such as the *Barbus anoplus* complex (2n), the *Barbus andrewi*, *Barbus serra* complex (4n), the yellow-fish group (6n) and the *Pseudobarbus* lineage (4n).

## HOPEFUL AND REAL SEED PLANTS OR CODING OBSERVATIONS IS BETTER THAN CODING PHYLOGENETIC HYPOTHESES

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Recent morphological and molecular cladistic analyses of seed plant relationships have resulted in considerable controversy, particularly focused on the question of the monophyly of the "gnetopsid" clade. We propose that the question of whether the gnetopsids form a clade has been over-emphasized. Of greater

interest is the overall structure of the trees. A clade that excludes cycads, with the form (Ginkgo (conifer(gnetopsid(angiosperm is present in the morphological analyses of Loconte and Stevenson and Nixon et al., as well as recent analyses of rbcL, rRNA and combined total evidence analyses. This clade is characterized by simple leaves, axillary branching, and seeds borne on axillary structures. Of the several analyses by Doyle and Donoghue, only their most recent analysis supports the (Ginkgo(conifer(gnetopsid(angiosperm clade. Their previous disparate results are attributable to the incorporation of phylogenetic hypotheses into coding of cycads and various fossil taxa. They also selected more recent equivocal fossils instead of older unequivocal fossils to establish some of these hypotheses. Although their latest analysis was more congruent with those of others, it still suffers dramatically from the same problems. Monophyly of some extant groups such as conifers was assumed by Doyle and Donoghue: an assumption that led to further assumptions in terms of polymorphic and pleisiomorphic states. The reproductive morphology of the gnetopsids has been over-simplified in such a way as to support wishful hypotheses on the reproductive morphology of a gnetopsid–angiosperm clade. In our most recent analyses, the simple-leaved clade also lacks the "cycadeoids" or bennititalean fossil taxa which have primate leaves, uncertain attachment of the seeds, and have not been definitely established to have axillary branching. In contrast, the analyses of Doyle and Donoghue emphasize the cycadeoids as important in understanding the "anthophyte" clade. Instead, we find the cycadeoids are more parsimoniously placed near the cycads as in the more traditional treatments by practicing morphologists of the past.

## CHALLENGES TO SCORPION CLADISTICS: EFFECTS OF SEX, SEGMENTATION AND PSAMMOPHILY

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Phylogenetic analysis of scorpions is complicated by effects of sexual dimorphism, metamerism and psammophily. Sexual dimorphism creates difficulties in cases of intersexual niche divergence, when the same characters are observed to exhibit different states in the sexes. They must be therefore scored twice, as distinct from the situation in which characters observed in the sexes are mutually exclusive. This problem is not analogous to the issue of polymorphic taxa, in which states of the same character are treated as inapplicable/missing. In cases of sexual dimorphism, treatment as missing data results in the potential exclusion of phylogenetically important information and exclusion of much of the data set. The question therefore becomes one of combined vs separate analysis of the data sets obtained for both sexes or downweighting of dimorphic characters. Metamerism, characters repeated across segments, creates difficulties when characters vary spatially across segments and among taxa. In such situations, each segment is scored as a multistate character. However, since such characters are clearly linked, repetition is introduced into the analysis. Repetition is compounded when metameric characters are also sexually dimorphic. Separate vs combined analysis and downweighting of repetitious characters are among the options for dealing with this repetition. Psammophily, or ecomorphological adaptation of life on/in sand, involves the evolution of characters that facilitate locomotion and burrowing, including the loss of characters found in non-psammophilous taxa. As character loss generally involves metameric characters, cladistic analyses are confounded through the introduction of many absences. This can lead to pseudo-parsimonious trees with artificial clades dominated by psammophiles. The problem may be obviated by coding absences as inapplicable/missing data, thereby rendering them neutral. In a phylogenetic analysis of the southern African burrowing scorpions (Scorpionidae: *Opisthophthalmus*), separate analyses of male and female data sets were conducted, and the data were analysed in combination, with and without downweighting. Metameric data were analysed with and without

downweighting. Psammophilous "absence" characters were analysed coded as zeros or inapplicable/missing data. Combined data, without downweighting, in which psammophilous "absence" characters were coded as inapplicable/missing data, produced the most informative result biogeographically and are probably less vulnerable to the effects of convergence. Repetitious sexually dimorphic and metameric characters do not "swamp" non-repetitious characters. A combined approach, without downweighting, is advocated in phylogenetic analyses of taxa for which the majority of characters are sexually dimorphic and metameric. "Absence" is to be avoided as a character and, preferentially, treated as inapplicable.

#### PARALLEL CLADOGENESIS, COEVOLUTION AND SEQUENTIAL EVOLUTION IN INSECT-PLANT ASSOCIATIONS: A TEST CASE

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Parallel cladogenesis is rare in insect-plant associations, but few analyses of phylogenetic congruence in these interactions have been conducted. Two conflicting theories have been proposed to account for the evolution of insect-plant associations: escape-and-radiation coevolution postulates that diversification and divergence in plants and phytophagous insects are brought about by reciprocal selective pressures, whereas sequential evolution proposes unidirectional adaptive radiation of an insect lineage subsequent to diversification of its host plants. Parallel cladogenesis is predicted by both theories, hence evidence of reciprocal selective influence must be produced for coevolution to be inferred; where this is absent, sequential evolution may be inferred. This

study was undertaken to assess congruence between putative phylogenies of cephaline leafhoppers (Homoptera: Cicadellidae) and their host plants, the Restionaceae, as a test of the above hypotheses. TREEMAP was employed for reconstructing all optimal scenarios of parallel cladogenesis. These optimal reconstructions postulated an equal number of cospeciation events, but differed in the number of host-transfers, independent speciations, and sorting events. Since TREEMAP provides no option for dealing with widespread species, analyses were conducted with and without Assumption 2. In both cases, the number of cospeciation events postulated was not significant. Phylogenetic covariance probability (PCP) was also computed, and the number of steps was not significant. Coevolution is therefore falsified, and sequential evolution suggested as a plausible evolutionary scenario, given the evidence of parallel diversification and phylogenetic conservatism in the association. In this proposal, partial parallel cladogenesis may be the outcome of counter-adaptation by the leafhoppers to novel attributes that may have evolved incidentally on the part of the plants.

### THE SPHECID WASP GENUS *GASTROSERICUS*: A WORLDWIDE REVISION AND ITS RAMIFICATIONS

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The wasp genus *Gastrosericus*, now known to include 61 species, ranges from South Africa to the Mediterranean Sea, east to Vietnam. Tropical Africa is the center of species diversity. One unusual feature of the genus' biology is the ability to collect species of various insects and even spiders as prey for the larva. The cladistic analysis, although partly unresolved, indicates that the highly derived *attenuatus* and *lamellatus* (a pair of sister species) are descended from the genus' basal stock. The

former species occurs north and the latter occurs south of the Congo Basin, and it is likely that they evolved from their common ancestor when its range became divided by the large Tertiary lake that filled the Congo basin.

### MOLECULAR PHYLOGENIES AND EVOLUTIONARY SPECULATIONS FOR THE POTYVIRIDAE AND GEMINIVIRIDAE

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The Potyviridae and Geminiviridae are the two best-studied taxonomic groups of plant viruses in terms of amount of sequence information available for their members: upwards of 50 partial and many complete genomic sequences have been obtained; by far the largest database(s) of plant virus sequences currently extant. The two virus families are also possibly the most significant in terms of economic importance/crop damage, meaning information on their variation may be of considerable agricultural importance. They differ significantly in their nature, as Potyviridae have filamentous particles and linear ssRNA genomes of  $\pm 10$  kb, while Geminiviridae have geminate spherical particles and circular ssDNA genomes of 2.5–5.4 kb. Three genera of Potyviridae are non-obligately insect- or arthropod-vectored (Poty-, Rymo- and Ipomoviruses), while Geminiviridae are obligately vectored by a single whitefly species, or by leafhoppers and a treehopper. Multiple sequence alignment and phylogenetic analysis has shed much light on relationships within the families, which has been of great taxonomic benefit, as well as on possible evolutionary scenarios which may have led to the diversity we see today. For instance, there is evidence in both families of "explosive radiation", perhaps in synchrony with plant host and/or vector species; moreover, evolutionary bottlenecks appear to have played a significant role in the evolution of Subgroup III Geminiviridae. Sequence

analysis has been of great value in determining that even viruses with different numbers of genome components obviously belong together in a taxonomic family due to the preponderance of shared characteristics. The merits and demerits of various phylogenetic analysis methods were discussed, and their use in practical identification schemes highlighted.

## TAXONOMIC INCONGRUENCE—A CASE IN POINT FROM PLANTS

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Molecular sequences and phylogenetic hypotheses accumulate at a constantly increasing rate. In some groups, hypotheses based on several different genes and morphologies are available. The hypotheses based on individual sets of information are often in conflict. Despite strong theoretical arguments in favour of a total evidence approach, taxonomic congruence may still provide useful information. A case in point is given from an analysis of a number of plastid genes, a nuclear gene, and morphology in the grass genus *Psathyrostachys*.

## RANDOM CLADISTICS: NEW FRONTIERS IN MOLECULAR PHYLOGENETICS OR OLD HAT?

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The latest installment of Random Cladistics (The Ohio Edition) remains free of charge. Executables in the package allow phylogeneticists to perform a variety of popular and unpopular data perturbation strategies without the requirement for a Macintosh operating system. Bootstrapping, taxonomic jackknifing, tests of data set combinability, matrix compression routines, random taxon addition sequences and other pre-existing algorithms remain. New algorithms included in HeyJoe permit determination of the effects of random deletion of characters or of scopes of characters, and random weighting of characters on finding monophyletic groups. New algorithms, in MooToo and MoJo, assess the effects of the introduction of noise on phylogeny reconstruction. The finding that the results of most of these routines are strongly correlated suggests that there is nothing particularly special about the bootstrap, save that Felsenstein thought of it first, and that equally arbitrary ways of insulting data sets can be conceived of. Whereas these methods can be "interesting", phylogeneticists should once again be admonished to abandon neojustificationist statistical interpretations.

## PHYLOGENETIC AND GEOGRAPHIC ORIGINS OF THE DEVASTATION OF ATLANTIC OYSTERS: PHYLOGENETICS AND THE ECOLOGICAL HOT ZONE

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Until the late 1950s the oyster *Crassostrea virginica* was a plentiful resource in the Chesapeake and Delaware Bays. Reefs of oysters used to break the surf at low tide and hundreds of millions of bushels were harvested yearly without compromising stock levels. In 1958 oyster levels started on a 4-decade decline. The oystering industry, once the mainstay of watermen, is all but dead, oyster reefs and the fauna they supported are

scarce and the time taken for the Bay to be naturally filtered has increased from 7 weeks to 7 years. The principal causes of this devastation are two protistan parasites: *Haplosporidium nelsoni* and *Perkinsus marinus*. Field studies show that, on average, over 95% of market-size oysters are decimated each year from these parasites. Well-corroborated hypotheses regarding to what other protists these parasites are related are a prerequisite for designing disease intervention strategies and for determining the ultimate source of the problem; yet the uniqueness of their morphological characters precluded any reasonable hypotheses for the Haplosporidia and was misleading for *Perkinsus* species. Use of 18S rDNA and actin gene sequences show that both parasites are related to the ciliates/dinoflagellate clade. The Haplosporidia represent a phylum in their own right whereas *Perkinsus* species are parasitic dinoflagellates. Moreover, subsequent investigations, predicated on these phylogenetic determinations, have shown that the most lethal of these, *Haplosporidium nelsoni*, arrived in the Chesapeake Bay with the clandestine introduction of Japanese oysters. Concerns regarding introducing exotic taxa should not be limited to over-growth issues—in this case the parasite got loose.

## WHS-WWW: THE HENNIG SOCIETY ON LINE

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In September of 1995 the Hennig Society went on line and interactive on the World Wide Web at <http://www.vims.edu/~mes/hennig/> This new resource was exploited in order to facilitate ease of communication and dissemination of information through electronic media. The design of the web site has been and remains the presentation of the Society's priorities, events, personalities and mandate in a visually pleasing and contemporary manner. In the first year the web site has received thousands of internet "hits". The

pages are continually modified and improved to include the most up-to-date information and to avail ourselves of the most recent technology. This has included the development of Javascript enhancements, animated images, full colour renderings, a directory of Fellows and Members, meeting proceedings and participants, access to search engines, lists of courses in phylogeny and systematics worldwide, and up-to-date information about these meetings, all at the touch of a mouse button. The WHS now also has an anonymous ftp site for the free exchange of software and data at <ftp://ftp.vims.edu/pub/hennig/>

## PHYLOGENETIC ANALYSIS OF AFRICAN PISAURINE NURSEY WEB SPIDERS, WITH REVISION OF *TETRAGONOPHTHALMA* AND *PERENETHIS* (ARANEAE, LYCOSOIDEA, PISAURIDAE)

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The nursely-web spiders (Family Pisauridae) currently contain 54 nominal genera, many of them only poorly known. Members of the family are distributed worldwide, displaying great variations in habitus, size and life style. Several genera contain large species (up to 30 mm body length) hunting on the surface of freshwater (e.g. members of the world-wide genus *Dolomedes* and the Africa-Asian genus *Thalassius*), or hunt in trees like spiders of the African genus *Tetragonophthalma*. Other genera contain small spiders (body length 3–4 mm) hunting on permanent webs, (e.g. in the American genus *Architis*). No apomorphies are known to suggest monophyly of the family, but at least two monophyletic clades can now be distinguished. One group of 18 pisaurid genera, the Pisaurinae, are here recognized as a monophyletic clade and their apomorphic characters, mainly based on copulatory organs, are discussed. Within the Pisaurinae, the genera *Charminus*, *Cispius*, *Tetragonophthalma*, *Afropisaura*, *Perenethis*, *Maypacijs*, and *Polyboea*

form a monophyletic group, here called *Perenethis* genus group. A cladistic analysis of the *Perenethis* genus group is presented ((*Charminus*+*Cispius*) ((*Afropisaura*+*Tetragonophthalma*) (*Perenethis* (*Polyboea*+*Maypaci*))))). The distribution of members of the *Perenethis* genus group is noteworthy. *Charminus*, *Cispius*, *Afropisaura*, *Tetragonophthalma* and *Maypaci* are restricted to Africa, the currently monotypic genus *Polyboea* to Asia, and the genus *Perenethis* is widely distributed in Africa, Asia, and Australia. The Afro-Asian distribution of members of the clade *Polyboea*+*Maypaci* and the *Perenethis* clade is hypothesized to be the result of independent range extensions during the expansion of suitable habitats between the Miocene and the beginning of the Pleistocene.

#### PHYLOGENETIC AFFINITIES OF THE FRUITCHAFER GENUS *RHINOCOETA* (COLEOPTERA: SCARABAEIDAE), BASED ON LARVAL CHARACTERS

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Beetles of the fruitchafer genus *Rhinocoeta* are recognized as being relatively primitive, but there is disagreement over whether they represent part of the relatively ancestral subtribe Xiphoscelidina, or lie near the root of the advanced subtribe Cetoniina. Cladistic comparison of 50 larval characters of *R. sanguinipes* with those of a member of the Cetoniina and two other tribes confirms that species as the most plesiomorphic of the sample, while numerous synapomorphies unite the other tribes. The representative of the Cetoniina is the most phylogenetically derived taxon. This suggests that *Rhinocoeta* belongs to the subtribe Xiphoscelidina

rather than the Cetoniina, as part of a relict lineage derived directly from the most primitive Cetoniinae.

#### A MOLECULAR PHYLOGENY FOR WOODHOOPES (BUCEROTES: PHOENICULIDAE) USING DNA FROM MUSEUM SPECIMENS

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The woodhoopes are a group of coraciiform birds endemic to sub-Saharan Africa and closely related to the more widespread hoopoe, *Epupa epops*. Relationships within the Phoeniculidae are poorly understood, with seven to eight species and one to three genera recognized. The family was recently split in two on the basis of DNA–DNA hybridization data suggesting the existence of two monophyletic groups, the scimitar-bills (Rhinopomastidae) and the woodhoopes (Phoeniculidae). For this study, total genomic DNA material from all 23 species and subspecies of woodhoopes/scimitar-bills has been extracted from a combination of fresh, ethanol-preserved and feather samples. In order to infer a molecular phylogeny for the group, a 300–700 base pair section of the mitochondrial cytochrome b gene (depending on preservation constraints) has been amplified using PCR and sequenced directly. Although sequence data have so far been obtained for only five of the eight species, they suggest a deep divergence between scimitar-bills and woodhoopes. There is also evidence supporting the specific status of the Violet Woodhoopoe (*Phoeniculus damarensis*), often considered a subspecies of the Green (Redbilled) Woodhoopoe (*Phoeniculus purpureus*). A preliminary phylogeny for the woodhoopes is inferred using the hoopoe as an outgroup.

## PHYLOGENETICS OF THE MONOCOTYLEDONS

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We report preliminary results of a phylogenetic analysis of the monocotyledons. The study is based upon variation in four character sets, these being a set of "morphological" characters (i.e. morphological, anatomical, embryological, palynological, developmental, and phytochemical characters) and three molecular character sets. The three molecular data sets in the restriction site vary in the inverted repeat region of the chloroplast genome, and nucleotide sequence variation in the chloroplast-encoded gene *rbcL* and in the mitochondrion-encoded gene *atpA* (the latter of which codes for the alpha-subunit of ATP synthase). The mitochondrial genome has been used in studies of many animal groups, and the plastid genome, and *rbcL* in particular, have been widely utilized in plant systematics, but there have been few previous analyses based on the plant mitochondrial genome. *atpA* is approximately the same length as *rbcL*, and for the taxa for which we have parallel sampling of all four data sets, *atpA* exhibits about half as many informative characters as *rbcL* per nucleotide site examined. The *rbcL* data set includes a greater number of informative characters than the sum of the other three data sets, and also the lowest CI, RI, and Data Decisiveness, in both simultaneous and separate analyses. Previous disparate results in topologies between *rbcL*-based data sets and morphological data sets and the combination of the two result in part from the use of non-parallel data sets. In the *rbcL* data set, each terminal is a single species considered for purposes of analyses to represent a higher taxon. In morphological data sets, the various sources of data, e.g. embryological, anatomical, etc., are rarely from the same species.

Thus, the terminal is a synthetic taxon made up of data from several species in a genus or several genera in a family. Problems in the scoring and sampling have been tested with respect to the increased number of missing values and increases in subset polymorphisms. Of particular interest is the various placement of problematic terminals such as *Hanguana*. These terminals have a single position in the trees derived from each data set, but the position varies between data sets (e.g. as sister group to the Zingerbales in the morphology analysis and as sister group to the palms in the *rbcL* analysis).

## CHROMOSOMAL POLYTYPY IN SOUTHERN AFRICAN RODENTS: IMPLICATIONS FOR SPECIES CONCEPTS

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This study reviews cases of chromosomal polytypy in southern African rodents. Previous studies of chromosomal speciation have favoured the biological species concept by stressing the singular role of negatively heterotic chromosomal changes as post-zygotic isolating mechanisms. Adherents of the phylogenetic and recognition species concepts have maintained that chromosomal differences are simply incidental "species markers" that are not necessarily implicated in the speciation process. Particularly where "chromosomal species" correspond with independent character sets (e.g. allozymic, morphometric), as is the case in sibling species of multimammate mice *Mastomys* and tree rats *Thallomys*, such "diagnosable clusters" would be considered good species under the phylogenetic species concepts. However, multidisciplinary studies of the chromosomally polytypic vlei rat *Otomys irroratus* and the striped mouse *Rhabdomys pumilio* have

revealed widespread discordance between chromosomal and non-chromosomal (e.g. morphometric, allozymic, immunological and molecular) characters. The recognition species concept emphasizes characters associated with mate recognition. Such characters are often difficult to obtain without great effort and cost. Where such data exist for related taxa of southern African rodents (e.g. in the vlei rat and the gerbil genera *Tatera* and *Gerbillurus*) they appear to demonstrate incomplete pre-mating isolation under laboratory conditions. Divergence in mate recognition systems is often greater in sympatric species pairs than in allopatric species pairs, lending some support to the notion of reproductive character displacement. Research to date has failed to locate stable hybrid zones between chromosomal races of southern African rodents. Taxonomic treatments of chromosomal species complexes should be based on multidisciplinary studies employing cladistic analyses of independent character sets.

## A GENERALIZED PARSIMONY APPROACH TO BIOGEOGRAPHY

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A property of Brooks Parsimony Analysis that has been criticized in the past is that dispersal and extinction events are usually optimized as parallelisms or reversals in multiple characters. In general, the extinctions (or dispersals) of two different taxa will not carry equal costs. In contrast, all speciation events due to vicariance are weighted equally. Using generalized parsimony, vicariant speciation, dispersal and extinction events can be assigned costs that are the same for all nodes, while at the same time the relative weight of these three types of events can be adjusted. By varying the dispersal and extinction values, reconstructions can be made to reflect pure vicariance scenarios, pure dispersal scenarios, or mixes of the two. So-called missing taxa no longer present a problem, while

widespread taxa are treated under the assumption that at most one of their occurrences is due to vicariance, the others requiring ad hoc explanations. The same approach can also be of value in reconstructing e.g. taxon cladograms from (multiple) gene trees or host cladograms from parasite cladograms.

## CONVERGENT EVOLUTION IN FIG WASPS (AGAONIDAE, CHALCIDOIDEA, HYMENOPTERA)

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Similar morphological adaptations have arisen independently across separate lineages within the fig wasps in response to the extreme selective pressure provided by the morphological constraints of their host fig trees (*Ficus*, Moraceae). Evidence is put forward that supports the convergence of female head shape between two distinct fig wasp lineages, the Agaoninae (pollinators) and Sycoecinae (non-pollinators), utilizing the same host *Ficus* species (Section *Galoglychia*). In contrast to the vast majority of the non-pollinating fig wasps, that oviposit from the outside of the fig, the Agaoninae and Sycoecinae must negotiate the fig ostiole for internal oviposition, with the result that these independent lineages are simultaneously exposed to the selective pressure by ostiolar morphology. Selection will favour a head shape that facilitates successful penetration of the fig cavity and this has resulted in the evolution of similar head shapes in the two lineages. Female head shape in both subfamilies was found to correlate with fig size, with elongate heads associated with large fig size. Given that ostiole bract arrangement is uniform within section *Galoglychia*, it appears that ostiole length may be the main factor contributing to head shape determination. The high degree of coadaptation of head shape suggests that both the Sycoecinae and Agaoninae have coevolved with their host *Ficus* species.



## A MOLECULAR PHYLOGENY OF SOUTHERN AFRICAN TESTUDINIDAE

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Sixteen of the world's 42 species of land tortoises occur in Africa, 10 of which are endemic to southern Africa. South Africa itself, which occupies 0.8% of the world's total land mass, has the highest tortoise biodiversity in the world, with 13 species. This is the first study to use molecular techniques to investigate the evolutionary history of this group, which displays an unusually high level of speciation on the continent. 400 base pairs of mtDNA cytochrome b sequences were obtained, using direct PCR-based sequencing, from 32 individual tortoise blood samples, comprising 13 different species from six genera. PAUP 3.1.1 and Mac Clade 3.06 were used to infer a phylogeny using *Chrysemys scripta elegans* (an Emydid) as an outgroup. The molecular phylogeny generated is congruent with the previously proposed morphological topology, with two main differences. The molecular data imply that *Chersina* should be placed within the *Homopus* clade, and that the *Kinixys* clade should include *Malacochersus*. Some additional specific and subspecific designations are suggested.

## THE USE OF DIFFERENT DATA SETS TO RESOLVE AND ROOT INGROUP TOPOLOGIES

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Extreme character divergence between ingroup taxa and their closest relatives may prohibit effective out-

group inclusion in cladistic analysis, both because these taxa cannot be coded for characters used to resolve ingroup relationships and because ingroup-outgroup homologies are too difficult to establish. Under such circumstances the estimation of ingroup-outgroup relationships and, therefore, ingroup root position, may lie at a higher level than the resolution of ingroup topology, and may best be achieved using a second, more conserved data set. Where the ingroup topology is known, not all ingroup taxa need be resampled for the second "rooting" data set, and this paper provides an ingroup-sampling procedure aimed at establishing a root position most efficiently. This approach is tested using real data from an earlier study on asteroid echinoderms, and is found to perform very well both in terms of its efficiency (effort saving) and its accuracy (ability to estimate the same root as a more inclusive analysis). However, where a "rooting" data set has an intrinsic tendency to identify multiple root positions, the subsampling procedure may converge on the wrong solution.

## A COMPARISON OF CLADOGRAMS OF SOUTHERN AFRICAN PACHYCONDYLA ANTS (HYMENOPTERA: FORMICIDAE) BASED ON CHARACTERS OF WORKERS, MALES AND LARVAE

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Recent revision of the ponerine ants has sunk eight other genera into the genus *Pachycondyla*. However, the relationships between these taxa are still not clear. The status quo is based mainly on characters of workers, which are diploid. Males are haploid, which might affect expression of phenotypic traits and provide a new source of characters. In particular, males are winged and their only social role is to disperse and mate, which suggests that their morphology may be less constrained by adaptations to other social roles. Larvae also play no significant social role, and their

morphology might also be expected to show fewer adaptations and a rich source of new characters.

Cladistic analyses of 20 southern African *Pachycondyla* species were carried out using *Plectroctena* as an outgroup, and including *Streblognathus* because of its uncertain phylogenetic position. All characters were treated as unpolarized. The data included 59 worker characters, 112 male characters, and 90 larval characters. Worker characters yielded 17 equally parsimonious cladograms, reflecting current systematic confusion. Analysis of males yielded a unique solution that reflected many historically recognized generic relationships based on worker morphology. However, many characters had parallels in workers, so that differences in ploidy and social role did not produce independent character sets. Data for larvae were limited (only 10 of the 22 species), but the characters were all novel. A unique solution was found that shared several branches with cladograms of adults. Total evidence supported most traditional generic groupings, and allowed placement of several monotypic genera. Of practical importance is the association of *Streblognathus* with the *Bothroponera* clade, and the splitting of *Pachycondyla* s.l. into two major clades.

## CHELICERATES, OPTIMALITY AND TOTAL EVIDENCE

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The phylogeny of the extant chelicerate orders is examined in the light of morphological and molecular evidence. Representatives from each of the chelicerate "orders" and mandibulate and onychophoran outgroups were examined. Molecular (small and large ribosomal subunit DNA) and morphological information are combined in a total evidence regime to determine the most consistent picture of extant chelicerate relationships possible with these data. Multiple phylogenetic analyses were performed varying analy-

sis parameters yielding largely consistent results. A normalized incongruence length metric is used to assay the relative merit of the multiple analyses. The combined analysis with lowest character incongruence yielded the scheme of relationships (Pycnogonida+(Xiphosura+((Opiliones+((Solifugae+Pseudoscorpiones)+Scorpiones))+((Ricinulei+Acari)+(Palpigradi+((Thelyphonida+Schizomida)+(Amblypygi+Araneae)))))). This result is fairly robust to variation in analysis parameters with the placement of solifugids and the status of the pedipalps responsible for most disagreement. Issues of character incongruence and cladogram optimality are discussed.

## IS TAXONOMY FINISHED?

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Analysis of 26 years of the BIOSIS database shows that, in terms of both total number of publications and literature share, the field of systematics was growing up until 1988, but has recently ceased to grow. In spite of this, species description is still an important part of taxonomy, with more than one-third of all papers published over the time period incorporating the description of at least one new species. On average, at least one new genus is described in about 8% of papers over the time period, a new family in about 3%, a new order in one paper in 1000 and a new phylum in one in 10,000. Papers on nomenclatural aspects of taxonomy show no upward trend over the same time period, but the proportion of revisionary work has increased somewhat. Other trends of interest include the ever-increasing dominance of cladistic over phenetic methods (but not the disappearance of phenetics) and a rapid increase in use of molecular methods, with sequencing now leading in popularity.