



## Abstracts of the 23rd Annual Meeting of the Willi Hennig Society. “Phylogenetics and Evolutionary Biology”

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The 23rd annual meeting of the Willi Hennig Society took place in Paris with the support of Muséum national d’Histoire naturelle and CNRS (Centre National de la recherche Scientifique), from the 18th to the 23rd of July 2004. Ninety four participants from 16 countries presented 67 talks and 11 posters. The symposia comprised both methodological contributions and strong analyses of case studies, focusing on hot topics in systematics, methodological advances in phylogenetic analysis, epistemology, phylogenetic analysis of behavioral and ecological traits, phylogeny and coevolution of microbial symbioses, taxon and character sampling, biogeography, and the evolution of arthropods. The student participation was very high with 30 student talks (45%) distributed among all symposia, showing the same healthy trend seen in previous meetings. The present abstracts show how much systematics and phylogenetics are scientifically growing and contribute significantly to all research fields of evolutionary biology in the framework of comparative biology.

The Student Awards Committee (Cyrille D’Haese, Diana Lipscomb, John Wenzel) nominated the following winners: Johannes Bergsten, the Hennig Prize (\$1000) for “Antagonistic coevolution between the sexes in diving-beetles (Coleoptera: Dytiscidae); phylogeny and experiments in reciprocal illumination”, Mahé Ben Hamed, the Brundin Prize (\$500) for “Reconstructing the history of Chinese through lexicon. Cladistics, distances and trees” and Lara Lopardo, the Rosen Prize (\$250) for the poster “Chilean Anapids and Their Webs, a Phylogenetic Approach (Araneae, Anapidae)”.

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**How did pentastomids get there?** Mikaël Agolin\* and Cyrille D’Haese. FRE 2695 CNRS, Département Systématique et Évolution, Muséum national d’Histoire naturelle, 45, rue Buffon, 75005 Paris, France

Pentastomids constitute a group of about 130 described species of worm-like parasites of the respiratory tract of tetrapod vertebrates. Their phylogenetic affinities have remained enigmatic until recently. Consequently, the evolution of the group is unclear and none of the previously proposed evolutionary scenarios was ever tested through a phylogenetic framework. More and more evidence has been found to conclude that Pentastomida is an arthropod group, closely related to the free living ectoparasite Branchiura (Crustacea: Maxillopoda). In order to address evolutionary questions concerning pentastomids, we first sequenced the complete 18S gene for *Raillietiella* sp. and *Kiricephalus* sp. and a fragment of 16S rDNA for *Kiricephalus* sp. Then the morphological matrix produced by Giribet et al. (in press) was completed and slightly modified

according to the literature on pentastomids morphology and anatomy. We performed a class-level total evidence phylogenetic analysis including 54 taxa for 2 genes and 358 morphological characters, using direct optimization with a Sensitivity Analysis plus Tree Fusing strategy. The inferred topology shows a robust sister group relationship between Pentastomida and Branchiura, forming the clade Ichthyostraca. The relationships between Ichthyostraca and Ostracoda remains unclear, since our taxonomic sampling includes only one Podocopa, no Myodocopa. Our results do not support previous publications arguing Pentastomida is a basal arthropod group, making the hypothesis of a very ancient origin of the group based on Cambrian fossils attributed to the phylum Pentastomida unsupported.

**Taxonomic position of *Nipponolejeunea* (Steph.) Hattori.** Inkeri Ahonen. Botanical Museum, Finnish Museum of Natural History, University of Helsinki, PO Box 7, 00014 University of Helsinki, Finland

Liverwort genus *Nipponolejeunea* is morphologically intermediate between genus *Jubula* and the family

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Lejeuneaceae. It has been assigned to the Lejeuneaceae especially because the ventral lobe of its leaves form a pocket like ‘water sac’, like that found in all Lejeuneaceae. *Jubula* instead, has a very different kind of helmet shaped ventral lobe. However, recent molecular analyses have suggested that genetically *Nipponolejeunea* is much closer to *Jubula* than Lejeuneaceae. In the present study the taxonomical position of *Nipponolejeunea* was studied using both morphological and molecular data from three genomic regions, *rbcL*, *trnL* from chloroplast, and ITS2 from nucleus. Morphological matrix contained 26 characters. The data was analyzed both with direct optimization data method (program POY) in parsimony framework, and with Bayesian inference (Mr Bayes) using static Dialign alignment. In addition to different principles in searching the optimal tree (parsimony versus imposing evolutionary models, dynamic alignment versus static alignment), the treatment of gaps is different in these programs (fifth base versus missing data). Despite these differences both programs give almost the same tree as result, simultaneous analysis of all data resolving *Nipponolejeunea* as a sister group to *Jubula*. The morphological data alone gave ambiguous result in both parsimony and Bayesian analyses.

**Phylogenetic analysis of the genus *Arrhipis* Bonv. (Coleoptera: Eucnemidae).** Diane Alaruikka\* and Jyrki Muona. Finnish Museum of Natural History, PO Box 17 (Pohj. Rautatiekatu 13), University of Helsinki, Finland FIN-00014

Situated within the eucnemid subfamily Melasinae and tribe Dirhigini, the genus *Arrhipis* Bonv. consists of 28 described species. The species are tropical and mostly southern hemisphere forms, only one species occurs in the more northern regions (Florida). The larvae develop in dead wood and show strong hypermetamorphosis. Previously, the taxonomy of the African and American species was clarified. No phylogenetic analyses of this genus have previously been completed. The main goals of this study were to examine the phylogenetic relationships of the genus *Arrhipis* and to revise the species occurring in Africa and Australia. The study resulted in the discovery of eight new species. Parsimony analysis of 32 unordered multistate characters (corresponding to 72 binary ones) resulted in two most parsimonious trees (L = 185, CI = 0.41, RI = 0.65). The American *Arrhipis* species formed a clade including the type-species, *A. subacuta* Guérin-Meneville. The remaining “*Arrhipis*” species formed a mixed lot. Two Asian species grouped with the Palearctic genus *Farsus* DuVal, and the sister group of this clade included the remaining Asian and all of the Australian and African species. A previously synonymized genus group name, *Nematodinus* Lea, is available for this clade. The relationships within the genus *Nematodinus* remain partly resolved, but both the Asian and African faunas appear to have multiple

origins. The genus *Arrhipis* turned out to be a paraphyletic group. It should be divided into three genera: the American *Arrhipis*, the European and Asian *Farsus*, and the African, Asian and Australian *Nematodinus*. Eight previously undescribed *Nematodinus* were detected. Future research will include molecular characters and a total evidence analysis. At present, sufficient material for the molecular studies was not available.

**New circumscription of *Mussaenda* (Mussaendeae: Rubiaceae) inferred from ITS and trnT-F Data.** Grecebio D. Alejandro<sup>1,2\*</sup>, Sylvain Razafimandimbison<sup>3,4</sup> and Sigrid Liede-Schumann<sup>1</sup>. <sup>1</sup>Department of Plant Systematics, Universität Bayreuth, Universitätstr. 30, 95440 Bayreuth, Germany; <sup>2</sup>Research Center for the Natural Sciences & College of Science, University of Santo Tomas, España, Manila, 1008 Philippines; <sup>3</sup>Department of Systematic Botany, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-752 36, Uppsala, Sweden; <sup>4</sup>The Bergius Foundations at the Royal Swedish Academy of Science, PO Box 50017, SE-104 05, Stockholm, Sweden

*Mussaenda* s. str., a widely accepted genus of the tribe Mussaendeae, is mostly paleotropical with ca. 160 species of small trees, erect or scandent shrubs, rarely, true lianas. Its center of diversity lies in tropical Asia with ca. 97 species, followed by tropical Africa with ca. 35 species, Madagascar with ca. 24 species, and the Mascarenes with four species. Earlier circumscriptions of *Mussaenda* included species with or without enlarged calyx lobes and fleshy or dry, capsular fruits. Succeeding studies transferred all the capsular-fruited *Mussaenda* species creating its segregates. This situation raises question as to whether *Mussaenda* s. str. is monophyletic. Evidence from parsimony analyses using both the internal transcribed spacer (ITS) regions of nrDNA and *trnT-F* regions of cpDNA strongly suggests that *Mussaenda* s. str. is not monophyletic. The Malagasy *Mussaenda* is more closely related to *Landiopsis* and *Schizomussaenda* than to Asian and African *Mussaenda*. Furthermore, the Asian genus *Aphaenandra* is nested within the Afro-Asian *Mussaenda* clade. Consequently, *Aphaenandra* should be merged in *Mussaenda*, the Malagasy *Mussaenda* needs a new genus circumscription, and *Mussaenda* s. str. should be restricted to the African and Asian representatives. The Asian *Mussaenda* is nested within the African *Mussaenda* clade suggesting an African origin of the genus.

**Progress in the phylogenetics of the spider family Tetragnathidae, with emphasis on the ‘Metinae problem’ (Araneoidea, Araneae).** Fernando Alvarez-Padilla\* and Gustavo Hormiga. Department of Biological Sciences, The George Washington University, 2023 G. St., Washington, DC 20052, USA

The family Tetragnathidae includes some of the most common and intensively studied spider genera like

*Tetragnatha*, *Leucauge* and *Nephila*. The taxonomic separation between the families Tetragnathidae and Araneidae has varied widely in traditional classifications. In most classifications tetragnathid species have been assigned to three groups, usually ranked as subfamilies: Tetragnathinae, Nephilinae and Metinae. A previous cladistic analysis based on 22 taxa (14 tetragnathids) coded for 60 morphological and behavioral characters recovered Tetragnathidae as a monophyletic group, Nephilinae as sister to all the remaining tetragnathids, and ‘metines’ as a paraphyletic assemblage with respect to Tetragnathinae. We will report progress on our ongoing research on tetragnathid phylogenetics, particularly on our efforts to untangle the phylogenetic relationships of ‘metines.’ At the core of the ‘metine problem’ lies its definition: ‘all forms intermediate between *Tetragnatha* and *Nephila*.’ Under this definition metines have been the taxonomic ‘trash-can’ of Tetragnathidae for more than one century. At present time metines represent 73% of all generic circumscriptions within tetragnathids. Unraveling the phylogenetic relationships of metines is crucial to understanding the evolutionary history of tetragnathid spiders. We will discuss the cladistic relationships of ‘metines’ based on a character matrix that includes 31 tetragnathid species plus 12 araneoid outgroups scored for 112 morphological and behavioral characters. Twenty of these taxa have been previously classified as ‘metines’; we have also included in the character matrix two new tetragnathid genera (one from Chile and the other from Australia). The three minimal length trees resulting from the parsimony analysis of this matrix corroborate the monophyly of Tetragnathidae, Nephilinae and Tetragnathinae, as well as the paraphyly of ‘Metinae.’ Traditional ‘metines’ comprise two separate lineages which we have informally labeled as ‘leucaugines’ and ‘metines *sensu stricto*.’ We will discuss in some detail the phylogenetic placement of ‘leucaugines’, ‘metines *sensu stricto*’ and the empirical support for these lineages.

**Sequences and fossils: influencing the topology of extinct ‘clades’ with data from living taxa.** Robert Asher. Museum für Naturkunde, Institut für Systematische Zoologie, D-10099 Berlin, Germany

For reasons of economy and tradition, it is still rare for paleontologists to include large bodies of sequence data in phylogenetic analyses that focus on fossil vertebrates. Because of the lack of sequence data for pre-50KY fossils, and based on the widespread perception that large radiations of Mesozoic and/or early Tertiary vertebrates (e.g., sauropods, condylarths, stem eutherians) are completely extinct, it remains fairly common practice to use one or a few fossil taxa as exemplars for a given radiation of living taxa, sampled only for the morphological data accessible from fossils.

Here I discuss several examples, focusing on mammals, of how the addition of sequence data for living taxa can affect clades perceived to be totally extinct. For example, extinct ‘condylarths’ are often reconstructed as stem taxa to living groups of ungulates. With the inclusion of sequence data, by necessity coded as missing for the fossils, modern ungulates are demonstrably polyphyletic, making it possible to be much more precise about the relationships of ‘condylarths’ relative to their living sister taxa. Less intuitive is the potential effect of sequence data from modern placental mammals on extinct stem eutherians. By altering the optimization of morphological character(s) found in both the living and fossil taxa, addition of sequences can change relationships among stem eutherians, and potentially remove support for a group that would otherwise be recognized as monophyletic.

**Reconstructing the history of chinese through lexicon. Cladistics, distances and trees.** Mahé Ben Hamed<sup>1,2\*</sup> and Feng Wang<sup>3</sup>. <sup>1</sup>Laboratoire Dynamique du Langage CNRS UMR 5596 Lyon, France; <sup>2</sup>Génétique épidémiologique et Structure des populations humaines, INSERM U535, Villejuif, France; <sup>3</sup>Language Engineering Laboratory, City University of Hong Kong, Kowloon, Hong Kong, PRC

The Chinese linguistic domain has known a rich history of migrations and admixture between populations, which has left a strong imprint on dialects geography, making their relationships hardly decipherable. Major families of dialects are recognizable, but the deep connections between them are very controversial. In the line of the recent applications of phylogenetic methods to linguistic issues, we attempt to see what contribution phylogenetic analyses can have, at smaller geographic and time-depth scales, in disentangling the relationships between Chinese dialects. The data used is a compilation, for 24 dialects sampled from the major families recognized within Chinese, of the Swadesh list 200 lexical items. The Swadesh lists (1950, 1952) constitute a fraction of basic core vocabulary. It is assumed to be the most conservative fraction of the whole vocabulary and most immune to horizontal transfers (borrowing of words or concepts). The 200 wordlist is further divided into 100 (Swadesh, 1950, 1952) and 35 (Yakhontov, 1991) wordlists. The shorter the list, the more conservative and more immune to borrowing it is assumed to be. In this study, these three imbricate lists appear congruent, as shown by an Incongruence Length Difference test. We first proceed to alternative phylogenetic analyses (parsimony, Bayesian and distance analysis of the lexicostatistical distance (Swadesh, 1950, 1952)), on alternative coding of wordlists (multistate versus binary). The acknowledged dialect groups are recovered only when the parsimony approach is used on the linguistically grounded

multistate coding of the 200 wordlist. However, although we obtain a good fit of the data on the resulting trees (CI > 0.8), dialect groups and tree topologies are virtually broken by bootstrap analyses. This suggests that the tree might not be appropriate to model how these dialects have evolved. This is further supported by Neighbor-Net analyses (Bryant and Moulton, 2002, 2004) which show that dialects have developed rather in a continuum than in a tree-like pattern. Such a dialect continuum is in agreement with the particular diglossic context and the rich migratory history to which Chinese has been submitted throughout its development. The methods/coding, which appear efficient in analyzing Indo-European, prove, on the contrary, totally inadequate when applied to Chinese dialects. Neighbor-Nets also show that these two domains have followed very different developmental patterns. This analysis calls for caution in using Indo-European as a paradigm for the application of phylogenetic methods to languages evolution.

**The role of Africa in the history of oscine passerines: molecular systematics of several ‘enigmas’.** Pamela Beresford<sup>1</sup>, Frederick K. Barker<sup>2</sup>, Peter G. Ryan<sup>1</sup> and Timothy M. Crowe<sup>1,3\*</sup>. <sup>1</sup>Percy FitzPatrick Institute, University of Cape Town, Private Bag, Rondebosch 7701, South Africa. <sup>2</sup>Bell Museum of Natural History, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA. <sup>3</sup>Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 1024-5192, USA

Recent molecular work has shown that two enigmatic, endemic Africa species (rockjumpers, *Chaetops* spp. and rockfowl, *Picathartes* spp.) share a most recent common ancestor with Australo-Papuan robins (Petroicidae) and Passerida (~3500 species). Following the general expectation that taxonomically isolated entities are relatively older, 10 more ‘enigmatic’ African birds were added to a large nuclear genetic dataset of Passeri (Barker et al., in press). These results resolve many long-standing questions about the phylogenetic affinities of the enigmatic birds, not all of which were predicted by traditional approaches. Several higher taxa have basal nodes subtending endemic African taxa: Promeropidae in a monophyletic assemblage of Passeroidea and the *Sphenoeacus* group in one of Sylvioidea. These results suggest a previously unsuspected role for Africa in the Tertiary cladogenesis of Passerida, and the implications for reconstructing their historical biogeography and understanding the roles of migration and breeding systems are discussed.

**Antagonistic coevolution between the sexes in diving-beetles (Coleoptera: Dytiscidae); phylogeny and experiments in reciprocal illumination.** Johannes Bergsten\* and Kelly B. Miller. Systematics, Department of Ecology

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Antagonistic coevolution between the sexes due to differential investment in the offspring has recently been suggested to explain characters and conflicts seen in many insect mating systems. Male fitness increase linearly with the number of matings and sired offsprings while female fitness usually is at optimum at one or a few matings and additional superfluous mating are more costly than beneficial for her. Theoreticians predicted from this that males and females in such systems should evolve morphological characters, chemical substances and behaviors to control the mating rate which could lead to an arms race between the sexes. Traditionally in the field of evolutionary ecology experimental work have dominated in trying to find examples of such arms race scenarios. From a systematist’s point of view however, it is obvious that the only way to study coevolution is to include a phylogenetic perspective. Till now examples with inferred character transformations on a phylogeny supporting a coevolutionary arms race between the sexes are scarce. Here we consider within a phylogenetic context the case of coevolution of male adhesive morphology and female dorsal modifications in the subfamily Dytiscinae of diving-beetles. Male diving-beetles have on their pro- and sometimes mesotarsi adhesive discs used to grip the female at copulation. Female response to a male mating approach, lacking any courtship behavior, is a rapid erratic swim in an attempt to dislodge the male. Thus, the mating system involves conflict and there is a basis for a possible arms-race scenario between male adhesive morphology and female antiadhesive adaptations. Crucial data to evaluate this are experimental studies of the antagonistic nature of the characters and a phylogeny. The phylogeny is based on morphology, two nuclear-(Histone 3 and Wingless) and one mitochondrial (CO1) protein coding gene and includes all tribes and most genera of Dytiscinae. Mapping the configuration of male adhesive protarsal discs onto the resulting phylogeny we find a single origin of symmetrical suckers and that various female modifications follow independently in several lineages (corroboration of Miller, 2003). A moderate number of medium-sized discs are inferred to be ancestral for males within Dytiscinae, but, and notably, subsequent to female modifications in various lineages we find deviations from this pattern. Although independently derived the male disc response, or counter-adaptation, in these lineages all takes in various ways the shape of a few discs increasing in size while the remaining get smaller and more numerous. That increased disc differentiation is advantageous to grip a granulate or wrinkled surface is something that can be tested in mechanical experiments. There are additional

sex-limited character transformations the role of which is not yet completely understood, including male claws, mesotarsal modifications and elytral margins. Here a phylogenetic perspective and experimental observations can reciprocally illuminate each other in developing and testing hypotheses to eventually gain an increased knowledge of the system.

**Name-bearers in the phylogenetic system, or why the PhyloCode names natural kinds rather than clades.** Yann Bertrand, Södertörn Högskola, Sweden and Muséum national d'Histoire naturelle, Département Systématique et Evolution, UMR CNRS 7138, 43, rue Cuvier, 75005 Paris, France

A basic entity in historical sciences is conceptualized as a continuous sequence of events bounded in time and connected through time by an integrating force. In the phylogenetic system I introduce the phylogenetic entity, which is a historical entity generated by an ancestor-descendant relationship. From an ontological point of view the phylogenetic entity displays some individual features along with some natural kind features. Furthermore, I compare some fundamental mechanisms in the Linnaean and the phylogenetic systems of taxonomy and nomenclature. Classically, the former distinguishes the fixation from the application of a name, whereas the latter attaches and applies a name to the same entity: the clade defined by the phylogenetic definition. The entities managed by each system are not equivalent, since the Linnaean system does not provide taxa with explicit temporal boundaries. Arguably, the clade concept is equivocal and therefore the phylogenetic entity concept may be a replacement. Moreover, I tackle the sameness issue in the phylogenetic system, namely what should count as the same entity in successive phylogenetic hypotheses. To accommodate the sameness problem I suggest that the phylogenetic definition is the defining property of a natural kind. I label such a natural kind a phylotype. Therefore in the phylogenetic system, the name is fixed by a definition to a natural kind and applied inside the phylogenetic context discussed by the scientific community. Thus, I point out similarities between the Linnaean and the phylogenetic system, forming a basis for their comparisons.

**Biogeographical relationships of New Zealand Pettalidae (Arachnida, Opiliones).** Sarah L. Boyer\* and Gonzalo Giribet. Department of Organismic & Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, US7A

The fauna of New Zealand has characteristics that are typical both of continents and islands, leading researchers to categorize it variously as a mega-island or microcontinent. The New Zealand archipelago is a fragment of the ancient southern supercontinent, Gondwana, which has resulted in a biota strongly

affected by vicariance. In addition, New Zealand has been isolated from Australia for 80 Myr, resulting in biotic features typical of oceanic islands, such as radiations within several animal groups. One animal group which typifies both vicariance and radiation in the New Zealand fauna is Cyphophthalmi, a suborder of Opiliones (harvestmen). These tiny arachnids are small and slow-moving, and spend their entire life cycle in leaf litter habitats. Therefore, they are poor dispersers and provide an excellent system in which to study vicariance events. The cyphophthalmid family Pettalidae has a typical Gondwanan distribution; in addition, this family has a spike in diversity in New Zealand, which is home to 60% of described pettalid species. We explore relationships of Pettalidae from New Zealand, Queensland (Australia), South Africa, and Chile, as well as relationships of pettalids within New Zealand (North Island, South Island, and Stewart Island). We have generated molecular sequence data from 18S rRNA, 28S rRNA, 16S rRNA, cytochrome c oxidase subunit I, and histone H3 for Pettalidae from New Zealand, Queensland (Australia), South Africa, and Chile. These data were analyzed with POY 3.0 with direct optimization under different parameter sets.

**The family Sironidae (Arachnida, Opiliones, Cyphophthalmi) in Europe; the characterization of a Balkan radiation and eastern Mediterranean biogeography.** Sarah L. Boyer\*, Ivo Karaman and Gonzalo Giribet. Department of Organismic & Evolutionary Biology and Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138 USA; Department of Biology and Ecology, Faculty of Sciences, Trg D. Obradovica 2, 21000 Novi Sad, Serbia and Montenegro

Cyphophthalmi is a suborder of small to medium sized arachnids within the order Opiliones. These leaf-litter dwelling animals resemble mites and are distributed worldwide, with families following neat biogeographical patterns. Perhaps the best studied family, the Laurasian family Sironidae includes species from all over Europe, Asia, North America, and Japan. *Siro* is the most diverse sironid genus, with 27 described species, some with up to five named subspecies. Several undescribed species are known in Eastern Europe and North America. The Mediterranean Basin can be divided into four quadrants, the north-west, north-east, south-west, and south-east. Of special interest to this study is the NE quadrant delimited in the north by a chain formed by the Alps, the Dinaric Alps, the Balkan Mts., and the Black Sea, and from the east by the Pontic Mts., the Taurus Mts. and the Lebanon Mts. This region is also known as the E. Mediterranean biogeographical region. A large portion of this region is formed by the Balkan Peninsula, one of the four large Mediterranean peninsulas, which shows high endemism of plants, freshwater fish, and herpetofauna.

Monophyly of certain Balkan reptile groups has also been demonstrated, suggesting an independent biological history for some time. The area has also been demonstrated to have a high degree of genetic isolation in large mammals and fish, due to its role as a glacial refugium during the Pleistocene. In order to test (a) the phylogenetic relationships of selected members of the Sironidae, and (b) the existence of a radiation of cyphophthalmids in the Balkans, we sequenced DNA from five loci, two nuclear ribosomal genes (18S rRNA, and partial 28S rRNA), two mitochondrial genes (the ribosomal 16S rRNA and the protein coding gene cytochrome c oxidase subunit I), and one nuclear protein-coding gene (H3). The data were analyzed using POY 3.0 h with direct optimization under several parameter sets. Our results clearly indicate that the large diversity of Cyphophthalmi occurring in the Balkans and adjacent areas forms a monophyletic clade.

**Phylogenetic relationships of Ithomiinae and Danainae (Lepidoptera: Nymphalidae) inferred from DNA sequences.** Andrew Brower. Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

Ithomiinae and Danainae are unpalatable butterflies with mainly tropical distributions. Many of the species are members of mimicry rings. Their close relationship has been hypothesized for a long time, but there are few morphological features that unambiguously unite them as sister taxa. For this study, 51 ithomiine and danaine genera were sampled for the mtDNA COI-COII region and segments of nuclear DNA from the Ef-1 alpha and wingless genes. Equal-weighted parsimony analysis provides a hypothesis of relationships that largely corroborates prior hypotheses based on morphology, behavior and taxonomic gestalt.

**Phylogenetic analysis of the corbiculate Apinae based on morphology of the sting apparatus (Hymenoptera: Apidae).** Sophie Cardinal. Department of Biology and Faculty of Environmental Studies, York University, 4700 Keele St., N. York, ONT. M3J 1P3, Canada

This paper aims to test the various competing hypotheses regarding the relationships among the four tribes of corbiculate apine bees (Euglossini ‘orchid bees’, Bombini ‘bumble bees’, Meliponini ‘stingless bees’, and Apini ‘honey bees’) against a completely new set of previously unstudied morphological characters. A cladistic analysis based on morphological characters derived from the sting apparatus was performed. In all of the morphological analyses to date, the posterior abdominal segments including the sting apparatus have been largely ignored. The result was one most parsimonious tree of 49 steps, CI = 89, RI = 93 that is perfectly congruent with most studies based on morphological and combined morphological/molecular data, i.e., Euglossini + (Bombini +

(Meliponini + Apini)), but does not support the results based upon just molecular data.

**Phylogeny of the leafhoppers of the *Abana* group (Insecta: Hemiptera: Cicadellidae: Cicadellinae).** Paula Cavalcanti Ceotto\* and Gabriel Mejdalani. FRE 2695 CNRS, Département Systématique et Évolution, Muséum national d’Histoire naturelle, 45, rue Buffon, 75005 Paris, France; Departamento de Entomologia, Museu Nacional, Universidade Federal do Rio de Janeiro (UFRJ), Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil

The subfamily Cicadellinae is composed of leafhoppers that feed from the xylem of vascular plants. Some species of this subfamily are important pests that transmit the bacterium *Xylella fastidiosa*. Species of the genera *Acrogonia* Stål and *Homalodisca* Stål, for example, are vectors of a strain of this bacterium that causes *Citrus* variegated chlorosis. The Cicadellinae are divided into two tribes: a cosmopolitan Cicadellini (about 1600 spp.) and a New World Proconiini (about 350 spp.), which is especially rich in the Neotropical Region. Young (1968) divided the latter tribe into two groups, one in which the meron of the hindlegs is exposed when the forewings are in the rest position, and another in which the meron is covered by the forewings. A cladistic analysis of the group with the meron exposed resulted in two clades, the *Abana* and *Cleusiana* groups (Mejdalani, 2000). The *Abana* group *sensu* Mejdalani (2000) includes the genera *Abana* Distant, *Acrobelus* Stål, *Acrogonia* Stål, *Deselvana* Young, *Omagua* Melichar, *Raphirhinus* de LaPorte and *Teletusa* Distant. A comparative morphological study of these genera and six outgroup taxa (*Homalodisca* Stål, *Molomea* China, *Tretogonia* Melichar, *Cicciana* Metcalf, *Diestostemma* Amyot & Audinet-Serville and *Desamera* Young) yielded 74 characters of the head, thorax, and male and female genitalia. The structures of the female genitalia, studied for the first time in a phylogenetic analysis of proconiine genera, provided informative characters. Phylogenetic analysis conducted to estimate the relationships among these genera revealed eight equally most parsimonious trees with length = 144, CI = 0.52, RI = 0.72 and RC = 0.42. Goloboff’s implied weights method resulted in two trees and successive weighting selected one of the original trees. The latter shows the following relationships for the genera: (*Cicciana* ((*Acrogonia*, *Homalodisca*) (*Molomea*, *Tretogonia*)) (*Diestostemma* (*Desamera* (*Acrobelus* ((*Abana*, *Omagua*) ((*Raphirhinus* (*Deselvana* sp., *D. ornata*, *D. excavata*)) (*Deselvana dorsivitta*, *Teletusa*)))))). The monophyly of the *Abana* group was not recovered, but a monophyletic group including *Abana*, *Acrobelus*, *Deselvana*, *Omagua*, *Raphirhinus* and *Teletusa* appeared in all eight trees. The genus *Deselvana* seems to be polyphyletic.

**Phylogenetic inferences about the nodule-forming abilities and host specificities of the actinorhizal symbiont *Frankia*.**

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Nitrogen-fixing nodule-forming angiosperms are found among 10 plant families. These families have been grouped by *rbcL* phylogenetic analysis into a single clade (Soltis et al., 1995). Characterization of the bacterial partners found in some of these root nodules revealed three major groups (Moulin et al., 2001; Soltis et al., 1995):  $\alpha$ - and  $\beta$ -rhizobia, and actinobacteria of the genus *Frankia*. Several  $\alpha$ - and  $\beta$ -rhizobial genera have been found to harbor nodule-forming and nitrogen-fixing strains. The best studied ones are the *Rhizobium*, *Sinorhizobium*, and *Azorhizobium* genera of the  $\alpha$ -Proteobacteria, and the *Burkholderia* and *Ralstonia* ones from the  $\beta$ -Proteobacteria. Some of the bacterial genes, named *nod*, involved in the nodule-forming ability of these rhizobia were shown to have a common origin but to have been acquired by horizontal genetic transfers by the  $\beta$ -rhizobia. Highly conserved *nod* genes among rhizobia have been searched for in *Frankia* but without success. These bacteria are distantly related to Proteobacteria; they are Gram-positives and filamentous, they can produce sporangia, spores and diazovesicles. Diazovesicles are specialized cells creating a barrier to oxygen diffusion and allowing functioning of the oxygen-labile dinitrogenase complex involved in nitrogen-fixation. These actinobacteria have a much broader host range and can colonize plants from eight families. Rhizobia have, so far, only been found in nodules of the Fabaceae and Ulmaceae plant families. *Frankia* strains have been isolated from five of these plant families. Host-range and modes of infection of these strains were investigated using a panel of model plants of the *Myrica*, *Alnus*, *Casuarina* and *Elaeagnus* genera (Baker, 1987; Callham et al., 1979; Miller and Baker, 1985). *Frankia* strains were found to be adapted to two distinct host-plant responses to invasion resulting in either an infection process named the root hair infection process (RHI) or another process (IP) involving direct penetration of the root and intercellular migration toward a nodule primordium. Phylogenetic groupings obtained using several genetic markers (*rrs*, *nifHDK*, *glnA*, *glnII*, etc.) show a clear divergence between sequences from the culturable *Frankia* strains able to colonize plants by RHI or IP (Cournoyer et al., 1993). Phylogenetic analysis of *rrs* and *glnA* from unculturable micro-symbionts (Clawson et al., 2004) of the other plant families, colonized by the IP process, suggested an early divergence of unculturable *Frankia* IP strains, prior to the separation of the culturable RHI and IP strains. The IP process could have thus been the ancestral mode of infection. Plant host-specificities at the genus, species or ecotype levels among these main *Frankia* phylogenetic

clusters have been observed. Some of these *Frankia* host-specificities were found matching particular phylogenetic lineages. As an example, among the RHI phylogenetic cluster, all gene sequences from the *Casuarina*-infective *Frankia* strains are grouped (Baker, 1987). All these phylogenetic inferences support the idea of a strong impact of the actinorhizal plants on the diversity and evolution of *Frankia*. However, the rhizobial and *Frankia* nodule-forming abilities might have emerged and evolved independently. The upcoming genome sequences of three *Frankia* strains should bring light on this key issue.

**Phylogenetic relationships of the arcoidea: a preliminary molecular investigation.**

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The Arcoidea is an extant order of bivalves, characterized by possession of a shell microstructure suited to form a strong, interlocking hinge and a duplivincular ligament. Relationships among the families of the Arcoidea are not well understood and there have been many alternative classifications proposed for this group. While most taxonomic studies divide the order into two superfamilies – Arcoidea and Limopsoidea – others have raised the three limopsoidean families of Wilson (1998) to superfamilial status. Moreover, though recent molecular analyses of the Bivalvia support monophyly of Arcoidea, they do not support monophyly of the superfamily, Arcoidea, which is paraphyletic with respect to Glycymeridoidea. A preliminary cladistic analysis of selected members of this bivalve order is investigated using DNA sequence data from nuclear ribosomal (18S rDNA and partial 28S rDNA) and mitochondrial ribosomal (16S rDNA) genes. These data were analyzed using optimization alignment and provide an insight into the evolution and diversification of the group.

**A tale of two characters.** Jan De Laet. Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, B-1000 Brussels, Belgium

Hennig opened his 1950 classic on phylogenetic systematics with Bacon's aphorism that truthfulness comes out of error more readily than out of confusion. Grant and Kluge, in their treatment of the character concept as it arises from Hennig's works, recently paid tribute to these grand old men by providing a superb example how confusion easily leads to error. It is shown that the character concept of Grant and Kluge is at odds with Hennig's ideas as well as with current usage and understanding. The cladistic character concept is briefly reviewed against the historical context of Hennig's work, which allows to address such various topics as the defects of absence/presence coding for the purpose

of phylogenetic analysis and the not so novel concept of dynamic homology.

**Measuring similarity between cladograms.** Jan De Laet\* and Steve Farris. Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, B-1000 Brussels, Belgium; Molekylärsystematiska laboratoriet, Naturhistoriska riksmuseet, Box 50007 SE-104 05 Stockholm, Sweden

Quartet-based measures of tree similarity as originally proposed by Estabrook and coworkers do not account for logical dependences between quartet subtrees. To figure out if this has consequences for their validity when comparing trees, two general conditions that should be met by any useful tree similarity metric are discussed. Examples are provided in which existing quartet-based measures fail these conditions. Modified measures are proposed that properly take into account logical dependences and that meet both conditions.

**Treatment of multiple trees in resampling analyses.** Jan De Laet, Steve Farris\* and Pablo Goloboff. Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, B-1000 Brussels, Belgium; Molekylärsystematiska laboratoriet, Naturhistoriska riksmuseet, Box 50007 SE-104 05 Stockholm, Sweden; Instituto Superior de Entomología 'Dr Abraham Willink', Miguel Lillo 205, 4000 S.M. de Tucumán, Argentina

When Felsenstein first used bootstrapping in phylogenetic analyses he did not discuss how to treat multiple optimal trees that might be found for a single pseudoreplicate. He subsequently introduced a method in which all optimal trees found for a pseudoreplicate are passed to the majority-rule summary tree calculation, each tree being weighted by the inverse of the number of trees found for the pseudoreplicate. While this method is still used in both PHYLIP and PAUP, no justification has ever been offered for it, and in fact it seems to have been adopted originally simply because the old PHYLIP consensus program could not process multifurcating trees. We point out here that this method is defective in that it can yield high resampling frequencies for groups that are actually unsupported by the data, and this can occur in both parsimony and likelihood analyses.

**Phylogeny as explanation: where does progress in knowledge come from?** Pierre Deleporte. UMR 6552 Ethologie-Evolution-Ecologie CNRS, Université Rennes 1, Station Biologique, 35380 Paimpont, France

A given phylogeny is not phylogenetically predictive in itself, nor does a given phylogeny inference consist in a test properly. Rather, character evolutionary scenarios may be predicted from evolutionary theories, and tested against a given phylogeny and the scenarios it implies. But phylogeny inference per se consists in explaining a

data matrix with a historical, evolutionary sketch. Different data matrices can trivially give rise to different and possibly topologically incompatible phylogenetic explanations. In this context, progress in knowledge can come from: – improved computing devices; – improved models of character evolution supporting phylogeny inference; – improved relevant representation of life (data matrix). Our comments will focus on the two last points.

**Convergence and parallelism: is a new life ahead of old concepts?** Laure Desutter-Grandcolas\*, Philippe Grandcolas, Tony Robillard, Jérôme Murienne and Frédéric Legendre. FRE 2695 CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 45, rue Buffon, 75005 Paris, France

In comparative biology, character observations separate from the start similar and dissimilar characters. Only similar characters are considered for phylogeny reconstruction and their homology is attested in a two-step process, firstly a priori of phylogeny reconstruction by accurate similarity statements, and secondly a posteriori of phylogeny analysis by congruence with other characters. Nonhomology then refers to homoplasy s.l., and is commonly, but vaguely, associated with 'convergence'. In this logical scheme, there is no way to analyze characters which look roughly similar but do not meet usual criteria of primary homology statements, even though such characters may represent evolutionarily significant patterns of character transformations. With this prospect, and because phylogenies are not patterns of taxa relationships but also, and most importantly, references for studies in evolutionary biology, we propose to redefine the traditional concepts of parallelism and convergence s. str. in order to associate them with explicit theoretical contexts. This will allow us first to describe unambiguously evolutionary patterns of character transformations which correspond to nonhomology, and second to perform tests of evolutionary hypotheses for characters which evolution cannot be related to common ancestry.

**Multiple data combinations to assess clade reliability.** Agnès Dettai\* and Guillaume Lecointre. Muséum National d'Histoire Naturelle, Département Systématique et Evolution, UMR CNRS 7138, rue Cuvier, 75005, Paris, France

There is a low probability of finding a given clade through separate analyses of independent molecular datasets by chance alone: therefore, a clade found repeatedly might be considered as reliable, given that we accept and incorporate some background knowledge for delineation of independent datasets. Yet separate analyses run the risk of loss of information due to stochastic errors or marker-dependent biases. Data combination lowers this risk because of longer sequences and overall



character congruence. By analyzing all possible combinations of datasets, one gets the advantages of both separate and combined analyses, given that only independent combinations are taken into account for analysis of repeatability of clades. The problematic phylogeny of the wide clade of acanthomorph fishes (more than 15 000 species in 314 families) has been used to study this. Five independent datasets totaling more than 3500 base pairs have been analyzed with this method. Four of the datasets had been published before (12S-16S, 28S, and rhodopsin: Chen et al. 2003; and MLL: Dettai and Lecointre, 2004, submitted), and the other one features IRBP, a new gene for Teleostei. The results have confirmed most clades found by previous works on these markers, as well as results of other teams on the complete mitochondrial genome (Miya et al. 2001, 2003).

**What is the origin of hexapods: wet or not wet?** Cyrille A. D'Haese. FRE 2695 CNRS, Département Systématique et Évolution, Muséum national d'Histoire naturelle, 45, rue Buffon, 75005 Paris, France

It is often considered that the first hexapods went from the sea through intermediate freshwater environments to colonize fully terrestrial ecosystems. To understand the ancestral ecology of hexapods, a phylogenetic analysis using Direct Optimization for exemplars representing all the major lineages of hexapods is provided. By mapping ecological attributes onto the obtained phylogeny, it is shown that hexapods colonized terrestrial environments directly from marine environment without a transition through freshwater. An edaphic life-style is the basal state for hexapods as a whole. Aquatic ecology is inferred to be a secondary change that occurred several times independently, particularly in some groups of Collembola and Pterygota. The answer is ambiguous for Pterygota, whether the first Pterygota had aquatic larvae and reversed toward fully terrestrial in Neoptera or aquatic larvae appeared independently in Odonata and Ephemeroptera. Subsequently, aquatic larvae were secondarily acquired in various groups independently (e.g., Plecoptera, Trichoptera, Coleoptera).

**Reticulation and suppressed concerted evolution in agamospermous polyploid dandelions (*Taraxacum*, Compositae).** Lenka Drábková<sup>1</sup>\*, Jan Kirschner<sup>1</sup> and Cestmír Vleck<sup>2</sup>. <sup>1</sup>Institute of Botany, Department of Taxonomy, Academy of Sciences, Zámek 1, 252 43 Pruhonice, Czech Republic; <sup>2</sup>Centre for Integrated Genomics and Institute of Molecular Genetics, Academy of Sciences, Flemingovo nám. 2, 166 37 Prague 6, Czech Republic

In the genus *Taraxacum*, a genus characterized by the coexistence of sexual reproduction and agamospermy, a complex reticulation combined with polyploidization represents one of the major evolutionary processes. We

analyzed the association between dandelion ITS sequence polymorphism, agamospermy, polyploidy, hybridization, and the phylogenetic information. Up to now, phylogenetic analysis of *Taraxacum* was limited to the study of plastome, a method able to reveal major trends in the evolution of cpDNA, but not fully appropriate to identify pathways of multiple reticulation events due to uniparental inheritance and relatively low level of phylogenetically relevant variation within the *Taraxacum* cpDNA. Our project is aimed at tracing parental genomes of polyploid hybridogenous dandelions in order to reconstruct the complicated reticulation history. As a material, we selected polyploid (tri- and tetraploid) agamosperms of the *Taraxacum* sections *Leucantha*, *Stenoloba* and *Suavia*, and compared them with related or similar sexuals, usually diploids. We selected nrDNA ITS regions, and expected that, under the condition of suppressed concerted evolution, the variation would represent a thesaurus of parental sequences, together with results of the later mutation process. Internal transcribed spacers (ITS1 and ITS2) of nuclear ribosomal DNA (nrDNA) of 31 species of three C Asian sections of *Taraxacum* were sequenced. Individual plants of *Taraxacum* taxa contain polymorphic nucleotide sites in the ITS1 and ITS2 regions. To characterize the intragenomic variation, we sequenced 10 clones from each individual. These sequences show polymorphism among clones. This polymorphism supports the hypothesis of the suppressed ITS homogenization in agamospermous polyploid dandelions. Moreover, the preliminary results show that the interclonal variation involves minor variants very close to one another, and a group of major variants, occupying very remote branches of the cladogram. To sum up, the main goals of this work were (1) to test a hypothesis that a comparison of ITS clones is a suitable tool for phylogenetic reconstruction of the reticulation in *Taraxacum*, and (2) to reveal probable evolutionary relationships among selected hybridogenous apomicts in C Asia. What remains is a comparison with the most important related groups of dandelions, including the diploid sexuals, probably close to the parental taxa of C. Asiatic dandelions.

**Phylogeny and evolution of spider parasitoids within Pimplinae (Hymenoptera, Ichneumonidae).** Jacques Dubois\* and Ian D. Gauld. FRE 2695 CNRS, Département Systématique et Évolution, Muséum National d'Histoire Naturelle, 45, rue Buffon, 75005 Paris, France; The Natural History Museum, Entomology, Cromwell Road, London, UK

The subfamily Pimplinae displays the most diversified patterns of parasitism within the Ichneumonidae. They are associated with a wider host range than in any other subfamily of Ichneumonidae, and species are known to parasitize many groups of a phytophagous or xylopha-

gous endopterygote larvae or pupae, including those of Lepidoptera, Diptera, Coleoptera and Hymenoptera. Hosts may be concealed or more or less exposed and most of the time these hosts are permanently immobilized prior to parasitization. Pimplinae can develop as primary or as obligate or facultative secondary, ecto- or endoparasitoids. The subfamily Pimplinae is composed of three tribes: Ephialtini, Pimplini, and Delomeristini. Within the Ephialtini a single evolutionary lineage has diversified to attack spiders. It is composed of two groups. The larvae of the first group develop as predators on spider's eggs (*Tromatobia* genus group). Some of these species larvae complete their development by eating the spider female that the parasitoid wasp has killed before laying eggs. The larvae of the second group (*Polysphincta* genus complex) are strictly ectoparasitoids of active spiders, an unique behavior within the Ichneumonidae. The female wasp only paralyzes temporarily the spider before laying eggs. Many species use the ovipositor only to sting and subdue the spider, and the egg is laid directly onto the host, not passing down the lumen of the ovipositor as is the case for most other nonaculeate parasitoid Hymenoptera. Unlike other pimpline species, spider parasitoids are associated with a restricted host range. Attacked spiders are either hunting spiders or web-building spider, all belonging to a few families of the Araneomorpha clade. Hypotheses on Pimplinae phylogeny have already been proposed for the whole subfamily. Here we propose a new insight in the phylogeny of the spider parasitoids in order to clarify their taxonomy and elucidate details of the origin and development of this unique life style.

**Phylogenetic analysis refutes symbiont-host co-speciation in bioluminescent symbiosis.** Paul V. Dunlap. Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University Avenue, Ann Arbor, MI 48109, USA

Bioluminescent symbiosis between luminous marine bacteria and fishes and squids is thought to provide a compelling example of cospeciation. Several features of these associations, which indicate historically intimate symbiotic interactions, could reflect a linked evolutionary divergence of the bacteria with their host animals. Equally convincing, however, is the contrasting view, arising from ecological independence of the bacteria, that these associations are simply loosely coupled mutualisms exhibiting no evidence of cospeciation. To test the cospeciation hypothesis, we analyzed the congruence of symbiont and host phylogenies for three associations, *Photobacterium leiognathi* symbiotic with leiognathid fishes, *Photobacterium fischeri* with sepiolid squids and monocentrid fishes, and *Photobacterium phosphoreum* with various deep-sea fishes. Phylogenetic analyses were based on 16S rRNA, *gyrB*, and *luxABE* gene sequences for the bacteria and 16S rRNA and COI

gene sequences or morphology-based taxonomy for the animals. For *P. leiognathi*, three evolutionarily distinct lineages were diagnosed; however, the same host species often harbored representatives of two or all three of the bacterial lineages. For *P. fischeri*, several distinct bacterial lineages were resolved; again, the same host species often harbored representatives of different symbiont lineages. Furthermore, the same bacterial strain type, defined by DNA fingerprinting and sequence analysis, was symbiotic with the sepiolid squid *Euprymna morsei* and the monocentrid fish *Monocentris japonicus*. For *P. phosphoreum*, the single resolved bacterial lineage was found to be symbiotic with members of four families of deep-sea fishes in three orders, Chlorophthalmidae (Aulopiformes), Macrouridae, and Moridae (Gadiiformes), and Trachichthyidae (Beryciformes). These results, in demonstrating a lack of congruence between the phylogenies of luminous bacteria and their symbiotic host animals, refute the cospeciation view. Rather than cospeciation, the specificity of these loosely coupled mutualisms instead may be a consequence of coincident ecologies of symbiont and host.

**Why are olfactory systems similar across phyla?** Heather Eisthen. Department of Zoology, Michigan State University, 203 Natural Science Building, East Lansing, MI 48824, USA

Despite recent advances in understanding the molecular basis of olfactory transduction, the nature of information coding in the olfactory system remains mysterious to neurobiologists. Studies of olfactory system function in nematodes, arthropods, molluscs, and vertebrates reveal striking anatomical, physiological, and biochemical similarities. Common features include the presence of odorant binding proteins in a liquid medium surrounding the receptor cells; the use of G protein-coupled receptors to detect stimuli; the presence of a two-step biochemical pathway underlying transduction of odorant signals; and receptor cells with unbranching axons that project to tangles of neuropil (glomeruli) in the central nervous system. The available data indicate that these features evolved independently several times, suggesting that they represent examples of convergent evolution. While some of these cases of convergence may be due to developmental or mechanical constraints, others may have arisen because of functional demands on the nervous system. For example, glomerular structures have evolved many times independently in chemosensory portions of the nervous system, but are not commonly found in other regions of the nervous system. This observation indicates that glomerular structures play a specific function in processing odorant signals, and suggests that research on glomerular processing mechanisms may help us understand the coding of odorant identity in the central nervous system. I will describe convergent features in

olfactory systems and analyze the factors that may have led to the repeated appearance of these features in olfactory systems across phyla.

**Crinoid phylogeny: a preliminary analysis.** Marc Eléaume<sup>1\*</sup>, Nadia Améziane<sup>1</sup>, Greg Rouse<sup>2</sup>, Fredrik Pleijel<sup>3</sup>, Jérôme Murienne<sup>4</sup> and Bernard L. Cohen<sup>5</sup>. <sup>1</sup>UMR 5178 BOME, Département Milieux et Peuplements Marins, Muséum National d'Histoire Naturelle, 57, rue Cuvier, F 75005 Paris; <sup>2</sup>Marine Invertebrates, South Australian Museum, Nth Terrace, Adelaide, Australia (SA 5000); <sup>3</sup>UMR CNRS 7138, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 43, rue Cuvier, 75005 Paris; <sup>4</sup>FRE 2695 CNRS, Département Systématique et Évolution, Muséum national d'Histoire naturelle, 45, rue Buffon, 75005 Paris, France; <sup>5</sup>IBLS Division of Molecular Genetics, University of Glasgow, Pontecorvo Building, 56 Dumbarton Rd, Glasgow, G11 6NU, UK

We describe the first combined molecular and morphological analysis of extant crinoid high-level interrelationships. Nuclear (18S rDNA, internal transcribed spacer 1, 5.8S rDNA, and internal transcribed spacer 2) and mitochondrial gene sequences (16S rDNA) and a cladistically coded matrix of 45 morphological characters are combined and analyzed by phylogenetic methods. The ingroup molecular and morphological analyses include data from the bourgueticrinid *Bathycrinus*; the antedonid comatulid *Florometra*; the cyrtocrinids *Gymnocrinus* and *Holopus*; the isocrinids *Endoxocrinus*, and two species of *Metacrinus*; as well as from *Guillecrinus* and *Caledonicrinus*, whose ordinal relationships are uncertain. Two outgroups were chosen among the sister group of the crinoids, respectively, representing the Asterozoa and Echinozoa. The phylogenetic analysis was processed by direct optimization using POY 3.0.11 with equal weighting, 2000 replicates and ratchet. Results show that *Bathycrinus* is sister group of all extant crinoids, including comatulids. Comatulids are therefore not sister group of stalked crinoids and stalked crinoids are found paraphyletic. *Guillecrinus* is sister group of two clades: the isocrinids (*Endoxocrinus* + *Metacrinus*) and the cyrtocrinids (*Holopus* + *Gymnocrinus*) + *Caledonicrinus*. As a consequence we re-evaluate the interpretation of *Gymnocrinus* calyx as compared to *Caledonicrinus*. The calyx of *Gymnocrinus* is a polycrystalline, i.e., a complex arrangement of plates of different origins, structure composed of two distinct areas: an outer and an inner region. The outer component may represent covering radials while the inner part may be interpreted as the basals fused to the radials. Another consequence is that the 'isocrinid' nervous system cannot be considered as the ancestral type. A fast optimization of the ancestral states of the nervous system characters indicates that the ancestral nervous system displays five aboral nerves and absence of the aboral ganglion.

**Gutless marine oligochaetes and their bacterial symbionts.** Christer Erséus\*, Nicole Dubilier and Olav Giere. Department of Zoology, Göteborg University, Sweden; Molecular Ecology Group, Max-Planck-Institute of Marine Microbiology, Bremen, Germany; Zoological Institute und Zoological Museum, University of Hamburg, Germany

A marine group among the aquatic oligochaetous Clitellata (Annelida), comprising the tubificid genera *Inanidrilus* and *Olavius*, are characterized by the total absence of a normal alimentary system. These gutless worms, today with about 80 named species, are dependent on nutrition provided by their endosymbiotic bacteria, the latter present in high numbers between the cuticle and the underlying epidermis of the hosts. The presentation will give a general overview of the complexity emerging from ongoing investigations of these associations. Ultrastructural and molecular studies have revealed the existence of multiple bacterial phylotypes in the gutless oligochaetes, including the coexistence of sulphate-reducing  $\delta$ -Proteobacteria and sulphide-oxidizing  $\gamma$ -Proteobacteria in the same host. Some of the symbionts of a particular host species are closely related to corresponding symbionts of other annelid worms, in other cases the symbionts are more closely related to free-living phylotypes isolated from sediments. The establishment and evolution of the bacterial symbioses in oligochaete hosts, however, are still far from fully understood.

**The inferential structure of the concepts of semaphoront, species taxa, and supraspecific taxa.** J. Kirk Fitzhugh. Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, USA

Hennig (1966: fig. 6) recognized three classes of relationships within biological systematics: ontogenetic, tokogenetic, and phylogenetic. The nature of these relationships are best interpreted as representations of causal hypotheses which have been derived from abductive, or explanatory inferences: (a) ontogenetic relations – a causal accounting of life history stages of individuals, i.e., semaphoronts; (b) tokogenetic relations – a causal accounting of shared properties among individuals that are the products of tokogenetic events, i.e., species taxa; note that tokogeny is not limited to sexual reproduction, but also includes asexual and heterogenetic events; (c) phylogenetic relations – a causal accounting of shared properties among individuals which are members of two or more species, i.e., supraspecific taxa. Hypotheses of semaphoronts, species taxa, and supraspecific taxa are inferred for the purposes of providing explanatory accounts for observed properties instantiated by individuals. The distinctions between these causal relationships are consistent with Hennig's insistence that phylogenetic systematics differs from other classes of systematics, such as ontogenetic and tokogenetic. Assuming these three

classes of causal relations accurately represent natural events, then the terms semaphoront, species (as a taxon), and supraspecific taxon require formal definitions that accurately convey each of these relations in the explanatory contexts intended for each. In recognizing the inferential bases for our uses of these three classes of causal hypotheses in biology, defining these terms becomes straightforward, as each illustrates our inferential actions: (1) Semaphoront: a hypothesis of ontogenetic relationships derived from ontogenetic theory, and applied to a particular individual or individuals. The term denotes a causal hypothesis accounting, by way of ontogeny, for the characters of individuals at a particular time in their life history relative to the characters observed at some other time. (2) Species: a hypothesis of tokogenetic relationships, a 'lineage', derived from tokogenetic theory, and applied to a group of semaphoronts. This definition is inclusive of causal hypotheses derivable from any recognized tokogenetic theory. For instance, general demarcations of at least three classes of tokogeny can be recognized for the present purposes: sexual (interbreeding), asexual, and heterogenetic ('alternation of generation'). (3) Supraspecific taxon: a hypothesis of phylogenetic relationships among a set of semaphoronts, derived from tokogenetic and speciation theory, and applied to semaphoronts in different species. This is a causal hypothesis accounting, by way of the phylogenetic theory of 'descent with modification', for the same characters among semaphoronts in two or more species relative to different characters in semaphoronts of other species. A consequence of defining semaphoront, species, and supraspecific taxon as representing ontogenetic, tokogenetic, and phylogenetic explanatory hypotheses, respectively, is that there are distinct limitations on what current methods qualify as being 'phylogenetic' as opposed to 'tokogenetic.' For instance, 'maximum likelihood' methods, which invoke the notion of 'branch lengths', only address why-questions of tokogenetic relevance, not phylogenetic relevance.

**Molecular phylogenies of parabasalid symbionts of termites.** Delphine Gerbod<sup>1\*</sup>, C. Noël<sup>2</sup>, M.F. Dolan<sup>3</sup>, V.P. Edgcomb<sup>4</sup>, E. Sanders<sup>5</sup>, S. Moriya<sup>6</sup>, O. Kitade<sup>7</sup>, M. Ohkuma<sup>8</sup>, N.M. Fast<sup>9</sup>, J.D. Palmer<sup>5</sup>, M. Capron<sup>10</sup>, T. Kudo<sup>8</sup>, M.L. Sogin<sup>4</sup>, P.J. Keeling<sup>9</sup> and E. Viscogliosi<sup>10</sup>. <sup>1</sup>Dalhousie University, Halifax, Canada; <sup>2</sup>The Natural History Museum, London, UK; <sup>3</sup>University of Massachusetts, Amherst, USA; <sup>4</sup>Marine Biological Laboratory, Woods Hole, USA; <sup>5</sup>Indiana University, Bloomington, USA; <sup>6</sup>Yokohama University, Japan; <sup>7</sup>Ibaraki University, Japan; <sup>8</sup>RIKEN, Wako, Japan; <sup>9</sup>University of British Columbia, Vancouver, Canada; <sup>10</sup>Institut Pasteur, Unité INSERM U547, Lille, France

On the basis of cytological studies, parabasalid taxa were classified into two classes: Trichomonadea (subdivided into four main families) and Hypermastigea.

Small subunit rRNA sequences were obtained by polymerase chain reaction from trichomonad symbionts of termites that belong to Devescovinidae (*Devescovina* sp.) and the polymastigont taxon Calonymphidae (*Snyderella tabogae*, *Calonympha grassii*, *Metacoronympha senta* and *Stephanonympha* sp.). These new sequences were analyzed by parsimony, distance and likelihood methods in a broad phylogeny including all identified parabasalid sequences available in databases. Our analyses demonstrate that both classes and all families of parabasalids are not monophyletic, indicating that a revision of parabasalid systematics is necessary. Moreover, we note the emergence of a very well supported Devescovinidae/Calonymphidae group, and an unexpected dichotomy of the Calonymphidae. This suggests that the polymastigont state observed in the Calonymphidae might be explained by two or more independent evolutionary events. In parallel, new sequences from seven diverse parabasalids (six trichomonads and one hypermastigid) were added to data sets of glyceraldehyde-3-phosphate dehydrogenase (GAPDH), enolase, alpha-tubulin and beta-tubulin. For the first time in parabasalids, this allows phylogenetic trees with the same species sampling to be inferred from several molecular markers, as well as comparison of protein- and rRNA-based trees.

**A combined phylogeny of penguins (Aves: Sphenisciformes).** Norberto Giannini\* and Sara Bertelli. Department of Mammalogy, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

Penguins are a homogeneous group of austral marine birds that exhibit remarkable adaptations for diving. Phylogenetic relationships among penguins received little attention. We developed a morphological matrix including 151 morphological characters of osteology (63 characters), myology (15), integument (66), and breeding (7 characters) scored in 18 extant forms (all currently recognized species plus one distinct subspecies). A gaviiform was placed at the root, and 11 species of representative procellariiform groups completed the outgroup. A heuristic parsimony analysis under equal weights was performed. We also compiled DNA sequences available in GenBank for the mitochondrial genes 12S rDNA and cytochrome b. We include the two data partitions in a combined analysis under direct optimization. Both analyses recovered monophyly of Sphenisciformes and all the traditional polytypic genera. Morphological characters performed optimally at the ordinal and generic level, also providing resolution and varying degrees of support at the supra- and intrageneric levels. The comparison of molecular and morphological results indicates that the most significant problem in the phylogeny of extant penguins is rooting the ingroup. The mutual interaction of molecular and morphological

data decreases the ambiguity regarding the placement of the root and provides a resolved phylogeny of extant penguins.

**A total-evidence phylogeny of megachiropteran bats.** Norberto Giannini\* and Nancy Simmons. Department of Mammalogy, American Museum of Natural History, Central Park West at 79th street, New York, NY 10024-5192, USA

The suborder Megachiroptera comprises > 160 species of fruit bats (Pteropodidae). Molecular phylogenetic results have generally contradicted most currently recognized taxonomic groups, implying high levels of morphological homoplasy, particularly in traits related to feeding habits. However, a recent study has shown that the alleged conflict between morphology and molecular data may be less significant than previously thought. To further investigate this, we generated a morphological matrix of over 200 characters for 44 representative megachiropterans and six microchiropteran outgroups. We combined this matrix with sequences from the 12S, 16S, t-valine, cyt b and the nuclear c-mos oncogene from previous studies. We used direct optimization under equal weights. Exploratory analyses using implied weights suggest that maximal topological congruence between the combined analysis and trees based on separate data sets can be achieved using strong concavities (k equal to 3 or 4). The combination of the two sources of evidence easily accommodated the morphological and molecular signals, yielding a well-resolved, well-supported phylogeny of the Megachiroptera that agrees remarkably well with the current taxonomy of the group.

**Continuous characters analyzed as such.** Pablo A. Goloboff\*, Camilo I. Mattoni and Andrés Sebastián Quinteros. Instituto Superior de Entomología 'Dr Abraham Willink', Miguel Lillo 205, 4000 S.M. de Tucumán, Argentina; Diversidad Animal I, F.C.E.F.y N., Universidad Nacional de Córdoba, Av. Velez Sarsfield 299, 5000 Córdoba, Argentina; Cátedra de Anatomía Comparada, Facultad de Ciencias Naturales, Universidad Nacional de Salta, Av. Bolivia 5150, 4400 Salta, Argentina

Continuous characters have rarely been included in cladistic analysis of morphological data; when included, they have always been discretized, using a variety of ad hoc methods. Since continuous characters are typically additive, they can be optimized with well known algorithms and thus they could be easily analyzed without discretization. TNT has recently incorporated continuous characters, and three real matrices (for scorpions, spiders, and lizards) are analyzed to study the performance of continuous characters analyzed as such. One of the problems that has been pointed out (Farris, 1990) with some existing methods for discretization is that they

can assign terminals that do not differ significantly to different states. With the implementation in TNT, this problem can be easily avoided by simply assigning to each terminal a range that goes from the mean minus one standard deviation to the mean plus one standard deviation; given normal distributions, terminals that do not overlap thus differ significantly (more significantly if using more than one standard deviation). One of the matrices has a reduced number of continuous characters, and thus continuous characters cannot be analyzed by themselves; adding the continuous characters to the discrete characters, however, increases the support of several groups. The other two matrices have larger numbers of continuous characters, so that the results of separate analyses for the discrete and the continuous characters can be more meaningfully compared. In both cases, the continuous characters (analyzed alone) result in trees that are relatively similar to the trees produced by the discrete characters alone. These results suggest that the continuous characters carry indeed phylogenetic information, and that (if they have been observed) there is no real reason to exclude them from the analysis.

**Transaptation, a new concept to describe historical continuity of function with change of the associated structure.** Philippe Grandcolas\*, Laure Desutter-Grandcolas, Tony Robillard, Frédéric Legendre and Jérôme Murienne. FRE 2695 CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 45 rue Buffon, 75005 Paris, France

From the early times of systematics and evolutionary biology, structure and function have been considered as related concepts. More or less tightly coupled, they have always been associated within the definition of adaptation, preadaptation and more recently, exaptation. In the last decades, several seminal papers have shown that phylogenetics is absolutely necessary for the study of the historical component of these adaptational concepts. Phylogenetics permits us to reconstruct whether an apomorphic/plesiomorphic structure is associated with an apomorphic/plesiomorphic function at a given phylogenetic node. In that way, adaptation can be distinguished from preadaptation or exaptation, all concepts invaluable to the study of evolution which show how organisms can evolve little but adapt significantly. However, one case of combination of character's states of structure and function has not been characterized until now: an apomorphic structure with a plesiomorphic function. That case has been evoked indirectly in the literature while it appears to be widespread and potentially biologically meaningful. Therefore, we propose the name of 'transaptation' for that adaptational situation where the same function is continuously present, 'trans-cending' a change of structures or 'aptations'. The evolutionary significance of this concept is discussed in the light of several examples. It refers to the 'recruitment' of structures in the

framework of a continuous function and a selective regime. Transaptation represents the polarity-symmetrical situation of the exaptation where the structure is historically continuous and the function changes. Each of these situations has deeply different biological implications and must be termed differently to be properly recognized and studied.

**The poverty of phylogeny, the poverty of taxonomy, the poverty of natural history, ... their richness altogether as shown by a case study on cockroaches.** Philippe Grandcolas\*, Roseli Pellens, Pierre Deleporte and Joan Van Baaren. FRE 2695 CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 45 rue Buffon, 75005 Paris, France; UMR 6552 Ethologie-Evolution-Ecologie CNRS, Université Rennes 1, Station Biologique, 35380 Paimpont, France

It has recently been argued with reason that systematics should remain a balanced discipline if inflation of molecular phylogenetics is not to hamper advances in basic taxonomy (Wheeler, 2004). From this perspective, the recent overwhelming scientific interest in tree-thinking may be found too strong, preventing the remainder of the work being correctly done. I would argue that the same is true for natural history, the basic data of which are completely neglected both by systematists and by ecologists, who focus either on sophisticated tree analyses or species *morphological* descriptions only. This situation prevents the 'natural system' being currently informative (some would say 'predictive', but the term is not appropriate). What for a natural classification of organisms without any biological knowledge associated with them? In this perspective, a case study is presented where 15 years of taxonomic and natural history sampling followed by phylogenetic analyses have been undertaken on a worldwide tropical cockroach clade. The effect of the increase of taxonomic knowledge on phylogenetic and evolutionary reconstruction is shown, contrasting the situation before and after this sampling effort. It is shown that increasing only taxonomic knowledge does not improve significantly the reconstructions of life styles evolution. When new or revised natural history knowledge is added together with new taxonomic knowledge, the reconstructions become different, showing that an input of information is required both in taxonomy and in natural history in a phylogenetic framework for providing evolutionary syntheses.

**Heterochrony in Tingidae (Insecta: Heteroptera): paedomorphosis or peramorphosis?.** E. Guilbert\*, P. Grandcolas and L. Desutter-Grandcolas. FRE 2695 CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 45 rue Buffon, 75005 Paris, France

Tingidae exhibit a lace-like body structures that can have very diverse shapes. The larvae also bear structures

(tubercles) on the dorsum that are also of very diverse shapes. These structures integrated in a phylogenetic study of the Tingidae, evolve from simple to complex, in two clades independently. Also, some apical species exhibit reversal evolution and exhibit then "ancestral" character states. These homoplasies are thought to be heterochronic events. The case of larval tubercles, particularly cephalic ones, evolving from simple to complex during the evolution and conserved in adult in their simple forms is analyzed combining phylogenetic results and ontogenetic sequences. A general peramorphosis combined with paedomorphic cases is hypothesized.

**Do closely related *Stereocaulon* species share same types of cephalodia?.** Filip Högnabba. Department of Biological and Environmental Sciences, University of Helsinki, PO Box 65, FIN-00014 Finland

Most of the species included in the lichen genus *Stereocaulon* form symbiotic associations with cyanobacteria. The cyanobacteria are usually concentrated in structures referred to as cephalodia. Based on the morphology of the cephalodia a number of different types can be distinguished. The aim of the present study is to investigate whether closely related species of *Stereocaulon* share same types of cephalodia. The phylogenetic relationships of the included *Stereocaulon* species have been examined by using direct optimization of DNA sequences from the ITS 1-5.8s-ITS 2 rDNA gene cluster and the protein-coding  $\beta$ -tubulin gene. In the obtained cladogram the occurrence of different types of cephalodia has been investigated. The results shows that some of the different types of cephalodia are restricted to closely related species while others are distributed in several monophyletic groups.

**Convergent evolution of parental care and sympatric speciation in hydrobiid gastropods of New Zealand.** Martin Haase. National Institute of Water and Atmospheric Research, Hamilton, and University of Waikato, Hamilton, New Zealand

In order to investigate the evolution of parental care in hydrobiid gastropods of New Zealand, I conducted a phylogenetic analysis using Bayesian and maximum likelihood methods. This analysis was based on fragments of two mitochondrial genes, COI and 16S rDNA (1130 bp). All but eight of the 29 included species brood their eggs in the distal female genital system and all but four species occur in freshwater, mainly in springs and in the groundwater. Using a maximum likelihood approach I compared the most parsimonious optimization of brooding comprising two steps with three step scenarios. Similarly, I compared the three different three-step scenarios of habitat transitions. In a combined analysis I investigated whether both ovoviviparity and habitat transition evolved interdependently. These

analyses indicated that brooding has evolved twice after freshwater had been invaded, which was achieved by three lineages independently. Tightly linked with these questions was the finding that three pairs of species may have originated in sympatry. This was suggested by mitochondrial similarity, morphological distinctness used as a control for nuclear hybridization, and present-day sympatry.

**A review of zooxanthellate systematics.** Megan Harrison Cevalco. American Museum of Natural History, Division of Invertebrate Zoology, Central Park West and 79th Street, New York, NY 10024, USA

First recognized by Brandt (1881), endosymbiotic zooxanthellae are a defining feature of tropical reef communities. Reef zooxanthellate symbioses characterize a wide variety of invertebrate host taxa ranging from metazoan cnidarians to protozoan foraminifera. Yet, despite the ubiquity and ecological importance of these symbiotic associations, species diversity of zooxanthellae has yet to be resolved. Historically zooxanthellae were classified as a single panmictic species (*Symbiodinium microadriaticum*), as described by Freudenthal (1962) from the cultured symbionts isolated from Caribbean *Cassiopeia* (jellyfish) and *Condylactis* (anemone). Prior to molecular characterization a paucity of taxonomic information retrievable from the coccoid symbiotic state of *Symbiodinium* mired comprehensive phylogenetic studies of the genus. However, within the past decade molecular sequence data generated from ribosomal, chloroplast, and mitochondrial genes has revealed complex patterns of diversity have been recognized among *Symbiodinium* ‘phylogenotypes’ although specific epithets have yet to be given. These patterns challenge the familiar paradigm in which hosts and symbiont coevolve. A review of the systematics of the genus *Symbiodinium* is presented, as well as, cladistic analyses using Genbank deposited sequences. In addition, the placement of *Symbiodinium* within the family Symbiodiniaceae and the larger dinoflagellate order Suessiales is examined.

**Menispermaceae (Ranunculales) phylogeny: statistical tests and fossils contributions to the resolution.** Frédéric Jacques\* and Cyril Gallut. Muséum National d’Histoire Naturelle, Département Histoire de la Terre, UMR CNRS 5143, 8 rue Buffon, 75005 Paris, France; Université Pierre et Marie Curie, Bât. Cuvier, 12 rue Cuvier, 75005 Paris, France

This study uses different methods (Reduced Cladistic Consensus, NoiseSnapper and inclusion of fossils) to retrieve more information from an apparently unresolved component consensus. Those methods are illustrated on the phylogeny of Menispermaceae, a pantropical family of basal Eudicots. A Reduced Cladistic Consensus profile combines consensus with

pruned taxa (though included in cladistic analysis). It limits the loss of information frequent in strict component consensus. Nevertheless, its interpretation has to be made carefully in order to avoid overinterpretation. *NoiseSnapper* evaluates characters’ information content. For a given topology, *NoiseSnapper* retrieves the characters that cannot be discriminated from random ones. As the most sustained cladograms are those with the fewest random characters, *NoiseSnapper* allows us to find them in a set of minimal length trees. An independent analysis with menispermacean fossils from Lower Eocene of Paris Basin confirms the results obtained by the former analysis. After such analyses, Menispermeae DC. is the only nonmonotypic tribe found to be monophyletic. The need of a reassessment of Menispermaceae classification is confirmed therefore by these results.

**Towards a new phylogeny of Menispermaceae (Ranunculales).** Frédéric Jacques. Muséum National d’Histoire Naturelle, Département Histoire de la Terre, UMR CNRS 5143, 8 rue Buffon, 75005 Paris, France

The family Menispermaceae is composed of 71 genera and is mostly pantropical. The present used classification, consisting of eight tribes (Menispermeae DC., Tiliacoreae Miers, Anomospermeae Miers, Coscinieae Hook.f. & Th., Tinosporeae Hook.f & Th., Peniantheae Diels, Fibraureae Diels, Hyperbaeneae Diels), was established by Diels in 1910. It was principally based on morphology of fruits and seeds because of the highly recognizable and diverse shapes of endocarps. Since then only regional revision have been undertaken by Troupin (Africa), Forman (South-East Asia), Moldenke, Krukoff and Barneby (South America). I started a worldwide phylogenetic revision of the family. The present study focused on 22 extant genera representing all the tribes and eight extinct genera. A cladistic analysis was undertaken with 58 morphological characters (leaves, inflorescences, flowers, fruits, seeds and pollen). The results show that only the tribe Menispermeae, well characterized by its horseshoe-shaped endocarp, can be maintained. No geographical structure can be retrieved. This work is however, too preliminary to propose a reassessment of classification. The endocarp’s sclerification shows a higher diversity than expected and is a way of further investigation. Other perspectives are the wood anatomy and molecular analysis.

**Phylogeny of isophyllous liverworts.** Aino Juslén. University of Helsinki, Department of Biological and Environmental Sciences, Plant Biology, Finland

It has been traditionally assumed that erect growing-form and isophylly are primitive characters among leafy liverworts. However, our first comprehensive molecular phylogeny of leafy liverworts resolved isophyllous families as one the youngest lineages. Vetaformaceae,

Lepicoleaceae, Mastigophoraceae, and Herbertaceae are all isophyllous, i.e., the lateral leaves are similar with underleaves, and they all have deeply divided leaf lobes. The aim of this study is to answer whether these four families are monophyletic, and to test the monophyly of the included genera. The relationships of especially Mastigophoraceae to the rest of the families have remained ambiguous, and special emphasis was given to this family. I also tried to resolve intrageneric relationships of the largest genus of the study group, *Herbertus*, in order to evaluate division to sections suggested formerly. The dataset consisted of 44 taxa, seven of which belong to the outgroup. Phylogenetic analyses were conducted using morphology and sequence data from the chloroplast gene region trnL-F and the nuclear encoded ITS 2. The data was analyzed using direct optimization as implemented in the program POY, and additionally also based on static alignment with the program Nona. The results show that the four isophyllous families form a monophyletic group. The study confirms the close relationship of Mastigophoraceae to the rest of the families. All the genera are resolved as monophyletic, and the results give support for some subgeneric groupings of *Herbertus* and *Lepicolea*, and also challenge monophyly of some currently recognized species of *Herbertus*.

**Quantitative phylogenetic systematics: a new/old paradigm in phylogenetic inference.** Arnold G. Kluge. Cladistics Institute, Ann Arbor, MI 48103, USA

The evolutionary paradigm of Quantitative Phylogenetic Systematics (QPS) is largely founded on the concepts articulated by Farris (1967), Farris, Kluge, and Eckhardt (1970), Baker (2003), and Grant and Kluge (2004). Farris' long forgotten concept of patristic difference focuses the inference directly on the transformation of the character state, from the ancestral condition, not on the synapomorphic similarities of the terminal taxa. It is because these transformation events occupy the same place in the causal sequence, i.e., have the same causes and effects, that they can be considered identical and additive. And, it is on the basis of this kind of additivity that I formulate a new antisuperfluity rationale for choosing among competing cladistic hypotheses, which I designate Farris Parsimony (FP): choose the hypothesis of cladistic relationships that minimizes the overall patristic difference, because that hypothesis explains more independently heritable transformation events as propositions of homology. QPS is concerned with the spatio-temporally restricted; the class concepts of similarity and homoplasy are not parameters. QPS is an ideographic, not a nomothetic, science. Severity of test (Popper, 1959), and the objective measure of support that follows from falsification (Grant and Kluge, 2003), are logically consistent with the discovery of the ideographic history of species

(Kluge, 2002, 2003), and may therefore be considered important aspects of QPS. W. Wheeler's (1996) direct optimization/dynamic homology method employs the concept of patristic difference, and for which FP now provides an epistemological justification for choosing the most parsimonious cladistic hypothesis.

**Evolution of aposematic warning colors in parasitic wasps (Hymenoptera: Braconidae).** Jason W. Leathers. Oregon State University, USA

Hymenoptera, with their painful stings, bites, and noxious chemical defenses, are the most frequently mimicked organisms in the world. Natural selection has yielded an assortment of aposematic warning color patterns to advertise these properties, and these patterns are copied by members of nearly every other order of winged insect. Such aposematic color patterns are found in parasitic wasps of the Neotropical *Compsobracon* group (Braconidae: Braconinae). This group contains 22 described species in seven genera: *Compsobracon* Ashmead, *Calobracon* Szépligeti, *Cyclaulax* Cameron, *Compsobraconoides* Quicke, *Cyclaulacidea* Quicke and Delobel, *Gracilbracon* Quicke, and *Sacirema* Quicke. Many members of this group have color patterns similar to several thousand species of Braconidae, Ichneumonidae, sawflies, assassin bugs, flies, moths, and beetles. One explanation for this observation is that the members of the complex and their colors are generated by multiple cospeciation events resulting in the constituent genera having isomorphic phylogenetic trees. An alternative explanation is that the organisms have colonized existing color pattern niches independently and do not have topologically similar phylogenetic histories. In order to test the hypothesis that these are the result of cospeciation events the patterns will be described and mapped onto a phylogenetic tree. If clades are found to have isomorphic topologies; evidence will suggest cospeciation. However, if clades are not found to have similar topologies, evidence will suggest independent colonization of color pattern niches.

**Phylogeny of the african Murinae: the *Praomys* group as a case of extreme adaptive convergences.** Emilie Lecompte\*, Christiane Denys and Laurent Granjon. Muséum National d'Histoire Naturelle, Département Systématique et Evolution, FRE 2695 CNRS, 45 rue Buffon, 75005 Paris, France; Laboratoire de Mammalogie (CBGP, UMR R022), IRD, BP 2528, Bamako, Mali; Institut für Virologie, AG ter Meulen, Robert-Koch-str. 17, 35 037 Marburg, Germany

The murine African fauna is mainly characterized by endemic genera and their phylogenetic relationships with the Eurasiatic Murinae are not well understood. A previous molecular work based on DNA/DNA hybridization suggests that African murine fauna is the result of several waves of immigration from Asia. In order to



test this hypothesis, we realized the partial IRBP nuclear gene (exon 1) phylogeny among the Murinae, comprising about 30 genera and including species from the *Praomys* group and the Arvicanthines, the two major African Murinae groups. Assuming the molecular clock, the emergence date of these African Murinae groups were calculated. The NJ, MP and ML trees are congruent and confirm the monophyly of these two major groups. As main results of these analyses, we find that the African Murinae are polyphyletic and are issued from at least 3 different immigration waves. The relationships within the *Praomys* group are analyzed in detail, combining the complete cytochrome b gene and the partial IRBP gene sequences. The confrontation of the different morphological and molecular phylogenetic trees obtained, shows that the morphology within the group is very convergent and the observed variations between taxa are probably adaptive. Moreover, the majority of characters used for determination are completely homoplastic, such as the number of mammae or the incisive foramen. There are many indications that this group results from an adaptive radiation which occurred at the end of the Miocene probably around 8–7 Ma. An evolutionary scenario is proposed for the divergences observed within this group.

**Phylogenetics and biogeography of *Cryptocercus* Scudder, 1862: the old cockroach out (Dictyoptera: Blattaria).** Frédéric Legendre<sup>1\*</sup>, Philippe Grandcolas<sup>1</sup>, Xavier Bellés<sup>2</sup>, Maria-Dolors Piulachs<sup>2</sup>, Yung Chul Park<sup>3</sup> and Jérôme Murienne<sup>1</sup>. <sup>1</sup>FRE 2695 CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 45 rue Buffon, 75005 Paris, France; <sup>2</sup>Department of Physiology and Molecular Biodiversity, Institut de Biologia Molecular de Barcelona (CSIC), Jordi Girona 18, 0834 Barcelona, Spain; <sup>3</sup>School of Biological Sciences, Flinders University of South Australia, GPO Box 2100, Adelaide 5001, Australia

The woodroach *Cryptocercus* has been considered for a long time as a key taxon for understanding the relationships and the evolution in Dictyoptera and Isoptera. It has been mainly studied in North America, even if it has an amphiberian distribution, occurring both in East Asia and North America. Little is known about *Cryptocercus* in Asia, which prevents any historical study of its distribution. For example, it has never been tested properly until now whether disjunctions between East Asia and North America occurred only once or several times. To improve that situation, new taxa from East Asia and Ohio in the USA are included in this study. The former are useful for understanding the evolution of the distribution of the whole genus while the latter are interestingly located at the northern boundary of the genus in eastern North America. The phylogenetic analysis carried out with two portions of

mtDNA genes 12S and 16S provides a pattern where Asian and North American taxa are two monophyletic sister groups, respectively. Within the American clade, populations from Oregon are monophyletic and sister group of Eastern populations. Diversification during the late Cretaceous (with Euramerica and Asiamerica lands) would imply another pattern where American populations would not be monophyletic. During the Tertiary and Quaternary, Beringian and North Atlantic land bridges could not have been used except in the Miocene for climatic and biotic reasons. This pattern considered together with the paleogeographical data shows that *Cryptocercus* diversification is merely recent, dating back to Miocene, as also shown independently by some attempts of molecular dating. This Miocene age suggests that *Cryptocercus* cannot be the sister group of Termites, a group presently dated from lower Cretaceous period according to the fossil record.

**Accuracy of biological identification through DNA barcodes.** Diana Lipscomb. George Washington University, Washington, USA

**Building trees from ESTs: what can ribosomal proteins tell us about metazoan phylogenies?** Stuart J. Longhorn\*, Peter Foster, Kosmas Theodorides, Anna Papadopoulou and Alfried Vogler. The Natural History Museum, Cromwell Road, London, UK

Molecular systematists are beginning to exploit 'genomic technologies' to explicitly address phylogenetic issues, generating large volumes of sequence data from the nuclear genome. The expressed sequence tag (EST) approach exploits reverse-transcription of mRNA to generate cDNA libraries of multiple nuclear genes. As part of the translational machinery of the cell, ribosomal proteins (RPs) have among the highest transcription rates in the eukaryotic genome, and are readily detected within cDNA libraries. Using sequences curated from EST data, we investigate ribosomal proteins as a character set capable of reconstructing both well-established and contentious aspects of the Metazoan (animal) phylogeny. We curated EST data from multiple vertebrate taxa from public databases to investigate the behavior of RPs across a stable phylogeny, which we show RP sequences can reconstruct robustly, with results of cladistic analysis broadly congruent other methodological approaches. These data suggest that, for the ribosomal proteins at least, increasing gene sampling leads to improvements in signal and support, with simultaneous analysis leading to the recovery of increased (hidden) branch support at most nodes. We apply the RP dataset to investigate taxonomic questions where single gene phylogenies (mainly rRNA) are typically at odds with morphological viewpoints, such as the position of the nematodes relative to arthropods, and the relationships of the Holometabola insects (with

complete metamorphosis). Results suggest that, when gene sequences are carefully selected and analyzed, new molecular sequence data from EST libraries can be used to provide new inferences on some relationships, but that multiple nuclear genes may be affected by shared biases that can confound phylogenetic analyses, such as differences in compositional differences and mutation rates among taxa. Across the Arthropoda, we generated new EST libraries for around 30 taxa, effectively doubling the number of insect taxa with large EST libraries (> 200 nonredundant sequences) in the public domain. Within the insects, we aim to show how phylogenetic analysis with ribosomal protein can reconstruct the monophyly of groups such as the Lepidoptera and Diptera well, and provide new inferences on beetle (Coleopteran) evolution.

**Chilean anapids and their webs, a phylogenetic approach (Araneae, Anapidae).** Lara Lopardo\* and Martín J. Ramírez. Department of Biological Sciences, The George Washington University, 2023 G St NW, Washington, DC 20052, USA; Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; Current Address: División Aracnología, Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina

In a recent paper, the orb webs of the Chilean anapid genera *Crassanapis*, *Sheranapis*, and *Elanapis* were described for the first time. *Crassanapis* and *Sheranapis* species spin a typical anapid web, with one to several above the orb-plane radii. Their webs are intraspecifically variable in architectural details and size. *Sheranapis villarrica* often constructs smaller webs close to the water surface of streams. The web of *Elanapis aisen* is bidimensional, without out of the orb-plane threads, like those of some Symphytognathidae. Moreover, the mysmenid genus *Maymena* builds three-dimensional orb webs typical of anapids. The bidimensional symphytognathid-like web and the protruding labrum typical of Anapidae among other characters make *Elanapis* an interesting taxon in the phylogenetic analysis of symphytognathoids. Three anapid species representing the three genera were added into three different published data matrices, and the matrices were reanalyzed under parsimony and equal weights. The original cladograms were not drastically different after the inclusion of Anapidae representatives, and Anapidae is monophyletic. While orb web architecture and the behaviors used for its construction comprise the main group of synapomorphies defining Orbiculariae, the convergence in its architecture is flamboyant, at least within symphytognathoids. This convergence questions the membership of some representatives within their families, as well as the phylogenetic content of orb

webs structural details, at least in this big group of small spiders.

**An empirical test of DNA taxonomy in Diptera based on cox-1 sequences.** Rudolf Meier\*, S. Kwong, G. Vaidya and P. K. L. Ng. Department of Biological Sciences, University Scholars Programme, Special Programme in Science; National University of Singapore, 14 Science Dr 4, Singapore 117543

Identification of specimens using traditional techniques has always been unpopular with most biologists. It is thus not surprising that recently population biologists, developmental biologists, and ecologists have proposed an obvious improvement: identification based on DNA sequences ('DNA barcodes'). It is also not surprising that these proposals have attracted a lot of attention from organizations and journals firmly committed to the advancement of taxonomy (e.g., Nature, Science, Sloan Foundation, GBIF). Here we present the results of an empirical test of specimen identification through 'DNA barcodes' based on 1390 sequences of cytochrome oxidase c subunit 1 for 458 species of Diptera (Insecta). We find considerable intraspecific sequence variation which overlaps extensively with the congeneric interspecific variability. In simulating a real-life identification situation, we pretend for each sequence that its species identity is unknown, compare it against the remaining sequences, and determine whether it can be accurately identified to species. Based on pairwise-distance, we find that 69–89% of all sequences are correctly identified depending on whether all or only those species are included that have multiple sequences in the database. 5.2% of all queries are misidentified and 6% are ambiguous. 7.7% of all barcode pairs with identical sequences are allospecific. The success of tree-based identification is lower with fewer than 50% of all sequences forming species-clusters. We discuss the potential shortcomings of using data from GenBank and demonstrate for Diptera why it is misleading to propose a fixed percentage-distance for distinguishing intra from interspecific variability.

**New molecular data on Iberian *Merodon* species (Diptera, Syrphidae).** Ximo Mengual\*, Gunilla Ståhls and M<sup>a</sup> Angeles Marcos-García. CIBIO. Universidad de Alicante. 03080. Alicante. Spain; Finnish Museum of Natural History. PO Box 17, FIN-00014 University of Helsinki, Finland; CIBIO, Universidad de Alicante, 03080, Alicante, Spain

The genus *Merodon* Meigen, 1903 (Syrphidae, Diptera) with more than 50 European species is one of the most widespread in the Mediterranean region. In the Iberian peninsula 32 species of *Merodon* occur, 20% of these are endemic, and we obtained molecular data of 16 of them for this work. Most of the species are insufficiently treated in taxonomic works, and life histories and

biology are poorly known. The lack of the description of the females of many species increases the difficulty of identification. The doubtful species limits in some species of *Merodon* with a high intraspecific variability, prompted us to evaluate the utility of molecular characters for this question. The mitochondrial protein-coding gene cytochrome c oxidase subunit I (COI) was chosen for sequencing, as well as the nuclear 28S ribosomal gene and the nuclear internal transcribed spacer (ITS2) region. Parsimony analysis identified three well supported clades within *Merodon* that are concordant with previously established morphological species groups/clades. The molecular noncoding ITS2 as well as the COI data supported clear delineations of all species, and linked doubtful females to males in two cases, *M. ottomanus* and *M. tricinctus*. Molecular data of the COI and ITS2 gene regions were informative for defining new taxa that previously had been poorly established with morphological characters.

**BOGEN/BLANCE: a faster parsimony program for larger trees – with an example of reconstructing ancestral sequences of enzymes detoxifying microcystin of the blue-green algae.** Nobuhiro Minaka<sup>1\*</sup>, Haruo Yamamoto<sup>2</sup>, Takashi Suemura<sup>3</sup>, Takahiro Asano<sup>2</sup>, Kouki Machii<sup>3</sup>, Kunihiro Okano<sup>4</sup> and Norio Sugiura<sup>4</sup>. <sup>1</sup>National Institute for Agro-Environmental Sciences, Japan; <sup>2</sup>Bogenpfeil; <sup>3</sup>Turaltech; <sup>4</sup>University of Tsukuba, Japan

BOGEN/BLANCE is an updated version of a program for building parsimonious trees from large molecular sequence data. Both DNA and amino acid sequences can be input data matrices. The upper limit of the current version is 30 000 OTUs and 50 000 base pairs. There are also some improvements of tree-searching strategies using simulated and real data. Several new features are demonstrated with a graphical user-interface which makes easier manipulations of data and calculations of trees. As an example of using BOGEN/BLANCE we reconstructed the most parsimonious cladogram of bacterial antitoxic enzymes acting on an algal toxin ('microcystin' of the blue-green algae) based on 16S-rDNA data. All known antitoxic bacteria form a compact clade. Ancestral reconstruction of the antitoxic gene ('mlrA') was done on the estimated 16S-rDNA cladogram. We are now working on the activity of hypothetical ancestral 'mlrA' genes. Preliminary results are given.

**A phylogeny for the family Characidae (Teleostei, Characiformes).** Juan Marcos Mirande. Fundación Miguel Lillo, San Miguel de Tucumán, Argentina

The family Characidae is one of the most diverse among the Neotropical fishes, with approximately 1000 described species. A phylogeny of this family as a whole has never been published, and its monophyly is uncertain. Only a few subfamilies (Cheirodontinae, Glandulocaudinae, Serrasalminae, Stethaprioninae) and genera

(*Creagrutus*, *Deuterodon*, *Bramocharax*, *Jupiaba*, *Chalceus*) that include less than 30% of the species of the family were treated phylogenetically. These analyses, however, did not treat the relationships of these supposedly monophyletic subunits with the remaining species of the family. The species not included so far in any phylogenetic analysis are in its majority included in a few, probably paraphyletic, genera with more than 50 species each one (*Astyanax*, *Bryconamericus*, *Hemigrammus*, *Hyphessobrycon* and *Moenkhausia*), and numerous monotypic genera. Most of these species are anatomically alike and belong to the subfamily Tetragonopterinae. This subfamily is currently considered as paraphyletic, although its paraphyly has not been demonstrated cladistically. This research is intended to provide a phylogeny for the family, focusing in a cladistic definition, the relationships of subunits phylogenetically defined, and the position of genera and species never treated in phylogenetic studies. The dataset was constructed with morphological data (mainly osteological) and consists of 54 species representing the diversity of forms within the family, scored for 269 informative characters (of which roughly two thirds are unpublished). The trees were rooted at *Parodon* sp. (Parodontidae), and *Cyphocharax pilotus* (Curimatidae), *Leporinus striatus* (Anostomidae), *Hoplias* sp. (Erythrinidae), and *Characidium* sp. (Crenuchidae) were included as outgroups. The analysis was performed using implied weighting. An experimental method to choose concavity was implemented and compared with alternative methods proposed in literature. The concavity selected produced a single tree, rather coherent with ideas previously proposed in literature. The monophyly of the family Characidae is well supported. Other well supported groups are the genera *Oligosarcus*, *Aphyocharax*, *Roebooides* + *Galeocharax*, and the subfamilies Serrasalminae and Cheirodontinae. Tetragonopterinae, as traditionally defined, is paraphyletic in terms of Cheirodontinae and Glandulocaudinae; the genera *Astyanax*, *Bryconamericus*, and *Moenkhausia* are non-monophyletic.

**Evolution on a shaky piece of Gondwana: a phylogenetic analysis of the endemism in the cockroach genus *Angustonicus* in New Caledonia (Blattaria, Tryonicinae).** Jérôme Murienne,<sup>1\*</sup> Philippe Grandcolas,<sup>1</sup> Maria Dolors Piulachs,<sup>2</sup> Xavier Bellés,<sup>2</sup> Cyrille D'Haese,<sup>1</sup> Frédéric Legendre,<sup>1</sup> Roseli Pellens and <sup>1</sup>Eric Guilbert. <sup>1</sup>FRE 2695 CNRS, Département Systématique et Évolution, Muséum national d'Histoire naturelle, 45, rue Buffon, 75005 Paris, France; <sup>2</sup>Department of Physiology and Molecular Biodiversity, Institut de Biologia Molecular de Barcelona (CSIC), Jordi Girona 18, 0834 Barcelona, Spain

New Caledonia is well known as a hot spot of biodiversity whose origin as a territory can be traced back to the Gondwanan supercontinent. The local flora

and fauna, in addition to being remarkably rich and endemic, comprise many supposedly relictual groups. Does the New Caledonian biota date back to Gondwanan times, building up its richness and endemism over 100 Myr or does it result from recent diversifications after Tertiary geological catastrophic events? Here we use a molecular phylogenetic approach to answer this question with the study of the endemic genus *Angustonicus* (Blattaria, Tryonicinae). Both geological and molecular dating show that the diversification of this group is less than two millions years old and is consistent with hypotheses of Tertiary bottlenecks in the New Caledonian biota.

**Toward a phylogenetic analysis of Listriodontinae (Suidae, Mammalia).** Maeva Orliac. Muséum National d'Histoire naturelle, Département histoire de la Terre, UMR 5143 CNRS, 8 rue Buffon, 75005 Paris, France

There has been a long running debate about the classification of Listriodontinae. Recent revisions made by Pickford (1986, 1988, 2003) and Made (1996) resulted in highly incongruent classifications and phylogenies. The trees proposed by these two authors are based on the characterization of small lines of descent constructed with characters arbitrarily deemed relevant, conflated in agreement with the stratigraphy. The aim of this work is to clarify the systematics of the subfamily by a real phylogenetic analysis based on parsimony. The synonymy between taxa is highly controversial. Hence, the material from the type localities was included without regard to synonymy. The results support the monophyly of the Listriodontinae *sensu lato* as well as the monophyly of the two entities 'Kubanochoerinae' and 'Listriodontinae'. However, the monophyly of 'Lopholistriodontinae' is not recovered. A special attention has been paid to the species *Bunolistriodon lockharti*, which consists in a 'paraphyletic assemblage'. These preliminary results include only dental characters, but show that a reassessment of the systematics of this group is needed.

**A brief report from a phylocode mole.** Kurt M. Pickett. American Museum of Natural History, 79th Street at Central Park West, New York, NY 10024, USA

(Eukaryota/Metazoa/Bilateria/Deuterostomia/Chordata/Craniata/Vertebrata/Gnathostomata/Sarcopterygii/Tetrapoda/Amniota/Synaspida/Therapsida/Mammalia (Whew!)/Eutheria/Insectivora/Talpidae/*Scalopus*; or for brevity, 'the most recent common ancestor of *Scalopus* and all extant organisms or species that share a more recent common ancestor with *Scalopus* than with something non-*Scalopus*'). A brief report from the Phylocode meetings will be presented.

**The persistence of clade prior influence in Bayesian phylogenetic analyses.** Kurt M. Pickett\* and Christopher P. Randle. American Museum of Natural History, 79th

Street at Central Park West, New York, NY 10024, USA

In Bayesian phylogenetics, two phenomena pertain to topological prior influence: 1. the influence that nonflat clade priors have on clade values, and 2. the amount of data required to overwhelm this influence. A brief review of the first point is presented. Given the knowledge of how flat topological priors affect clade values, the role of prior influence in these values given increasing data can be investigated. Bayesian theory provides that the likelihood function will overwhelm the influence of priors given sufficient data. However, the amount of biological data necessary to accomplish this has not been established. The persistence of flat topological prior influence on clade values is examined for varying amounts data simulated using a simple model of substitution.

**Assembling the scorpion tree of life: phylogeny of extant scorpions based on morphology, molecules and exemplars.** Lorenzo Prendini\* and Ward C. Wheeler. Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

Recent attempts to reconstruct the phylogeny of extant scorpions by Soleglad and Fet are inadequate. The analyses are based on supraspecific terminal taxa representing genera, the monophyly of which has either been previously falsified or remains untested and (in many cases) doubtful. Essential outgroup taxa, e.g., eurypterids, xiphosurans and other arachnids, are omitted entirely. Composite terminals, assembled from the anatomical fragments of disparate genera, are created for fossil scorpions. The analyses are riddled with unjustifiable assumptions concerning character evolution and primary homology, none of which are tested. This approach is deliberately adopted to reduce 'homoplasy' and attain a preconceived result. As such, homologous structures in different taxa are assigned separate (often autapomorphic) states. Reversals are coded as separate characters. Character transformation is forced with additive binary coding and Sankoff optimization through allegedly intermediate states for which there is no empirical evidence. Characters are often poorly defined. States display overlapping variation in some but probably encompass several characters in others. Polymorphic 'states' are created for terminals with intrageneric variation. Many characters are not even evaluated for most terminal taxa, but merely scored 'inapplicable' although the structures in question are present in these taxa and the characters are therefore applicable to them. This contribution addresses these problems in a reanalysis and provides preliminary results from a competing programme to reconstruct the phylogeny of extant scorpions based on multiple sources of character data (DNA sequence from six loci in the nuclear and mitochondrial genomes, and

morphology) acquired from multiple exemplar species, currently representing all scorpion families and more than half of all scorpion genera. Results of this exercise highlight the futility of recent familial and generic reshuffling, predicated on insufficient evidence, preconceived notions, and questionable analytical practices, in the face of phylogenetic instability.

**Aligning morphologies.** Martín J. Ramírez. CONICET, Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina

The sequential application of first resolving primary homology, and second searching for optimal phylogenetic trees is not granted to produce optimal results when there are more than one plausible primary homology schemas. This problem is well known for the analysis of DNA sequence data, but has received little attention in the case of more complex data, like morphology and behavior. The interaction between comparative studies and phylogenetic inference is most patent in the favoring of comparisons between close relatives at the time of deciding on homology. The traditional problem of alternative anatomical interpretations affecting morphological characters is identified as belonging to the same conceptual problem as the alternative alignments of DNA sequences. Gains and losses are equivalent to insertions and deletions, respectively, but not all homology shifts in morphology structures are equally costly; homology shifts in anatomical interpretations must take account of heterogeneous bounds in the number of conditions observed in morphological characters (differing from the four possible states in nucleotide sequence data); and transformations in anatomy are frequently multidimensional (differing from the one dimension of sequence transformation events). I present an example case of 93 representative species of the spider family Anyphaenidae. The homology of some sclerites in the male copulatory organ is disputed, and that region involves phylogenetic information scored in more than 20 characters (out of 200). The alternative interpretations of the anatomy produce different optimal tree sets and different ancestral reconstructions of the structures over the trees. I discuss the requisites, and present a proposal, for scoring and analyzing a morphological dataset for the simultaneous evaluation of alternative homologies and phylogenetic hypotheses. The most parsimonious trees are identified together with the most parsimonious homology schemas.

**Problems in accumulation of phylogenetic data: an example case of a morphology based analysis of dionychan spiders.** Martín J. Ramírez. CONICET, Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470, C1405DJR Buenos Aires, Argentina

As phylogenetic analyses accumulate, there is more and more overlapping in characters and terminals

among different studies. Taking the example of spiders, this accumulation of phylogenetic analyses did not imply much of an accumulation in knowledge. Fusing datasets (i.e., combining two or more datasets in a broader analysis) is at best laborious, and most often impossible. Differences in character state definitions, and in representative taxa are the obvious limitations, but the ways in which phylogenetic data are recorded, documented, and disseminated impose important restrictions as well. These problems are exemplified with the construction of a cladistic dataset of *Dionycha*, an informal group of 17 families of two-clawed spiders. Sometimes regarded as the crown group of spiders, *Dionycha* comprises about 2000 genera and more than 13 000 species, 35% of the spider species known to date, including the charismatic jumping spiders, and crab spiders. I reviewed most morphological systems and previously proposed characters, and built a unified homology system spanning much of the spectrum of variation within spiders. The dataset comprises about 400 characters scored for about 140 taxa, and is documented with 4800 original SEM images. I discuss the issues of documentation, scoring of noninformative characters, and the priority of databases over cladistic datasets. The construction of character states is not a naive procedure, and in general must be done after the data is collected. Storing observations in the most unprocessed form increases the possibilities for data growing and accumulation. I discuss possibilities for a layered structure of phylogenetic data.

**Matching the evolution of reproductive behavior and associated structures in Eneopterinae (Orthoptera, Grylloidea, Eneopteridae).** Tony Robillard\*, Laure Desutter-Grandcolas and Urs Ziegler. FRE 2695 CNRS, Département Systématique et Evolution, Muséum national d'Histoire naturelle, 45 rue Buffon, 75005 Paris, France; Institute of Anatomy, University of Zürich, Y42 H 4, Winterthurerstrasse 190, CH-8057, Zürich, Switzerland

Crickets are well known for their very stereotyped reproductive behavior which often includes, during the spermatophore transfer, the mouthing by the female of glands located on the male dorsum. In most crickets, glandular structures associated with this behavior correspond to the metanotal glands first described by Hancock in *Oecanthus*, but are also associated with a great diversity of structures located on tergites, forewings and hindtibiae. We focus here on the subfamily Eneopterinae. The phylogeny of Eneopterinae has been previously reconstructed using morphological data on exemplars of almost every genus, and used to optimize mouthing behavior and glandular structures. Mouthing behavior is ancestrally ambiguous, yet evolutionarily labile within the subfamily. Optimizations of glandular structures

document several kinds of patterns of transformation and evolutionary processes, such as parallelism, reversal and convergence. Structures associated with mouthings are mostly absent ancestrally: matching their evolution with that of the mouthings behavior involves repeated occurrences of both structures and behavior, multiple modifications of glandular structures in association with a plesiomorphic behavior, and also shifts in structures involved in an ancestral function.

**An exemplar phylogeny of the Ranidae (Anura: Neobatrachia: Ranoidea), based on the analysis of morphological and molecular data.** Elizabeth Scott. Vertebrate Section: Herpetology, Transvaal Museum, PO Box 413, Pretoria 0001, South Africa

Ranidae is one of the largest families of Neobatrachia, but its taxonomy is in a state of flux. This study presents results of a simultaneous cladistic analysis of morphological and molecular data for ranoid frogs, the primary aim of which was to test the monophyly and proposed relationships of the major clades of Ranidae, variously ranked as subfamilies or families in the past. Exemplars of all additional ranoid families were included (Arthroleptidae, Astylosternidae, Hyperoliidae, Hemisotidae, Mantellidae, Microhylidae, Petropedetidae, Rhacophoridae), as their relationships to the various clades of Ranidae are untested, and the basal relationships in Ranoidea are poorly understood. The study used approximately 600 bp of DNA sequence from loci in the mitochondrial 12S rDNA and 16S rDNA genes, combined with 192 characters from morphology, for 78 exemplar species. Results confirm that Microhylidae is the sister taxon of Ranidae, and that *Hemisus* is a member of the Microhylidae. The Malagasy mantellids are confirmed to be part of the rhacophorid lineage, although morphological synapomorphies for this group were not apparent from the taxa and characters included here. The rhacophorid lineage is embedded amongst clades traditionally considered to be part of Ranidae *sensu lato*, prior to the implementation of the current phenetic classification. The recognition of the family Petropedetidae, as separate from Ranidae, is incorrect. This is clearly a paraphyletic assemblage of up to three clades (petropedetines, cacosternines and phrynobatrachines), whose ranks remain to be determined, as they are embedded in Ranidae. The phylogenetic hypothesis obtained here indicates that two of the seven putative ranid subfamilies (Dicroglossinae and Raninae) are demonstrably grossly paraphyletic, according to their current definitions. Three of the putative ranid subfamilies (Tomopterninae, Ptychadeninae and Pyxicephalinae) appear to represent small, divergent monophyletic lineages, but two of these are deeply embedded in other putative clades of Ranidae, and therefore of questionable rank as

subfamilies. Results obtained here suggest that all clades of ranid frogs (including Rhacophoridae and its subfamily Mantellinae) should be relegated to subfamilial or tribal rank within a larger Ranidae, until further clarification of their appropriate rank and content is obtained. Major reshuffling of the taxa comprising the putative subfamilies is required to restore monophyly of the classification. As such, the current classification should be used simply as a working hypothesis to be tested, not a reflection of the evolutionary history of these frogs.

**Symbiosis, pathogenesis and phylogenetic relationships of the insecticidal nematode bacteria complex *Steinernema-Xenorhabdus*.** Mathieu Sicard<sup>1\*</sup>, Noël Boemare<sup>2</sup> and S. Patricia Stock<sup>3</sup>. <sup>1</sup>Laboratoire Génome, Populations, Interactions, Adaptation, CP 105, Université Montpellier II, UMR 5171 CNRS, 34095 Montpellier Cedex, France; <sup>2</sup>Laboratoire de Pathologie Comparée, CP 101, Université Montpellier II, INRA-CNRS no. 2209, 34095 Montpellier Cedex, France; <sup>3</sup>Div. Plant Pathology and Microbiology, Department of Plant Sciences, University of Arizona, 1140 E. South Campus Dr, Tucson, AZ, 85721, USA

An emerging model of terrestrial animal-microbe mutualism is represented by the association between *Steinernema* spp. (Nematoda: Steinernematidae) nematodes and their symbiotic bacteria *Xenorhabdus* spp. (Gram-negative Enterobacteriaceae). Together, *Steinernema* and *Xenorhabdus* form an insecticidal complex that is effective against a wide range of insect hosts. Interest in studying steinernematid nematodes and their symbiotic bacteria mainly arose because of their use in the biological control of insects and other arthropod pests. Currently numerous laboratories worldwide are implementing this nematode-bacterial complex in agriculture, medicine and industry. Furthermore, progress in these areas coupled with the inherent experimental tractability of *Steinernema* and *Xenorhabdus* has spurred developments across a far broader scientific front such that this mutualism is now viewed as a model for basic research in ecology, evolution, biochemistry, molecular genetics and symbiosis. Taxonomic studies indicate that each *Steinernema* species has a specific natural association with only one *Xenorhabdus* species, though a single *Xenorhabdus* bacterial species may be associated with more than one nematode species. In this presentation, the level of specialization of this symbiotic association and its implications for the success of nematode reproduction and bacteria dissemination will be discussed. Furthermore, to understand the pattern of coevolution in this nematode-bacteria association, the phylogenies of these two organisms (28S rDNA and 16S rDNA genes for *Steinernema* and *Xenorhabdus*, respectively) will be compared and discussed.

**On BPA.** Mark E. Siddall. Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

Brooks Parsimony Analysis (BPA) is found to be lacking an optimality criterion and more generally to be lacking the coherence of a research program. Published defenses of the method are found to include several fabrications. Published descriptions of the methodology are self-contradictory regarding whether BPA can be used on a priori specified host trees and whether it can be used in host-parasite cospeciation at all. Rules for a posteriori duplication of entities in secondary BPA and the concatenation of associate codes are never specified and are found to be applied both capriciously and unparsimoniously. Claims that modifications of coding strategies solve known problems at best are incomplete. Such modifications introduce new difficulties and can defy logical interpretation.

**Phylogeny of glossiphoniid leeches, their endosymbiotic bacteria and implications for understanding the history of bloodfeeding-related bacterial symbioses.** Mark E. Siddall\* and Susan L. Perkins. Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA; University of Colorado, Boulder, CO, USA

Several monophagous animals have tight coevolutionary relationships with a bacterial partner that provides the host organism with otherwise unavailable nutrients. In some of these symbioses, the bacteria are transmitted vertically from parent to offspring and have undergone massive genomic rearrangements, some of which are predicted to be similar to the early stages or organellar evolution. Hematophagous leeches have also been found to harbor symbionts. North American *Placobdella* species possess specialized organs containing symbionts belonging to the subdivision alpha-proteobacteria and closely related to Rhizobiaceae. The European medicinal leech, *Hirudo medicinalis*, cultures a unique strain of *Aeromonas veronii*, which is obtained from the environment. Here we report two additional lineages of organ-specific bacterial symbionts, one from the giant Amazonian leech, *Haementeria ghilianii*, and another from *Placobdelloides jaegerskioldii*, a leech that feeds exclusively from the recta of hippos. Via DNA sequencing and fluorescent *in situ* hybridization, these symbionts were shown to belong to two clades in the subdivision gamma-proteobacteria. These results, combined a phylogenetic hypothesis for the Glossiphoniidae and for the Arhynchobdellida based on morphology and molecular characters, indicate that hemotophagous leeches have acquired lineages of symbionts at least four times during their evolutionary history.

**Phylogeny of the Scopulini moths unraveled (Lepidoptera: Geometridae).** Pasi Sihvonen. Finnish Museum of Natural History, Department of Entomology, PO Box 17, FIN-00014 University of Helsinki, Finland

Systematics of the species-rich, cosmopolitan geometrid tribe Scopulini (Lepidoptera: Sterrhinae) has been based on regional faunas, and the lack of a broad view has resulted in relatively regional generic classifications. This is the first analytical attempt to study the phylogenetic relationships of its constituent genera throughout its entire distribution area. A cladistic analysis that was based on extensive examination of characters from adult morphology and ecology revealed several equally parsimonious trees but a strict consensus cladogram of those was well resolved. The results were found to contradict earlier phylogenetic hypotheses, and, many of the previously recognized genera were found to be nonmonophyletic. Based on the present revised, synapomorphy based classification, the number of recovered genera is reduced considerably and numerous new species combinations are introduced. The results clarify homology statements and demonstrate that many of the earlier proposed generic delimiting characters are homoplastic, and, more importantly that a global perspective in the taxonomy of the Scopulini is necessary to achieve a more stable classification.

**Molecular data and syrphid phylogenetics: placement of tribe Pipizini.** Gunilla Ståhls. Finnish Museum of Natural History, PO Box 17, FIN-00014 University of Helsinki, Finland

The family of hoverflies (Diptera, Syrphidae) comprises > 5000 described species. Adults of this large group of flies feed on nectar and pollen of flowers, and pollinate plants. A classification system of three subfamilies, the Microdontinae, Eristalinae and Syrphinae, was adopted > 25 years ago. The tribe Pipizini, with syrphine-like larvae and eristaline-like imagos, was variously placed with the syrphines or the eristalines. A recent study using a combined parsimony analysis of morphological and molecular characters placed the pipizines separate if equal weighting was used, while using gap cost of 2 and higher and same cost for morphological characters resulted in hypotheses with the pipizines as basal in the Syrphinae. As taxon bias towards easily available specimens in studies of phylogenetic relationships is common in molecular systematic studies the taxon sampling was increased for the subfamily Eristalinae, the most diverse and possibly nonmonophyletic subfamily. The mitochondrial cytochrome c oxidase subunit I (COI) and the D2-3 domain of the nuclear ribosomal 28S rRNA gene (28S) were sequenced for 83 taxa altogether, including six syrphines, three pipizines. This molecular data was analyzed using optimization alignment.

**Nomenclatural use and abuse: comments on the PhyloCode.** Dennis Stevenson. New York Botanical Garden, New York, USA

The proponents of the PhyloCode seem to think they have discovered the nomenclatural problem of turning the tree of life into a taxonomic system, either through arrogance or through ignorance, given that numerous papers and textbooks since 1967 have addressed the issue but remain uncited by PhyloCoders. Although claiming to represent the systematics community and offering to classify the tree of life, the PhyloCoders do not have represented among themselves entomologists, pteridologists, gymnosperm specialists, mycologists, and prokaryote specialists to name a few. One of their notions is to replace the binominal with just the uninominal. Recognizing that the uninominal may have been used more than once, such as *alba* being used at least 645 times in the flowering plants, they would add the authors name as in *alba Linnaeus*. However, Linnaeus used *alba* many time so we would have to have *alba Linnaeus 1*, *alba Linnaeus 2*, etc. It has even been suggested that the date follow so we could have *alba Linnaeus 1 1759*, etc. So from binomial to uninominal to polynomial. Simpler and improved communication? At least both get rid of Linnaeus!

**Evolution of egg powdering behavior in proconiine sharpshooters (Insecta: Hemiptera: Cicadellidae).** Daniela M. Takiya\*, Roman A. Rakitov and Christopher H. Dietrich. Center for Biodiversity, Illinois Natural History Survey, 607 East Peabody Drive, Champaign 61820, IL, USA

The leafhopper tribe Proconiini (subfamily Cicadellinae, commonly called sharpshooters) comprises approximately 350 species in 56 genera restricted to the New World. Sharpshooters are among the most speciose groups of tropical herbivores and are common vectors of the bacterium *Xylella fastidiosa*, which causes diseases in over 20 economically important plants. Proconiine females of 14 genera powder their eggs with microscopic proteinaceous particles (brochosomes) produced by the Malpighian tubules and used by most leafhoppers as a coating to their integument. Such females usually display associated modifications: (1) large and elongated (rather than spherical) brochosomes; (2) forewings with areas of differentiated setae that facilitate storing brochosomes prior to oviposition; and (3) hindlegs with setae modified for scraping brochosomes off wings onto egg-nests. The egg powdering (EP) behavior may be viewed as an example of the evolution of a novel complex of traits associated with a new function. Among extant proconiine species, not all display the complete set of EP-related modifications, indicating that these traits did not necessarily evolve in concert. The objective of this work was to estimate the phylogeny of the tribe Proconiini and

elucidate the evolution of such traits. Our preliminary dataset included 22 outgroup taxa (Cicadellini and Phereurhininae) and 68 species belonging to 45 genera of Proconiini. Characters examined included partial sequences of the genes COI, COII, 12S, 16S rDNA, and histone H3 (2461 bp), and 100 external morphological characters. Combination of molecular and morphological datasets was supported by the ILD test. Maximum parsimony analyses of the morphological and combined datasets were carried out. Non-parametric character bootstrap and partitioned Bremer index (combined evidence dataset) were calculated as clade support measures. The phylogenetic estimate suggests a single origin of EP behavior with a concerted origin of associated structural traits, and multiple secondary losses, rather than a stepwise gradual acquisition of the modifications. Our data suggest that EP behavior is always present when both forewings and hindlegs are modified, but not necessarily absent if these structures are unmodified. Furthermore, species that appear to have lost EP behavior sometimes display vestigial structural modifications, making predictions of the presence of the behavior based on morphology difficult. More behavioral observations are needed to determine the extent to which the presence of EP behavior can be predicted by morphology. The present phylogenetic analysis suggests that the classification of the tribe Proconiini should be revised. Monophyly of Proconiini was not consistently recovered, but clades not supporting this relationship received low support. There is strong support for the presence in this tribe of two main lineages, which are incompatible with the previously recognized generic groupings based on a single morphological character – whether or not the posterior meron is concealed by the forewings. Based on our analysis, the cicadelline genera *Pamplona* and *Pamplonoidea* should be included in Proconiini, and the proconiine genus *Ochrostacta* should be placed in Cicadellini. *Homalodisca* and *Phera* are apparently not monophyletic.

**Total evidence phylogeny of *Childia* (Acoela), worms with inside-out muscles.** Yonas I. Tekle<sup>1\*</sup>, Olga I. Raikova<sup>1,2</sup>, Afsaneh Ahmadzadeh<sup>1</sup> and Ulf Jondelius<sup>1</sup>. <sup>1</sup>Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University; <sup>2</sup>Zoological Institute, Universitetskaya nab., St.-Petersburg, Russia

The Childiidae *sensu* Dorjes, 1968 comprises the acoel worms characterized by a cone shaped penis with muscular or sclerotized elements. Its phylogeny was inferred by means of a total evidence analysis including Histone H3, 28S rDNA and new 18S rDNA sequences, as well as 50 morphological characters. New characters related to muscular system and copulatory organs obtained by using confocal laser scanning microscopy of phalloidin stained specimens are included in the



phylogenetic analysis. A total of 12 taxa (9 in the ingroup and 3 outgroups) were used in the parsimony analysis of the 18S data set, which was aligned with different parameters for a sensitivity analysis, and the combined data set (18S + 28S + H3 + morphology). The incongruence (as assessed by Bremer Partitioned Support) in the node support of the groups among the four partitions was very low in the total evidence tree; except for the H3 partition. All data partitions support the split between *A. beklemischevi* (Actinoposthiidae) and the Childiidae (comprising *Childia* Graff, 1910 and *Paraphanostoma* Westblad, 1942). The monophyly of *Childia* and *Paraphanostoma* is strongly supported by both the 18S and 28S data partitions. Our study also reveals additional apomorphies uniting *Childia* with *Paraphanostoma* from body-wall musculature, statocyst muscles and male copulatory organ. Muscular system, statocyst muscles, male copulatory organ and nervous system characters proved to be the best characters for taxonomic delimitations of subtaxa within the Childiidae, whereas the seminal bursa (a frequently used character in the taxonomy of Acoela) was highly homoplastic. We also describe the body-wall musculature of six *Paraphanostoma* species, which is characterized by the reversed arrangement of the longitudinal and circular muscle layers, and by the absence of diagonal muscles on the ventral side of the body and the presence of two types of diagonal muscles on the dorsal side. *Childia groenlandica* is nested among the *Paraphanostoma* species in our total evidence tree, so we synonymize *Paraphanostoma* with *Childia*.

**The molecular phylogeny of *Miarus campanulae* (Coleoptera: Curculionidae) species group in Finland.** Varpu Vahtera\* and Jyrki Muona. Finnish Museum of Natural History, PO Box 17, FIN-00014; University of Helsinki, Finland

*Miarus* is a Holarctic weevil genus with morphologically very similar species, all breeding on *Campanula* plants. *Miarus campanulae* (L.), the type species, occurs throughout Europe except in Finland. Here it is replaced by a seemingly endemic weevil known as *Miarus fennicus* Kangas. The separation of these two species is based on the differences in the soft parts of the male aedeagi. However, these characters vary considerably and the species status of *Miarus fennicus* has remained doubtful. In order to clarify the situation, molecular data was gathered from specimens originating from a number of locations in Finland, Estonia, Denmark and Sweden. The regions sequenced were CO1 (cytochrome oxidase 1) and ITS2 (internal transcribed spacer 2). In addition to *M. fennicus* and *M. campanulae*, two other *Miarus* species, *M. distinctus* and *M. graminis*, were included in the study. Both combined and separate data sets were analyzed using the optimization alignment program POY and parsimony as the optimality criterion.

All included *Miarus* species were characterized by numerous synapomorphies, except for *M. campanulae* and *M. fennicus*, which proved to be indistinguishable from each other. Hence, we propose them to be synonymized.

**DNA based taxonomy and the tree of life.** Alfried P. Vogler\*, Toby Hunt, Joan Pons and Michael Balke. Department of Entomology, The Natural History Museum, London SW7 5BD, and Department of Biological Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK

Should we aim to establish a taxonomic system based on DNA sequences alone, and how could this be done? We are exploring methods for the use of large DNA databases in taxonomy, using sequence data from newly sequenced samples of unknown species membership, or from publicly available databases which are increasing quickly in taxonomic coverage. A reiterative procedure is proposed for data extraction, tree building and inclusion of multiple gene datasets and periodical update of trees. The Blast algorithm can be used to assign an initial placement of newly added taxa, providing starting trees for more extensive searches. A preliminary demonstration of the approach is provided using large data sets for Coleoptera (beetles) using all Genbank data of a particular size and level of similarity to query sequences for COI, 16S rRNA and 18S rRNA, in total representing over 3000 species. We use this system to assign a newly described family of Coleoptera of unknown affinity. We also demonstrate the utility of high-throughput sequencing for taxonomic studies at the species level, using examples from tiger beetles (genus *Rivacindela*) of Australia and aquatic beetles (genus *Copelatus*). Species delimitation was highly successful based on sequences only, and the distribution and phylogenetic history of sequences provided excellent information about historical biogeography, dispersal patterns, age and persistence of populations, phylogeography and dynamics of species evolution, without the need to establish a morphology based taxonomic system. The fast increasing taxonomic representation in public databases provides a great resource for compiling comprehensively sampled trees, and will quickly result in a taxonomic resource of great utility to Biology.

**Untoussling the early metazoan radiations: on the phylogenetic position of the comb jellies (Ctenophora) and the importance of taxonomic sampling.** Andreas Wallberg\*, Mikael Thollesson, James S. Farris and Ulf Jondelius. Department of Evolution, Genomics and Systematics, Uppsala University; Molecular systematics laboratory, Swedish Museum of Natural History, Sweden

The transition to a vermiform body shape with nervous and sensory systems concentrated at one end

of the body represent perhaps the most important event in animal evolution, triggering the impressive radiations of the Bilateria. But the sister group of the Bilateria has remained obscure and it has therefore been difficult to hypothesize how this transition could have been taking place. Cladistic analyses of morphology indicate that the Ctenophora is the sister group of the Bilateria. But previous analyses of SSU rRNA sequences have yielded contradictory results; in many cases the Ctenophora form the sister group of Cnidaria + Bilateria, but in others the ctenophores instead group with the poriferans. Here we re-examine the phylogenetic signal in the 18S SSU rRNA sequence by analyzing a dataset with 528 metazoan + outgroup sequences, including almost 120 poriferan and diploblast sequences. This is by far the most inclusive dataset to date in terms of the number of included diploblast taxa. We use parsimony ratchet and jackknife methods, as well as bayesian methods, to analyze the data. The results indicate strong phylogenetic signals for a cnidarian + bilaterian group and for the comb jellies to have branched off early within a group uniting all epithelial animals [(Ct,(Cn,Bi))]. By constructing randomized subsets of the large dataset, we demonstrate the importance of inclusive taxonomic coverage of ribosomal sequences for resolving this problematic tangle of the metazoan tree: not only does the topological consistency increase dramatically with the addition of taxa, but the jackknife frequencies of the internal nodes uniting the lineages [(Cn,Bi) and ((Ct,(Cn,Bi)))] increase as well. We consider the reconstructed topology to represent the current best hypothesis on the interrelationships of these old lineages. The result is consistent with an hypothesis suggesting that a planula larva-like animal could have been the ancestor of both cnidarians and bilaterians. Similarities between developmental features of planula larvae and basal bilaterians (Acoela) and between cnidarian and bilaterian Hox gene clusters add further support to the hypothesis. Some morphological features supporting alternative hypotheses are discussed in the light of this result.

**Buffon's grave: the death of natural history.** John W. Wenzel. Department of Entomology, Ohio State University, Columbus, OH 43210 USA

The original purpose of comparative biology was to explain the phenotypes of living things around us. Old fashioned 'natural history' seems to have given rise to modern studies of evolutionary pattern and process, fields that are essentially complementary. However, comparative study of phenotypes is falling out of favor in both of these fields. On one hand, phylogenetic studies are now driven in part by funding priorities that reward large-scale analyses of arbitrarily chosen gene sequences. Patterns are often generated without particular connection to the phenotypes that make the organisms interesting in the first place. Relevant biological features are often taken from the literature without further study. On the other hand, researchers studying process largely use an epistemology that relies on model organisms or systems. As such, these studies prefer ever more detailed exploration of a few chosen species or selection pressures rather than broader study of the greater diversity of organisms. This fundamental narrowness of focus necessarily yields narrow understanding. Each of these approaches is incomplete, and we will have to integrate pattern and process if we are to fulfill the promise of explaining the world around us.

**General character optimization.** Ward Wheeler. Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA

A method of parsimonious character optimization is derived which accommodates, diverse and hierarchically related transformation events from binary changes to genome-level transformations. An expression is presented which encompasses the minimization of weighted nucleotide/character change, insertion-deletion, locus rearrangement and insertion-deletion, chromosomal origin-loss and change as well as translocation and transposition of information between chromosomes and finally, transformation events between lineages.