

The Systematist

Newsletter of the Systematics Association

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Spotlight on
Agnes Arber

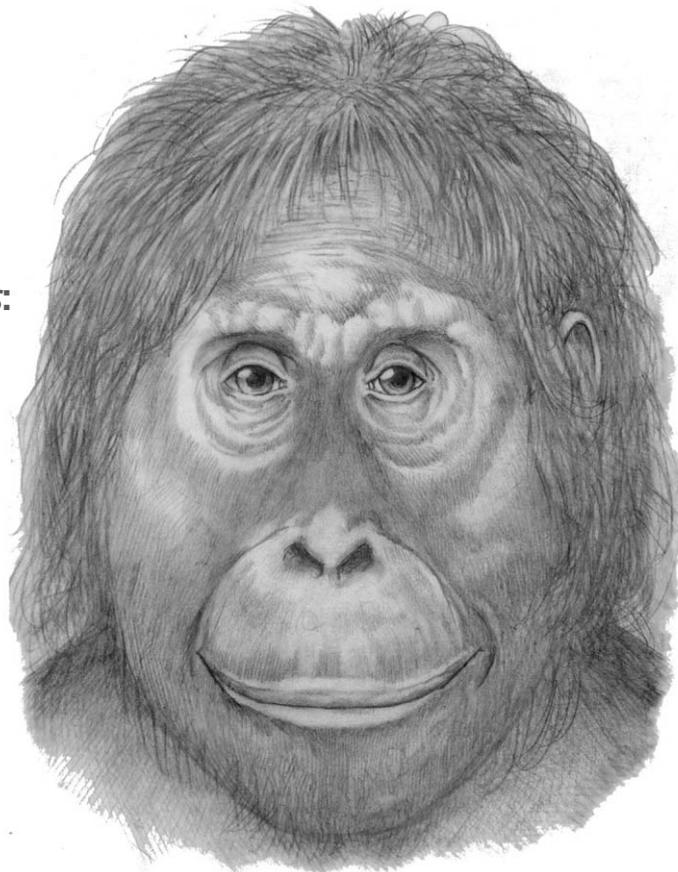
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Lucy?

The orangutan and the enigma of human origin

Editorial

Our cover will have already told you that the evolution of "The Systematist" continues apace. We hope that you like the content and new front page design: please let us know your thoughts. Issue 24 highlights include an excellent article on morphology vs. sequence data in hominid systematics by John Grehan (p. 3-7), which is accompanied by the specially commissioned cover illustration by William Parsons, a report on the Evolution of Protozoa and other Protists Meeting last September (p. 7-9), and a personal account of the PhyloCode meeting in Paris in July 2004 (p. 9-12). We also enjoyed reading Maura Flannery's piece on Agnes Arber (p. 13-17). A hard copy of the Systematics Research Fund application form is available, and SA programme information for 2005 is can be found in its usual place on the back page. Our thanks are particularly due to Dr. Rudi Schmid of UC Berkeley for providing the photograph of Agnes Arber on p. 14.

The role of *The Systematist* should be to inform, stimulate and entertain the membership. Perhaps the best way to ensure that this happens is for SA members to write and submit articles themselves. We are always seeking interesting copy and arresting images, so please get writing now for the Summer, 2005 issue. We and your colleagues look forward to hearing what you have to say, and perhaps to giving our own point of view in return. It's one way to convince the outside world that our discipline is alive, relevant and effective in meeting its challenges.

Hope you all have a systematically productive 2005.

For those interested in contributing a letter, article, a response, news item to *The Systematist*, please note that the deadline for the next issue is **June 1 2005**.

Malte C. Ebach & Paul Wilkin
Editors

Please visit the SA website:
www.systass.org

Letter from the President

Greetings for 2005!

The New Year is a time for taking stock of what has recently past but more particularly it is a time for looking forward. As I mentioned in my introduction to the Summer Edition, 2004 was a year for navel gazing. Council reviewed the extent and detail of our activities and decided upon a number of innovations. Above all, we were keen to engage more frequently with the membership of the Association and with this in mind we instigated 'The Sir Julian Huxley Lecture' which took place on July 7 at the Linnean Society and was followed by a wine reception in the library. This event was such a success that it will now become an annual occurrence - suggestions for speakers and topics are always welcome. In 2005 the lecture will take place on July 6 at the Linnean Society. The AGM on December 6 2004 was followed by the annual address given by Joel Cracraft which generated much lively debate. The following day the Sixth Young Systematists Forum was hosted at the Natural History Museum. As has become customary,

these are excellent events attracting substantial numbers of postgraduate students who have an opportunity to present talks and posters. The overwhelming impression following this year's event was the enthusiasm and professionalism generated by the participants.

2005 heralds our fifth biennial meeting, this time to be held in Cardiff (August 22nd-26th). The biennials have now become events not to be missed both for their science and the conviviality. The three themes chosen for this year address highly topical issues - *The New Taxonomy; What is Biogeography? and Compatibility Methods in Systematics*. In addition there will plenty time for contributed papers and, as usual, we will be awarding prizes for the best student oral and poster presentations. Please note this event in your diaries now.

Several changes have taken place amongst the Officers. Donald Quicke and David Williams have completed their terms of office as Zoological and Botanical Secretaries respectively. Eileen Cox, after nine years as Programmes Secretary, has earned a well-deserved respite. We offer them our warmest thanks for their respective contributions and look forward to their continuing support. As a result of our discussions last year we decided to dispense with the roles of two of the secretaries and to replace them by a Programmes Secretary and an Awards and Grants Secretary. Bill Baker (RBGK) and Tim Littlewood (NHM) respectively have duly been elected to these positions. Together with the new 'ordinary' members of Council we welcome them on board.

Finally on a purely personal note I have much enjoyed my first year as President of the Association and look to meeting you at the Cardiff Biennial in August. A happy and productive New Year to you all.

Barry Leadbeater
President

Cover illustration : "Lucy" Copyright 2005 William Parsons (published with permission). Artistic interpretation of Lucy by William Parsons using a recent skull reconstruction of *Australopithecus afarensis* and additional soft tissue features implied by a cladistic sister group relationship between humans and orangutans.

The orangutan and the enigma of human origin

John R. Grehan

Buffalo Museum of Science, Buffalo, USA

Orangutans are our nearest living relatives. That is the unequivocal story of morphological systematics. Ignoring this evidence, in favor of genetic similarity linking humans and chimpanzees, calls into question the continued existence of morphological systematics as a science.

Over 20 years ago the primate and hominid systematist Jeffrey Schwartz made a startling and challenging proposition that should have turned human evolution upside down. Schwartz proposed that the orangutan (*Pongo pygmaeus*) was more closely related to humans than were either chimpanzees or gorillas. This proposal went against the almost universally accepted view that the chimpanzee is our closest living relative.

Schwartz's reasoning was based on cladistic analysis showing that

chimpanzee relationship rests on genetics - principally the similarity of matching DNA base sequences. Greater similarities of DNA sequences were widely seen by geneticists and even morphologists to be a reliable predictor of a closer phylogenetic relationship since humans and chimpanzees differ by only about 1.1% of all base sequences compared to 2.2% for humans and orangutans, chimpanzees became the nearest relative of choice (Schwartz 1987). The similarity of human and chimpanzee sequences was seen to be so close

ing only if it conforms to a genetic relationship (Collard and Wood 2000; Pilbeam 2000).

The subordination of morphology to DNA similarity leaves the scientific study of evolution in a precarious position because it would appear to invalidate the entire endeavor of morphological systematics. What is the answer to this problem? According to Timothy Littlewood of the Natural History Museum in London, incongruities between molecular and morphological data highlight the need for additional data rather than representing a barrier to resolving the tree of life (Pennisi 2003). But what is 'more data'?

Schwartz's work shows that the key might not simply be the addition of more data, but the addition of data that comes from asking the right kind of questions. So the orangutan relationship is more than just a minor question in systematics. It reaches into the heart of systematic theory and method, and in turn, the veracity of evolutionary modeling.

In this article I will briefly review the nature of the morphological connection between humans and orangutans (defended in detail by Schwartz 1987, 1988, 2001, 2004a). I will show that the morphological evidence marshaled by Schwartz is a better predictor of the hominid fossil record than the DNA sequence

In any other group of organisms the comparative level of cladistic support for orangutans would attract intense scrutiny and detailed critique. Instead there ensued two decades of almost total silence.

there are about 40 uniquely shared characters between humans and orangutans compared with only 7-10 uniquely shared between humans and chimpanzees (Schwartz 1984, 1987, 1988, 2001, 2004a). In any other group of organisms the comparative level of cladistic support for orangutans would attract intense scrutiny and detailed critique. Instead there ensued two decades of almost total silence.

The reason for the silence is not hard to find. The foundation of the

that some authors called for the incorporation of both primates within the genus *Homo* (Diamond 1993; Goodman *et al.* 1998). If the genetic relationship is the sole predictor of phylogeny, as has been widely accepted in primate systematics, does morphology continue to have any evolutionary meaning, and can morphology continue to exist as a science if it has no predictive power? The answer, according to some practitioners, is "no" because morphology has evolutionary mean-

support for the chimpanzee. I will also argue that the correlation of living and fossil morphology supports the contention of Schwartz (2004a) that morphology need not be subordinated to DNA sequence similarity for the systematic resolution of primates or any other group of organisms.

Unique similarities between humans and orangutans are immediately visible in their external appearance. Both have the longest hair of any primate (head for humans, body for orangutans), a receded hairline leaving an exposed forehead (the hairline of gorillas and chimpanzees, like gibbons and monkeys, begins at the eyebrows), cranial hair that grows forward rather than to the back or sides as in other primates, and a well developed beard and mustache in males. Another all too obvious uniquely shared feature is the complete absence of keratinized calluses on the buttocks. This absence might be attributed to the evolution of bipedalism in humans if it were not for the non-bipedal condition of the orangutan.

When an orangutan opens its mouth one might well be looking into a mirror to see the low cusped molars otherwise found only in humans. The molars of orangutans are also like humans in being covered by a thick layer of dental enamel.

Humans and orangutans show several uniquely shared developmental and structural features of the skeleton including timing and sequence of ossification for the proximal humerus, distal radius, proximal ulna, and humeral head. They also share the shortest and deepest scapula, the most horizontal orientation of the scapular spine, and the most reduced area above the scapula spine.

The skull of orangutans and humans includes two uniquely shared characters involving openings or foramina. The first is the

incisive foramen, a small opening (wide in humans, narrow in orangutans) near the front of the upper palate, which allows blood vessels and nerves to pass through from the floor of the nasal cavity. All other primates, including chimpanzees, have two foramina. The other opening is the foramen lacerum at the base of the petrosal bone. This is filled with cartilage and connective tissue in humans and orangutans, but is absent in all other primates.

A variety of internal soft tissue features are also unique to humans and orangutans. They share the greatest level of brain asymmetry, which may raise the question of whether there are also correlated cognitive characteristics (Schwartz

ductive hormone estriol.

Humans and orangutans stand apart from chimpanzees, gorillas, gibbons, and most monkey species in having concealed ovulation because there is no female genital swelling or color change during the peri-ovulatory phase of the menstrual cycle. In addition, the female genitalia of juvenile orangutans are more like humans in structure than are those of juvenile chimpanzees.

Orangutans, like humans, can and do, copulate throughout the menstrual cycle and while orangutans appear to show increased preference for mating near mid-cycle, this pattern may also occur in humans. Interest in mating by male humans and orangutans is not cued by the female reproductive condition.

In reproductive biology humans and orangutans are similar in many respects just as chimpanzees are very different.

1987) such as the well-known persistence and patience of orangutans with mechanical problems compared with the frustration of chimpanzees (Parker and Mitchell 1999).

Orangutans and humans have a medial forelimb vein, the least developed accessory lobe of the parotid gland, the most linear shaped gall bladder, the largest fetal adrenal gland, and the most vallate papillae on the tongue. Orangutans and humans also have the most widely spaced mammary glands of all primates.

In reproductive biology humans and orangutans are similar in many respects just as chimpanzees (including bonobos) are very different. Mating by orangutans and humans is an extended affair (compared with a matter of seconds in chimpanzees), the duration of gestation (adjusted for body weight) is the longest of any primate, and both have the highest levels of the repro-

Other features of sexual biology so far reported only for humans and orangutans include female initiation of copulation with males, the use of foreplay, and a preference for face-to-face mating. Although face to face mating in bonobos is widely compared to humans, it is limited to only about 30% of all matings (de Waal 2001: 52).

When Harvard University geneticist Maryellen Ruvolo recently asserted that there is no evidence for the orangutan relationship she identified the non existence of morphology as a predictive or informative evolutionary science. She also noted that the genetic view of chimpanzees as our closest living relative led the Federal US government to spend millions of dollars to sequence the chimp genome (*Pittsburgh Post-Gazette*, October 15, 2004).

So, what is the evidence supporting the status given to the DNA

sequence similarity? In looking at the literature and asking systematists, I have so far only found a rhetorical defense: morphology is subject to the imagined effects of selection and is therefore unreliable (Diamond 1988) or morphological homology is too subjective (Pilbeam 2000).

In an extensive review of the literature, Schwartz (2004a) was only able to find an admission that the correlation of DNA sequence similarities with evolutionary relationship was an assumption, and the general match between morphological and DNA sequence similarities justified priority to the latter. These defenses appear to be just rationalizations.

Another layer of defense for DNA similarities is widely invoked in the form of cladistics. In DNA sequence studies, outgroups are used to polarize sequences and so sequence similarity trees are now said to be 'cladistic'. This approach is justified by claiming that an *a priori* polarization of individual characters is no longer necessary (e.g. Nixon and Carpenter 1993).

Using a compilation of unpolarized (primitive and derived) characters and relying on the 'outgroup' to give the correct phylogenetic tree assumes that the selected outgroups will automatically represent the plesiomorphic state for all characters as if the characters were correctly assigned in the first place. I agree with Schwartz's argument that DNA sequence analysis is more a case of phenetic characters being dressed up in cladistic language and techniques than cladistics as such (cf Schwartz 2004a).

If one considers a good theory to be one that successfully predicts other lines of evidence (Craw and Weston 1984) this criterion could be applied to the respective predictions of morphological and DNA sequence models for the hominid fossil record. The most obvious prediction of the DNA sequence theory is that early fossil hominids will

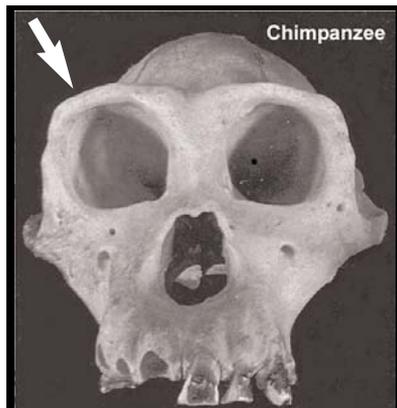


Figure 1a. Skull of chimpanzee illustrating the supraorbital margin (arrowed) forming a true brow ridge with forward, and especially vertical, distension. Note the absence of a large, forward-facing cheekbone. Image courtesy of JH. Schwartz.

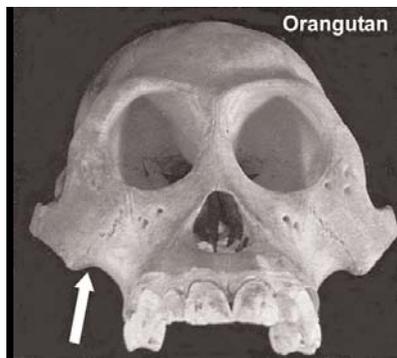


Figure 1b. Skull of orangutan showing the large forward-facing cheekbone (arrowed), and supraorbital margin comprising a low mound instead of a brow ridge. Image courtesy of JH. Schwartz.



Figure 1c. Skull of *Australopithecus 'africanus'* (Sts 52) illustrating the large forward-facing cheekbone (arrowed) and absence of a brow ridge. Image courtesy of JH. Schwartz.

show a definitive resemblance with chimpanzees rather than any other primate because chimpanzees are our nearest living relative. If one were to read the popular science media, that prediction would indeed seem to be confirmed. Look at all the museum paintings and television documentaries (e.g. BBC *Walking with Cavemen*) representing Lucy and other early hominids as some sort of upright chimpanzee. All of these renditions show faces with the broad, fleshy African ape nose (a feature absent in humans), deep set eyes, and short black hair projecting away from the forehead. These are features built up on a great deal of imagination and extrapolation.

If one were to look carefully at the hard tissues of early hominids (the genus *Australopithecus*) there are some direct contradictions to what might be anticipated by the chimpanzee theory. Chimpanzees and gorillas have a brow ridge extending above and between the eyes that also projects forwards and upwards so there is a depression behind the brow (Fig. 1a). In contrast, the eyes of orangutans are bordered above by a slight mound of raised bone that follows the eye orbits and there is a smooth transition from the superior margin of the eye orbits to the forehead (Fig. 1b). Which feature characterizes fossil hominids? The answer is the latter. *Australopithecus* skulls lack the African ape brow ridge, and like orangutans, australopiths have a smooth transition between eyebrow and forehead (Fig. 1c).

Absence of the brow ridge in australopiths could be dismissed as the result of an evolutionary loss following separation of hominids from the last common ancestor with chimpanzees. This kind of explanation cannot, however, be applied to orangutan features that are *present* in australopiths and absent in African apes. For example, the broad, forward-facing australopith cheekbone (Fig. 1c) is unlike anything found in modern African apes,

but it is otherwise unique to orangutans (Fig. 1b) and their fossil relatives (such as *Sivapithecus* [*Ramapithecus*]) (Schwartz 2004b). The thick dental enamel and low molar cusps place australopiths firmly within a human-orangutan clade, as do the presence of the foramen lacerum and a single incisive foramen (Schwartz 2004a; Schwartz & Tattersall in press). Altogether, these features in the australopith skull represent an entirely predictable finding for a sister group relationship between humans and orangutans.

A recent reconstruction by Kimbel

ets and thin eye brow ridges. Using these contours as a guide, Buffalo Museum of Science artist Willaim Parsons consulted with Jeffrey Schwartz to produce the world's first new interpretation of Lucy. This reconstruction includes those soft-tissue features predicted by the orangutan theory such as a clearly delineated hairline, forward orientation of cranial hair, and even a Mona Lisa-like smile that is all too human, but is also sometimes seen in orangutans (Fig. 2).

The new painting is on exhibit at the Buffalo Museum of Science as part of the world's first museum pre-

are otherwise perplexing contradictions of human and chimpanzee biology. Also, gone is that vexing evolutionary problem of trying to derive human bipedalism from a knuckle-walking quadruped chimpanzee-related ancestor since orangutans are not specialized knuckle walkers.

Lucy and other early hominids need not be subject to the anatomically constrained mating patterns of chimpanzees, and it would not be necessary to invent concealed ovulation, prolonged mating, or undergo any other evolutionary contortions to produce humans out of a common ancestor with chimpanzees (Schwartz 2004c).

Corroboration of the fossil record supports Schwartz's theory as a progressive research program (*cf.* Craw & Weston 1984). Consequently, it now becomes incumbent upon DNA sequence theorists to address the contradiction other than by simply rejecting morphology.

To retain its scientific integrity the Tree of Life web page will, at the very least, need to include the orangutan alternative alongside the DNA sequence model for the chimpanzee. Perhaps it is now also time for alternative morphological approaches to be funded by the National Science Foundation at levels commensurate with the financial commitment currently given to DNA sequencing. After all, the book of human origins is still open - at the first chapter.

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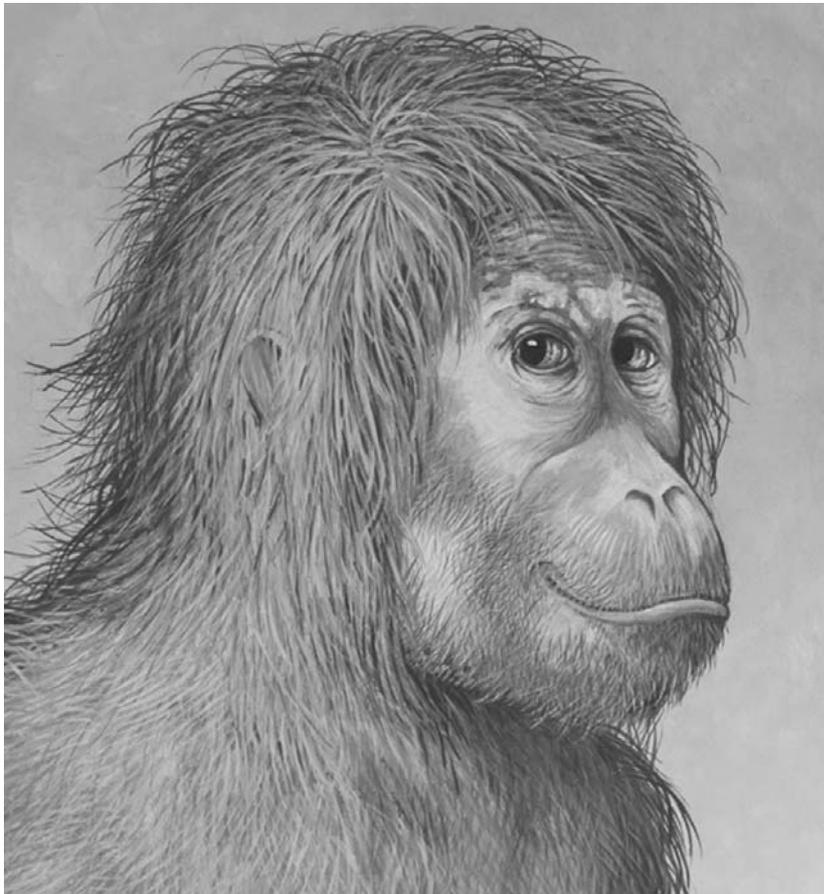


Figure 2. Artistic representation of 'Lucy' (*Australopithecus afarensis*) by William Parsons (Buffalo Museum of Science). Copyright 2004 William Parsons.

et al. (2004) for *Australopithecus afarensis* skull AL444-2, found at the same site as Lucy, gives new emphasis to the orangutan resemblance. Their reconstruction shows a very orangutan-like configuration with forward-facing cheekbones, a flat facial plane below the eye sock-

sentation showing the public how alternative scientific models for human evolution are generated by differential emphasis of the same 'evidence' (see http://www.science-buff.org/human_origin_and_the_great_apes.php). The orangutan theory for human evolution removes what

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Meeting Reports

Meeting Report Evolution of Protozoa and Other Protists

Linnean Society, London,
September 13 2004

Protozoa were the first eukaryotes and gave rise all the higher kingdoms of life: animals, fungi, plants and chromists. At roughly the same time as the famous Cambrian explosion of animal phyla, protozoa and other protists (notably algae) underwent a similar massive radiation. The origin of the eukaryote cell and how it diversified to produce the major groups of Protozoa and other unicells, some heterotrophic, some autotrophic, thus continues to be a fascinating and often controversial topic that has ramifications for all major eukaryote groups.

Protozoan evolution was last addressed by the Systematics Association in 1996 at a joint meet-

ing with the British Section of the Society of Protozoologists (BSSP) and the Linnean Society. During the eight years since that meeting some breathtaking advances have been made in our understanding of protozoan evolution and phylogenetics. It was therefore thought timely to revisit this topic, so the same three societies brought their expertise to bear in organising a one-day meeting at the Linnean Society. The meeting was chaired by Keith Vickerman (who also chaired the 1996 meeting) and comprised eight invited talks given by internationally recognised experts, and a poster session. A total of 80 participants from 8 different countries were registered at the meeting.

The first two talks dealt with the acquisition and evolution of mitochondria and mitochondria-like organelles, a key event in eukaryote evolution. Martin Embley (Newcastle University, UK) presented compelling evidence that all extant eukaryote lineages so far investigated evolved from a mitochondria-bearing ancestor. The absence of mitochondria in some groups is due to secondary loss since investigations so far carried out on all these anaerobic forms have revealed the presence in the nucleus of mitochondrial genes and/or the presence in the cytoplasm of mitochondrial homologues such as hydrogenosomes and mitosomes. Carmen Rotte (Institut für Zytobiologie, Germany) presented further evidence: (1) for the early acquisition and common origin of mitochondria and hydrogenosomes, and; (2) that basic metabolic functions essential for all eukaryote cells, such as the biogenesis of Fe/S proteins, is conserved in both organelles. Evidence from nuclear protein coding genes was also presented to suggest that yeast cells harbour more genes of eubacterial than of archaeobacterial origin whereas the current phylogenetic paradigm based on ribosomal RNA gene sequences suggests that

eukaryotes and archaeobacteria are sister groups.

Andrew Roger (Dalhousie University, Canada) explored methods for inferring the deep phylogeny of eukaryotes using multiple gene data sets. Obtaining robust, `deep` phylogenies has hitherto been difficult due to phenomena such as saturation of sequence changes and lateral gene transfers. A software tool was described that helps overcome these difficulties by identifying gene sets with similar histories and analyzing them separately from other sets. Professor Roger also introduced us to the term `dendrophobia`, or the fear of trees, a condition that is likely to be detrimental to the careers of botanists and phylogeneticists alike.

In common with most disciplines, protozoology has become increasingly specialized and one of the deepest and long-standing divides is that between those who work on extant vs. fossilised protozoa. In an attempt to bridge this gap four speakers were invited to review important aspects of protozoan evolution from both extant and fossilised faunas. Foraminifera are the best represented protozoa in the fossil record and provide a rich source of material for investigation. Jan Pawlowski (University of Geneva, Switzerland) examined the early history of foraminifera by analyzing SSUrRNA and actin-coding genes and found evidence of a large radiation comprising numerous heterogeneous lineages, rather than a gradual, step-wise process as had previously been supposed. Similar morphotypes apparently developed independently in different lineages thus throwing the present morphology-based classification of early foraminiferans into disarray. Encouragingly, however, there was a good congruence between the molecular and fossil data for dating the major radiation event.

The colonisation of the pelagic environment was the last major step in the ecological expansion of the

foraminifera and first occurred around 180 million years ago. Using a combination of molecular and fossil studies, Michal Kucera (Royal Holloway, University of London, UK) reviewed the causes and mechanisms of the speciation events that then followed. He noted that non-vicariant speciation models have been suggested as the main mechanism of plankton evolution, with isolation being mediated by mechanisms such as divergence in the depth and timing of reproduction, mate recognition systems, etc. However, molecular genetic investigations reveal that genetically distinct types with a greater degree of endemism are common among morphologically defined species, lending support to the plausibility of

Encouragingly, however, there was a good congruence between the molecular and fossil data for dating the major radiation event.

allopatric speciation in the plankton.

Continuing the planktonic theme, Jeremy Young (Natural History Museum, UK) explored the evolution of life cycles and of biomineralization in two protist groups: the coccolithophores and the calcareous dinoflagellates. Both groups are well represented in the fossil record and both exhibit superficially variable life-cycles with haploid and diploid phases. However, molecular genetic and stratophenetic data suggest that fundamental aspects of the life-cycle are highly conserved within groups and that innovations in one ploidy phase of the life-cycle, such as biomineralization, can be transferred to the other phase.

Traditionally, our fossil-based understanding of protozoan evolution has relied on a fossil record that comprises almost exclusively forms with durable, calcareous shells such as foraminifera, radiolarians and dinoflagellates. Fossil representatives of the soft-bodied fauna, or even those with proteinaceous

shells, are virtually unknown. Wilhelm Foissner reviewed some recent reports that indicate such forms do exist, including testate amoebae in 800 million year-old Neoproterozoic rock and tintinnid ciliates in ~500 million year-old deposits, thus significantly extending the period over which these groups are known to have existed. This suggests that protists are significantly more than 1,000 million years old. Professor Foissner went on to present compelling evidence that certain testate amoebae from 15 million year-old volcanic crater-lake sediments, and ciliates from 100 million year-old amber, have such a high degree of similarity with extant forms as to be conspecific with their modern-day equivalents. This sug-

gests that protist morphotypes may persist for very long periods.

The final address was given by Tom Cavalier-Smith (Oxford University, UK) who undertook the not insignificant task of summarizing the key events in the evolution of the protists and in their diversification into the five eukaryote kingdoms we recognise today. A few of the key features of this scenario include: the first eukaryotic cell was a facultatively aerobic, phagotrophic, heterotroph with a cilium (flagellum) but no chloroplast; there was a fundamental bifurcation between two major eukaryote clades with an ancestrally uniciliate unikont giving rise to the protozoan phylum Amoebozoa and the opisthokonts (including the kingdom Animalia and kingdom Fungi); meanwhile an ancestrally biciliary bikont gave rise to all other protists and to the kingdom Plantae. The key evolutionary events that gave rise to the major protozoan (and other protist) groups were also highlighted. Professor

Cavalier-Smith ended his talk on an optimistic note concluding that our large-scale picture of diversification of the kingdom Protozoa, with its 13 phyla, is probably now reasonably complete.

Three posters were also displayed. These included one by R. Moore, A. Simpson, D. Green, K. Heimann, C. Bolch, M. Obornik, D. Patterson, O. Hoegh-Guldberg and D. Carter, who presented molecular evidence (i.e. nuclear SSU rDNA, LSU DNA and plastid psbA sequence data) for two taxa that suggests evolutionary relationships between apicomplexans and certain lineages of autotrophic protists. Another was presented by H. Smith and D. Wilkinson on the global distribution of the testate amoeba *Nebela vas* and its biogeographical and evolutionary implications.

During the previous meeting in 1996 John Corliss reviewed the status of protozoan/protistan classification and posed the question whether, by the beginning of the 21st century, we might have a classification scheme for the Protozoa that is clear, uncomplicated and accurately reflects known phylogenetic relationships. Although we have clearly failed to meet the deadline set by John Corliss, progress reported at the 2004 meeting gives cause for optimism that we may not be too far from that goal.

Alan Warren (meeting co-organiser)
Terry Preston (meeting co-organiser)
Keith Vickerman (meeting chairman)

Phylocode - May the Force be with us: An attempt to understand

University of Paris
6-9 July, 2004

The Meeting

Is 2004 "Year Zero for Nomenclature"? This is what I overheard someone call the inauguration of the PhyloCode while attending the *First International Phylogenetic Nomenclature Meeting* in Paris (6-9 July, 2004). Many articles exist debating the merits and shortcomings of the PhyloCode and I will not add another. This is instead a personal account of my experience of that meeting. Which was, according to one of the authors of the PhyloCode, an historic event.

The Code

Most people reading this newsletter will be familiar with the PhyloCode, but for the sake of clarity an

I also knew that very few people at the conference knew me or my opinion, so it was a sort of undercover mission.

extremely brief rundown is that it is a new code of Nomenclature based solely on phylogeny. Put very simply the underlying principle is the naming of clades. It sprang from work by de Quieroz and Gauthier in the 1980s and has gathered a following and much literature pro and against since. The code itself is authored by Cantino and de Queiroz and can be found at: <http://www.ohiou.edu/phylocode> [last revised June 17, 2004]. A very good review of many relevant issues is given by Jake Alexander in an essay that can be found on the Systematics Association website at: http://www.systass.org/Jake_Alexander_Essay.pdf.

The Motivation

I had heard about this code and the waves it was making mostly from TAXACOM and discussions around

my lab at The University of Melbourne. The thing that struck me when I raised my head from my daisy encrusted thesis, was the vitriol with which people were participating in (or dismissing) the debate about the PhyloCode. I'm not keen on witch hunts and think the status quo should always be questioned. On the other hand, I don't like change and am a firm believer in the old adage 'if it ain't broke, don't fix it'. I heard about the meeting at a conference in Melbourne, where Brent Mishler gave a talk about the PhyloCode. At that point I think I was fairly vocal about thinking it was not the best idea I had ever heard.

There were several reasons I chose to go to the meeting in Paris. Firstly, I live in Europe now and it

was only a 6 hour train trip away, which is nothing for an Australian. Secondly, I am a student and managed to get the registration fee waived. And thirdly, and most importantly, I was interested to know what all of the hype was about. I also knew that very few people at the conference knew me or my opinion, so it was a sort of undercover mission. This made it as exciting as a conference about a new code of Nomenclature could be, as it is not renowned for being the most scintillating of topics.

I was genuinely interested in why people thought a new code would be better than the existing codes and how exactly a purely phylogenetic approach could work. As a user of the International Code of Botanical Nomenclature (Greuter *et al.* 2000) I wanted to be up to date with the state of the field. I also only really know people who are opposed to it and I wanted to give the idea a

chance to see if there was something in it that I was missing. There was also the attraction of being at a big, potentially historic conference which could have an impact on my field of study in either a positive or negative manner. And let's face it, it was in Paris, why pass up an excuse to go to wonderful European city?

The Expectation

I didn't realise that I had expectations, but when I got there I found I did because the meeting did not match them. I had expected a large attendance because the amount of literature devoted to the subject seemed to indicate that a lot of people had opinions about the

champing at the bit to have their say. Also some popular science media, eg *BioScience* and *Science* had run articles on how ground breaking this was and I half expected journalists and members of scientific funding bodies to come. The reality was quite different. There were very few people. I counted a maximum of 50 at the fullest session, although official numbers (reported in Laurin and Cantino 2004) are given as 70. There were often as few as 20 in a given session and there were no parallel sessions. The advertised venue was sufficient for around 200 people, but the meeting was moved to a smaller hall in the museum.

Phylogenetic Nomenclature (20 minutes), The name Aves (20 minutes) and all other names (45 minutes) and, finally, discussion on any topic pertaining to the meeting (40 minutes). I am not sure where the organisers had experienced speed debating before but this was not sufficient time. They were apparently surprised as Laurin and Cantino (2004) reported that "we had hoped to reach a consensus in the discussions at the meeting, but the time devoted to this debate proved insufficient." At the Environmental Youth Alliance conference I remember spending - literally - two hours on where to put a full stop. On the amusing side, despite the time constraints someone claimed "I am not a hominid person" in the middle of a name debate.

I wish I had had my camera on me the day someone was wearing a T-Shirt that said "PhyloCode - may the force be with us".

Something that struck me from the first talk to the last was the assumption that we were all on the same side and that side was right. Something about the phrase "winning hearts and minds" in the title of a seminar suggests a certain religious zeal. On the second day someone admitted to not being a supporter of the PhyloCode and still waiting to be convinced. Naively I thought this might change the tone somewhat. The following speaker began by asking why everyone in the audience was there and the answer, apparently, was because we all like the PhyloCode.

PhyloCode. I also expected a lot of opponents to be present and I like lively discussion and looked forward to huge debates about the relative merits of the different codes. I expected the meeting to be about the Code and it's final form, how to implement it, and other such practical issues. I also expected copies of the code to be in the conference pack and extensive sessions debating unresolved issues like what to do about species. I did some reading but not the actual code in detail as I assumed that would be the main topic of the conference. I was wrong.

It was not a ferocious debate between the proponents and those who think it's a less than spectacular idea. In fact it wasn't that sort of debate at all. I think the expectation may have been based on my previous experience of the Environmental Youth Alliance in Australia where our national conference attracted about 300 members to argue for three days straight about the details of our new constitution. This was an altogether different experience. It was one of shoulder patting and agreement and earnest discussions about how to overthrow the evil empire. Many of the people in attendance were involved with creating the code. There were also groups of students following their pro-PhyloCode lecturer. The seminars were applications of the proposed code. In many different ways. And the PhyloCode itself was not part of the conference kit and hardly scheduled for discussion!

Because people assumed I was a big fan of the PhyloCode they said all sorts of things that they perhaps might have reserved otherwise, like conspiratorially telling me that it was important to make sure the code wasn't too controversial so that we could sneak it past the critics and then do whatever we wanted with it. No-one bothered to check if I was part of 'we'. I wish I had had my camera on me the day someone was wearing a T-Shirt that said "PhyloCode - may the force be with us".

The Reality

Firstly the attendance surprised me. From the response on TAXACOM and in the literature (for example a whole volume of *The Botanical Review*) vehemently opposed to the code, I got the impression it was a large threat with a lot of support behind it and many opponents

There were several sessions allocated for discussion: The theory of

The Symposium Volume

What astonished me the most were the comments of de Queiroz regarding the conference proceedings which are to be the companion volume for the PhyloCode. It is not going to consist of the contributed papers at the conference as is usual. The 'extraneous' text (i.e. the contributors papers) will be avoided and the work just used as examples of how to apply the PhyloCode. He suggested that the trees may not even be included in the publication although how you can name a clade without a tree is beyond me. Now I understand that the code was not officially in existence when the papers were given and none of the names proposed at the conference have any sort of official sanction but there has been a draft code on the web for years and the people present were proponents who had applied that code to their research and offered papers as the conference had instructed them to. Instead of that work being acceptable as offered by the researcher de Queiroz thinks it is necessary to oversee the publication and use them simply as examples.

This wish to retain control over the application of PhyloCode came through in other ways as well. Many suggestions were made regarding some unresolved issues and no conclusion was arrived at - or deemed necessary as 'the committee (composed of the instigators) will take the suggestions into consideration'. It may simply be naïve that I believed input from users (supporters no less) should be appreciated. If the code is to be used, taking the users opinions seriously seems like an elementary step. But I very much got the impression that it is a closed society of those who create the code who behaved like parents saying "yes dear, that's a good idea but we're the adults and we'll make the decisions". At the conference two different conversions of the name Amniota to a

clade name were offered.

Considering that the companion volume is to be edited (in the manner noted above) by de Queiroz and Cantino who offered one version of Amniota it seems obvious which definition is likely to make it into print.

Despite this approach being made clear at the conference, in their glowing report of the meeting, Laurin and Cantino (2004) blithely claim that "Papers presented at the meeting (and a few other contributions) will be assembled into a symposium volume whose publication, tentatively scheduled for 2006, will coincide with the implementation of the PhyloCode. This volume will be edited by K. de Queiroz, J. Gauthier and P. Cantino".

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The same names come up over and over again in the advisory group for the actual PhyloCode, the organising committee for the conference and the people who offered themselves for election to the council. Of the ten people elected seven were involved with writing the code. There were two options for President and President-Elect, as in all good democratic elections: these were de Queiroz and Cantino and de Queiroz and Cantino.

The Species Issue

An ongoing bug-bear for the PhyloCode has been the lack of resolution regarding treatment of species. This issue remains unresolved. A nomenclature that wishes to replace the current systems but has not figured out a way to deal with species which are the fundamental unit seems like a bit of a

joke to me.

The party line, given at the conference by de Queiroz regarding species was: "[the meeting] is not the time for debate, we [the committee] will come up with something and you [the members] can comment". Perhaps it was just that my hackles had well and truly risen by this point, but sending the 'chosen people' off to make something up about species and bring it back smacked of 'we know better than you'. A show of hands was offered for whether this was something the larger group condoned, but the impression was that they'd do it anyway even if it was a resounding 'no'.

My uneasiness was confirmed when I read in Laurin and Cantino

(2004) that "[t]wo important papers presented at the Paris meeting, one by Benoit Dayrat and the other by Julia Clarke, addressed these problems and set the stage to start work on a species code. In a 'straw vote', the participants in the business meeting approved de Queiroz's proposal that he, Clarke, Dayrat, and Cantino would draft a code for species names that will be separate from, but compatible with, the code for clade names." My problem is that the most interesting talk regarding species level application with a solid example came from a seminar by Kirsten Fisher, a student working with Brent Mishler, neither of whom are listed above. They advocated an extension of the rank free philosophy to the species level. This was not in line with the party line and subsequently ignored.

The Public Perception

De Queiroz in particular is a very charismatic quietly spoken smooth character and the public relations associated with the code seems to be a well oiled machine. There are several popular science journals or magazines that have covered this issue under sensational titles like "Is it 'So Long, Linnaeus?'" (Withgott 2000) or "Linnaeus's Last Stand?" (Pennisi 2001). In the former in *BioScience* the PhyloCode authors are described as "gentle revolutionaries" who "...are using feedback from allies and opponent alike to strengthen their code". They are apparently "...eager to allay fears". I'm not sure who they sent to the interviews, but this was not my experience.

An issue that was raised at the conference and was a surprise to many of the attendees was that of Pan being automatically added as a prefix for the stem of every crown clade. The example given was Panreptilia for the stem of Reptilia. This seemingly negated one of the arguments offered for the PhyloCodes' supremacy over existing codes. People outside of phylogenetic nomenclatural circles (i.e. most users of biological information) are likely to equate names that all begin with 'Pan' as being at a comparable level, just as they have always done with families.

It's all very well to come up with a good idea and run with it, heck, base a career on it if you can, but if you are not willing to listen to the people who are interested in using your idea and incorporate external suggestions, you seemingly shoot yourself in the foot. It struck me that most people were not impressed with the idea of 'Pan' - especially not as an automatic option, but I'll be quite surprised if it is not in the final PhyloCode because it was suggested by Gauthier and de Queiroz among others. The popularity of the idea can be gauged by a conference

in-joke: Pan-Demonium.

The Verdict

Many people have published opinions but I have to agree with Greuter (2004). "After careful analysis I can find no merit in the PhyloCode, can perceive no need for it, and consider it potentially dangerous to the present systems of scientific naming as a whole."

There are a lot of impatient people out there and it will be interesting to see how many actually adopt this approach.

The idea that the group is somewhat arrogant and outside governing bodies is noted in Pennisi (2001). "Phylocoders seemed to have bypassed both the codes and their congresses. 'They are going to erect a shadow government and [set up] a coup'". This quote is attributed to Kevin Nixon and sounds paranoid in the article, but from my experiences at the conference this is not so far from the truth.

I listened to four days of PhyloCode work and have no clearer an idea of how, practically, this system could replace the current ones especially in relation to biodiversity work and inventories, not to mention field work and identification particularly at the species level (which is my bias, because that's where I work and have worked in a few different capacities). It strikes me that this is a nomenclatural code for impatient people who want to name things before the phylogeny is stable enough to support change. There are a lot of impatient people out there and it will be interesting to see how many actually adopt this approach. I may be being hopeful but I do not give it a high likelihood of changing the face of nomenclature.

The Bottom Line

I considered myself fairly impartial, a non believer but also not a serious opposer. I was willing to be convinced. I was not convinced. The adversarial and smug approach really bothered me a lot. But I'm glad I went to the conference because the free dinner was wonderful.

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Spotlight

Agnes Arber in the 21st Century

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Agnes Arber (1879-1960) is a name that may not be familiar to many present-day biologists, but she was a distinguished plant morphologist of the first half of the 20th century. Educated at Cambridge University and the University of London, she wrote three major works and over sixty research articles on plant morphology (1920, 1925, 1934), and she was only the third woman elected to the Royal Society, receiving that honor in 1946. Married to the Cambridge paleobotanist, Newell Arber (1870-1918), she remained in Cambridge after his death, raising her daughter and receiving various fellowships, but never having an official appointment. However, there is much more to her background than I have sketched so far, and it is because of the richness of her work that I would argue she deserves to be better known today.

The very fact that Arber achieved scientific recognition despite the lack of an academic position speaks highly of her research and also speaks to the place of women in British science in the first half of the 20th century. While she was in school and again after she obtained her doctorate, up to the time of her marriage, Arber worked in the private laboratory of another woman botanist, Ethel Sargent (1863-1918). This laboratory was in Sargent's home and there Arber took up research on grasses and other monocotyledons which was to be her

life's work. At Cambridge, Arber worked at the Balfour Laboratory, a facility for women researchers and science students, until it closed in 1926. Then her request for space in the Botany Department was turned down, and so, borrowing a microscope and microtome from the Balfour, she set up a laboratory in a tiny room of her home, thus following in Sargent's footsteps (Packer 1997).

(Arber 1912). In his Royal Society memorial to Arber, H. Hamshaw Thomas (1960) writes that Arber developed an interest in herbals as a teenager, when her father brought home one which he had been asked to appraise, and that her fascination with Goethe's ideas date from the same time. In 1946, she published a translation of Goethe's *Attempt to Interpret the Metamorphosis of Plants* with an extended introduction and commentary. Through the years, she wrote pieces on figures in botanical history such as Nehemiah Grew (1906) and John Ray (1943) for *Isis* and other publications. Her two major works in the philosophy of biology are *The Natural Philosophy of Plant Form* (1950), which she described as a metaphysical view of plant morphology, and *The Mind and the Eye* (1954), an introduction to the philosophy of biology and another classic, being

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Arber was not only a fine botanist but a fine artist as well and this skill influenced her approach to research. She received early art training from her father, Henry Robertson, a landscape painter by profession. Botanically accurate watercolors of plants done in her teens attest to her skill, and she did almost all the drawings for her scientific papers and books; several of the latter have well over a hundred figures. She was also very interested in the history and philosophy of science. Her first book was a history of early printed herbals that has become a classic and is still in print today

reissued in 2003. This is the most accessible of her books and provides an interesting introduction to her ideas. Arber begins her book by outlining what she sees as the steps in biological inquiry. The first three are to find a question to explore, investigate it, and interpret the results of the investigation -- of the observations or experiments involved. Next comes testing the validity of this interpretation, followed by communicating the work to the scientific community. This is a relatively standard rendition of scientific inquiry, but Arber then adds one more step, that of reflect-

ing on the research and its relation to large issues in science and even in philosophy.

Arber sees this as something a researcher might do toward the end of their career, just as she had done in publishing *The Natural Philosophy of Plant Form* when she was over 70 years old. She sees philosophical reflection as important work because only when the larger implications of research are understood can its real value be appreciated and the scientific endeavor truly enriched. In *Natural Philosophy* Arber traces the history of ideas about plant form from the time of Aristotle. She gives particular attention to Goethe's idea of the leaf as the basic form in plants to which all other structures are related, but she then argues for a different fundamental form. She links Goethe's concept to Casimir de Candolle's of the leaf as an inhibited branch. From this, she develops her idea of the basic plant form being the leaf as a "partial-shoot." After providing a defense of this concept with a great deal of morphological evidence, she ends the book with a chapter on a philosophical interpretation of plant morphology. She argues for a special place for morphology as different from, but equal in importance to, more analytic modes of inquiry such as the experimental methods used in biochemistry and cell biology.

Having described her view of biological inquiry in *The Mind and the Eye*, Arber then goes on to spend over half the book exploring some of the philosophical aspects of such inquiry, including the importance of metaphor and analogy in scientific thinking, the relationship between creating in science and in art, and the nonverbal aspects of inquiry. It is important to remember the context in which Arber was working in

order to appreciate how prescient she was. In the 1950s, physics was still seen as the paradigmatic science for philosophers and positivism was still widely accepted as describing the way science is done.



Agnes Arber (1879-1960). Photo 1916 or 1917 reprinted from: Arber, MA. 1968. List of published works of Agnes Arber, EAN. Arber and Ether Sargent. Biographical notes by WT. Stearn. *Journal of the Society for the Bibliography of Natural History* 4: 370-384.

Arber bucked these trends, and this makes her views remarkably fresh even today. She argued that biology itself needs to be examined philosophically rather than being subsumed under some general philoso-

crucial role of metaphor in human thought processes was widely appreciated. Finally, she valued the aesthetic aspects of scientific inquiry before it became fashionable to look more broadly at the process of science, outside of the positivistic box, and to draw parallels between science and art.

Before I get to Arber's significance to systematists today, I would like to mention one more general reason why she deserves more attention: she is fun to read. She writes extremely well, and extremely clearly. She is learned without being at all dense or obtuse; she is learned in an unselfconscious way that was always rare but is almost unheard of today. To take just one page at random from *The Mind and the Eye* (p. 34), there she cites work by Isaac Newton, Nehemiah Grew, D'Arcy Thompson, and Charles Singer and she does so without making the text seem bloated with erudition. She can also be self-deprecating and a bit satiric as when in *Natural Philosophy* she describes Turpin's interpretation of Goethe's archetypal plant form: "The whole thing is a botanist's nightmare, in which features, which could not possibly coexist, are forced into the crudest juxtaposition" (p. 62).

Arber's last book, *The Manifold and the One*, is not really about science at all. It is a work of philosophy, which some have labeled a work of mysticism, yet it is very much about Arber's philosophy of science as well. As she discusses in the book's preface, from an early age she was fascinated by the question of the relationship between unity and diversity, and obviously the study of botany is a good outlet for such curiosity. This question did indeed occupy Arber's thinking for

much of her life, and her approach to plant morphology is an indication of this. She was very much interest-

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phy of science that is physics-oriented. She wrote of the importance of metaphor in science well before the

ed not only in the structural differences between species, but also in their similarities. She took a dynamic approach to the study of structure; she wanted to know how structures developed and how they changed through time, from one species to another.

This is where we get to a major reason why Arber is not better known today: she is often labeled as being anti-evolution, when in fact, what she questioned was not the fact that species change over time, but the idea that natural selection is the dominant mechanism for that change. It must be remembered that Arber is writing just as the evolutionary synthesis is becoming the dominant paradigm in biology, and that her research essentially ended around 1940, when the beginning of World War II made it impossible for her to continue her lab work. So it is not surprising that Arber's views are different from those of today, and it is unfair to judge her in light of what we now know.

Interestingly, some of her rather unpopular ideas are now gaining ground in new contexts, showing once again that really fundamental ideas keep recurring in science.

Arber repeatedly cited evidence which she saw as arguing against adaptation as the sole engine of evolutionary change. Like other botanists -- even Anthony Huxley as late as 1987--she wonders at the many variations on morphological themes and how these could all be adaptations. One of the major arguments she uses against natural selection is parallelism, the appearance of similar traits in species which are otherwise not closely related to each other. She argues for parallelism as a more accurate description of what Goethe called type: "when such related forms are seen from the standpoint of parallelism, there is no question of a basic type to which they all conform" (Arber 1950:159). While the concept of parallel evolution is often ignored or renamed as convergent evolution, there is a

renewed interest in it today (Hoekstra and Price 2004).

Recently, there has been research on parallel evolution in two very different arctic birds, lesser snow geese (*Anser c. caerulescens*) and arctic skuas (*Stercorarius parasiticus*). While they are not closely related, these species both display melanic plumage polymorphisms, with the melanism associated with variation in the same gene *melanocortin-1 receptor* (MC1R). In fact, in each species the darker phenotype is due to the same mutation, a point substitution resulting in the change of a valine to a methionine (Mundy *et al.*

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2004). While feather color is often the result of the action of a complex of genes, the effect with the snow geese is quite striking; they are white without the mutation and a deep blue-gray with it. This is one of the first cases where a parallelism has been tracked down to the genetic level and been found to be the result of a single point mutation, but it is unlikely to be rare. And such genetic studies are going to put a new light on parallelism.

One of the problems in science is

that, because the nature of the process, scientists are always trying to explain the big issues in light of incomplete data, and at any one time, they really have no idea just how incomplete the data is. In the first half of the 20th century, biologists were attempting to understand evolution with very scant genetic information. Even today that information is still very spotty. Think of it; only a handful of genomes have been sequenced, and even sequencing tells very little about what genomes actually *do*. Granted, Arber's interpretation of parallelism left a lot to be desired. At one point she writes of the "urges" of plants to develop in certain directions. But still it must be granted that she focused on phenomena -- similar traits appearing again and again in relatively unrelated species -- that others chose to ignore because these traits didn't fit neatly into the selectionist paradigm. What Arber was calling an urge, or force, we know now to be a genetic storehouse of potential traits that are found in each genome with only a small fraction of the possibilities actually expressed and with other possibilities capable of being expressed as a result of minor genetic changes.

There is also another area of genetics research that casts light on Arber's ideas. She has been labeled as taking an unpopular idealist and essentialist view of morphology (Edye 1975). She did indeed seek the unity underlying the diversity at a time when most biologists were focusing on the diversity and attempting to explain how natural selection generated all that diversity. She did indeed see Goethe's emphasis on type as a guide in viewing plant form, though she replaced type with parallelism. There are a number of present-day observers who have espoused views similar to hers, though they, too, are still seen as outside mainstream biological thinking. In *Form and Transformation*, Gerry Webster and Brian Goodwin (1998) attempt to revive the pre-

Darwinian tradition of rational morphology. Webster, in his portion of the book, rejects David Hull's argument that organisms belong to particular species "because they are part of that genealogical nexus, not because they possess any essential traits" (p. 66). Webster instead argues for a rational system of forms that, if constructed, "what *actually* happened in history would become of relatively minor interest" (p. 124).

Goodwin's approach is close to Arber's in that it is based on a rational morphology with the focus on a comparative study of form. He argues that taxonomy based on evo-

lutionary relationships may not always be the most revealing, and a taxonomy based on similarities in the development of form could be more instructive than a phylogenetic taxonomy. Both Arber and Goodwin argue that that organisms are shaped by more than just natural selection, that there is something inherent to them that drives their form. The difference between the Arber/Goodwin viewpoint and that of more traditional biologists concerns the role of genes in morphology and evolutionary change. Are genes just the products of selection as strict selectionists contend, or are there other issues to be considered? The discovery of homeotic genes, and of gene clusters that work together indicate that the structure of the genetic environment itself is crucial to development and to the forms which arise from developmental processes.

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While Arber hints at a vitalistic explanation for some commonalities

among species, what she at one point calls an "urge" toward self-completion (1950:93), Goodwin would explain more mechanistically as the result of the self-organizing characteristics of matter, the creation of pattern even in the absence of life. Goodwin (1993) thus provides an explanation for the "parallelism" that Arber found striking, and like Arber, focuses on these similarities and away from evolutionary relationships. There is still an idealistic element to his work since the morphogenetic fields he sees as essential to self-organization are not always clearly defined in physiochemical terms. At the end

of *The Gramineae*, Arber asks: "What is the meaning of the differences that separate the Gramineae so delicately, yet so definitely, from any other order" (p. 409). For her, genetic explanations were merely "descriptive." Perhaps she would see Goodwin's explanations in terms of organization as a step closer to the meaning she was looking for. For Goodwin, diversity in form is generated by an interplay of self-organization with genetic and environmental influences. Like Stuart Kauffman (1995) and Philip Ball (1999), Goodwin sees self-organization as a powerful force basic to the organization of matter, even the organization of living matter. While Kauffman (2000) takes a vitalistic approach by arguing that there are yet-to-be-discovered basic laws governing the self-organization of living things, Goodwin is more circumspect and focuses on how self-organization principles could channel evolutionary change. He devel-

ops a theory of biological form that is "based upon whole organisms as dynamically transforming systems that are technically described as fields" (Webster and Goodwin, 1998:129). He sees these fields as grounded in the self-organization of matter and then fine-tuned by genetic influences.

Since principles of self-organization are so fundamental, and the conservation of genes so marked, it is not surprising to find similar forms in unrelated taxa. Goodwin considers morphogenetic fields to be manifestations of self-organized form, as the material cause of form, while the genetic makeup is the efficient cause, to follow Arber and use Aristotelian causal categories. This view is beginning to be considered credible in mainstream evolutionary biology as indicated by Wallace Arthur's (2002) recent review of emerging concepts in evolutionary developmental biology. At several points, Arthur discusses the possibility of directional biases in evolutionary change, with some forms more likely to emerge than others.

At the 16th International Congress Botanical Congress in 1999, there was a symposium on the relationship between Arber's work and new explanatory models for vascular plant development; these papers were later published in the *Annals of Botany* (December 2001). As Bruce Kirchoff (2001a) one of the organizers of the symposium notes, systematics and molecular biology are creating huge amounts of new data about plants, but these data are only as useful as the models used to explain them. What is lacking is Arber's sixth step: taking the long view and examining the philosophical underpinnings of this work, finding ways to see the unity and meaning behind this information. Kirchoff (2001b) also argues that while present-day morphologists do not usually take Arber's holistic approach, there is a greater shift to the use of visual information, which is very much in keeping with her

work. This shift "allows systematists to capture more information, including some of the context in which the character occurs" (p. 1203), thus indirectly leading to a more holistic viewpoint.

Kirchoff argues for visual databases in botany to avoid the narrowing of information which occurs when visual data is translated into words. He sees this as in keeping with Arber's drive for "a better way to see what is already visible. . . to draw our attention to the interrelation among a number of phenomena to help us to see the plant with fresh eyes, and to speak about the results of this 'seeing,' and to place results in the context of botanical thought" (p. 1204). This may be Arber's most important contribution to the future of biology: to focus our attention on the importance of the visual. Philip Ritterbush (1968) has said that biology is the most visual of the sciences, but unfortunately biologists don't always behave as if this were the case. Their work is so involved with the visual that they fail to notice the complexities and difficulties of observation and representation. Arber did not shy away from these issues, and perhaps in our effort to deal with them more forthrightly, her work might be a good place to begin.

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THE LINNEAN SOCIETY OF LONDON

THE SYSTEMATICS RESEARCH FUND



THE SYSTEMATICS ASSOCIATION

- The Linnean Society of London and the Systematics Association have pooled resources in order to provide a fund for systematic research. These are small grants made available to all researchers regardless of nationality except where indicated*. The fund is a combination of small sources of funding that are being made available under one scheme (Systematics Association Small Grants, Linnean Society grants under the Side, Bonhote, Omer-Cooper & Westwood fund, Natural Environment Research Council. Grants are **not** available for attending conferences or for routine research expenses where other monies would be expected to be available.
- Applications for funding are to be made by completing this form and appending a single page (one side) of A4 paper outlining the objectives and methodology of the proposed project, emphasising its broader significance. Where appropriate, please give (a) starting and completion dates of specific activities, and (b) details and costs of equipment and/or facilities to be funded by the grant.
- * - the NERC Fund for Taxonomic Publication is only available for people based in the UK (although not necessarily UK nationals) and firm evidence of publication potential must be provided. The purpose of this fund is to provide costs for the publication of taxonomic research over and above the costs of normal scientific publication; tick the appropriate box on the form if you and the application are eligible for this fund.
- Applications must reach: Dr Tim Littlewood, The Chair – Systematics Research Fund, c/o The Linnean Society of London, Burlington House, Piccadilly, London W1J 0BF, UK by 31 December for consideration for the following year's awards. There are no exceptions. Submission by e-mail is also possible: T.Littlewood@nhm.ac.uk with 'Systematics Research Fund' in the subject line. Further details and additional forms are downloadable from: www.linnean.org or www.systass.org

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Book Reviews

A review of R.T. Pennington, Q.C.B. Cronk, and J.A. Richardson (eds.), 2004. *Plant phylogeny and the origin of major biomes*. *Phil. Trans. R. Soc. Lond. B* 359 (1450)

This account of biome evolution glorifies the 'powerful tool' of molecular sequencing but overlooks a simple logical error which undermines the whole enterprise. Despite this fundamental flaw (hinted at in several comments in the volume about problems with calibration) the tone is dogmatic and triumphalist: molecular evidence is 'clear'; it 'demonstrates' that long-distance dispersal 'must' have occurred; vicariance is 'refuted'.

Ages of taxa (nodes on phylogenetic trees) have been equated with the age of the oldest known fossil of the group, with the age of strata the taxa are endemic to, and with the age of relevant paleogeographic events. The first method has been the most popular, but both this and the second method involve serious difficulties. The third method seems the most promising but has often been used in a simplistic way, for example in assuming that all divergence across the Isthmus of Panama dates to its final rise.

Pennington *et al.* discuss how to choose between using geological events or fossils in calibrating nodes on a tree. They conclude that the high frequency of long-distance dispersal 'highlights the danger' of using geological events, especially 'old' ones, because patterns will have been obscured. However, we only know that long-distance dispersal is frequent because the dates of many nodes in many papers (e.g. in the current volume and in Givnish and Renner 2004) are recent. And we only know they are recent because they were calibrated with

fossils. This sort of reasoning is hardly convincing.

Pennington *et al.* write that 'until recently, the fossil record was the only source of information' on origin and evolution of the biomes and their species. This overlooks a tremendous amount of work dating evolutionary events using correlation with tectonics. They write that new theoretical methods (using methods for calibrating branch lengths that do not assume a strict clock) 'offer a means of placing a dimension of absolute time on [molecular] phylogenetic trees', but with or without a clock this can only be done after at least one node (on this or another tree) has been calibrated using geological evidence. As they note, this method involves 'considerable assumptions, not least that the initial calibration often relies upon the fossil record'. Furthermore, although 'less attention' has been paid to calibration than to techniques and algorithms, 'calibration is potentially the largest source of error in the dating'. So just exactly how is it done?

The method is basically Matthew's (1915) 'literal reading' of the fossil record, although Croizat pointed out many times that the age of fossilisation of a taxon is not the same as (and is younger to much younger than) its age of being. In their introductions, molecular studies often, correctly, acknowledge this principle and describe oldest known fossils as providing only minimum ages for divergences; *later* geological events can be deemed irrelevant to the origin of the taxa. However, in the actual analyses of molecular data, estimated ages of taxa based on oldest fossils often mysteriously transmogrify from minimum ages into absolute ages and *earlier* geological events are deemed irrelevant to the phylogeny. This 'switch', made in nearly all phylogeographic papers, shows that the habit of assuming age of fossilisation equals age of being has, after a century, become deeply ingrained.

So, for example, while Pennington *et al.* claim, for example, that Renner *et al.* 'demonstrate' that endemic radiations of Melastomataceae etc. on Madagascar 'date only from the Miocene' and so are due to long-distance dispersal, these dates were based on calibrations from fossils and so are all minimum, not absolute, dates. Earlier vicariance cannot be ruled out.

New oldest fossils are constantly being reported and provide practical reminders that fossils only provide minimum ages of taxa. For example, over the last couple of years new oldest fossils have been found for loriform primates (previously known back to 20 Ma, now known back to 41-37 Ma), crown-group salamanders (previously 60 Ma, now 160 Ma), metatherian mammals (previously 75 Ma, now 125 Ma), and hummingbirds (previously 1 Ma, now 30 Ma) (references in Heads, in press).

Pennington *et al.* also note that simply assigning fossils to the stem of the clade they belong to - 'a tendency in many studies - will also underestimate divergence times.

Pennington *et al.* conclude that 'A clear message emerging from all these studies is that long-distance, trans-oceanic dispersal has been a major force determining plant distributions', that 'dated phylogenies show clear evidence of recent long-distance dispersal events', that 'it is clear that long-distance dispersal must have had a substantial influence' on plant evolution, and that 'recent rapid speciation has clearly played a role'. But is all this really so 'clear'?

New methods of estimating branch lengths do not assume a strict molecular clock (cf. many contributions in the reviewed volume and in Givnish and Renner (2004a). However, Near and Sanderson note that 'With respect to rate heterogeneity, once the model of molecular evolution departs from a simple one-rate molecular clock,

the divergence time problem enters a realm of model selection in which the number of models is effectively infinite.' Despite this, most authors seem reluctant to accept large differences in rates between closely related clades (and in the same lineage over time), although the biogeographic evidence suggests that this is a common phenomenon.

While many authors have abandoned the idea of a strict, universal molecular clock, and despite Near and Sanderson's caution, most authors continue to assume a 'rough clock', in which evolution proceeds more or less continuously. In this model, morphological and molecular divergence is taken to be roughly proportional to time. For example, Pennington and Dick infer that the 'high degree' of sequence divergence between neotropical and African palm taxa 'does suggest antiquity', while 'remarkably short branch lengths' in transatlantic Zingiberaceae 'imply' that these patterns are due to recent trans-oceanic dispersal followed by rapid speciation. Using another model, panbiogeography has suggested instead that evolution generally proceeds by bursts or phases of modernisation, followed by millions of years of stasis. There is thus no relation between depth of divergence and age of divergence. Shallow divergence may represent ancient events, deep divergence may be recent. Any distribution pattern involves taxa of widely differing rank, implying that different groups have diverged to different degrees (some not at all) during the same phase of modernisation. Renner observed that 'divergence events thought to date back to well-understood Gondwanan events, for example the break-up of South America and Africa, occur at very different distances from the phylogenetic trees' roots... Accordingly, hypotheses of trans-oceanic long-distance dispersal were put forward to explain the shallowest geographical disjunctions. Explaining them other than by different absolute ages

would have required assuming tremendous rate heterogeneity.' Exactly; the biogeographic data are very good evidence for just this. Renner calibrated the tree using oldest fossils, thus assigning nodes minimum ages. The data were then transmogrified and the ages treated as maximum ages. The Madagascar-India Melastomataceae were then seen as 'too young' for Cretaceous vicariance and the pattern 'must be' due to multiple dispersal events. The alternative vicariance model would require 'tremendous rate variation'. Thus, 'molecular data continuously bring to light new examples of trans-oceanic long-distance dispersal in groups traditionally thought to be poor dispersers.'

They described the fossil record of fishes as 'misleading'

Near and Sanderson write that 'systems in which divergence time estimation from sequence data are needed most critically are the ones with few or no good calibrations (e.g. Darwin's finches, East African cichlids)'. However, in exemplary molecular studies of cichlid fishes, Sparks (2004) and Sparks and Smith (in press) found two main clades in the family, one in Madagascar, Africa and America, and one in Madagascar, India and Sri Lanka. They concluded that these relationships 'are congruent with prevailing hypotheses regarding the sequence of Gondwanan fragmentation and a vicariance scenario to explain the current distribution of cichlid fishes'. They described the fossil record of fishes as 'misleading', with 'notable gaps', but also cited recently identified Eocene cichlids, 10 m.y. older than previously known oldest fossils and 'very derived and similar to modern African lineages'. They did not attempt to date nodes. Their paper, and many others in the literature, illustrate that molecular phylogenies as tree topologies have tremendous value, while date calibrations based on fossils and

approximate molecular clocks are virtually worthless.

Richardson *et al.* calibrated trees based on fossil material and in their 'Material and Methods' section 'emphasized that all timings are therefore minimum ages'. Nevertheless, following transmogrification, they were able to conclude that 'Rhamnaceae and most lineages within Annonaceae are too young to have had their distribution patterns influenced by break-up of previously connected Gondwanan landmasses... long-distance dispersal appears to have played a more significant role... than had previously been assumed'. They assert that Africa-South America disjunctions 'have been demonstrated' to be too recent

for migration by land routes, and 'long-distance dispersal must therefore be invoked'. They note that 'long-distance dispersal does occur, as evidenced by the molecular trees and the presence of Annonaceae on volcanic islands in the Antilles'. These islands occur at a subduction zone, and it is the age of this that is important, not the geologically ephemeral islands currently on it. Taxa survive on islands around subduction zones as metapopulations, colonising new islands from nearby older ones by ordinary means of survival, not by long-distance dispersal from a mainland. Studies correlating age of nodes with age of volcanic islands often overlook the fact that these islands have been produced at plate margins or hot spots where small, individually ephemeral islands are constantly being produced and disappearing, and a metapopulation can survive indefinitely.

Crisp *et al.* discuss the flora of Australia and suggest that the chenopods there (300 species, mainly endemic) 'all probably originated as post-isolation immigrants, given the absence of fossils before that

time'. They explain the close affinity between inland desert floras and coastal ones by dispersal (rather than stranding): phylogeographic studies 'may reveal pathways between these habitats, perhaps along riverine floodplains'. As for Myrtaceae, 'given the uncertainty of any eucalypt fossil before the Miocene..., it would be reasonable to conclude that a Cretaceous date for the basal node is too old'. Again, these conclusions follows transmigration of minimum (fossil-based) ages of taxa into maximum dates, with older events deemed

large, recalcitrant seeds cannot survive immersion in sea-water...'. In these cases trans-oceanic dispersal is inferred because a node on a tree 'has a geological date' during which there were no stepping stone migration routes. Renner (2004) presented examples of transatlantic plant distributions at various taxonomic ranks 'that are all dated at 11 Myr ago or less, and therefore explicable only by long-distance dispersal'. However, all these were based on oldest fossils (or personal communications) and are therefore minimum ages. Pennington and Dick con-

recent origin, were assigned lesser importance'. But the fossil record was not really given 'lesser importance' in this work; what Pennington and Dick mean is that the fossil data were not transmogrified into giving absolute ages. A 'young' fossil record is not truly conflicting with an old actual age (only with a younger age), and systematic position (tree topology) by itself (i.e. without calibration) cannot tell anything about age. Pennington and Dick write that in earlier work several families (e.g. in Lamiales) 'none of which has a pre-Eocene fossil record... were interpreted as originating earlier', but this is necessarily true. These families are 'now established as having relatively recent origins. For example, the order Lamiales is determined as ca. 44 Myr ago (Magallón et al. 1999) to 74 Myr ago (Wikström et al. 2001). This undermines the Gondwanan vicariance explanation...'. But both these ages are minimum ages derived by calibrating nodes using oldest fossils and vicariance can only be undermined if the data are transmogrified.

Matthew's (1915) biogeography was based on a literal reading of the fossil record, with the age of a taxon taken to be the same as the age of its (or an allied taxon's) oldest known fossil, and it is inevitable that a molecular biogeography based on the same premise will reach the same conclusions. Despite the technical advances of molecular biology, in basic concepts phylogeography involves a regression to the science of the 1910s-20s. For example, in the volume reviewed here authors cite many key Matthewian concepts, such as the 'critical role of fossils', 'recent long-distance trans-oceanic dispersal', 'Plio-Pleistocene diversification', 'founder populations', 'waif dispersal', 'sweepstakes dispersal', 'stepping stone dispersal' and 'filter bridges'.

Like Pennington *et al.*, Near and Sanderson note that while fossil calibration of trees is a 'critical issue'

Matthew's (1915) biogeography was based on a literal reading of the fossil record, ... and it is inevitable that a molecular biogeography based on the same premise will reach the same conclusions.

irrelevant.

Pennington and Dick discuss South American biogeography and conclude that 'The vicariance model is too simplistic as evidenced by several recent molecular phylogenetic studies of plants which demonstrate arrivals from the Late Cretaceous [minimum ages] and through the Tertiary. They found that Gondwanan explanations for transatlantic Melastomataceae and Malpighiaceae 'have been refuted by molecular phylogenetic studies coupled to fossil calibrated molecular clock analyses'. Likewise, transatlantic Lauraceae are 'clearly' the result of recent radiation. Evidence from molecular phylogenies calibrated with oldest fossils indicates that 'waif' or 'sweepstakes' dispersal across the Atlantic Ocean 'has indeed occurred in multiple taxa and explains disjunctions at species, generic and higher taxonomic levels... It is remarkable that some of these examples are of plants that show little adaptation for over-water dispersal, such as [groups] whose

cluded that their examples 'demonstrate' that South America has received immigrant taxa throughout the Cenozoic'. Late Cretaceous fossil wood of *Weinmannia* (Cunoniaceae) from Antarctica 'implies' that this family 'probably migrated along this southern route', but this only follows in a model which relies on migration in the first place.

Pennington and Dick conclude: 'Given that the earliest [known] fossils' of many important rainforest families such as legumes date only to the Late Cretaceous 'the occurrence of shared genera between Africa and South America is probably most often the result of oceanic dispersal'. Again, this would only be true if fossils gave maximum, not minimum ages.

Pennington and Dick write that in earlier work on pantropical distribution, 'which is both tempting and parsimonious to explain by Gondwanic vicariance, conflicting data such as a young fossil record and a systematic position implying

which involves 'potential multiple sources of error', 'less emphasis' has focused on this. The fossil record 'necessarily leads to a consistent underestimation of any given lineage's age'. Near and Sanderson observed a 'strong and persistent desire' (Graur and Martin 2004, called it a 'great thirst') to know the divergence dates of clades and it seems a certain impatience has clouded judgment and led to rushed conclusions in many molecular studies. Good science requires a degree of caution and scepticism, and systematists should constantly, critically examine the basic assumptions their methodology involves, rather than taking them for granted or sweeping them under the carpet.

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SA Meeting: 1st Circular

Algorithmic approaches to the Automated identification Problem in Systematics

A symposium on the theory, technique, technology, current application, and future potential of automated taxonomic identification.

August 19, 2005
Flett Theatre, The Natural History Museum, Cromwell Road, London, UK.

Registration is free

The automated identification of biological objects (individuals) and/or groups (e.g., species, guilds, characters) has been a dream of systematists for centuries. Some of the first applications of multivariate methods in biology sought to address the perennial problems of group discrimination and inter-group characterization. Despite much preliminary work in the 1950s and 60s, however, progress in designing and implementing practical systems for fully automated object identification has proven frustratingly slow. Recent developments in computer architectures, however, as well as innovations in software design, have final-

ly made the development of reliable, generalized, automated specimen and/or group-identification systems a real possibility.

These advances could not come at a better time. The world is running out of specialists who can identify the very biodiversity whose preservation has become a global concern. This expertise deficiency cuts as deeply into those commercial industries that rely on accurate identifications (e.g., agriculture, biostratigraphy) as it does into a wide range of pure and applied research programmes (e.g., conservation, biological oceanography, climatology, ecology). Moreover, it is commonly, though informally, acknowledged that the technical, taxonomic literature of all organismal groups is littered with examples of inconsistent and incorrect identifications. Peer review only weeds out the most obvious errors of commission or omission in this area, and then only when an author provides adequate representations (e.g., illustrations, videos, recordings, gene sequences) of the specimens in question.

Systematics has much to gain, both practically and theoretically, from the creation and use of automated identification systems. It is now widely recognized that the days of systematics as the individualistic pursuit of knowledge in splendid isolation from funding priorities and economic imperatives are rapidly drawing to a close. In order to attract both personnel and resources, systematics must transform itself into a "large, coordinated, international scientific enterprise" (Wheeler 2003: 4). Many have identified use of the internet as the medium through which this transformation can be made. While establishment of a virtual, GenBank-like system for accessing morphological, audio, video, information etc., would be a significant step in the right direction, improved access to observational information and/or text-based descriptions alone will not address either the taxonom-

ic impediment or low identification reproducibility issues successfully. Instead, the inevitable subjectivity associated with making critical decisions on the basis of qualitative criteria must be reduced or, at the very least, embedded within a more formally analytic context. Properly designed, flexible, and robust, automated identification systems, organized around a distributed computing architectures, can, in principal, feed back much important information to systematics and play a key role in re-invigorating our science.

In order to summarize the current state-of-the-art in automated group-recognition systems, and assess their potential to make practical contributions to systematics and taxonomy both now and into the future, *The Systematics Association* and The Natural History Museum, London have agreed to jointly sponsor a free, one-day symposium entitled *Algorithmic Approaches to the Identification Problem in Systematics*, to be held in the Flett Theatre of The Natural History Museum, London on August 19, 2005.

The purpose of this symposium is to provide leaders of research groups, researchers, post-doctoral research assistants, and students working or studying in any area of systematics with an opportunity to (1) learn about current trends in quantitative approaches to the group-recognition problem, (2) become familiar with the capabilities of various software systems currently available for identifying systematic objects/groups and (3) evaluate various applications of this technology to present and future systematic problems. Special attention will be paid to showing how different approaches to automated identification can be applied to various organismal groups and in various applied research contexts (e.g., biodiversity studies, biostratigraphy, conservation, agriculture, curation). Ample programme time will also be provided for discussions of issues

relating to how these approaches and technologies can play a larger role in meeting the needs of current and future systematists.

This free symposium is being held in association with the Biennial Meeting of *The Systematics Association* which begins on Monday, August 22, 2005 at the University of Cardiff (for more information see below). Attendees of the Systematics Association meeting are encouraged to include attendance at this symposium in their Biennial Meeting plans.

Website:

www.nhm.ac.uk/hosted_sites/paleonet/aaips_symposium/

Organizers

Norman MacLeod
The Natural History Museum, London, UK.

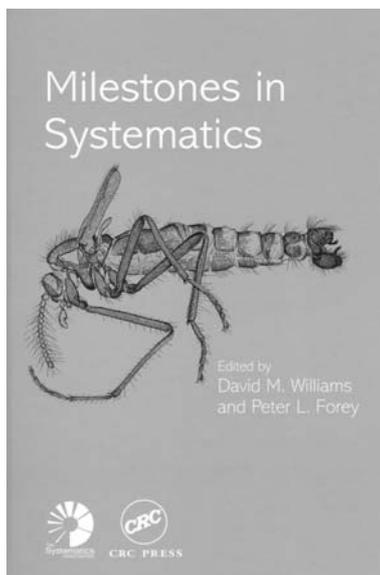
Mark O'Neill
University of Newcastle upon Tyne, Newcastle, UK.

Stig Walsh
The Natural History Museum, London, UK.

References

Wheeler, Q.D. 2004. Transforming Taxonomy. *The Systematist* 22:3-5.

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 future.

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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 Summer issue of *The Systematist*

BackPage

SA Events

April 6-8, 2005

The Palms - An international symposium on the biology of the palm family

Linnean Society and Royal Botanic Gardens, Kew, UK.

Contact: Dr. William Baker, Royal Botanic Gardens, Kew, UK.

Conference details at:

www.linnean.org

July 4-8, 2005

Fifth International Brachiopod Congress

Geological Museum, University of Copenhagen, Denmark.

Contact: Prof. David Harper, Geological Museum, Copenhagen, Denmark.

Conference details at:

www.geological-museum.dk

July 6, 2005

The Sir Julian Huxley Lecture

Linnean Society, London, UK.

Contact: Dr. William Baker, Royal Botanic Gardens, Kew, UK.

Lecture starts at 6pm.

August 19, 2005

Algorithmic Approaches to the Identification Problem in Systematics

Details of the SA research grants, conference bursaries and funding for the organisation of meetings can be found at:
www.systass.org

Flett Theatre, Natural History Museum, London, UK.

Contact: Dr. Norman MacLeod, Natural History Museum, London, UK.

Conference Details at:

www.systass.org. (See article on page 22).

August 22-26, 2005

Systematics Association 5th Biennial Meeting

National Museum and Gallery of Wales, Cardiff, UK.

Contact: Dr. Ray Tangney, National Museum of Wales, Cardiff, UK.

Conference details at: www.systass.org

Biennial Symposia

The New Taxonomy

Contact: Dr. Quentin Wheeler, Natural History Museum, London, UK.

What is biogeography ?

Contact: Dr. Malte Ebach, Natural History Museum, London, UK.

Compatibility Methods in Systematics

Contact: Dr. Mark Wilkinson, Natural History Museum, London, UK.

December 7, 2005

Systematics Association AGM and Lecture

Linnean Society, London, UK.

Lecture starts at 6pm.

December 8, 2005

Systematics Association Young Systematists' Forum

Flett Theatre, Natural History Museum, London, UK.

Contact: Dr. Mark Carine, Natural History Museum, London, UK.

Forum details at: www.systass.org

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 Association's 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.

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