

flower<sup>10</sup>, and although it is self-compatible, selfing rarely occurs without artificial pollination. Those seeds that occasionally do set are probably the result of small flower-visiting beetles, which can be seen crawling into the flowers. Therefore, to take advantage of generalist pollination, a preceding morphological change to shorten the corolla tube would be highly favourable. This has evidently happened in *Ramonda*, which has almost no corolla tube, though its closest zygomorphic relatives all have tubular flowers. Loss of tube has occurred several times in the Gesneriaceae, without loss of zygomorphy. This is often associated with a switch from a nectar reward to a pollen reward (which may involve trickery with false anthers as in the pollen-deceit flowers of the genus *Loxocarpus*). The African violet, *Saintpaulia* (which is closely related to the tubular-flowered genus *Streptocarpus* or Cape primrose) is zygomorphic but has almost entirely lost its corolla tube. Its protruding anthers may be adapted for buzz pollination (pollen release resulting from vibrations of some pollen collecting bees) but nothing is known of its pollinators in the wild. If it should lose its putative specialist pollinators, then a peloric mutant might not be sublethal, but even advantageous. For one thing, it would expand pollen output by increasing the number of anthers. So far, peloria is unknown in wild African violets, although peloric mutants exist as commercially available cultivars.

The need for a two-stage shift in pollination ecology may be the reason why reversions to actinomorphy are rare in nature, but there is still much to learn about major morphological shifts in plant evolution. However, the isolation of *cycloidea*, as with other morphologically significant genes, raises the challenge of putting the evolution of known genes in an adaptive and ecological context.

#### Acknowledgements

We thank B.L. Burt and E.S. Coen for stimulating discussion. M.M.'s work is supported by the Leverhulme Trust.

#### Quentin Cronk

*Institute of Cell and Molecular Biology,  
University of Edinburgh, Kings Buildings,  
Mayfield Road, Edinburgh, UK EH9 3JH and  
Royal Botanic Garden,  
20A Inverleith Row,  
Edinburgh, UK EH3 5LR  
(q.cronk@rbge.org.uk)*

#### Michael Möller

*Royal Botanic Garden,  
20A Inverleith Row, Edinburgh,  
UK EH3 5LR  
(m.moeller@rbge.org.uk)*

#### References

- 1 Weberling, F. (1989) *Morphology of Flowers and Inflorescences*, Cambridge University Press

- 2 Coen, E.S. and Nugent, J.M. (1994) **Evolution of flowers and inflorescences**, *Development* (Suppl.) 107–116
- 3 Coen, E.S. *et al.* (1995) **Evolution of floral symmetry**, *Philos. Trans. R. Soc. London Ser. B* 350, 35–38
- 4 Luo, D. *et al.* (1996) **Origin of floral symmetry in *Antirrhinum***, *Nature* 383, 794–799
- 5 Dafni, A. (1992) *Pollination Ecology, a Practical Approach*, Oxford University Press
- 6 Manning, A. (1956) **The effect of honey guides**, *Behaviour* 9, 114–139
- 7 Manning, A. (1956) **Some aspects of the foraging behaviour of bumblebees**, *Behaviour* 9, 164–201
- 8 Mather, K. (1947) **Species crosses in *Antirrhinum*. I. Genetic isolation of the species *majus*, *glutinosum* and *orontium***, *Heredity* 1, 175–186
- 9 Proctor, M., Yeo, P. and Lack, A. (1996) *The Natural History of Pollination*, Harper Collins
- 10 Darwin, C.R. (1875) *The Variation of Animals and Plants under Domestication*, John Murray
- 11 Carpenter, R. and Coen, E.S. (1990) **Floral homeotic mutations produced by transposon mutagenesis in *Antirrhinum majus***, *Genes Dev.* 4, 1483–1493
- 12 Tucker, S.C. (1984) **Origin of symmetry in flowers**, in *Contemporary Problems in Plant Anatomy* (White, R.A. and Dickison, W.C., eds), pp. 351–395, Academic Press
- 13 Muenchow, G.E. and Grebus, M. (1989) **The evolution of dioecy from distyly: a re-evaluation of the hypothesis of the loss of long-tongued pollinators**, *Am. Nat.* 133, 149–156
- 14 Delph, L.F. (1990) **The evolution of gender dimorphism in New Zealand *Hebe* (*Scrophulariaceae*) species**, *Evol. Trends Plants* 4, 85–89

## An infinitude of connecting links

Darwin<sup>1</sup> said it first: life on earth shares a bond forged through 'an infinitude of connecting links' and it is the reconstruction of this network 'which naturalists have been unconsciously seeking' in their drive to place all organisms in a single, comprehensive classification. Naturalists are still seeking to reveal this network (subsequently dubbed 'phylogeny' by Haeckel<sup>2</sup>), but certainly not unconsciously. In fact, over 200 participants from a myriad of organismal and methodological disciplines met in October last year at the University of Arizona in Tucson, USA for a symposium entitled 'The Phylogeny of Life and the Accomplishments of Phylogenetic Biology' to celebrate and contemplate the field of phylogenetic analysis. Organized by John Lundberg and Martin Wojciechowski (University of Arizona – Tucson), the symposium was an affirmation of the achievements and continuing evolution of the discipline variously known

as cladistics or phylogenetic systematics. Apparently, David Maddison (University of Arizona – Tucson) is not alone in believing that the ever-branching tree of life is 'one of the most romantic notions in all of biology'.

It was clear from the earliest moments of the symposium that the barriers that often separate biological disciplines become porous with respect to phylogenetics. Although several of the 23 invited speakers admitted (with some chagrin) that they had never generated a cladogram, nonetheless it seemed that to have an interest in the workings of the organic world is to have the need for an accurate phylogeny. This was certainly the case for investigators exploring the complexities of genomic evolution. Laura Landweber (Princeton University, Princeton, NJ, USA) presented her findings on the bizarre mechanism of RNA editing in the mitochondria of kinetoplastid protozoa. Her work

has shown that in numerous lineages, the resident DNA template is a wholly incomplete representation of the genetic material that is essential to the organism's survival. Rather, through the addition and/or deletion of numerous uridine residues, RNA editing creates over 90% of the functional amino acid codons. By investigating the phylogenetic distribution of RNA editing patterns in trypanosomatids, Landweber has discovered that extensive RNA editing may be an ancient mechanism that has only recently disappeared in some lineages, perhaps obviated by the introduction of reverse transcriptase. Landweber's talk was complemented by those from a cadre of investigators from the University of Arizona – Tucson, all of whom, via phylogenetic analysis, were able to postulate the relative timing of and potential mechanisms for a number of intriguing genetic phenomena: the acquisition and distribution of intron sequences (Richard Hallick), bacterial/insect endosymbiosis (Nancy Moran), the evolution of homeobox genes (Lisa Nagy), and the process of gene family diversification (Elizabeth Waters).

However, the symposium by no means focused on genotype to the exclusion of phenotype. Indeed, it may have served to extinguish forever the false dichotomy between molecules and morphology that appears so frequently in the literature. By exploring genetic and morphological data, the symposium illustrated that many of life's obscure phenomena are only revealed through the analysis of both types of data. Lucinda McDade (University of Arizona – Tucson) demonstrated in her study of plant hybridization that conflict between morphological and genetic data may, in fact, be one of the only available clues in the effort to identify parent species and the resultant offspring species. If anything, morphology carried the day as the indispensable window to the past. Nicholas Strausfeld (University of Arizona – Tucson), a neurobiologist by trade, illustrated the value of morphological characters for defining major arthropod clades. Several paleontologists (Simon Conway Morris, University of Cambridge, UK; Douglas Erwin, Smithsonian Institution, Washington, DC, USA; Andy Knoll, Harvard University, Cambridge, MA, USA; Michael Novacek, American Museum of Natural History, New York, NY, USA) drove home the point that fossils are the only unequivocal indicators of past organisms and lifestyles, and (despite the fantasies of science fiction writers and the best efforts of molecular systematists) are usually preserved in the form of morphology, not DNA.

Nonetheless, there are cases where DNA offers the only traceable connection to the first node on the tree of life. In a startling presentation, Susan Barns (Los Alamos National Laboratory, Los Alamos, NM, USA) described the fishing expedition that she and her colleagues have undertaken in their search for new microbial life forms. Using a 'shotgun' PCR (polymerase chain reaction) approach, ribosomal RNA sequences from environments such as high-temperature aquatic pools can be blindly amplified and then submitted to phylogenetic analysis along with known organismal sequences. The results have been astonishing, suggesting the existence of countless undescribed genera and even phyla. Moreover, the phylogenetic analyses have supported the idea that a thermophilic lifestyle is ancestral for both prokaryotes and eukaryotes. In Barns' view, this raises the possibility that life on earth may well have arisen in what she called 'a burning hell hole'.

A number of speakers unflinchingly presented results that either refuted established truisms or raised paradoxical conundrums. Elizabeth Kellogg (Harvard University), in her struggle to understand the phylogeny of the world's grasses, has discovered that the biochemically elaborate

C<sub>4</sub> photosynthetic pathway has probably evolved many times in this group, thus refuting the adage that complex adaptations evolve infrequently. David Hillis (University of Texas, Austin, USA), in a similarly unsettling moment, revealed that selection at the molecular level can generate sufficient signal to provide a tree-like structure for a data set that is actually devoid of phylogenetic signal. This result emerged from an experiment in which four bacteriophage lineages, simultaneously derived from a common ancestor (thereby creating a 'star' phylogeny), were placed in one of two bacterial hosts grown in one of two temperature regimes. Surprisingly, when DNA sequences from the four bacteriophage lineages were subjected to phylogenetic analysis, a bifurcating tree-like pattern was reconstructed as a result of molecular convergence induced by the host-phage interactions. This should raise a cautionary flag for molecular systematists who have assumed that DNA sequences are not subject to the same selection effects that can be problematic for morphological data.

Alan Templeton (Washington University, St Louis, MO, USA) cited the low genetic variation that appears to be typical of humans as evidence that we are an ancient lineage for which global gene flow has been a powerful force for the past million years or so. In contrast, these data are usually cited as support for the 'out-of-Africa' replacement hypothesis that posits that humans arose much more recently (200 000–100 000 BP) as a single lineage in Africa, portions of which migrated into other parts of the world, replacing *Homo erectus* as they went. Although Templeton does not dispute an African root for the human tree, his interpretation lends support to the older view that anatomically modern traits arose gradually among *H. erectus* populations and were spread and maintained by low-level, sporadic gene flow among geographically distant populations (a hypothesis commonly referred to as the 'multi-regional' model of human evolution).

Hillis explored the paradox of 'tree space' and 'long-branch attraction'. In recent years, phylogeneticists have become aware of a vexing problem associated with the simultaneous phylogenetic analysis of many taxa. When 100 or more taxa are analyzed, the possible number of bifurcating trees that could describe their interrelationships is greater than an astounding  $2 \times 10^{182}$ , which by Hillis's calculations exceeds the volume of the universe as measured in 'cubic Planck distances' (Planck distance =  $10^{-35}$  m). Whatever the unit of measure, such a number of trees is clearly enough to boggle the mind of even the best computers (and systematists). The contradiction arises with the discovery that,

with the addition of taxa, branch lengths between nodes on a given tree tend to become shorter. Thus, the problem associated with spurious convergence owing to long-branch attraction (the infamous 'Felsenstein Zone') is alleviated. In Hillis's words, 'adding taxa may be the most important thing we can do to enhance accuracy'. He has therefore presented systematists with a conundrum: when have we included enough taxa to break up long branches but not too many for realistic calculations of tree topology?

This is not a trivial issue. Presentation after presentation focusing on taxa ranging from arthropods (Richard Brusca, University of Charleston, Charleston, SC, USA) to angiosperms (Michael Donoghue, Harvard University) to eutherian mammals (Novacek) to passerine birds (Scott Edwards, University of Washington, Seattle, WA, USA) grappled with the phylogenetic enigmas that Novacek described as evolutionary 'hotspots'. In these cases, interrelationships within well-defined clades defy resolution resulting from rapid bursts of lineage diversification (cladogenesis) followed by long periods of independent evolution (anagenesis). The systematist is therefore trying to resolve the tiny internal branches that separate and give structure to the taxon-specific long branches that are so problematic for accurate resolution. Systematists enjoy a challenge, however, as evidenced by the atmosphere of optimism that pervaded the symposium. Donoghue's declaration that 'It's a good time to be alive!' was echoed by many other participants as was the sentiment that the dramatic advances in phylogenetic theory and methods will permit the resolution of many, if not all, of these hotspots within the next decade. Participants were also enlivened by the knowledge that 'so much remains to be done' in that there are untold numbers of undescribed taxa out there (90% of microbial taxa, for example), and with them, universes of trees to be estimated. Thanks to the efforts of David and Wayne Maddison (University of Arizona – Tucson), who have been working tirelessly on their Web-based Tree of Life<sup>3</sup>, these trees may one day merge into one through a parallel 'infinite of connecting links' among phylogeneticists and their computers.

In a closing moment of introspection, Wayne Maddison posed the question 'Has phylogenetic analysis entered the realm of normal science?' Kuhn defined normal science such that '[n]o part of the aim of normal science is to call forth new sorts of phenomena' (Ref. 4, p. 24). The Phylogeny of Life symposium showed that, if anything, phylogenetic systematics is the antithesis of normal science. Rather, phylogeneticists seem to be actively seeking new

## Characterizing human psychological adaptations

phenomena and are therefore continually reformulating the paradigm in which they work. Rod Page (University of Glasgow, UK) predicts that it is the study of associations (such as genes within organisms, parasites within hosts, organisms within geographical areas) that will inform future phylogenetic studies. This theoretical forecast has already appeared in practice. Rytas Vilgalys (Duke University, Durham, NC, USA) has found that biogeographical patterns are indispensable for defining species and modes of speciation within the fungi.

Stuart Nichol (Centers for Disease Control, Atlanta, GA, USA) described the uncanny co-evolutionary patterns displayed by a variety of hantavirus strains and their rodent hosts. One of these strains, the Sin Nombre virus, was responsible for the sudden-death pulmonary syndrome that wreaked momentary havoc in the southwestern USA in 1993. Through phylogenetic analysis, Nichol and his colleagues were able to demonstrate that Sin Nombre is not a terrifying new organism but one that has actually been present in deer mouse populations throughout North America for a very long time. Thus, they were able to identify the ecological factors responsible for the outbreak. This elegant example of what is now routine phylogenetic analysis in the study and control of pathogens raises an intriguing (and perhaps fanciful) question: could the very survival of the human species depend on phylogenetic analysis? Those that were gathered in Tucson would undoubtedly respond, 'Yes!'

### Acknowledgements

Thanks to T. Eriksson for lively discussion concerning the symposium. Abstracts for platform and poster presentations are available from the Department of Ecology and Evolutionary Biology, University of Arizona – Tucson, USA web site ([http://eebweb.arizona.edu/RTG/RTG\\_symp.html](http://eebweb.arizona.edu/RTG/RTG_symp.html)).

### Anne D. Yoder

Dept of Cell and Molecular Biology,  
Northwestern University Medical School,  
303 E. Chicago Ave, Chicago, IL 60611-3008,  
USA (ayoder@worms.cmb.nwu.edu)  
and Dept of Zoology, Field Museum of  
Natural History, Chicago, IL, USA

### References

- 1 Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection*, John Murray
- 2 Haeckel, E. (1866) *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie*, Georg Reimer
- 3 Morell, V. (1996) **Web-crawling up the tree of life**, *Science* 273, 569
- 4 Kuhn, T.S. (1962) *The Structure of Scientific Revolutions*, University of Chicago Press

The central aim of evolutionary psychology is to identify domain-specific cognitive subsystems that may have arisen as a result of the organizing forces of evolution by natural selection to solve particular adaptive problems faced by *Homo sapiens* over millions of years<sup>1</sup>. In October 1996, psychologists, anthropologists, animal behaviourists, geneticists and sociobiologists with a darwinian bent met at The Ciba Foundation, London, UK to discuss the future of evolutionary psychology as it approaches its 30th birthday\*.

There are theorists from biology to social science who dismiss evolutionary psychology as 'common sense'. They see what evolutionary psychologists call 'human universals' as nothing but learned cultural artefacts<sup>2</sup>. Martin Daly (McMaster University, Hamilton, Canada), who chaired the symposium, is incensed by this attitude: 'there is no more mischievous dichotomy than "social" versus "biological" – sociality has no meaning outside of the biological world'<sup>3</sup>. Leda Cosmides (University of California, Santa Barbara, USA), one of the founders of evolutionary psychology, agrees: 'Learning cannot take place without some kind of innate hardware, thinkers have realised that since Plato.' Or, as fellow symposiast Steven Pinker puts it in his book *The Language Instinct*<sup>4</sup>: 'complexity in the mind is not caused by learning; learning is caused by complexity'.

To isolate specialized cognitive modules for remorse, honour or gratitude is rather more difficult than identifying evolved entities in anatomy or physiology – some would say impossible. Cosmides and John Tooby (University of California, Santa Barbara, USA) have produced some of the most convincing evidence for custom-designed social inference 'circuits' in their work on cheater detection and coalition formation. Their studies of small, isolated tribal societies have revealed that people are acutely aware of the loyalties and strength of other group members. Tooby and Cosmides find women confident and outspoken on the subject of warriorship hierarchies, but less concerned with coalitions and allegiances than men. They argue that in an evolutionary context it makes sense for men and women to be able to assess accurately the risk of conflict with another group member. However, for a woman, 'taking sides' could jeopardize her children's safety or their social position, and so she is 'programmed' to remain as impartial as possible.

One aspect of our mechanisms for making character assessments of fellow humans – mate choice – has become the 'flagship domain of evolutionary psychology'. There is an enormous body of work on the physical cues that motivate mate choice: symmetry, walking speed, waist:hip ratio, full lips and so on. Steven Gangestad (University of New Mexico, Albuquerque, USA) has shown that fluctuating asymmetry – an average measure of external bodily symmetry – can be directly correlated with violence, number of sexual partners, metabolic efficiency, developmental health and even indicate some forms of brain asymmetry. Gangestad reasons that asymmetry is a measure of developmental stress such as pathogens, parasites or pollutants. Since sexual selection is all about maximizing fitness, it is no surprise that men of lower symmetry have fewer sexual partners, are less violent (i.e. less mate-competitive) and are judged less able to protect a mate. Gangestad has, however, found that highly asymmetric men make better, more-modest long-term partners. They describe themselves as nice guys, are more honest, invest more heavily in their females, and are more faithful.

Some of the most exciting work discussed at the meeting came from the animal behaviour camp. Dr Marc Hauser (Harvard University, Cambridge, MA, USA) presented an excellent illustration of the potential of animal behaviour to inform our theories about the human brain with his studies on infant and primate mathematics. Awareness of, and the ability to manipulate numbers conceptually is often assumed to require language. It has long been known that many non-human animals have some concept of number, which they use for assessing group sizes and food quantities, but is it only humans who can add and subtract?

A fascinating series of 'preferential looking time' (PLT) studies (where a subject's interest in possible and impossible exhibits is timed) indicate that pre-linguistic infants and chimpanzees have primitive computational awareness, at least up to the number four. One chimp was even able to manipulate arabic numerals, giving rise to a delightful experiment demonstrating the inability of animals, however intelligent, to override instinct: Sheba (the A-grade chimp) was shown a tray with six food treats and one food treat; whichever one she pointed at she