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Letter from the President

'Times change, and we change with them'

Welcome to the Summer issue of The Systematist, the new title for our re-vamped newsletter. So far this has been a year of review; a year when we have taken stock of our activities to assess the current challenges that we face and how we might best respond. The decision to carry out a review was taken under the chairmanship of Christopher Humphries, our past-President. The reasons for this were various but they particularly focussed on our publishing activities and finances. It seemed timely that, whilst our activities were in the ascendancy, we should take a look into the crystal ball.

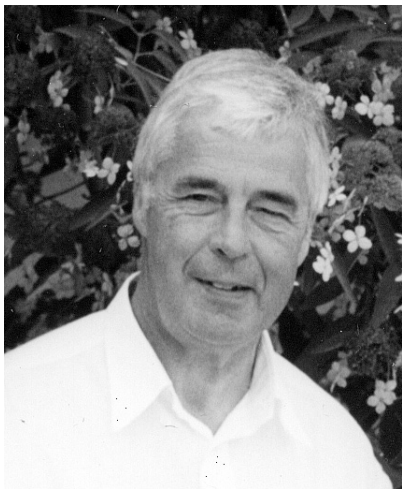
Last autumn David Williams, a Secretary of the Association, Bill Baker (RBG Kew) and Malte Ebach (NHM) produced a report on the business of the Systematics Association and its possible development. As their starting point they went back to the original article in Nature (1937), in which the aims of the Association were stated. Of the ten aims listed, all but one of them, the publication of a British Fauna and Flora, remain as relevant as ever to our activities today. The 'Rules' (Constitution) came later and from these it is worth quoting the three aims of the Association:

1 To promote facilities for the study of the theory and practice of systematics.

2. To promote the exchange of information between scientific workers of all branches of biology and palaeontology with particular reference to matters of taxonomic interest.

3. To encourage, assist and improve research and teaching in systematics and taxonomy.

Currently our activities can be categorised under three headings: Firstly, we organise meetings of various kinds. Traditionally we have supported three-day Symposia; starting in 1997 with the meeting in Oxford we have sponsored Biennial meetings; each year in December we host a talk after the AGM and on the day after the AGM we host the Young Systematists Forum which provides an opportunity for post-



Professor Barry Leadbeater, President

graduates and postdocs to present their results to an audience consisting largely of their peers.

Secondly we publish books under two headings: The Systematics Association Publications (11 volumes so far) and; The Systematics Association Special Volume series (64 Volumes) most of which have arisen from Symposia and again many have been landmark books.

Our third activity stems from our role as a charity and this is to administer Grants and Awards. Here we contribute in two areas, for the last 10 years we have distributed grants for research and secondly we have provided bursaries for attendance at meetings, particularly the

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Biennials.

This is a list of worthy activities but all in one way or another are under pressure. Three-day meetings are less attractive now because of time and financial constraints. The success of the Biennials has deflected attention away from individual meetings. From our deliberations this year and following the initiatives taken during the last Presidency, we have tried to address all of these pressures. With respect to meetings we are now supporting more single-day meetings. With regards to publication we are encouraging the organisation of 'themes' in the Biennials to be accompanied by a publication. In relation to grants, we have just undergone a successful collaboration with the Linnean Society to form the new Systematics Research Fund, and this year jointly we were able to offer a total of £26,000 worth of grants to 26 applicants. In addition to these changes, this year, for the first time, we hosted a summer talk, *The Sir Julian Huxley Lecture* on July 7th. In spite of the inclement weather we welcomed a good audience for Mike Benton's talk on the comparison of palaeontological and molecular dating methods. The Sir Julian Huxley Lecture will now become an annual event.

I have been greatly impressed by the vitality and enthusiasm of members of the Association. The Young Systematists Forum attracted a wide range of contributions by postgraduates and post-docs from around the world.

The 2005 Biennial, to be held in Cardiff (August 22nd - 26th), is at an advanced state of planning with three themes arranged. Ultimately, of course, the success of all our activities depends on the active participation of all members of the Association. We hope that by making our activities as relevant, attractive and varied as possible we will continue to be worthy of our Founders' aspirations.

The Future of Systematics: Assembling the Tree of Life

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Phylogenetic information is the centre of biology (Pagel 1999), and has proven useful in many fields, such as choosing experimental systems for biological research, tracking the origin and spread of emerging diseases and their vectors, bioprospecting for pharmaceutical and agrochemical products, preserving germplasm, targeting biological control of invasive species, and evaluating risk factors for species conservation and ecosystem restoration (Cracraft *et al*. in press).

Acknowledging that many branches in the tree of life remain unanalysed and unresolved, and that we have only limited information of most species on Earth, have been a major impetus behind the National Science Foundation's (USA) recent initiative to assemble the tree of life (see www.nsf.gov/bio/progdes/bioatol.htm). Assembling the tree of life is Big Science and its planetary scope makes is mandatory that all countries realise their responsibility for adding to this endeavour. Sadly this view does not seem to be shared in the larger extent of the EU, were efforts to include the topic even with minimal funding in the 6th framework programme has been in vain.

The Scale of the Problem

The estimated number of extant species varies enormously, ranging from three to 50 millions taxa or even more (Hammond 1995). According to Groombridge & Jenkins (2002) the most likely estimate is in the vicinity of 14 million. However, another recent estimate (May 1999: 38, table 4) places the number closer to seven million. Of these between 1.5 (May 1999) and 1.75 million (Groombridge & Jenkins 2002) have already been described. The uncertainty of the number of described species is aggravated by synonymy. Hammond (1995) have proposed a generally applicable, average figure of 20% synonymy, but recently, Scotland & Wortley (2003) have predicted that almost 80% of the already published names in the angiosperms are synonyms. For the present purpose I will accept Groombridge & Jenkins'

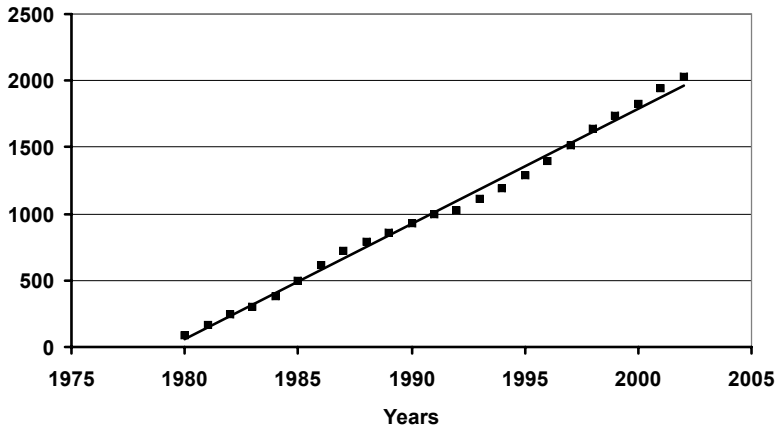

Figure 1. Cumulative number of publications in WebSPIRS (ver. 5.02) since 1980 that cite the term taxonomic revision in the title or abstract (r2=0.99).

numbers as realistic estimates.

In marked contrast to the nearly exponential increase in number of papers that deal with molecular phylogenies (Pagel 1999), the number of published taxonomic revisions has been remarkably constant over the last 20 years and has steadily been in the neighbourhood of about 90 per year (Fig. 1). Due to the bias of *WinSPIRS* this figure is very likely too verging on the insignificant, but it is unlikely that in the near to middle future the figure still required will be orders of magnitudes higher.

It has been suggested that new species are described at a rate of approx. 10 000 per year by May (1999), and 7000 per year by Wheeler (1995). Given the numbers shown here (Table 1) for several major taxa it seems more probable to guesstimate that the figure is in the vicinity of 13.000 per year. This is close to the estimate by Stork (1997) and in agreement with the estimate of Hammond (1995). Within these annual rates of new taxic description I reckon that a 1,000 fold increase in rate would be necessary should the scientific community aim at describing all undescribed taxa (e.g. Mandibulata insects plus myriapods is one group within this undescribed legion) in one year. Put in a different way the current rate would take at least ~980 years to describe all remaining undescribed species of Mandibulata. In total, if there are still 12 250 000 undescribed species out there, and we describe them at a rate of 13 000 each year it will take us slightly more than 940 years to describe them all (Table 1).

All estimates of course ignore the fact that one has to find new species first. If the accumulation of type specimens at the Royal Botanic Gardens, Kew and the US National Herbarium is an indication of taxonomic activities, the description of new plant species have decreased dramatically since 1909 (Wheeler 2004: figure 2). Invocation of revolutions in taxonomic methods (May 1999: 43) will not solve this problem. For this reason alone, it seems overtly optimistic to assume that the task of describing all species will be done in only 25 years (Wilson 2003; www.all-species.org). Consequently the systematic community is faced with a tremendous task even to obtain the basis material for assembling the tree of life. It has been suggested that somewhere in between 50 000 and 80 000 species (Cracraft 2002: 132; Donoghue in Pennisi 2003: 1692) are currently placed in a phylogeny. Accordingly the mere job of gathering the basic building blocks for assembling the tree will require an effort that in magnitude by far surpasses the effort that went into sequencing the human genome. Hence, to describe unknown biodiversity and to assemble the tree of life within reasonable time, it is tempting to develop shortcuts to reach these goals. One such recent attempt has been DNA taxonomy (Tautz *et al*. 2002, 2003).

	New	Described	Total
Bacteria	120[2)]	10.000	1.000.000[2)]
Fungi	1.700[1)]	72.000	1.500.000
Algae	Unknown[2)]	40.000	400.000
Plants	1.700[2)]	270.000	320.000
Nematods	365[1)]	25.000	400.000
Mandibulata	7.200 [1)]	963.000	8.000.000
Birds	5 [1)]	9.750	-
Mammals	26 [1)]	4.630	-
Total	~13.000	1.750.000	14.000.000

Table 1. Showing the number of new species described per year, total number of described species, estimated total number of species in selected groups. The total number of new species of Mandibulata described covers insects only.
The two latter set of figures are from Groombridge & Jenkins (2002), except for Bacteria and Algae where the figures stems from Hall & Hawksworth (1996). The number of new species described stems from 1) Hammond (1992) and 2) Hawksworth (1991).

Shortcuts in Systematics? - DNA Taxonomy

The basic procedure of DNA taxonomy is simple (Tautz *et al*. 2003: 70, 71-72): A tissue sample is merely taken from a collected individual and DNA extracted. One or more gene regions are sequenced and an unambiguous link between the collected individual and the sequence (or sequences) is made. The sequence serves as a first approximation, an identification tag for the species from which the DNA sample was extracted. The sequence is compared against existing sequences and made available to the scientific community though appropriate databases together with other types of information, ideally including its taxonomic status. The sequence is a standard for future reference, ideally together with the type specimen and the DNA preparation. As a prerequisite, existing Linnaean names should be matched with appropriate

DNA sequences. However, many or most existing types are not useful for this purpose. In such instances DNA preparations should be based mainly on sequences from newly collected individuals preferable from the type locality and identified by experienced taxonomists - nomenclaturally they should have status as neotypes! While in principle acknowledging the importance of morphological information it emerges that DNA data have preference over all other types of data - even if it involves total destruction of the specimen (or type) and replacement by a photograph. Following the suggestion of Tautz *et al*. (2003: 73) routine identification of specimens collected during ecological studies should be done by high-throughput DNA-sequencing facilities. Such facilities "could routinely handle ~ 1000 samples per day" at a cost of E5 per sample [a calculation that of course disregards all other expenses (e.g., equipment, technical, and scientific staff)]. According to the proposers DNA taxonomy will solve a number of pertinent problems:

1. The identification problem - The fact that the knowledge of taxonomists is frequently lost when they retire.
2. The inherent instability of the Linnaean "naming system."
3. The undue emphasis on particular groups (e.g. vertebrates, insects, flowering plants).
4. The "taxonomic impediment."
5. The inadequacy of taxonomic data/standards in existing databases.

However, a whole suite of new problems will be created by implementing DNA taxonomy, and it remains highly questionable as to what extent it will be able to provide a solution to the problems identified above.

Most importantly it remains a moot point why DNA data should have preference over all other types of data? Species descriptions are based on a synthesis of a broad range of different data making it possible to create interesting hypotheses about the distribution of attributes among organisms. Contrary to what Tautz *et al*. (2003:72) envisage phylogeny is not merely a by-product of taxonomy, but is integral to its core, being used to explain the observed patterns of taxonomic diversity. In this respect DNA data certainly plays a major role, but if we know nothing about the organisms except a very tiny part of their DNA, there are no patterns of interest to explain - apart from sequence similarities. DNA taxonomy will reduce taxonomy from being a hypothesis-driven science to a purely technical discipline (Lipscomb *et al*. 2003, Cracraft et al. in press) - or, at best, a cataloguing device for other biologists. To relegate taxonomy to a high-tech service industry centred around a few DNA sequences will deprive evolutionary biology of its most important function: the testing of evolutionary hypotheses at all levels from the evolution of characters, over the evolution of species, to the evolution of clades, i.e. species concepts, species delimitations, phylogenetic reconstructions, homology statements, character polarizations, and ultimately classifications are all scientific hypotheses that do not hinge upon a few DNA data points, but change as science progresses. The identification problem will be dealt separately with below.

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The assumed instability of the Linnaean naming system seems to be a major concern not only of Tautz *et al*., but also to adherents of the Phylocode (see e.g. Carpenter 2003; Keller *et al.* 2003; Nixon *et al.* 2003, and the *Systematic Association* webpage (www.systass.org/).

Admittedly, it is a nuisance for everyone that names, which have been in use for a long time, suddenly disappear. However, it is difficult to see how linking a name with a sequence will solve this problem. The instability of the current system is caused by changes in knowledge, e.g. previously recognized species are split into two species, or subsumed into others. Hypotheses about relationships are always subject to revision as new information becomes available, or existing data are reinterpreted. The taxonomy of species is not fixed (Groombridge & Jenkins 2002: 14). In taxonomy 'stability is ignorance' (Gaffney 1979) and the mere idea behind creating a unitary taxonomy (Godfray 2002) runs counter to scientific practice (Vane-Wright 2003). If *Pan paniscus* and *P. troglodytes* are subsumed into *Homo* - which in light of the low sequence divergence (if that is of any importance) between *Homo* and *Pan* is an obvious option - two species names disappear no matter whether they were linked to physical types or electronically stored sequences.

Admittedly the undue emphasis on charismatic taxonomic groups is a problem for our scientific understanding of life on Earth. To express it differently, it is a general problem that the typical bird or mammal species on the average will be mentioned in one scientific paper per year, whereas the average invertebrate species will only be mentioned in 0.1 to 0.01 scientific papers per year (May 1999: 32). It would certainly be advantageous if more scientists turned their research interests towards lesser known groups, but we must not neglect how important are to the general public groups like

birds, butterflies, and whales. To a large extent these are the groups that shape public opinion on threats to biodiversity. However, it is difficult to see how DNA taxonomy can divert more scientific attention to orphan groups (Hyde 1997). Would it be any more interesting to study mite sequences than mite morphology? It is difficult to persuade anyone that we will know more about mites because we have a sequence and a photograph of one, than if we know something about its morphology.

Obviously, there are better solutions to the 'taxonomic impediment' than to become ignorant of the organisms we work with. One is the training of a new generation of taxonomists (Schram & Los 1996) and the other is funding. It is perhaps no coincidence that a recent attempt to centralize registration of plant names was rejected by the last International Botanical Congress in 1999. The move was lead by taxonomists from developing nations fearing that wealthier countries would monopolize taxonomic information.

Evidently there is only limited control on the taxonomic standards of the submissions to *GenBank*, or, most other molecular databases - for that matter. The biggest efforts are concentrated on keeping nomenclature up-to-date - which is a noble effort in its own right. Apart from the large genome projects, which work with well-known model organisms, most information on the origin of individuals is deposited in *GenBank* by people (mostly taxonomists) that hopefully know the kinds (and indeed the types) of organisms upon which they work. It would be naïve and against scientific practice to think that one can create an authoritative body of taxonomists that supervise this aspect.

It may be that there are no solid taxonomic standards in current repositories of sequence data, but neither is there solid control of the sequences themselves: As a natural consequence of this, Harris (2003) has recently appealed for a much greater authentication of the sequences deposited in *GenBank*. There is every reason to be cautious when three out of 16 sequences from the mitochondrial cytochrome b gene from different reptile genera contain either 'stop codons' or indels that disrupt the reading frame (Harris 2002). Indeed, when Noor & Larkin (2000) failed to confirm any of 22 previously published polymorphisms in mitochondrial 12S rRNA genes from *Drosophila pseudoobscura* when resequencing them. By resequencing, checking vouchers, and adding four new sequences from the same genus, Kristiansen *et al*. (submitted) have recently unequivocally shown that both *rbc*L sequences in *Genbank* from *Oxychloë andina* (Juncaceae) are erroneous - at least one of them being a chimeric. The quality of taxonomy and sequences in *Genbank* relies solely on the quality and thoroughness of the researchers. Neither problem will be solved by DNA taxonomy.

Tautz *et al*. (2003: 72) claim that two of the main purposes of taxonomy are "identification of species and their assignment to higher level taxa," and the "sequences collected within the framework of DNA taxonomy are intended primarily to provide identification, rather than phylogenetic resolution."

Traditionally, taxonomy is based on a meticulous investigation of a large number of specimens prior to creating a classification. This is hardly the case in molecular studies where one often relies on just one sequence per taxon. Such an approach takes it for granted that intraspecific variation is less than interspecific variation - a proposition we really have little knowledge about. [Apart from the enormous amounts of sequences from model organisms and *Homo sapiens* in *Genbank*, an overwhelming majority of sequences of relevance to studies of biodiversity are unique - viz. all known sequence information stems from just one individual representing a species.]

How DNA taxonomy can assign anything to higher taxa (which are only historical constructs anyway), except through an existing classification of the species remain more than enigmatic. Felsenstein (2004: 145-146) has recently denounced classification, but seems to have forgotten that even recognising taxa (incl. species) represents classification.

If we imagine that all the described species are valid and were immediately available for sequencing it would require approximately seven years

Logistical Problems

If one accepts the rationale behind DNA taxonomy the sheer task of assembling the data points is formidable.

As of January 13, 2004 there are sequences from approximately 160 000 classified organisms in *GenBank*, of these approximately 110 000 are classified to species level and a further group of approximately 10 000 infraspecific categories. These sequences are from widely different parts of the genome(s), but lets for the sake of argument consider them all of relevance to DNA taxonomy. Hence, we need a further 13 840 000 sequences to have just one sequence from all species (undescribed as well as described) and just 1 590 000 sequence to have one sequence for all described species. If we imagine that all the described species are valid (= no synonymy) and were immediately available for sequencing it would require approximately seven years (given 225 work days per year) to produce a single sequence for each, given the availability of a high-throughput DNA-sequencing facilities, which "could routinely handle ~ 1000 samples per

day" Tautz et al. (2003: 73) at a cost of E5 per sample.

However, just doing the sequences is insufficient. They have to be checked and read. Even if we assume absolutely perfect sequences of ~1000 bp a minimal "handling time" of five minutes per sequence is not unrealistic. It would take approximately 10.5 year (225 working days per year and an eight hour working day) to handle one year's production of sequences. This amounts to more than 80 years for all known species (approximately 640 year to do it for all species), at a cost of approximately eight and E70 million (neglecting all other expenses such as equipment, and salaries for technical and scientific staff).

Evidently a much higher level of automation is possible at all stages in the process than is standard, but sequencing such an enormous diversity of species is not a straight forward process, and DNA extraction (which has not been included in the calculations) is far from trivial. In *GenBank* the acquisition rate of sequence(s) from new species has been constant over the last approximately nine years (1995-2003) at 2088 (r2= 0.991) new species per year. This also applies to green plants (Viridiplantae=Chlorobiota) were there has been a constant acquisition rate of 764 (r2= 0.954) new species per year. In comparison the accumulation of sequence from the very widely used *rbc*L-gene has also been constant but by a fourth of the total species acquisition rate, i.e. 191 sequences (r2=0.904) per year.

As stated by Tautz *et al*. (2003: 72) it may be possible to sample non-destructively large animals, insects, most plants and fungi in existing collections. However, the present reluctance by curators to accept destructive sampling of many collections makes it rather difficult to believe that such practise will ensue. Though of course theoretically possible, it seems to pay no attention to the fact many species are known only from the type collection, e.g. approximately 40% of all beetles are only known from one locality (May 1999: 33), and roughly half the 38 000 known spiders were originally described from a single specimen (Coddington & Levi 1991: 567). Are we willing to replace them by photographs and - if successfully extracted - with a DNA sample? Knowing that if the quality of the extraction and sequence(s) is far from perfect - all we might be left with is a lousy sequence and a photograph? Every practicing taxonomist is aware of the limited value of types that exist only as descriptions or drawings.

Additionally, a very large fraction of the existing types are in excess of 100 years old. Given the error rates in assembling the small fractions of sequence that may be amplified by PCR from low quality DNA should extraction and sequencing of these types be done solely by trial and error? Even though the proposed "neotypifications" seem straightforward it is not necessarily a simple matter given that 50-70% of all arthropod species only turn up as one or two specimens. It will be extremely difficult and labour intensive to find neotypes in all the megadiverse groups. Perhaps, even worse, given the postulated lack of taxonomic experience (and the complete lack of expertise in many fields) who are the experienced taxonomists that should undertake the task of verifying existing species identifications and identify the new samples in the many cases of "neotypification"? Although it is rather unlikely to happen, consider the havoc that would ensue when mixing the types of *Homo sapiens* and *Pan troglodytes*. There are innumerable examples far less likely to be spotted.

One of the alleged advantages of DNA taxonomy is - according to Tautz *et al*. - that sequence information is digital and not influenced by subjective assessment. That is certainly true from the very moment that the sequence is entered into the computer, but a series of decisions leading up to this particular moment are certainly not: Reading, interpreting, and translating the chromatogram into raw sequence involves subjective decisions, and additional problems may be caused by the sequences themselves such as alignment and distinguishing orthologs from paralogs, etc. Automation can perhaps be made such that it deals with the first set of problems - though this is likely to impede the throughput. The two latter problems are not so easy to handle.

When does it Work? - The Identification Problem

Though it's actual taxonomic status as a new species was based on extensive studies of morphology, behaviour etc. only a minimalist holotype (photographs, moulted feathers, and minute samples of blood) were used to designate the shrike, *Laniarius liberatus* by Smith et al. (1991). This created considerable furore among ornithologists (see e.g. Hughes 1992a, b; Peterson & Lanyon 1992) and the decision not to preserve a complete specimen seems ill founded. However, it is important to stress that neither the zoological nor the botanical codes preclude the inclusion of DNA data in the diagnosis or description of species, or the designation of tissues samples as types.

However, there are a number of obvious instances, beyond their use in phylogeny, were DNA data are extremely useful. Obviously when organisms "have no morphology" and are additionally unculturable as are most prokaryotes the only thing we can do is to collect sequence data from the environment, create databases of the results, and invent a 'classification', which only reflects sequence similarity. In such a system species are defined as entities that differ by less than 5% sequence similarity. This is of course a carica-

ture of a classification and a simple need for identification. Needless to say microbiologists and other scientists working with such groups would like to know considerably more about their organisms than this and they know that they can do far better if they are able to culture them (Lipscomb *et al*. 2003). However, to use this parody of a classification as an argument for revolutionising taxonomy (Godfray 2002: 16) seems bizarre).

In comparatively small and tightly-knit groups like birds, butterflies, and whales where *a*-taxonomy has largely been undertaken, identification of cryptic species, linking life history stages and sexes, separation of sibling species etc. can of course be guided by DNA data. DNA data may also help in identifying humane disease vectors and agricultural pests. The Barcode of life initiative has strongly emphasised, that barcodes are not a substitute for or an attempt to supplant existing taxonomic practice (phe.rockefeller.edu/BarcodeConference). The real strength of barcoding lies outside the taxonomic community as it will enable non-specialists able to identify unknown species. However, the identifications will never be better than the available a-taxonomy. It is noteworthy that the pivotal role of DNA data in taxonomic practice has recently been strongly downplayed by at least one of its key proposers (www.danbif.dk/conference2004/speakers.asp).

What do we need?

Standards for DNA extraction and storage are badly needed. Some museums are building up DNA storage facilities, but no unanimously agreed common ground exists on data sharing, safe-guarding etc. Current initiatives in the EU are aimed at solving these problems (www.synthesys.info).

To what extent organizations like *GenBank* should put standards for linking taxa with sequences is a contentious issue? In the majority of cases it suffices to require that traditional voucher information is available, either directly or indirectly through the journal in which the studies are published. This is of course the responsibility of the editors of refereed journals, who should never allow publications of sequence based studies without concomitant submission of the sequences to a public database and, of course, should never allow publication of such data unless the necessary voucher information (e.g. collection number, abbreviation of the institution holding the voucher) is available. Basically this amounts to nothing more but a little training of editors, mostly - but not exclusively - of editors of molecular journals. The cornerstone of scientific inquiry is repeatability. Specimens used in scientific investigations should be catalogued and vouchered in museums ensuring that species identification can be confirmed (Ruedas *et al*. 2000).

It is difficult to disagree with Wheeler *et al*. (2004: 285) that molecular data, abundant and inexpensive as they are, have revolutionized phylogenetics but not diminished the important of traditional work. The need for this research has largely been masked because molecular researchers have been able to drawn on centuries of banked morphology knowledge.

"The task of inventorying is sometimes mistaken for "stamp collecting" by thoughtless colleagues in the physical sciences [sadly one might add and among ecologists and microbiologists]. But such information is a prerequisite to the proper formulation of evolutionary and ecological questions, and essential for rational assignment of priorities in conservation biology. Lacking basic knowledge about the underlying taxonomic facts, we are impeded in our efforts to understand the structure and dynamics of food webs, patterns in the relative abundance of species, or, ultimately, the causes and consequences of biological diversity" (May 1999: 43). Implementation of DNA taxonomy and the widespread attitudes towards classification as recently articulated by Felsenstein (2004: 145-146) will only take us further away from the goal of Assembling the Tree of Life.

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The world of DNA barcoding and morphology - collision or synergism and what of the future?

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We systematists are ‘living in interesting times’ as Mr Spock would say in *Star Trek*. Well, at least some systematists and taxonomists are thinking that. Some are major political advocates of a largely DNA-based, barcoding future whereas others appear to be staunch adherents to a traditional morphospecies based approach. Who is more right? In this short piece I hope to argue that neither are perfectly right, but that a synergistic approach ought to be sought wherever possible. However, the answer should not be one guided by gut feeling, protectionism or prejudice, but based on

empirical evidence and statistical estimation of the error rates of each approach. Whether, a new amalgamated approach will provide a means of completing taxonomic treatments waits to be seen, but the results seem likely to be much more reliable and therefore useful.

Having done some revisionary taxonomy, it soon became obvious that most projects had a number of stumbling blocks. In rough order of increasing time consumption these were: getting all the necessary material together, assembling the relevant literature, preparing descriptions and illustrations, and deciding where the boundaries between taxa, especially between closely similar species, were. The last of these is one of the vital skills of any practicing taxonomist. Of course, the degree of the problem of species delimitation varied from project to project, but another thing also seemed to recur - most groups seemed to comprise a number of clearly separable morphospecies, easy both to diagnose and to key, and then one or occasionally a few, 'aggregates'. These might be conveniently imagined as the results of recent or ongoing rapid speciation or something like that. How big a hold-up these aggregates cause depends on the worker, but at least some taxonomists have metaphorically walked under a No. 10 London bus before publishing their magnum opus in all its completed glory. Something that is good neither for the individual taxonomist nor for the subject! I have always preferred a more pragmatic approach and revised what I felt reasonably confident of, and left the really tricky problems for some later date - with a warning like 'here be dragons'.

Such nutty species-level problems could always be skinned in a number of ways. Some workers turn to morphometrics, some to karyology or allozymes, some to behaviours such as courtship songs, and so on. Recently, DNA has offered a whole new box of tricks, some of which can even be applied to long dead museum specimens rather than requiring you to have a living organism at hand. The great advantage of this is that DNA provides a very powerful tool that, given careful interpretation, allows those difficult species boundary issues to be addressed sharply and clearly. Armed with the new DNA data, as with sonograms and enzyme gel data, we might now often discern quickly which of the morphological characters that previously bewildered us, is actually reliable for separating the species. Knowing, say, that it is the colour of the head rather than the length of the snout that works to distinguish two species, we can easily complete the key and complete the descriptions or synonymies. However, it is only usually on small local projects that this is completely feasible, because although it is sometimes possible to extract useable DNA from old material, this depends very much on the group, the genes involved, the nature of the killing and preservation and the age of the specimens (Quicke *et al*. 1999). Very much of the existing museum material upon which revisions are based simply will not work for DNA, and therefore collection of fresh specimens is essential. Further, in this day and age, new collecting is likely to involve very serious permitting issues, which although usually soluble, take a vast amount of time and will inevitably be limited to a small number of countries. If this is compared with the 200-plus years of collections accrual, from vast numbers of localities, that form many of the major collections, there is practical no way that comparably diverse/representative samples can be obtained for most groups. And even then, the world's museums do not contain any where near all the existing easily recognised morphospecies. For my own group, parasitic braconid wasps, recent collecting in west Uganda revealed a local fauna which appears to comprise an enormously large proportion of new species, not present in The Natural History Museum's collection, despite that as a result of a long British colonial history there, actually has rather a lot of Ugandan material. Another common observation is that there is little overlap of rarer genera and species between the major European and North American museums because each comprises material from lots of individual and independent collecting trips, and the world is a big place. Thus a complete inventory of life is going to require an even more broadly-based collecting programme than all that of the past combined, and while I consider that a major priority, it is clearly going to be the ultimate limiting factor.

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So, OK, let's assume that we can live with the material we **can** obtain fresh which will at least help in resolving problems of species boundaries for the species available. Does that mean that all is solved? Well … no! In taxonomy as in all science we are faced with an essentially statistical question, and we choose the option we think is most probable. Thus we are similarly prone to Type I errors and Type II errors. These are specifically, recognising species boundaries where none exist and failing to recognise multiple species where they do exist. Below I'll briefly present a few examples, based on insects that I have been working with, and then consider the implications and what needs to be done. To pre-empt things, I think it is an important question whether Type I and Type II

errors are uniformly taxonomically distributed and whether DNA or morphology is consistently more likely to create one sort or the other.

The best studied insects are nearly all either pests or natural enemies of pests. What might come to you as a bit of a surprise is that we are now finding many examples where pest 'species' turn out actually to be a complexes of species, often with very different pest statuses or responses to control agents. For example, in the widespread leaf-miner fly genus, *Liriomyza*, three 'species' in particular are economically important: (*L. huidobrensis, L. trifolii,* and *L. sativae*). All of these have turned out to be complexes of two or more cryptic species (see, for example, Scheffer 2000; Scheffer *et al.* 2001). In each case, the possibility that a cryptic species might exist was suggested by anomalous results in trying to control them (this translates to 'a lot of work for just 3 nominal species').

With parasitic wasps we are finding just as many examples of cryptic species, sometimes with virtually no reliable distinguishing feature of external morphology but nevertheless with profound biological differences. For example, a chance discovery of karyological variation in the very widely studied pteromalid, *Anisopteromalus calandrae*, revealed that some labs had been working on an r-selected species, whereas others had a K-selected one in culture (Gokhman *et al.* 1998, 1999) differing in chromosome number and massively in terms of DNA sequence data as well as biology. Another chance 'fishing expedition', this time molecular, with a parasitoid reared from several Taiwanese zygaenid moths revealed yet another pair of apparently morphologically indistinguishable species that the DNA strongly suggests are actually quite separate (Quicke *et al*. 2003). We have since investigated molecularly another related group of braconid wasps from Uganda, and revealed three obviously distinct species that we cannot distinguish on morphological grounds (Mori *et al*. in prep.). These are just a couple of examples suggesting that cryptic species that are most easily distinguished using DNA are likely to be very common. At a rough guess, I estimate that about 40% of currently recognised insect species would be found, if studied appropriately, to comprise cryptic species complexes. This is roughly the same as karyology has found for mosquitoes. However, this is a guess, and what I think ought to be an absolutely top priority for barcoders and traditional taxonomists, is to get together and determine, as best as can be done at present, what the overall proportion of currently undetected cryptic species is, and whether this proportion is more or less constant or perhaps varies according to lineage. Perhaps butterflies, which have been so well collected and probably heavily split, are more or less OK. Though the continuing recognition of new species in Europe with its massively studied and collected fauna suggests that this may not be the case.

All the above examples are really just cases of suspected Type II errors in conventional taxonomic treatments - finding additional, previously unrecognised, species by applying molecular or other more sophisticated techniques. What then of Type II errors in DNA-based taxonomy - failing to detect cryptic species groups when they do actually exist? Of course that has been the complaint levied against traditional morphotaxonomy by advocates of DNA taxonomy, but there is the other possibility, that even rapidly evolving DNA sequences will fail to distinguish what are good biological species - throwing the ball out of the molecular lab back into the court of the morphologist, behaviourist, karyologist, etc. Such instances are harder to find but that may be a sampling artefact. When workers have clearly different biological species, they probably will find it hard to justify funding to do a DNA sequence study of them - after all, they already know the answer. Nevertheless, there are cases where what we can confidently call biologically distinct species, cannot be distinguished by DNA sequence data using any of the standard, rapidly-evolving genes we commonly use today, e.g. for entomologists, these are typically CO-I or cytochrome b sequences, EF-1alpha introns, and ITS-1 and ITS-2 fragments. In my lab we have recently been working on a complex of bees in the genus *Colletes*. Based on pollination biology, phenology and some less convincing morphology, there is a complex of three species in Britain near *C. succinctus*. We have sequenced multiple individuals of these for a variety of rapidly-evolving gene fragments including CO-I, ITS-2 and EF-1 alpha introns, but no single gene fragment examined was able to differentiate all three of the species, though individual genes could separate off individuals of what we consider to be good biological species (Else *et al*. in preparation). Similar results are emerging with some ichneumonid wasp species complexes. Thus, avoiding Type II errors in molecular species discrimination using the standard markers, doesn't seem to be straight forward either. Of course, at some level, even if it is only chromosomal, there must exist DNA differences between what are 'real' species, but question is: 'How many such species will be missed using a standard recipe of gene fragments?'

Detecting Type I errors in existing morphotaxonomies using DNA is a far harder issue. Failure to find a

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distinct fixed DNA sequence difference between forms that can be separated morphologically and which have been suspected as being separate species, is simply not proof that they are the same. Usually some different level of study will provide a resolution to such problems, such as rearing and crossing studies. Thus if, as in the above *Colletes* example, the DNA sequences obtained for two or three genes had failed to provide an positions that distinguished the phenological and pollination 'forms', it would not have proven that they were all conspecific. Indeed apparently identical polymorphisms are often shared between species - speciation events do not need to be accompanied by gene fixation at all loci. Molecular data are potentially more likely to succumb to Type I errors than morphology because the numbers of individuals of a species studied are almost invariably going to be smaller (except for exceptional cases) than are available for traditional morphological examination, and so stochastic factors are more likely to play a role with DNA sequences. What is clear is that we cannot specify a universal minimum level of DNA sequence variation in any given gene that will correspond to real species.

The importance of DNA and barcoding is of course not limited to its being able accurately to distinguish species within difficult complexes, but also because of its potential massively to increase the speed of recognising and defining species. It also goes without saying that the best estimate of taxonomy is likely to result from the application of as much evidence as possible, molecular and morphological. It is simply a matter of expediency, and given the generally accepted opinion that in the past 250 years of classical binomial taxonomy we have at most described 10% of animal species, DNA sequencing cannot just be ignored as it potentially can enable vast numbers of individuals representing large numbers of new (as well as described) species to be placed into an entirely DNA-based classification (ignoring the added complexities of working out relationships). Hardcore advocates of DNA barcoding would say that this was sufficient and that these barcode catalogues need only be tied into the existing literature when individual taxa are studied and sequenced. But barcoding to a high degree of reliability, while undoubtedly feasible, is not going to be as straight forward as advocates such as Hebert *et al*. (2003) might suggest, because there is now ample evidence that no one gene, or at least none of those commonly examined at present is going to be sufficient to guarantee that level of accuracy across a range of taxonomic groups. If a large proportion of traditional morphologically defined species are found actually to be complexes of cryptic species, we will have to question how to tie the potentially more reliable DNA taxonomy to existing published but unreliable information on the morphospecies. This is not going to be a trivial issue and there is no point in being able more accurately to distinguish species if we don't apply a quality control to linking them to the existing nomenclatural entitities. In a worse case scenario we may have to start doing it all again - though hopefully with hind sight, that would be an easier task. Again we need to know how group-dependent the accuracies of different methods of species discrimination are and whether it is possible to make any useful generalisations.

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Thus, while I envisage the future of taxonomy as being very largely molecular, we desperately need to know what level of genetic (DNA sequence) investigation, is going to be needed to achieve the level of accuracy in species recognition that we are seeking. And this will be determined by the proportion of Type I and Type II errors we are prepared to live with. For some projects we may be quite happy to accept a moderate error rate as long as it is not too biased - perhaps in things like biodiversity assessment; in other cases, such as food web studies, we might need a more stringent level of accuracy, whereas in medicine and pest control only the most stringent levels of species recognition are liable to suffice. Clearly, archiving DNA/tissue samples so that additional genes can be sequenced when necessary is also an issue that needs appropriate consideration.

In short, assuming we all agree that we want to create a taxonomy (i.e. recognising, distinguishing and placing species) that closely approximates some generally accepted biological reality of what species are - be that a biological or a phylogenetic species concept-based system - we are going to need more than just CO-I sequences. It will only be by comparing the Type-I and Type-II error rates between traditional and DNA-based taxonomies that we will know whether a taxonomy based on a given level of DNA sequence investigation will be a significant improvement or not. Inevitably, in the great majority of cases we will still have to rely on either arbitrary or subjectively-determined levels of difference to define species, whether we are using DNA or morphology for a long while to come.

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Quo Vadis?

Presumed primitive until proving derived: appreciating evolutionary loss

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What evolution is, is in the eye of the beholder. For an 18th century preformationist embryologist such as Charles Bonnet the word evolution meant the progressive and linear unfolding of complexity during the ontogenesis of an individual organism, which is close to the original vernacular meaning of the word. Although Bonnet's work already shows the first seeds of the shift in meaning of evolution from developmental change to species change (Richards 1992), it was the 19th century Victorian pundit Herbert Spencer who is chiefly responsible for popularising evolution as an umbrella term covering progressive change in general, from organic change in nature to change in human social systems.

Even if we just consider modern times, the meaning of evolution will differ according to a person's background. An astronomer will define stellar evolution as a one-way predictable process of transformation governed by immutable physical laws in which one type of star evolves into another. In contrast, for modern biologists evolution is a variational process based upon the sorting of variation offered to natural selection, and evolution's course is neither inherently directional nor predictable. For many university freshmen throughout the 20th century evolution initially takes on a meaning predicated upon their coursework in population genetics, such as "changing gene frequencies in populations." Later in their academic careers, when they manage to escape the clutches of reductionism, these students may redefine evolution to encompass all genetically based intergenerational change, irrespective of hierarchical level of organization.

Laypeople may have yet another conception of evolution. At the beginning of this year, for example, the inimitable Kathy Cox defined evolution as nothing more than "a buzz word that causes a lot of negative reaction," an opinion with rather strong consequences. Mrs Cox is State Superintendent of Schools in the state of Georgia, U.S.A., and because Mrs Cox is of the opinion that for many people the word evolution only calls up associations with "that monkeys-to-man sort of thing," it should be banished from the science curricula in high schools in Georgia. However, irrespective of whether you are an 18th century preformationist, 21st century astronomer, population geneticist, intelligent layperson, or just Mrs. Cox, all concepts of evolution are united in that they deal with change in time.

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The first prerequisite both for the possibility and the recognition of evolution in the natural world is the existence of differences between organisms. Genetic variation forms the basis of evolutionary change in populations, and observed differences between two taxa in the tree of life are the basis for inferring that evolutionary change has occurred in at least one of those lineages. Without the existence of organismic differences evolution will stop in its tracks as natural selection will have no substrate to take hold of, and in the absence of differences between organisms we can reasonably conclude that no evolution has taken place. After all, stasis has long been defined as the "absence of evolution", the realization of which in the 1970s created a niche for propo-

nents of punctuated equilibrium to devise their contrary slogan that "stasis is data." The recognition that organismic differences imply evolutionary change whereas similarities do not is also part of the necessary methodological foundation of systematics, which aims to group organisms on the basis of shared derived similarities, and which usually works well.

Consider, for example, my friends Pam, Simon and Charles. Pam is a tall, athletic, articulate brunette with long curly hair and beautiful teeth, and adamantly committed to maintaining the highest level of personal hygiene. She has an active sex life, is an avid cook, loves to talk and read, and is independently mobile with her brand new Honda. In contrast, Simon and Charles are practically bald, lack most of their teeth, and are of less than average height. Simon is unable to walk and spends most of his days in bed, while Charles is unfortunately bound to a wheelchair most of the time. Both Simon and Charles need to be fed specially prepared food at regular times each day, and they need help washing themselves. Being unable to either read or talk coherently, they enjoy being read to, or being taken on a ride through town. When we consider Pam, Simon, and Charles in terms of their sexes, anatomy, and behaviour, it appears quite unproblematic to sort them on the basis of their similarities and differences. Obviously, Simon and Charles have much more in common with each other than either of them has with Pam, and its seems therefore reasonable to provisionally group Simon and Charles to the exclusion of Pam.

However, this *prima facie* clear-cut case can be resolved in an entirely different manner if we depart from the adopted black and white approach to comparative morphology, and in addition also consider elements from the environment in which we find our protagonists. Pam lives by herself in an apartment, whereas Simon lives with his parents, and Charles lives in a home for the elderly. It turns out that Simon is a baby still dependent upon breast-milk, and not yet possessing either teeth or a full head of hair. Charles on the other hand is a balding centenarian in the last stages of Alzheimer's disease. This immediately casts doubt on the "homology" of the structural and behavioural similarities noted above between Simon and Charles. Specifically, Simon's primary lacks are Charles' secondary losses. Although apparently identical in many attributes when superficially considered, their different status as either rudiments waiting to be developed or vestiges in the final stages of deterioration debars their equation as meaningful indicators of affinity.

I think there are sufficient reasons to consider evolutionary loss a common phenomenon with the nasty quality of being very difficult to detect.

This light-hearted hypothetical example is intended to highlight what I think may be a serious and widespread, but not generally recognized, problem in the study of morphological phylogenetics: how to deal with so-called "absence" characters, and how to distinguish between phylogenetically uninformative primary absences and phylogenetically informative secondary losses of characters.

That accidental equation of independently evolved absences can have dire consequences for our attempts to phylogenetically order diversity can be nicely illustrated with the demise of two taxa residing on two very different branches of the tree of life, but with revealingly similar etymologies: the Archezoa and the Archiannelida.

The Archezoa was erected in the early 1980s by Tom Cavalier-Smith to house a variety of peculiar anaerobic, and morphologically extremely simple eukaryotes lacking many cell organelles typical of other eukaryotes. The morphological simplicity of archezoans, and in particular their lack of mitochondria led to the hypothesis that they were very primitive eukaryotes, which split off from the rest of the eukaryotes before the endosymbiotic origin of the mitochondrion (Keeling 1998). However, the presumed primitiveness of archezoans was not long-lived. The combination of molecular phylogenetic evidence and the presence of mitochondrial genes in the nuclear genomes of the archezoans clinched their fate as being nothing more than simple imposters (Keeling 1998; Gribaldo & Philippe 2002). In reality their simple appearance is the result of extreme secondary simplification.

A comparable tale can be told for the Archiannelida. This taxon has been recognized throughout most of the 20th century alongside the familiar Polychaeta and Clitellata. The Archiannelida grouped a broad variety of annelids of uncertain systematic position, and has for that reason also been considered a trash-can taxon. Most archiannelids are minute animals with simple morphologies, for example, often lacking parapodia, chaetae, and with relatively simple body musculature. However, systematists were hard-pressed to find even a single convincing synapomorphy shared by all archiannelids. Instead, detailed morphological investigations, which are now beginning to be backed up by molecular phylogenetic evidence, have shown that the Archiannelida is a polyphyletic taxon, the members of which have separately descended from larger-bodied polychaetes. It is now hypothesized that several archiannelids have retained larval features through progenesis while adapting to their mostly interstitial habitat. Another presumed primitive taxon turns derived after their simplicity is exposed as being

the result of secondary character loss.

I can scarcely hope to convince you of the prevalence of extensive character loss during evolution, and the concomitant problems for phylogenetics and the study of body plan evolution on the basis of two little examples. However, I think there are sufficient reasons to consider evolutionary loss a common phenomenon with the nasty quality of being very difficult to detect. Although the following examples will come from the animal kingdom I strongly suspect the conclusions hold for the other kingdoms of life as well. Convergent evolution is a widely recognized problem in evolutionary biology, and it has received due attention in the literature. Simon Conway Morris's recent book (2003) (see Jenner, 2003 for review), for example, discusses case after case of positive convergence across the entire tree of life, and across all levels of biological organization, leaving little room to doubt the prevalence of convergence. However, Conway Morris' book is a good example of the fact that convergence and parallelism are typically discussed in terms of the independent evolution of "positive" characters or evolutionary novelties. In general, convergent similarity between organisms as a result of independent losses seems to have received much less explicit attention, at least in the literature on animal evolution, except in such specific instances as the convergent loss of pigmentation, eyes, etc., in cave dwelling animals (so-called troglomorphisms). Yet, if convergence of positive structures is generally acknowledged to be present wherever we look, convergent absences must be even more common.

One important reason for this is obvious. If no remaining vestige betrays a seeming absence as secondary, independent absences are identical in appearance. The primary absence of wings in collembolans (springtails) looks exactly the same as the secondary absence of wings in lice, yet considering this similarity as homologous is clearly incorrect. Convergence of positive structures can often (although not nearly often enough) be suspected on the basis of differences between the structures involved. You don't need a phylogeny to see that the raptorial legs of a praying mantis and a mantis shrimp are not likely to be homologous. Although they are superficially similar no unique similarities indicate their correspondence. If character loss results in a return to the ancestral condition of total absence, their convergence will often go unnoticed, unless we are lucky enough to already possess a well-resolved phylogeny that indicates whether the absence can be explained by a common evolutionary origin.

... convergent absences must be even more common.

Another reason to believe that character loss is probably very common is the deeply engrained 'intuition' of many biologists that complex characters are more easily and frequently lost than independently gained. This should naturally rouse suspicion about the homology of many absences. Moreover, recent advances in molecular developmental biology have started to provide suggestive glimpses of the developmental genetic correlates of the loss of characters of different degrees of morphological complexity across different taxonomic levels. These studies show that relatively small and localized changes in genetic regulatory networks underlying the development of such diverse morphological features as tails in ascidian larvae, eyes in cavefish, and wings in ants, may be correlated with, or perhaps even cause, the loss of these features across a variety of temporal and spatial scales. The problem exacerbates if you try to tackle the phylogeny and evolution of taxa with ancient divergence times, such as the major metazoan lineages. Since most of the major animal phyla (no Linnaean rank connotation implied) or their stem groups appeared in the fossil record more than 500 million years ago there has been ample time for gain and loss of characters. If the extent of convergent evolution of positive characters between the major metazoan lineages is any indication, extensive loss is very likely as well. After a study of character evolution in fossil members of various animal phyla, Wagner (2000) concluded that irrespective of taxon in due time "clades appear to exhaust available character space." When the apparent evolutionary stasis of conservative animal body plans of such phyla as echinoderms, molluscs, or arthropods is considered on a finer scale, it becomes clear that within certain boundaries of morphospace characters flicker and fluctuate in and out of existence. Consequently, when one tries to assess phylogenetic relationships between such deeply diverged taxa as the animal phyla using comparative morphology one is in real danger of being mislead.

A final reason for taking the confusing effect of secondary losses on our studies of evolution seriously is that loss of complexity is likely to be inextricably linked to increase in complexity. All biological systems are hierarchically structured with several semi-independent levels existing simultaneously. During the evolution of this hierarchical organization lower-level entities, such as unicellular organisms, gave rise to higher-level entities, such as multicellular organisms, principally by means of forming associations or colonies. Interestingly, studies of the 'rules' that attend such processes of complexity increase have yielded evidence that lower-level entities generally lose complexity as they aggregate in the formation of new,

more complex higher-level individuals. This holds true, for example, for the evolution of multicellularity in plants and animals, and of ant colonies. The lower-level entities in both these cases lose complexity, numbers of different cell-organelles in the first case, and morphological and behavioral complexity of individual ants in the second case (Anderson & McShea 2001; McShea 2002). If evolutionary loss is indeed so ingrained in the evolutionary process we will ignore it at our own peril.

If evolutionary loss is indeed so ingrained in the evolutionary process we will ignore it at our own peril

I want to close this essay with an example where this unfortunate event may already have occurred. For more than a decade phylogeneticists have performed comprehensive morphological cladistic analyses of the Metazoa, however, without reaching a detailed consensus view. Strikingly, what little consensus can be discerned has been brutally upset by the emerging 'new view' of animal evolution, which is principally founded on the phylogenetic analysis of 18S and 28S rDNA sequences. However, it appeared to me that these phylogenetic conflicts between morphology and molecules were not randomly distributed across the Metazoa (see Jenner in press for full discussion). It seemed that in particular animal phyla that fall within either of three categories have a high chance of being placed in conflicting positions in molecular and morphological phylogenies: parasites, morphologically very simple taxa, and taxa that supposedly underwent a large change in habit or habitat during their evolutionary origin.

A look at character coding strategies in metazoan cladistic may explain this distribution of conflict. Over 90% of more than 800 characters included in comprehensive morphological data sets published in the new millennium are coded as binary absence/presence (a/p) characters. A/p coding is a very popular coding strategy for phylogenetic analyses of many different taxa on a variety of taxonomic levels. For the majority of these characters the absence character states are simply regarded as uninformative default plesiomorphies, and a large percentage of these characters are not even properly defined. The unfortunate result is that taxa are habitually scored for the same unspecified absence state, without actually exhibiting any special similarity in morphology or development. The many empirically empty absence characters states conflict fundamentally with the notion of transformational homology that is at the heart of standard cladistic analysis. Within a framework of transformational homology a parsimony analysis is operationalized by the transformation of different character states into each other, and this can only be meaningfully achieved if all character states are carefully delimited, and represent potentially informative primary homologies. Only in this way can character losses become phylogenetically informative. This widespread coding strategy led me to suspect that many potentially phylogenetically informative secondary absences, or character losses were simply overlooked.

If this is indeed the case, then the distribution of phylogenetic conflict between molecules and morphology noted above is no longer particularly surprising. Parasites and taxa adopting new habits or moving to entirely new environments (e.g. terrestrialization) are expected often to modify their morphology, sometimes extensively, which may lead to loss of key morphological features. Moreover, morphologically simple taxa will almost automatically be misplaced if they are secondarily reduced, when the few informative characters are simply a/p coded. As a result, all these taxa appear to be placed in more basal positions in morphological cladograms than in the molecular trees. Thus, insufficient attention to absence character states may largely be responsible for exaggerating molecular and morphological conflict in metazoan phylogenetics.

How to deal with this problem? Using molecular data is one obvious answer. If you still want to use morphology, and of course we do, either to reconstruct the phylogeny, or to dress up a naked molecular phylogenetic skeleton, one possibility would be to pay attention to functional morphology and the environmental setting of evolutionary changes. For example, parasites are prone to modifying or losing characters related to external sensory organs and the digestive tract, and if you are a burrowing reptile, you may feature the same set of reductions and bone fusions as other, but unrelated, limbless burrowers (Lee 1998). Of course, introducing evolutionary process considerations into a phylogenetic analysis is definitely no failsave method, and in the current cladistic era it seems a decidedly unpopular proposal. Yet, if you meet parasite Pam, simple Simon, or changing Charles in your data matrix, be warned!

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Ronald Jenner is a regular essayist for the Newsletter of the Palaeontological Association.

Book Reviews

A Review of 'Telling the Evolutionary Time: Molecular Clocks and the Fossil Record'. CRC Press, Boca Raton, Florida, by Donoghue PCJ. & Smith MP. (eds.) 2004. ISBN 041527542 (H back)£66.99

Time is everything. It is the course of life. It is priceless - most persons would pay a fortune to add 20 years to their own lives. We often have too little of it (think of all those great data waiting to be written up) or rarely too much (when the kids won't get out of the bathroom despite our urgent personal pleas)! Time fascinates us in context of our own evolutionary origins. Exactly when our species diverged from our nearest common ancestor is a question that nestles in the back of every biologist's mind. How old are we, really? This quickly leads to other time-oriented questions - the age of life, the first eukaryotes, the first land plants, the first chordates, angiosperms, etc. Putting a timestick to the entire Tree of Life is a desired goal for most biologists.

This book is all about time and how it can be measured best through fossils and molecular clocks. It is divided into an Introduction and 12 chapters as follows: (Introduction) Molecular clocks and the fossil record - towards consilience?, Donoghue & Smith; (1) Molecular clocks: whence and whither?' Rodríguez-Trelles, Tarrío & Ayala; (2) Molecular clocks and a biological trigger for Neoproterozoic Snowball Earth events and the Cambrian explosion, Hedges; (3) Phylogenetic fuses and evolutionary 'explosions': conflicting evidence and critical tests, Fortey, Jackson & Strugnell; (4) The quality of the fossil record, Benton; (5) Ghost ranges, Paul; (6) Episodic evolution of nuclear small subunit ribosomal RNA gene in the stem-lineage of Foraminifera, Pawlowski & Berney; (7) Dating the origin of land plants, Wellman; (8) Angiosperm divergence times: congruence and incongruence between fossils and sequence divergence estimates, Wikström, Savolainen & Chase; (9) The limitations of the fossil record and the dating of the origin of the Bilateria, Budd & Jensen; (10) The origin and early evolution of chordates: molecular clocks and the fossil record, Donoghue, Smith & Sansom; (11) Bones, molecules, and crown-tetrapod origins, Ruta & Coates; and (12) The fossil record and molecular clocks: basal radiations within the Neornithes, Dyke. It is a mixture, therefore, of chapters on fossils and molecular data plus animal and plant groups (with an emphasis on the former).

Measuring time is not easy. No modern clock is perfect, not even atomic ones. As we leave human history and go further back in time, the challenges increase. Fossils provide the only certainty for life forms being found at a particular time. Sometimes these dates change, such as the earlier report of the oldest known angiosperm from the Jurassic, *Archaefructus*, which has carpels but not typical flowers, at 140 million years ago (Sun *et al*. 1998). Subsequent geological studies, however, revealed errors of interpretation, the strata now being dated to the more believable Lower Cretaceous at 126 million years ago (Swisher *et al*. 1999; Sun *et al*. 2002). Other ways to date the divergence of a group (and/or structures) are major geological, atmospheric, or oceanographic events, plus radioisotopes. Correlation among these data allows extrapolation to time of other divergence points, allowing estimation of anatomical and morphological change, explanation of biogeographic patterns, etc.

Because there are often not enough fossils nor dates from other geological sources, we turn to phylogenetic information in the so-called 'semantides' (Zuckerkandl & Pauling 1965) in extant organisms. Molecules certainly do contain a record of the past history of each organism, and these are extremely important for determining relationships. But what parts of the genome can tell us best about times of divergence? Wouldn't it be especially nice if DNA base pairs changed clock-like, regular, steady?

It is well known and intuitively grasped, however, that a precisely functioning molecular clock does not exist. Rodríguez-Trelles *et al*. in Chapter 1 provide abundant evidence on this point. Different genes mutate at different rates, some are under selection and others not, and many DNA segments are non-coding and others are apparently nonsense. Further, rates of change in one particular gene sequence may be very clock-like in one lineage and completely erratic in another. That is, the clock works in both

cases, but it keeps better or worse time depending upon its owner. The challenge, therefore, is to assess the accuracy of the clock within a particular group before it can be used effectively. Some of the problems with molecular clock analyses are due to phylogenetic uncertainty (from small datasets and stochastic errors; Wikström *et al*. Chapter 8), unreliability of the calibration points, neglect of confidence intervals both on calibration points and clock estimates, and accurately relating sequence changes to rate variation (Fortey *et al*. Chapter 3). To me, the most interesting point of this book is its summary across many taxa (mostly animals) that the molecular age of divergence of groups is nearly twice that from fossil evidence. Focusing on this discrepancy, in fact, is one of the stated emphases of the book. This 'doubling' of the age of groups from molecular data in comparison to fossil data may be due to (1) gaps in the fossil record, or (2) rapid clock rates during times of divergence (i.e. not a constant rate; Benton, Chapter 4). For fossils, perhaps early in the evolution of a group the body parts are not well preserved and the taxa few, so that the fossils aren't easily found until later. This is called the 'phylogenetic fuse' (Fortey *et al*. Chapter 3). This specific label would certainly fit the recent transitional-combinational theory for the origin of the angiosperms (Stuessy 2004), which, among other things, seeks to reconcile the fossil record of angiosperms with molecular data from among extant vascular plants. Wikström *et al.* (Chapter 8) address many of these specific issues.

No book is perfect. There is an odd bibliographic point that should be mentioned. On the main title page the book is said to be published by CRC Press. On the reverse page, however, the publisher is listed as Taylor & Francis. The copyright is by the *Systematics Association* for 2003, which is not a problem. On the hard cover (imprinted with the title and art) is also the logo of *The Palaeontological Association* (along with that of the *Systematics Association* and CRC Press), and at the bottom of the obverse of the first title page, there is a short description of this association, but with no explanation whatever on their role in the book (or symposium). I have learned that Taylor and Francis has apparently been bought out by CRC Press, but such a business transition should not be reflected inconsistently in one book. It will be interesting to see how librarians deal with this odd problem. The ommission of letters [".ool..ical .ecord"] in the title of fig. 5.6 (p. 98) is unfortunate but minor.

Overall, for investigators interested in the time of divergence of their groups, this book is a valuable contribution to the subject. It puts the discrepancy of molecular and fossil data into clear focus (although without solution), it illustrates the methods used for molecular clock estimates, it clearly underlines the non-absolute clock nature of DNA sequences, and it gives abundant examples of all these problems. The volume is reasonably well-edited and the production is good. The price is high, but this is not untypical these days for scholarly publications.

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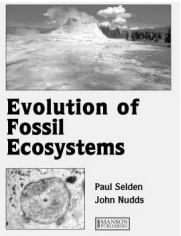
In 2003, Taylor and Francis Ltd., publisher of the Systematic Association's book series bought CRC Press, based in Florida USA.

A Review of 'Evolution of fossil ecosystems' Manson Publishing, London, by Selden P. & Nudds J. 2004. ISBN 1 84076 041 9 (Paperback). £



When conjuring up metaphors for the adequacy (or otherwise) of the fossil record, it is hardly surprising that reference is often made to either a moth-eaten tapestry or a high brick wall with only an occasional window. Either image implies a scene, either once-rich or largely invisible, of which we are afforded only a glimpse of its true nature, even its glory. In my moments of reverie, I sometimes imagine having a wish granted, whereby one could return to one instant in the geological past. My guide pulls back the curtain and there is the Cambrian world, or whatever your choice may be. All those years of research meet the reality: "Good heavens …… No, really …… I never imagined ….. Look at this ……Well I never ……" . Who knows if such a privilege will ever be bestowed, but in the meantime we can gather some comfort from the fact as our investigations continue so at least some of the threads of the tapestry will be restored or another chink made in the wall. I refer, of course, to those extraordinary instances of fossil

preservation, in the trade known as Fossil Lagerstätten, that here are beautifully documented by Paul Selden and John Nudds, both of Manchester University.

As they point out in their introduction, despite the widespread interest in the state of exceptional preservation, perhaps most famously the Middle Cambrian Burgess Shale or Upper Jurassic Solnhofen Plattenkalk, there is no adequate textbook suitable for students. To be sure the recent book by Dave Bottjer and colleagues, *Exceptional Fossil Preservation* [Columbia; 2002] goes some way to address this need, but Selden and Nudds steal a march by the use of striking colour illustrations and crisp style which although set in a uniform pattern for the description of each Fossil-Lagerstätte provides many vignettes of interest. Many will have heard of the fabulous Amber Room which vanished at the end of World War Two (and is still rumoured to exist), but how many of you knew of the use of amber as false teeth?

The choices of Fossil-Lagerstätten are not in themselves very surprising, chronologically spanning as they do the classic Ediacaran localities of the Flinders Ranges in South Australia to the Rancho La Brea tarpits of modern-day Los Angeles. Sandwiched in between are arguably the triumvirate of Fossil Lagerstätten, that is the Burgess Shale, Mazon Creek and Solnhofen, and nine others that range from the Hunsrückschiefer to Baltic amber. Each deposit is put in its appropriate context, with a succinct review of overall setting (be it quarrying or those false teeth) and stratigraphy. This is followed by a brief, if at times slightly dry, overview of the biota that, supported by many spectacular illustrations of fossils, provides a series of glimpses into vanished worlds. Given the interests of the senior author it is perhaps understandable why the marvellous record of insects (and other arthropods) receives particular notice, but in general the coverage is judicious rather than exhaustive. There will be few palaeontologists with an overall knowledge of Fossil Lagerstätten and for example I found the overview of the Rhynie Chert biota, and especially the plants, a very helpful update. Succeeding the review of each biota, the chapter is wrapped up with a short discussion of the palaeoecology, followed by a comparison with similar deposits.

I have no hesitation in recommending this book. It deserves to be a cornerstone text in undergraduate teaching, and will be a colourful counterpart to some of the rather staid textbooks in this area. Yet, some critical comments are called for. Perhaps most surprising is the omission of at least one or two of the Precambrian Fossil-Lagerstätten; the Gunflint Chert immediately comes to mind. To be sure it does not have the spectacular quality of such deposits as the Posidonienschiefer (Holzmaden), with its ichthyosaurs giving birth, or Solnhofen with its limulid death marches, but the microbial ecology of the Gunflint Chert is still sensational. Selden and Nudds are right to mention comparable deposits to each of the Fossil-Lagerstätte they discuss, but here too are some oversights. The remarkable Bear Gulch Limestone, from the Carboniferous of Montana, receives only passing mention, yet its fish fauna and the mysterious *Typhloesus*, are of considerable significance. Perhaps the most significant failure to do justice to a deposit is the case of the Ediacaran biotas. The Flinders Ranges are certainly important, but it is difficult to imagine a more spectacular locality than that of Mistaken Point in south-east Newfoundland. Here one can walk across a sea-floor, apparently frozen in Ediacaran time. Those who have been lucky enough to visit the locality or even view Dolf Seilacher's exhibition of Fossil Art with its striking casts of fossil surfaces will attest to the extraordinary nature of Mistaken Point. A similar point could be made with respect to the Burgess Shale. Despite its (over-)exposure it is now clear that the Chengjiang assemblages of Yunnan province, China, rival, if not exceed, the Burgess Shale in terms of importance. Nor should this surprise us, for at least two reasons. First, Chengjiang is closer to the detonation of the Cambrian "explosion"; the Burgess Shale is apparently much more of an "echo". Second, the outcrop area of productive strata is enormous, and it is little exaggeration to say that despite the spectacular progress achieved by several groups based in Xi'an, Kunming and Nanjing, we are still scratching the surface.

Many readers will also find helpful the further information of how localities might be visited, or museums with particularly important collections toured. A word of caution is, however, advisable. The stringency concerning visits to the Burgess Shale is well known, but in the case of the Flinders Ranges any prospective collector needs to be very well aware of the existing regulations both in terms of designated Park areas and export of fossils from Australia. Perhaps on a more positive note it is gratifying to learn that, in addition to the Burgess Shale, recently the Mistaken Point has been designated as a World Heritage Site. Thus this locality joins the Backs of Cambridge and the Dorset coast as a site of global significance.

Another criticism concerns the explanations of just how such extraordinary preservation came about. To be sure an outline of the preservational style is provided for each Fossil-Lagerstätte, but it would be useful to have a more enquiring tenor. This was brought home to me most forcibly when I was visiting a Changjiang locality near Haikou, site of the remarkable discovery of Cambrian fish. Here, in a small excavation, it is impossible not to find soft-bodied fossils. So abundant

are they that the collectors are simply not in a position to keep everything. What on earth is the special factor in the operation here?

This remark on the perennial mystery of how such soft-part preservation came about leads me to ask how we can best inspire the next generation of researchers. Certainly the clarity of exposition and quality of illustrations in this book will help to do their part. But the Fossil-Lagerstätten also excite our interest because they are the arena of some of the most interesting controversies in evolution. In this respect the Ediacaran assemblages stand out. So weird are they in terms of both their anatomy and preservation it seems difficult to avoid the conclusion that Seilacher's vendobiont hypothesis must have some relevance: the evidence is increasingly suggesting that here we have a glimpse of an extraordinary radiation of protistan diversity. This is not to deny that there is a metazoan component, but even these are (to our eyes) bizarre and cry out for some radical re-thinking. Similar remarks certainly apply also to the Burgess Shale-type faunas, where new discoveries continue to surprise even the most hardened of palaeontologists.

Let me conclude, however, by not only urging you to buy this book - for teaching and sheer enjoyment it is a very sound investment - but also praising the authors for writing a skein of geological history which in providing an underlying narrative of events serves to remind us that exceptional as these biotas are their real importance is when they are integrated into the wider picture of earth history and organic evolution.

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Spotlight

Biological systematics in Bulgaria

Pavel N. Nikolov & Boyko B. Georgiev

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Bulgaria occupies a relatively small territory of about 111 000 km^2. However, it has diverse natural conditions: an altitude between 0 and 2925 m; plains, deep valleys, gorges, highlands and peaks; karst areas with numerous caves; regions with typical continental, Mediterranean and transitional climate; glacial lakes, coastal lagoons and riverside wetlands; arable lands, natural grasslands, forests and coastal sands. All these formations are a prerequisite for the impressive biological diversity of this country. Numerous natural ecosystems in Bulgaria are well preserved, which has resulted in an extensive network of protected areas. These occupy about 5% of the territory of the country, including three national parks, 11 natural parks and 90 reserves.

Ten years ago, in the course of the elaboration of the National Biological Diversity Conservation Strategy, data about the species diversity of the country were re-evaluated. The list of the species recorded in Bulgaria included about 760 vertebrates, 26,200 invertebrates (19,600 insects), 1,800 protozoans, 3,800 vascular plants, 58 ferns, 670 bryophytes, 3,000 algae, 3,500 fungi and 710 lichens. Due to the fact that substantial parts of the country have never been affected by glaciations, the level of endemism is very high - about 8% of the species-group taxa of vascular plants are Balkan endemics and in some invertebrate groups the level of endemism exceeds 50% (myriapods, terrestrial isopods). Since numerous invertebrate groups are poorly studied, the expected number of animal species in Bulgaria is estimated at about 56 000 species.

The first data on Bulgaria's biological diversity were published by foreign travellers and scientists in the second half of the19th Century. The biological science in Bulgaria started its development after achieving a national independence in 1878, relatively late in comparison to many European countries. The University of Sofia was founded in 1888 and soon after that, the chairs of botany (1891) and zoology (1893) were organised. Largely due to the personal natural history interests of the members of the royal family, in 1890 the collections of the Royal Natural History Institutes (now National Museum of Natural History) were founded.

Over more than 110 years, biological systematics in Bulgaria made many essential achievements. Perhaps the most important of them are:

- The flora of vascular plants is relatively well studied. The first edition of the *Flora of Bulgaria* was published in two volumes in 1923 and 1925. This book, which is rather an identification key, had further three editions (1933, 1948 and 1967). Since 1963, a detailed work in many volumes on the vascular flora arranged in systematic order has been started by the Institute of Botany at the Bulgarian Academy of Sciences. Until now, 10 volumes have been published. These are a result of extensive taxonomic work and critical re-evaluation of the collections at Bulgarian and foreign institutions.

- Detailed taxonomic monographs were prepared on several groups of fungi (four volumes published in 1991-2001), bryophytes (1975) and seaweeds (2000).

- The series Fauna of Bulgaria was initiated in 1950 with the book

Birds of Bulgaria followed by Fishes of Bulgaria (1951). Until now, this series, maintained by the Institute of Zoology, Bulgarian Academy of Sciences, contains 26 volumes covering fishes, birds, mammals, various insect groups, ticks, polychaetes and terrestrial snails.

- The series *Catalogus Faunae Bulgaricae* started in the late eighties. Currently there are four volumes on insect and protozoan groups and on freshwater molluscs. At present, the main institutions carrying out studies and education in biosystematics are the Bulgarian Academy of Sciences, the University of Sofia "St. Kliment Okhridski" and the University of Plovdiv.

The Bulgarian Academy of Sciences is the oldest institution in the country. Bulgarian emigrants founded it as Bulgarian Literary Society in 1869 in Braila, Romania. After the resurrection of the Bulgarian state in 1878, it was relocated in Sofia and later, in 1911, was transformed into Bulgarian Academy of Sciences. In the second half of the Twentieth Century, the academy initiated numerous research institutions. Now, it encompasses about 80 institutes and has more than 7,000 employees. Studies in biological systematics take place mainly in the Institute of Botany, Institute of Zoology, National Museum of Natural History, and Central Laboratory of General Ecology, all located in Sofia, and the Institute of Oceanology in Varna. The main research of these institutes is addressed to the biological diversity of Bulgaria, with special emphasis on natural resources, protected areas and environmental monitoring.

The Universities of Sofia and Plovdiv provide a good level of education in biology. These universities have well-equipped departments of botany and zoology, employing experienced taxonomists in various plant and animal groups. PhD education in biosystematics is carried out at both universities and Bulgarian Academy of Sciences. This brief review will not be complete if the major problems of the biological systematics in Bulgaria are not outlined. The main problem is the lack of reliable funding bodies in the country because the economic instability during the last 15 years. For instance, between 1990 and 2002, the annual support of the projects funded by the National Science Foundation has been limited to E200-500 - an amount covering postal expenses, stationery and some consumables and chemicals produced in the country (e.g., ethanol) but not allowing supplies of imported chemicals and literature, renovation of equipment or international travels. The situation has improved during the last two years when the annual supports of the projects have reached E1,500-2,000. However, this still cannot provide renovation of the laboratory equipment, mostly produced before (and much before) 1989.

The financial restrictions forced the universities and the academy to reduce strongly the subscriptions for international journals. For the first time after the Second World War, there was a disconnection of the series of the most important scientific journals (e.g. the library of the Bulgarian Academy of Sciences had regular subscriptions for 25 specialised parasitological journals before 1989; their number now is reduced to six).

The political restrictions for international travels before 1989 were replaced by financial limitations after that. Thus, many Bulgarian taxonomists, though being experts in their groups, had never the opportunity to participate international scientific meetings. This, in combination with the reduced access to foreign literature, resulted into the retarded distribution of the contemporary approaches in systematics in our country (e.g. the phylogenetic methodology is poorly known among Bulgarian taxonomists). The curriculum of the biological education does not include this subject and there are not experienced specialists in the field. Fortunately, the number of taxonomists interested in phylogenetic studies rapidly increases and its wider application in the systematic research is a matter for the next few years.

In spite of the economic difficulties and the low prestige of the academic professions during the transitional period, mostly because the enthusiasm of the people involved, biological systematics in Bulgaria is not only alive but improving its international reputation. The number of the publications in internationally recognised journals gradually increases, as it can be seen from the annual reports of the Bulgarian Academy of Sciences. The positive recent developments include the expansion of the studies on the flora and fauna of neighbouring countries or in wider geographical scale.

There are several active scientific societies in our country: botanical, parasitological, ornithological, herpetological, ecological, entomological, etc. In the next few years, Bulgaria will host several international scientific meetings covering taxonomic topics -arachnology, nematology, parasitology and others. The participation of members of the *Systematics Association* will be highly appreciated because it will assist the improvement of the methodological level of our studies and will facilitate the further integration of Bulgarian systematists to the international scientific community.

> ... biological systematics in Bulgaria is not only alive but improving its international reputation.

Pavel N. Nikolov won the prize for the best poster presentation at the

4th Biennial Conference of the Systematics Association in Dublin, 2003.

News

The Fifth Young Systematists' Forum

Russell Seymour
The Natural History Museum, London

There may be better days to visit the Royal Botanic Gardens at Kew than a grey December day with a piercing breeze; unless, of course, you were attending the most recent *Systematics Association* Young Systematists' Forum. This annual event, co-sponsored this year by the RBG Kew, CRC Press (the *Systematics Association's* publisher) and Science magazine, was held in the Jodrell Lecture Theatre at the RBG Kew on the 4th of December last year and was attended by approximately eighty delegates. The chill of the early winter's day was countered by the quality of the presentations given and the warm discussions that ensued.

The ethos and driving force of the Young Systematists' Forum is to provide a welcoming environment for young systematists (that is, current and recently completed PhD students) to present their work, often for the first time, to an audience of peers and interested 'senior' systematic biologists. The Young Systematists' Forum (affectionately known as the YSF) has grown year on year, and has always thrived on the variety of subject matter discussed. This year saw, perhaps, the greatest geographical diversity with young systematists registered from (in alphabetical order) Australia, Austria, Belgium, Brazil, Canada, Colombia, the Czech Republic, Finland, Iran, Ireland, the Netherlands and the UK.

The President of the Systematics Association, Dr. Barry Leadbeater, welcomed the delegates and introduced the welcoming address by the Director of the RBG Kew, Prof. Peter Crane. There followed a diverse program of fifteen oral presentations (two Iranian delegates, due to speak, were unable to obtain the necessary visitor's visas) with five posters on display.

The standard of science and the quality presentation was high throughout and the judges (Drs. Bill Baker, Paul Wilkin and Vincent Savolainen) had a difficult time deciding on the awards for best presentations and engaged in some serious discussion. Ultimately, the prize for the best poster presentation went to Silvio Nihei for *"A cladistic review of the tribe Muscini (Diptera, Muscidae) and how it can change our view on the biogeography of the family"*. The two runners up in the oral presentation category were Alexandra Muellner for the *"Evolution and systematics of Agaia (Meliaceae): inferences from DNA sequence data and secondary metabolites"* and Tim Waters for *"Concepts, morphology and molecules: delimiting species in the New Caledonian kauris (Agathis, Araucariaceae)"*. The winner of the best presentation was Chris Creevey, who attempted to answer the question *"Does a tree-like phylogeny only exist at the tips in the prokaryotes?"*.

The winners of each category were presented with a book from the *Systematics Association* publications series, donated by CRC Press. The winner of the best oral presentation category also received a year long subscription to Science (donated by Science International). All of the winners and runners up also received a quantity of book tokens. The abstracts of the winners and the full list of speakers are reproduced below. The abstracts of the other presentation are available on the association website (www.systass.org).

The day concluded with a "drinks and nibbles" reception where wide ranging discussions continued until the food and drink ran out!

The day was a fascinating insight into the depth and diversity of work being carried out by young systematists from all over the world. The quality of the work and the style in which it was presented amply demonstrate that systematics truly is a vibrant and exciting arena in which to be pursuing research. The date and venue for the 6th YSF has already been decided and the venue booked. So I commend you all to enter the date in your diary now; **Thursday 9th December 2004 in the Flett Lecture Theatre of the Natural History Museum, London.** If you want to present, please get in touch closer to the day. If you no longer fall within that 'young' category then please encourage your students or colleagues to present or to attend. For those of you who have already attended a YSF you will know what an exciting day it is. For those who have not, please do make the effort to come along this year, all are welcome to attend, whether young or not-so-young! I know that you will not be disappointed!

For more details on the YSF and other Systematics Association activites pleases visit our website: (www.systass.org)

Abstracts from Winning Presentations

Winner of the Best Poster category

Cladistic analysis of the tribe Muscini (Diptera, Muscidae)

Shigueo Nihei S. & Barros de Carvalho CJ.
Department of Zoology, Universidade Federal do Paraná, Curitiba, Brazil (Financial support from CNPq and CAPES).

The tribe Muscini exhibits a wide variety of morphologically and ecologically diverse forms, including

their reproductive strategy (female oviparous or larviparous), larval feeding habits (saprophagous, coprophagous, carnivorous) and adult colouration (metallic, pale, yellowish). This group, with 22 genera and about 350 species around the world, is regarded among the most basal clades within the Muscidae and is characterised by a number of diagnostic features. The aim of the present study is to reconstruct the phylogenetic relationships among the genera of Muscini using mainly adult morphological characters, and larval characters wherever available.

The preliminary results indicate that: (1) the monophyly of Muscini is supported; (2) the monophyly of some genera (e.g. *Polietes, Morellia, Eudasyphora*) is doubtful; (3) the New World and Old World species of *Morellia* do not form a unique clade; and (4) several clades are congruent with regard to the basal position of the genera endemic to Neotropical, Afrotropical and Australasian regions, which suggest the origin of the Muscini could be related to Gondwana.

Runner up in the Best Oral Presentation Category

Evolution and systematics of Aglaia (Meliaceae): inferences from DNA sequence data and secondary metabolites

Muellner AN, Samuel R. Chase MW, Pannell CM & Greger H. Institute of Botany and Botanical Garden, Department of Higher Plant Systematics and Evolution, University of Vienna, Austria.

Aglaia Lour. (angiosperm family Meliaceae, order Sapindales) is an arborescent genus occurring in the tropics of S.E. Asia, the Pacific islands and N. Australia. It comprises more than 100 species and presents more taxonomic problems in species delimitation than any other genus of the family. This resulted in the adoption of a wide species concept, by which taxa contain considerable morphological variation. We performed maximum parsimony and Bayesian analyses of sequence data from two regions (nuclear ITS and plastid *rps*16 intron) to estimate phylogenetic relationships within genus *Aglaia* and its relations to the other genera of tribe Aglaieae. Based on 67 newly sequenced accessions of *Aglaieae*, three taxa of Guareae and two taxa of Melieae (outgroup), this study provides the first reassessment of the current circumscription of *Aglaieae* and *Aglaia*, and of sections and species concepts. DNA data are compared to recently collected data on chemical profiles of the respective taxa.

Winner of the Best Oral Presentation Category

Does a tree-like phylogeny only exist at the tips in the prokaryotes?

Creevey CJ. Bioinformatics and Pharmacogenomics Laboratory, National University of Ireland, Maynooth, Ireland.

The extent to which prokaryotic evolution has been influenced by horizontal gene transfer (HGT) is unclear. Here we use supertree methods to ask whether a definitive prokaryotic phylogenetic tree exists and whether it can be confidently inferred using orthologous genes. We analysed two datasets, one spanning the deepest divisions of prokaryotic relationships and one spanning the relatively recent gamma-proteobacteria using species for which complete genomes are available. Compatibility between gene-trees spanning deep relationships is only slightly better than random. Contrastingly, a strong, almost perfect, phylogenetic signal exists in gamma-proteobacterial genes. We conclude that deep-level prokaryotic relationships are either difficult to infer due to systematic biases or are not tree-like because of extensive HGT, hidden paralogy or both. Although we used two small datasets, this approach will help decide the extent to which we can say that there is a prokaryotic phylogeny and where in the phylogeny a cohesive signal exists.

Complete list of Participants

(Note that only presenters are listed here. Co-authors are given on the website)

Speakers

Hannah Banks, Micromorphology Group, Royal Botanic Gardens, Kew, Richmond, UK. *"The evolution of pollen structures in caesalpinioid legumes"*.

James J. Clarkson, Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, UK. *" Phylogenetic relationships in Nicotiana (Solanaceae) based on glutamine synthetase sequences"*

Christopher J. Creevey, Bioinformatics and Pharmacogenomics Laboratory, National University of Ireland, Maynooth, Ireland. *"Does a tree-like phylogeny only exist at the tips in the prokaryotes?"*

Lenka Drábková, Institute of Botany, Deptartment of Taxonomy and Biosystematics, Academy of Sciences, Czech Republic. *"Phylogeny and evolution of the Juncaceae."*

Sophie Herden, Department of Zoology, University of Oxford, Oxford, UK. *"Genetic variation and ancient divergence between freshwater and marine Protozoa."*

Jennifer Jackson, Department of Zoology, University of Oxford, Oxford, UK. *"How to swim sideways: a systematics perspective on flatfish evolution."*

Aino Juslén, Division of Systematic Biology, University of Helsinki, Finland. Present address Nationaal herbarium Nederland, Utrecht University, Utrecht, Netherlands *"The phylogeny of liverworts - with special attention to the traditional "basal" leafy liverwort lineages."*

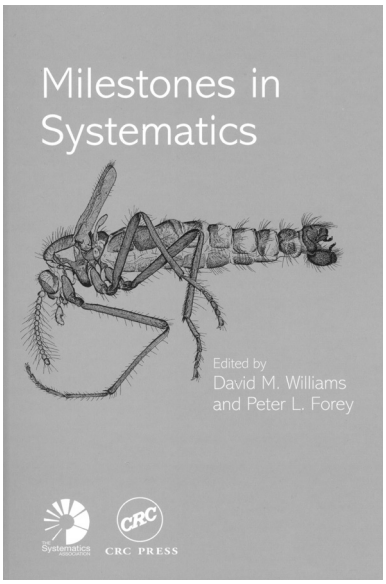
Stuart J. Longhorn, Department of Entomology, The Natural History Museum, London, UK. *"Phylogenomic Analysis of the*

Translational Machinery: The Cytoplasmic Ribosomal Proteins in Arthropods."
Louise M. Longridge, *"Biogeography, diversity and systematics of the Jurassic ammonite Badouxia."*
A. N. Muellner, Institute of Botany and Botanical Garden, Deptartment. of Higher Plant Systematics and Evolution, University of Vienna, Vienna, Austria. *"Evolution and systematics of Aglaia (Meliaceae): inferences from DNA sequence data and secondary metabolites."*
Maneezhe Pakravan, Alzahra University, Iran (withdrawn). *"Numerical taxonomy study of the genus Alcea."*
Davide Pisani, Department of Zoology, The Natural History Museum, London, UK. *"The Colonization of Land by Animals: A Molecular Perspective."*
Martyn P. Powell, Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond & Centre for Plant Diversity and Systematics, Department of Botany, University of Reading, UK. *"Floral mimicry in oncidioid orchids."*
Fariba Sharifnia, Department of Biology, Faculty of Science, Islamic Azad University, North Tehran Iran. *"Seed protein analysis in relation to taxonomic of Persian Linum species."*
Jan Strugnell, Department of Zoology, University of Oxford, Oxford, UK. *"Phylogeny, rates of evolution and estimating divergence time events in cephalopod molluscs"*
Timothy Waters, Department of Zoology, University of Oxford, Oxford, UK. *"Concepts, morphology and molecules: delimiting species in the New Caledonian kauris (Agathis, Araucariaceae)."*
Wim Willems, Center of Environmental Studies, Research Group Biodiversity, Phylogeny and Population Studies, Limburgs Universitair Centrum, Diepenbeek, Belgium. *"Flatworm taxonomy revisited? Molecular phylogeny of the 'Typhloplanoida' and its implications for the phylogeny of the Rhabdocoela (Platyhelminthes)."*

Poster Presentations

Blanca C. Huertas, Imperial College & The Natural History Museum, London, UK. *"Colombian EBA Project: Research in Biodiversity, Systematics and Conservation in the Colombian Andes."*
Leona Leonard, Department of Zoology, University College Dublin, Dublin, Ireland. *"Evolutionary relationships of palaeognathous birds, combining morphological characters and information from fossils."*
Zdenka Navratilova, Institute of Botany, Department of Taxonomy, Academy of Sciences, Czech Republic. *"Hybridization and introgression in Carduus crispus and C. personata."*
Silvio Shigueo Nihei, Department of Zoology, Universidade Federal do Paraná, Curitiba, Brazil. *"Cladistic analysis of the tribe Muscini (Diptera, Muscidae)."*

New Systematics Association Publications!



Milestones in Systematics

Edited by David M. Williams and Peter Forey *The Natural History Museum London*
ISBN 0-4152-7524-5 £66.99
This volume reviews the major issues in systematic theory and practice that have driven the working methods of systematists during the 20th century, and takes a forward look at the issues most likely to preoccupy systematists in the immediate furture.

Also out now

Organelles, Genomes and Eukaryote Phylogeny

Edited by Robert P. Hirt and David S. Horner
ISBN 0-4152-9904-7 £99.95

Organelles, Genomes and Eukaryote Phylogeny covers recent developments in the field of "deep level" phylogenetic inference of eukaryotes, especially with respect to the origin and evolution of eukaryotic cells and their organelles. It focuses on interpretation of data derived from molecular and cell biology, genome sequencing with respect to the timing and mechanism of eukaryogenesis, and the endosymbiotic events leading to mitochondria and plastids.

These publications will be reviewed in the Winter issue of *The Systematist*

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SA Business

Council Meetings

The next council meeting will be held at the Linnean Society, Burlington House, Piccadilly, London, UK. on Wednesday **October 6th at 1pm 2004.**

AGM December 8th2004

The AGM lecture to be given by Joel Cracraft, Department of Ornithology, American Museum of Natural History, New York, USA **at 6pm** in the Lecture Theatre, Linnean Society, Burlington House, Piccadilly, London
All members welcome.

SA Meetings

Evolution of Protozoa and Other Protists

13th September 2004
Linnean Society of London, Burlington House, Piccadilly, London W1J 0BF

Joint meeting organised by the British Section of the Society of Protozoologists, the Linnean Society and the Systematics Association

Organizers: Terry Preston (t.preston@ucl.ac.uk) and Alan Warren (a.warren@nhm.ac.uk)

Cost: £25 (students £12.50) includes registration fee, tea and coffee, lunch and evening reception.

Evolution of Pleurocarpus Mosses

6-8th September 2004, National Museum and Gallery of Wales, Cardiff

Please send the abstract of your poster or contributed paper by 1st August 2004. Poster presentations on the subject of the conference are welcome.

Organizers: Angela Newton (a.newton@nhm.ac.uk) and Ray Tangney (ray.tangney@nmgw.ac.uk).
Cost: £20.00

Do you want to contribute an article, letter or notice to *The Systematist ?* Please contact the editors. Deadline for contributions: 28th November 2004

6YSF: The 6th Young Systematists' Forum

9th December 2004 in the Flett Lecture Theatre of the The Natural History Museum, London.

Annual Meeting of young systematists (graduates, undergraduates and postdocs) held in association with The Natural History Museum, London

Organizer: Russell Seymour The Natural History Museum, London (r.seymour@nhm.ac.uk).
Cost: Free.

Further information about *Systematics Association* Meetings, including programme and registration forms can be found at www.systass.org

The Systematics Association Registed UK Charity No. 270429

The Systematics Association is committed to furthering all aspects of Systematic biology. It organises a vigorous programme of international conferences on key themes in Systematics, including a series of major biennial conferences to be launched in 1997. The association also supports a variety of training courses in systematics and awards grants in support of systematics research.

Membership is open to amateurs and professionals with interests in any branch of biology, including microbiology and palaeontology. Members are generally entitled to attend the conferences at a reduced registration rate, to apply for grants from the Association and to receive the Associations newsletter, *The Systematist* and mailings of information.

Please visit our website for more information: www.systass.org

For information on membership, contact the Membership Secretary, Dr G. Reid (membership@systass.org), Department of Botany, The Natural History Museum, Cromwell Road, London, SW7 5BD, U.K.

The Systematist Newsletter of the Systematics Association.

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