

The Systematist

Newsletter of the Systematics Association
Number 34 2012

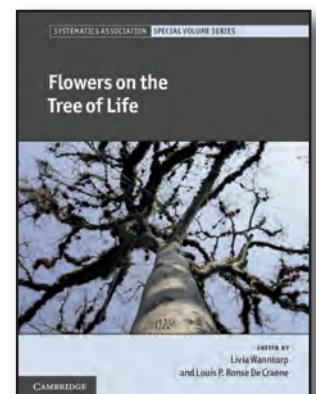
www.systass.org

ISSN 1744-5701



- Cichlid fish and the micro-macroevoolution continuum in the origin of species diversity
- Foundation Monographs - accelerating the pace of taxonomy
- One species or three? The Azorean butterfly-orchids
- Twitter for systematists
- Celebrating systematics - 75 years of the Systematics Association
- Young Systematists Forum 2011
- Cultivating common ground: biology and the humanities
- Inspirations: Anne Yoder

Book Reviews



Celebrating systematics

75 years of the Systematics Association

On the 20th June this year a special event took place at the Natural History Museum to celebrate 75 years of the Systematics Association. What better way to mark such an occasion than an authoritative, inspirational and animated conversation between Sir David Attenborough and Professor Richard Fortey? These generous gentlemen thoroughly entertained a large audience with tales of some of the characters linked to the Association in one capacity or another that they had known, from Sir Julian Huxley through Humphrey Greenwood, Arthur Cain and Ernst Mayr amongst others. Before the conversation, David Williams started the evening with a history of the Systematics Association. No-one else could present a history in such an unusual, fresh, provocative and lateral way, bringing both the subject and some of the colourful personalities to life. Every Society comes with its characters, scandal and intrigue.

How many evenings have two receptions? After the history, a reception provided the opportunity to connect and reconnect with colleagues and friends. Amongst the crowd there were former Presidents of the Association, three generations of one family and plenty of young people, many of whom have contributed to the Young Systematist's Forum in recent times. After the Attenborough and Fortey conversation a second reception commenced in the gallery 'From the beginning' next to the Flett theatre. What an excellent setting full of illustrations of such creatures as the wonderfully named *Hallucigenia* and fossils including ammonites, a huge oceanic predator, a plant eating reptile, mammoth bones and so on. At the far end of the gallery where we all entered for the second

reception, (I hoped not too many would notice the sign 'The end of the world is nigh?') I then saw humans exhibited alongside a moa skeleton—a bird which was hunted to extinction. And there we were treated to a delicious hot buffet and more refreshments.

So what about the future and direction of the Systematics Association? That will no doubt depend on many things, but I believe that the now and the future depend on the following fundamental aspects. I would argue that we are living in a new age of discovery. Never before has it been possible to study the diversity of the world in all its minutiae with the ability to explore the planet with the brilliant techniques that we have available to us. The Systematics Association can and should play a vital and leading role in both documenting and synthesising life on Earth. The Systematics Association also needs to become an excellent communicator of what it does and how it does it. Finally, we must have a new generation of people to take these ideas forward.

We need systematists and systematics more than ever before.



From left to right: Richard Fortey, Sir David Attenborough and Eleanor Adamson (copyright Eleanor Adamson)

Cover illustration: an as yet un-described new species of *Ipomoea* from the Andes of Bolivia (copyright R. Scotland)

Cichlid fish and the micro-macroevolution continuum in the origin of species diversity

Ole Seehausen

EAWAG Centre for Ecology, Evolution and Biogeochemistry, Kastanienbaum, Switzerland
Institute of Ecology and Evolution, University of Bern, Switzerland

Introduction

Perhaps the two most fundamental challenges to our understanding of species diversity are to explain, first, why species exist and second, why some species multiply a lot more than others. Why do some taxa undergo large evolutionary radiations, diversifying into many and varied species, while others do not? This essay is about cichlid fish diversification and what investigating it may teach us about that second question.

Both environmental factors such as the diversity of available resources, habitats or climates, and lineage-specific traits, such as behavioural or morphological traits, and perhaps genetic architectures, may influence the rates and extent of biological diversification. The large radiations of cichlid fishes in the African Great Lakes, Victoria, Tanganyika and Malawi, provide the most dramatic known cases of species diversification. That cichlids provide striking evidence for evolutionary stasis too and for failure to diversify is underappreciated. I argue that it is the combination of both within one taxon that makes cichlids so very suitable for addressing questions about biological diversification.

Thirteen percent of all species of freshwater fish are cichlid fish

Cichlids are perch-like fish, distributed in freshwaters of the tropics and subtropics. With some 1300 validly described species but at least 2200 species known, they are the second most diverse family of freshwater fish after the cyprinids (2700 described species). It also is the third most species rich family of all fish, (there are 2000 described species of mostly marine gobies, Gobiidae), and probably of all vertebrate animals. At least 13% of all species of freshwater fish are cichlid fish! Cichlids have fascinated biologists and aquarist-naturalists alike for over a century because of their extraordinary diversity in morphology, ecology, colour and behaviour. Their exceptional species proliferation and accumulation of sympatric species diversity, may both be unparalleled amongst vertebrate animals.

Cichlid fish diversity – age and distribution

Cichlid fish species richness is highly unevenly distributed in space. It is actually low everywhere except in tropical Africa, Madagascar and tropical South and Mesoamerica (table 1). Respectively, 450 and 110 species are known from tropical South- and Mesoamerica. The former number is not very high given the large area occupied in South-America, and is easily matched by several other South American freshwater fish families. In Africa and the Americas, the distribution of species richness in the cichlid fish family adheres to the latitudinal species richness gradient (Figure 1), but the exceptional species richness of cichlid fish only manifests itself in tropical Africa, where there are some 1575 known species. 1400 of these are endemic to single equatorial lakes, whereas lakes in subtropical Africa contain endemic species much less frequently, and only some 175 species are known from all the African rivers together, again predominantly in the tropical parts of the continent. In Madagascar, Meso- and South America on the other hand, most of the diversity occurs in rivers, and

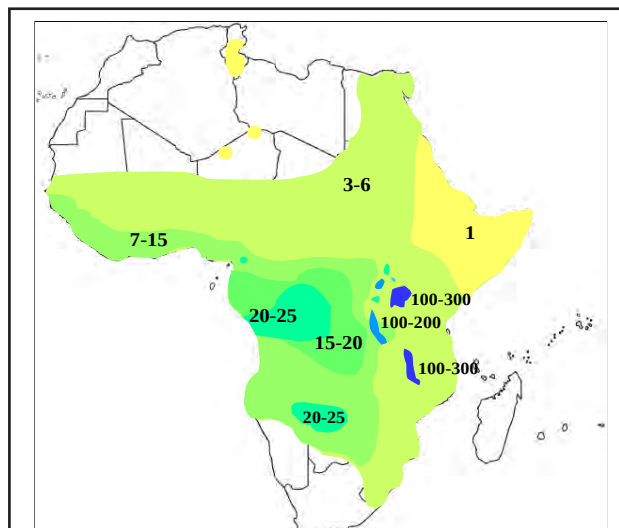


Figure 1. The continental distribution of cichlid fish species alpha-diversity. Approximate numbers of species coexisting within area plots of 10 × 10 km (Seehausen, unpublished).

lake endemism is rare.

Molecular phylogenies suggest that cichlids are monophyletic (Streelman and Karl 1997; Sparks and Smith 2004) and that with the exception of Madagascar, cichlid faunas of major biogeographical regions also make monophyletic clades, the branching order among which is congruent with the breakup of Gondwana (Sparks 2004; Sparks and Smith 2004). If this was suggestive of a Mesozoic origin during the Late Jurassic or Early Cretaceous, the oldest known cichlid fossils, *Mahengechromis* from Tanzania and *Proterocara* from Argentina, are dated only to the Eocene (46 MYA and 33.9–5.8 MYA; (Murray 2001; Malabarba et al. 2006). Even the earliest fossils of all the labroid fish (surfperches, damselfish, wrasses and cichlid fish, now considered a polyphyletic group (Santini et al. 2009) are only about 65 MY old (Lundberg 1993).

If the earliest cichlid fossils were approximately coincident with the origin of the family, their present distribution must instead be explained by intercontinental marine dispersal (Vences et al. 2001). To resolve this conflict, Genner et al. (2007) calibrated a relaxed molecular clock with geological estimates for the ages of either Gondwanan fragmentation or cichlid fossils. Timescales of cichlid evolution derived from fossil-dated phylogenies of other bony fishes most closely matched those obtained with Gondwanan breakup calibrations, suggesting that cichlids indeed originated prior to Gondwanan landmass fragmentation 121–65 MYA. Schwarzer et al. (2009) independently confirmed the Gondwanan origin of cichlids.

Applying Gondwanan calibrations to the cichlid tree, Genner et al. (2007), Schwarzer et al. (2009) and Wagner et al. (2012) showed that accumulation of genetic diversity within many African lakes began around or after the time of lake basin formation, but also that some lakes were colonised by more than one distantly related

lineage of cichlid fish. Moreover, at least some of the large radiations are apparently derived from several such lineages that hybridised (Joyce et al. 2005; Joyce et al. 2011).

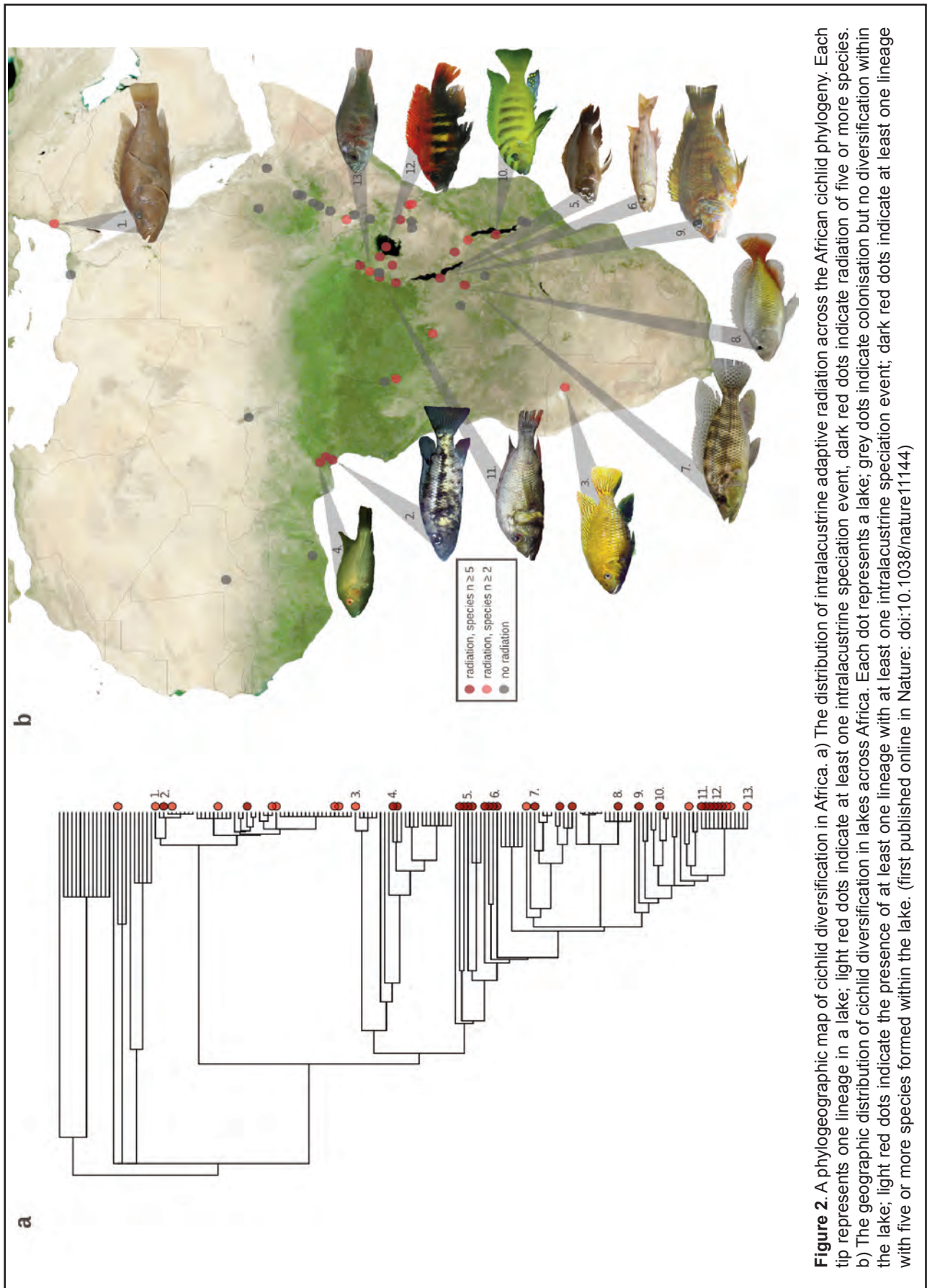
Species are real even in the most rapid cichlid radiations

Adaptive radiation is usually thought to be associated with speciation, but the evolution of intraspecific polymorphisms without speciation could be an alternative mechanism. The cichlid fish in Lake Victoria are perhaps the most incredible example of a very recent rapid adaptive radiation, with 600+ species that arose within the past 15–100,000 years. Key questions about the rapid origin of this diversity include those about speciation versus polymorphism, whether species persist on evolutionary time scales, and whether speciation typically occurs in small isolated or in large connected populations. Studying more than 300 individuals from 105 putative species in a radiation-wide AFLP genome scan, Bezault et al. (2011) demonstrated pervasive signatures of speciation supporting the classical model of adaptive radiation. A positive relationship between the age of lakes (within the Lake Victoria region) and the average genomic differentiation of the species that occupy them, and a significant fraction of molecular variance explained by above-species level taxonomy, suggested the persistence of species on evolutionary time scales, with sequential speciation instead of a single starburst. Bezault et al. further noted that very large gene diversity was retained throughout the process to individual species, implying large effective population sizes or repeated episodes of genetic exchange. This contrasts with classical mitochondrial DNA work (e.g. Sturmbauer et al. 2001), and makes speciation in small geographical isolates highly unlikely in Lake Victoria.

Very recent population genomic investigations using next

Area	Number of described and valid species	Number of known species
Africa	900	1575
Asia (South)	3	3
Middle East, Iran	7	7
South America	290	450
Mesoamerica	95	110
Madagascar	17	32
Total	1310	2200

Table 1. Natural distribution of cichlid fish diversity



generation sequencing of RAD tags revealed that species of Lake Victoria cichlids are phylogenetically very real entities, i.e. within a single community, all species were reciprocally monophyletic when ancestry was averaged over thousands of loci (Wagner et al. in press). Yet, gene flow between species in sympatry has sometimes been sufficient to make sympatric populations of different species more similar genetically than allopatric populations of the same species (Konijnendijk et al. 2011). Hybridisation is detectable not just as a signature of recent speciation, but hybridisation occurred between non-sister species too and apparently led to the evolution of hybrid species with novel gene combinations (Keller et al. submitted).

Mode and mechanism of speciation

The number of speciation case studies in African lake cichlids is surprisingly small. In a series of comparative investigations of speciation, the population genetics, phenotypic differentiation and ecology of 11 pairs of geographically sympatric phenotypically defined populations of very closely related Lake Victoria cichlids have been investigated. This project wanted to explicitly compare the role in speciation of three major classes of phenotypic polymorphisms that are often associated with incipient and sometimes full speciation: male nuptial colouration, trophic (dental) morphology, and X-linked (female) colouration (Seehausen and Magalhaes 2010). Some of this work is yet to be published. The data suggest that the extent of spatial segregation of spawning sites along the sloping lake floor is a fairly good predictor of the progression stage of speciation. Such speciation, even though completely sympatric at coarse geographical scale, is ecologically parapatric at finer spatial grain.

Seehausen and Magalhaes (2010) estimated that speciation occurred even when spatial segregation accounted for just a relatively small deviation from random mating. However, of the pairs that were spatially not segregated at all, none showed any significantly differentiated allele frequencies at microsatellite loci. Several of these fully sympatric morph pairs were phenotypically nevertheless strongly differentiated. Failure to proceed in speciation could hence not be explained by lack of suitable genetic variation.

Geographically sympatric speciation has been reported in lake-dwelling fishes more often than in any other vertebrates

The three kinds of trait variation studied are all very common in Lake Victoria cichlids, thus one might argue that ecologically parapatric (geographically sympatric) speciation may not be uncommon in cichlid fish of Lake Victoria. Ecologically fully sympatric speciation may, though, be rare if not absent. Seehausen & Magalhaes (2010) and Konijnendijk et al. (2011) reported generally weak population differentiation at neutral markers

between conspecific allopatric populations occupying habitat islands separated by many kilometres of unsuitable habitat. This suggests that the scope for completely allopatric speciation may in fact be limited in Lake Victoria. However, there is plenty of opportunity for parapatric speciation in all its geographical facets, from allo-parapatric to para-sympatric.

The shape of the evolutionary species area relationship for African cichlid fish (Seehausen 2006) suggests a combination of more sympatric-like and more allopatric-like speciation in the evolution of cichlid species flocks. The number of endemic species has a flat relationship with lake surface area across several orders of magnitude (speciation happens even in small lakes), but suddenly increases steeply when lakes are larger than 1000km². Hence, it seems that speciation did indeed occur in many lakes without opportunity for geographical isolation, but that many more species are produced in large lakes where there is greater opportunity for geographical genetic structure. The two arms of the curve are reminiscent of the relatively flat and steep slopes (z) respectively of intra- and interprovincial species area curves in island biogeography. There is much larger scope for allopatric speciation between provinces (or islands) than within (Rosenzweig 1997; Rosenzweig 2001). However, the increasing spatial species turnover that is expected even within a contiguous area, as sampled area exceeds species mean distribution ranges (Storch et al. 2012), can probably explain the steeper slopes at larger spatial scales. Speciation could have happened through any geographical mode.

Geographically sympatric speciation has been reported in lake-dwelling fishes more often than in any other vertebrates (Bolnick and Fitzpatrick 2007). Lakes (and the sea) differ from many terrestrial vertebrate environments (and many river environments) by the additional spatial dimension of water depth and the associated strong environmental gradients that exist within even small habitat patches. Water depth mediates gradients in light intensity and composition, oxygen concentration and temperature. These in turn affect resources, predators, parasites, sensory and signalling requirements, and hence call for divergent adaptation along the gradients. If variable depth adaptation causes deviation from random mating, traits relevant to fitness at different depth may act a little bit like “magic traits” in speciation, i.e. traits that are both under divergent natural selection and contribute directly to reproductive isolation (Servedio et al. 2011).

Our data suggest that such speciation may be typical in the rapid adaptive radiation of Lake Victoria cichlid fish. While geographically sympatric speciation may be more common in these fish than previously thought, a corollary of our observations is that spatial environmental structure does indeed have strong impact on the likelihood of ecological speciation with gene flow.

Macroevolutionary analyses of cichlid diversification

Adaptive radiation is thought of as an evolutionary response to newly arising ecological opportunity (Simpson 1953; Losos 2010). Extrinsic factors that have been suggested to facilitate such opportunity include a paucity of competitors (Schluter 2000), predators (Vamosi 2003), or parasites (Price 2008) and biotic insularity more generally (Mac Arthur and Wilson 1967; Price 2008). Alternatively, adaptive radiation may be a consequence of the evolution of lineage-specific traits that affect speciation rates, such as key morphological innovations (Liem 1973), the prevalence of sexual selection (Kraaijeveld et al. 2011), ecological specialisation (Farrell 1998), ecological versatility (Liem 1973) and spatial vagility (Kisel and Barraclough 2010). Since the discovery of the species-rich African lake cichlid faunas, hypotheses for the spectacular diversity of these fishes have proliferated, invoking environmental factors (Fryer 1959; Sturmbauer et al. 2001), intrinsic traits (Liem 1973; Seehausen and van Alphen 1999), and their interactions (Seehausen 2007) as influences on radiation. However, at macroevolutionary scales, these hypotheses had remained untested.

Wagner et al. (2012) placed all lacustrine African cichlids from 46 different lakes on a large molecular phylogeny (Fig. 2). They collated information on species richness and endemism, lake depth, surface area, net solar radiation (hereafter “energy”), latitude, elevation, the presence of predatory fishes, and time for diversification for each lake. Then they collected data on intrinsic traits of cichlid lineages, including the presence of a polygamous mating system, mouthbrooding, generalised egg dummies and/or morphologically derived “haplochromine” egg dummies (Greenwood 1979) (used in courtship and in fertilisation of eggs in the mouth of the female), and sexual dichromatism. Using ordinary and phylogenetic multiple regression models they tested for associations between these predictor variables and species radiation – that is, whether a lineage diversified or not upon entering a lake. The best-supported predictor variables included both environmental variables and lineage-specific traits: lake depth, energy and sexual dichromatism were the most consistently well-supported predictor variables, all affecting diversification positively.

Whereas in terrestrial systems like *Anolis* lizards, where very small islands never host adaptive radiations (Losos and Schluter 2000), many of the small lakes in Africa do have little cichlid fish radiations (Wagner et al. 2012). This revealed an important difference between cichlids and terrestrial taxa in that speciation is apparently not constrained by habitat surface area in cichlids. This is also consistent with other results, discussed above, that speciation in cichlid fish may not require allopatric conditions. The consistently significant positive effect of lake depth on cichlid diversification is consistent with depth being an important axis of ecological and reproductive niche differentiation in speciation in these

fishes (Seehausen et al. 2008), providing another independent confirmation of the results of the speciation case studies. More available depth also increases habitat area for fishes, and the resultant larger population sizes may influence speciation and extinction rates. Larger energy input to an ecosystem might similarly increase carrying capacities, leading to larger total population sizes, increased rates of speciation and/or lower rates of extinction (Evans et al. 2005; Mittelbach et al. 2007). Alternatively, high inputs of energy may lead to shortened generation times and/or increased mutation rates, perhaps permitting increased rates of population differentiation and speciation. The positive effects of sexual dichromatism on diversification suggested that the intensity of sexual selection is a key influence on the probability that cichlids radiate into many species, again confirming what case studies of the microevolutionary

The coincidence between environmentally determined ecological opportunity and sexual selection best predicts whether a radiation will occur

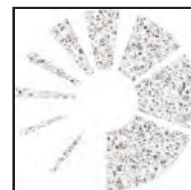
process had revealed about the importance of sexual selection in cichlid fish speciation.

Taken together, these studies suggest that cichlid fish diversification is not a simple function of any one predictor variable, but it is the coincidence between environmentally determined ecological opportunity and sexual selection that best predicts whether a radiation will occur. Biologists often considered cichlids in general an unusually speciation-prone taxon, but because only some cichlid lineages exhibit strong sexual selection, the propensity to evolve extraordinary diversity may only have evolved in some branches of the cichlid tree. Large and deep lakes appear to play a dual major role: firstly, they capture preexisting cichlid diversity, often from several riverine sources, and subsequently maintain it sometimes well beyond its extinction in rivers, and, secondly, they are the hotspots for production of new diversity through adaptive radiation. So it seems to me that diversification may in fact be predictable in cichlid fish – but it requires taking environmental factors, evolved lineage traits and environmental history jointly into account.

References

- Bezault E, Mwaiko S and Seehausen O. 2011. Population genomic tests of models of adaptive radiation in Lake Victoria region cichlid fish. *Evolution* 65: 3381–3397.
- Bolnick DI and Fitzpatrick BM. 2007. Sympatric speciation: Models and empirical evidence. *Annual Review of Ecology Evolution and Systematics* 38: 459–487.
- Evans KL, Warren PH and Gaston KJ. 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews* 80: 1–25.

- Farrell BD. 1998. "Inordinate fondness" explained: Why are there so many beetles? *Science* 281: 555–559.
- Fryer G. 1959. Some aspects of evolution in Lake Nyassa. *Evolution* 13: 440–451.
- Genner MJ, Seehausen O, Lunt DH, Joyce DA, Shaw PW, Carvalho PR and Turner GF. 2007. Age of cichlids: new dates for ancient lake fish radiations. *Molecular Biology and Evolution* 24: 1269–1282.
- Greenwood PH. 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part 1. *Bulletin of the British Museum (Natural History) Zoology* 35: 265–322.
- Joyce DA, Lunt DH, Bills R, Turner GF, Katongo C, Duftner N, Sturmbauer S and Seehausen O. 2005. An extant cichlid fish radiation emerged in an extinct Pleistocene lake. *Nature* 435: 90–95.
- Joyce DA, Lunt DH, Genner MJ, Turner GF, Bills R and Seehausen O. 2011. Repeated colonization and hybridization in Lake Malawi cichlids. *Current Biology* 21: in press.
- Keller I, Wagner CE, Greuter L, Mwaiko S, Selz O, Sivasundar A, Wittwer S and Seehausen O. submitted. Population genomic signatures of divergent adaptation, gene flow, and hybrid speciation in the rapid radiation of Lake Victoria cichlid fishes. *Molecular Ecology*.
- Kisel Y and Barraclough TG. 2010. Speciation has a spatial scale that depends on levels of gene flow. *American Naturalist* 175: 316–334.
- Konijnendijk N, Joyce DA, Mrosso HDJ, Egas M and Seehausen O. 2011. Community genetics reveal elevated levels of sympatric gene flow among morphologically similar but not among morphologically dissimilar species of Lake Victoria cichlid fish. *International Journal of Evolutionary Biology*, doi:10.4061/2011/616320.
- Kraaijeveld K, Kraaijeveld-Smit FJL and Maan ME. 2011. Sexual selection and speciation: the comparative evidence revisited. *Biological Reviews* 86: 367–377.
- Liem KF. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. *Systematic Zoology* 22: 425–441.
- Losos JB. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *American Naturalist* 175: 623–639.
- Losos JB and Schluter D. 2000. Analysis of an evolutionary species area relationship. *Nature* 408: 847–850.
- Lundberg JG. 1993. *African-South American fresh-water fish clades and continental drift - problems with a paradigm*. Yale University Press, New Haven.
- Mac Arthur RH and Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.
- Malabarba MC, Zuleta O and Del Papa C. 2006. *Proterocara argentina*, a new fossil cichlid from the Lumbra Formation, Eocene of Argentina. *Journal of Vertebrate Paleontology* 26: 267–275.
- Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeck MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM and Turelli M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* 10: 315–331.
- Murray AM. 2001. The oldest fossil cichlids (Teleostei: Perciformes): indication of a 45 million-year-old species flock. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 679–684.
- Price T. 2008. *Speciation in Birds*. Roberts & Company, Greenwood Village, Colorado.
- Rosenzweig ML. 1997. Tempo and mode of speciation. *Science* 277: 1622–1623.
- Rosenzweig ML. 2001. Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5404–5410.
- Santini F, Harmon LJ, Carnevale G and Alfaro ME. 2009. Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. *BMC Evolutionary Biology* 9: 1–10.
- Schluter D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press.
- Schwarzer J, Misof B, Tautz D and Schlieven UK. 2009. The root of the East African cichlid radiations. *BMC Evolutionary Biology* 9: 186.
- Seehausen O. 2006. African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society of London Series B-Biological Sciences* 273: 1987–1998.
- Seehausen O. 2007. Evolution and ecological theory – Chance, historical contingency and ecological determinism jointly determine the rate of adaptive radiation. *Heredity* 99: 361–363.
- Seehausen O and Magalhaes IS. 2010. Geographical Mode and Evolutionary Mechanism of Ecological Speciation in Cichlid Fish. In Grant PR and Grant BR (eds.), *In Search of the Causes of Evolution: From Field Observations to Mechanisms*. Princeton University Press, Princeton and Oxford: 282–308.
- Seehausen O, Terai Y, Magalhaes IS, Carleton KL, Mrosso HDJ, Miyagi R, van der Sluis I, Schneider MV, Maan ME, Tachida H, Imai H and Okada N. 2008. Speciation through sensory drive in cichlid fish. *Nature* 455: 620–626.
- Seehausen O and van Alphen JM. 1999. Can sympatric speciation by disruptive sexual selection explain rapid evolution of cichlid diversity in Lake Victoria? *Ecology Letters* 2: 262–271.
- Servedio MR, van Doorn GS, Kopp M, Frame AM and Nosil P. 2011. Magic traits in speciation: 'magic' but not rare? *Trends Ecol. Evol.* 26: 389–397.
- Simpson GG. 1953. *The major features of evolution*. Columbia Univ. Biol. Ser. No. 17: i–xx, 1–434.
- Sparks JS. 2004. Molecular phylogeny and biogeography of the Malagasy and South Asian cichlids (Teleostei: Perciformes: Cichlidae). *Molecular Phylogenetics and Evolution* 30: 599–614.
- Sparks JS and Smith WL. 2004. Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). *Cladistics* 20: 501–517.
- Storch D, Keil P and Jetz W. 2012. Universal species-area and endemics-area relationships at continental scales. *Nature*: in press.
- Streelman JT and Karl SA. 1997. Reconstructing labroid evolution with single-copy nuclear DNA. *Proceedings of the Royal Society of London Series B-Biological Sciences* 264: 1011–1020.
- Sturmbauer C, Baric S, Salzburger W, Ruber L and Verheyen E. 2001. Lake level fluctuations synchronize genetic divergences of cichlid fishes in African lakes. *Molecular Biology and Evolution* 18: 144–154.
- Vamosi SM. 2003. The presence of other fish species affects speciation in threespine sticklebacks. *Evolutionary Ecology Research* 5: 717–730.
- Vences M, Freyhof J, Sonnenberg R, Kosuch J and Veith M. 2001. Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. *Journal of Biogeography* 28: 1091–1099.
- Wagner CE, Harmon LJ and Seehausen O. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. *Nature* 487: 366–369.
- Wagner CE, Keller I, Wittwer S, Selz O, Mwaiko S, Greuter L, Sivasundar A and Seehausen O. Genome-wide RAD sequence data provides unprecedented resolution of species boundaries and relationships in the Lake Victoria cichlid adaptive radiation. *Molecular Ecology*, in press.



Foundation Monographs - accelerating the pace of taxonomy

Robert Scotland

University of Oxford, Department of Plant Sciences
robert.scotland@plants.ox.ac.uk

and colleagues from RBGE, NHM, and Kew Gardens successfully obtained a small grant of £27k through the second round of the NERC/BBSRC SynTax initiative. The initiative is an attempt by UK research councils in collaboration with the Linnean Society and Systematics Association to explicitly integrate or at least include the subject area of taxonomy and systematics within research council funding. The scheme finished with the third and final round of funding during 2012. A central aim of the scheme was to prime-pump the type of research that would lead to a full-scale research council grant and therefore the success or otherwise of the scheme will only become clear in the coming years. Here, nine or so months into our project, I outline our original proposal and progress made. Our overall rationale was to propose research that was firmly taxonomic in focus, but innovative and ambitious in its scope.

Project Title: Foundation Monographs - accelerating the pace of taxonomy

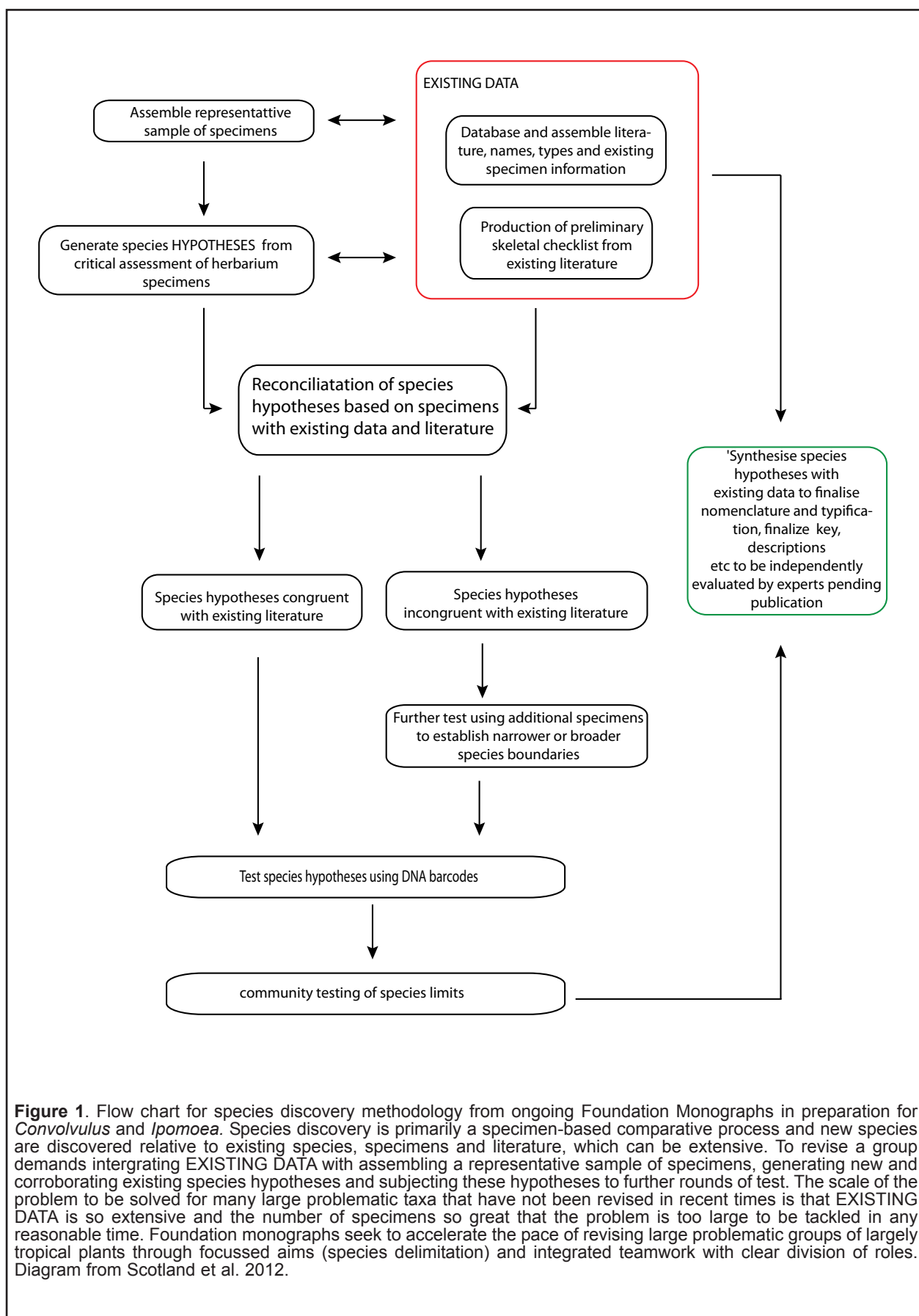
Background

Current estimates of the number of described species of flowering plants range between 230,000 and 420,000 (Scotland & Wortley 2003). The uncertainty surrounding these figures is largely due to unknown levels of synonymy for many taxa. In addition, there are estimated to be about 70,000 species of flowering plant (Joppa et al. 2010) yet to be described, of which it is estimated that more than half have already been collected and await discovery in herbaria (Bebber et al. 2010). Major impediments to the detection of these new species include the high levels of synonymy, lack of keys to currently recognised species and, in the case of most large genera, lack of any global treatment. We propose the Foundation Monograph as an innovative, pragmatic and fast approach for overhauling the taxonomy of species-rich, widespread, taxonomically neglected groups of plants. In contrast to modern global monographs, the Foundation Monograph approach aims

only to: (i) delimit taxa, establishing taxon circumscriptions and providing brief descriptions; (ii) resolve nomenclature; (iii) provide identification tools, specifically diagnostic keys and DNA barcodes; (iv) provide distribution data and (v) test the monophyly of the study group (make sure the group is a natural one).

Initially we propose to produce a Foundation Monograph for *Convolvulus*, estimated to contain 150-200 species, and to make this publicly available on a website within twelve months. Descriptions of new taxa and other necessary supporting papers will be submitted for publication within the same period. *Convolvulus* is selected as a reasonably large genus, which has not been monographed since the work of Choisy in De Candolle's Prodrômus in 1849. Using experience and lessons gained from the *Convolvulus* Foundation Monograph, the working method will be modified to provide a model for monographing other large, taxonomically neglected groups of plants (we intend to begin with *Ipomoea*, a genus of c. 600 species).

The last attempt to monograph the world's flora was that of De Candolle in the mid-19th century. Since that time the world has been explored intensively and the number of specimens in herbaria has increased enormously. One consequence of this has been the tendency to carry out taxonomic revisions only at national or regional, rather than global levels. Recent attempts to prepare global monographs such as the Species Plantarum project have met with delays due to overambitious aims, lack of appropriate authors or lack of finance. More limited monographic treatments of individual families or genera have been completed in the past 50 years, but these are few and often of groups that are relatively small. Part of the problem is the scope of most monographs: extremely detailed taxonomic accounts, and more or less comprehensive treatments of the phylogeny, biogeography, ecology and evolution of a particular group. This means that monographs generally require many years to be completed (often a life-time of work from a single dedicated botanist) with consequent high costs in terms of time and budget. Other aspects of the



problem include the sheer volume of material associated with any large taxonomic group, which may be housed in



Figure 2. An as yet un-described new species of *Ipomoea* from the Andes of Bolivia.

herbaria in many parts of the world, the burden of historical and contemporary literature and the lack of experienced taxonomists. The inevitable consequence of all this is that many species-rich groups of plants remain relatively unstudied today. If knowledge of the taxonomy of the world's flora is to be significantly enhanced, pragmatic, faster, and innovative solutions, focused on a single global agenda – the species level inventory – and making full use of all available tools, are necessary. This proposal aims to begin the process of developing such novel and innovative solutions (Figure 1).

Methodology

Electronic resources and informatics tools - Production of the Foundation Monograph will utilize electronic resources including information on names (e.g. from IPNI and the RBG Kew World Checklist project), specimens (e.g. GBIF, Tropicos), and types (e.g. API, LAPI). It will take full advantage of database/informatics technologies specifically the BRAHMS (Botanical Research and Herbarium Management Software) package to enable us to score and store specimen and nomenclatural data that can be used automatically to build descriptions. The project will identify any modifications necessary to ensure that BRAHMS meets the needs of the Foundation Monograph approach.

Morphological taxon delimitation - A central feature of all monographic approaches, including that proposed here, is that they treat the taxonomy of a group by assessing, sorting, comparing and evaluating specimens across the complete range of variation and the total global distribution of the group. This helps to resolve synonymy and has a much greater potential to unearth

often substantial numbers of new species that have escaped detection. Loan material coupled with specimen images will therefore provide the raw data for a morphological sort to delimit taxa. This will enable us rapidly to achieve a near complete coverage of unproblematic taxa. Where complex variation is encountered it will be flagged up and dealt with pragmatically by recognizing the smallest detectable, diagnostic taxa that are monophyletic. This approach distinguishes tractable taxonomic levels of variation from levels of variation that potentially represent hybridisation, introgression and other micro-evolutionary processes. Based on this information, we will produce original short diagnostic descriptions and keys. Images of specimens will be included and all names associated with the group will be accounted for. Our information will be collated and managed in a BRAHMS database and placed on the web for public access.

Molecular methods - Monophyly and taxon circumscriptions will be further tested using DNA sequence data. DNA barcodes (*rbcL* and *matK*) will be established for all recognised taxa (two accessions per taxon representing the extremes of the morphological variation). These data will be managed and published online using the Barcode of Life Data System (BOLD) (Ratnasingham & Hebert 2007), allowing their use for specimen identification. Barcode sequences will also be used to test monophyly in conjunction with other published *rbcL* and *matK* sequences for Convolvulaceae.

Aims, Outcomes and Future Plans

Development of the Foundation Monograph model - The aim of this project is to make available a scientifically sound Foundation Monograph for all potential users within a relatively short time. We wish to develop a method that integrates traditional herbarium-based taxonomy, DNA barcodes (Janzen et al. 2009) and a phylogenetic approach based on monophyly to overhaul the taxonomy of problematic plant groups in a short time-frame. A multi-institutional working group will monitor and evaluate progress and seek to establish widely-applicable norms from what is essentially a pilot project. The project and the working group will specifically:

1. Explore the trade-off between quality, cost and time with a view to establishing an ideal balance between these within the context of the needs of potential users of monographic outputs.
2. Identify important bottlenecks and problems, and explore possible solutions to these.
3. Establish a protocol including template databases etc. to accelerate monographic outputs from taxonomic research.

This project is distinctive and innovative for the

following reasons:

1. The Foundation Monograph aims to combine the global approach of the monograph with the level of detail of a good diagnostic field flora in combination with DNA barcodes.
2. The Foundation Monograph will harness modern electronic resources in both its preparation and output.
3. The Foundation Monograph aims to break the logjam in monographic work by establishing achievable taxonomic goals within a short timescale.
4. The Foundation Monograph will result in a product which is accessible to a wide audience interested in conservation, biodiversity, floristic and botanical studies in general, not merely a restricted group of people involved in taxonomic research.
5. The project as a whole will generate a model that can be followed by other plant taxonomists to produce similar foundation monographs without the necessity of a lifetime's dedication to a particular group.
6. For the above reasons we envisage applying for responsive mode research council funding for a multi-institutional research grant through the NERC or the LoLa scheme of the BBSRC.

Outputs - Peer-reviewed paper covering the Foundation Monograph methodology developed during the project, addressing timescale, quality, cost, bottlenecks, problems and solutions.

Peer-reviewed paper focused on the need for a new approach and the conceptual issues surrounding the documentation of the world flora (Scotland & Wood 2012).

Foundation monograph of *Convolvulus* to be available



Figure 4: Three colour variants of the morning glory, *Ipomoea purpurea* growing together.



Figure 3: An as yet un-described new species of *Ipomoea* from the cerrados of Bolivia.

online and published in a peer-reviewed outlet (e.g. *Phytotaxa*).

Descriptions of new species and taxonomic notes to be published in a peer-reviewed journal.

DNA barcode reference library published in BOLD.

State of play - We are now at a very advanced stage in finishing the monograph. We have revised in excess of 200 species, will have produced that number of species descriptions with identification keys, inferred a phylogenetic tree with 80% species-level sampling with associated DNA diagnostic barcodes for many species. We are in the process of preparing the monograph for publication in *Phytotaxa* later this year. We have also recently secured a Leverhulme grant to produce a foundation monograph for the genus *Ipomoea*, a tropical genus of some 800 species that has never been monographed.

References

- Bebber DP et al. 2010. Herbaria are a major frontier for species discovery. *Proceedings of the National Academy of Sciences of the United States of America* 107: 22169–22171.
- Janzen DH et al. 2009. Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Molecular Ecology Resources Supplement* 1: 1–26.
- Joppa LN, Roberts DL and Pimm SL. 2010. How many species of flowering plants are there? *Proceedings of the Royal Society of London Series B – Biological Sciences*. Published on-line July 7th, doi: 10.1098/rspb.2010.1004.
- Ratnasingham S and Hebert PDN. 2007. BOLD : The Barcode of Life Data System (). *Molecular Ecology Notes* 7: 355–364.
- Scotland RW and Wood JRI. 2012. Accelerating the pace of taxonomy. *Trends in Ecology and Evolution* 27(8): 415–416.
- Scotland RW and Wortley AH. 2003. How many species of seed plant are there? *Taxon* 52: 101–104.

The 13th Young Systematists' Forum

The 13th Young Systematists' Forum was held at the Natural History Museum, on 1st December 2011

The Young Systematists' Forum provides a place for students at the start of their careers in systematics and biodiversity research to meet each other and present posters and talks, often for the first time. This annual one-day event was established in 1998 primarily for UK based students to provide experience of a professional conference without the registration fees or the intimidating senior audiences. Following a steady increase in popularity, this year the Flett Lecture Theatre at the Natural History Museum was full with 137 registered participants from ten countries. The six institutions with the largest number of student representatives were the Natural History Museum, UK; Royal Botanic Gardens Kew, UK; Ruhr-Universität Bochum, Germany; Muséum National d'Histoire Naturelle, France; University of Amsterdam, Netherlands; and University of Bath, UK. Abstracts for the 18 talks and 25 posters are available at <http://www.systass.org/ysf>, with topics ranging from Mesozoic coelacanths, Heliconiini butterflies, and pollen of violets, to next generation sequencing technology and bio-ontologies.

The prize for the best talk was awarded to Alice Burridge for her talk entitled '*Shells, shapes and sequences: An integrated morphological, molecular and biogeographic study of Cuvierinidae (Gastropoda, Thecosomata)*'. The work was done as part of Alice's Master's thesis at the University of Amsterdam, Netherlands, and it was her first talk in a major venue. The prize for the second place talk was given to Elizabeth Cooke for her talk entitled '*Systematics and phylogeography of the emerging model plant Cardamine hirsuta*'. The talk showcased some of the work she is doing at RBG Kew, UK, as part of her PhD work. The first prize for the best poster was awarded to Meike Seefeldt from Ruhr-Universität Bochum, Germany, for her MSc work entitled '*Genetic and morphologic data unveil two overlooked Southern Ocean lysianassoid species (Crustacea, Amphipoda)*'. The second prize for the best poster was given to John Pfieffer, University of Alabama, USA, for his MSc work on '*Evolution of asymmetrical glochidia in the Unionidae (Mollusca: Bivalvia)*'. An honourable mention was awarded to the poster by Patrick Knopf, also from Ruhr-Universität Bochum, Germany, for his poster entitled '*Comparative phylogeny within Podocarpaceae (Coniferopsida)*'.

All the speakers did a great job of presenting professional level talks, keeping to time and answering tough but fair

questions from the audience. The authors of the posters presented their work with engaging pitches, providing feedback to the crowd of inquisitive viewers. We were lucky to be able to hold the evening reception in the historic and atmospheric Bird Gallery of the Natural History Museum. A really great time was had by all. Thanks are due to everyone who has helped on the day, especially Emily Saunders and Vera Uva (NHM) and Martin Xanthos, Katherine Challis (both RBG Kew) for their help with logistics and reception. The intense focus of the judges for a full day of talks and posters deserves special thanks, thus we recognise Gemma Bramley (Kew, Botany), Cédric Berney (NHM, Zoology), Alex Monro (NHM, Botany) and Lil Stevens (NHM, Palaeobotany) for their unflagging attention to the talks, and Juliet Brodie (NHM, Botany), David Hawksworth (NHM, Botany) and Maria Vorontsova (Kew & NHM, Botany) for their thoughtful scrutiny of the posters. We look forward to seeing you at the 14th Young Systematists' Forum, to be held on 29 November 2012.

The YSF Organising Committee: Ellinor Michel (Natural History Museum, UK), Jon Todd (Natural History Museum, UK) & Maria Vorontsova (Royal Botanic Gardens Kew, UK).

Cultivating common ground: biology and the humanities

John Holmes, University of Reading

What, if anything, can science learn from the humanities?

That is the question that a team of biologists, literary critics and historians at the University of Reading set out to answer in an AHRC-funded project that has generated new insights into the hoary old question of the 'two cultures'.

In July the team held a workshop, entitled 'Cultivating Common Ground: Biology and the Humanities', to introduce practising biologists to humanities research into biology. It provoked some rich and unexpected responses. In the scoping study, 'The Value of the Literary and Historical Study of Biology to Biologists', we draw upon the experience of the workshop and our respective specialisms to argue that the humanities can play an important role in transforming future biological research. We show that humanities research on biology can be of real interest and value to biologists; that there is enthusiasm for collaboration in research between the humanities and biology on both sides, and that it would be mutually beneficial; and that both biology and humanities students could benefit too from being taught

alongside one another in an interdisciplinary way for part of their degrees. With regard to specific humanities disciplines, we show, both in our view and the view of the biologists who came to the workshop that:

- history has practical applications for biologists, in positioning their own work in relation to earlier research and to contemporary culture;
- literature can assist in reflecting on science and its values, providing an important supplement to the work of science itself, particularly aesthetically;
- critical and theoretical approaches to texts can help scientists to be aware of their own assumptions and to improve their own writing.

We conclude that there is real potential for the humanities to play a part in the future development of biology, and that co-disciplinary collaborations between biologists and humanities scholars in research and teaching could lay the foundations for a new, more rounded and ultimately more complete approach to the study of human beings, our fellow organisms and the environments we share with them. To realize this ambition the team is now working together with colleagues from other universities on a pioneering co-disciplinary training programme for young academics as the next step towards bringing biology and the humanities together.

To read the report in full, please go to:

<http://blogs.reading.ac.uk/cultivating-common-ground/files/2012/10/The-value-of-the-literary-and-historical-study-of-biology-to-biologists-a-scoping-study.pdf>

Twitter for systematists

Ross Mounce, University of Bath

Despite, or perhaps because of, being limited to just 140 character messages at a time, Twitter is an excellent medium for the near instantaneous dissemination of information over the Internet. It's been successfully used to remotely sense earthquakes (Sakaki et al. 2010) and flu outbreaks (Culotta 2010), and to predict the outcomes of elections (Tumasjan et al. 2010) and box office success (Asur & Huberman 2010). It's also a very handy tool for academics, with ever-increasing usage amongst the population.

Here are my top tips for using Twitter for science (a far from exhaustive list):

•Remotely follow conferences you can't attend

There are too many interesting conferences these days. No one has the time or money to attend them all. Furthermore, some may occur simultaneously and one cannot be in two places at the same time! But with Twitter one can often get a reasonable description of what's going on at a conference by following the official conference hashtag e.g. #evol2012 #ievobio (Evolution, Ottawa), and #HennigXXXI (Hennig, Riverside). At some conferences remote participation via Twitter is possible, to ask questions from afar at panel discussions and such.

•Expand the impact of your conference talks

Expanding on the above, if you're giving a talk at a conference – put your Twitter handle on your conference name badge and on the title slide of your talk so tweeters in the audience can link to you on Twitter when describing your talk. This is particularly useful if you have a common name – John Smith could be anyone online but @JSmith69 exactly identifies who (and is shorter). If you can, put your slides online before your talk using a service like Slideshare or Prezi and use a URL shortener to provide an easily tweetable link to that online slidedeck. Put this short-link on your first and last slides, so tweeters can disseminate this link to everyone following the conference hashtag from afar to also view your slides. This can dramatically increase the number of people seeing your talk (albeit, a slide-only version of it). For example, my talk this year at #HennigXXXI once tweeted out by @rdmpage and others (thanks!) was seen by over 200 people online after just a couple of days. At the conference itself there were fewer than 100 people in attendance, so it really helped maximise the impact of the talk.

•Discuss, promote and critique papers on Twitter

Like a paper? Tweet about it including a link to the paper (attribution and links are key on Twitter) and maybe start a discussion with fellow academics. Don't just tweet-promote your own papers or those of your close colleagues – this is bad netiquette. Some groups even have journal clubs conducted in the open on Twitter, e.g. <http://www.twitjc.com/>

•Get help or canvass the opinion of your research community

Got a problem you can't solve yourself, but might easily and quickly be solved by someone else? One can't abuse Twitter for this all the time, but the occasional well-put question on Twitter often elicits good responses if you have enough followers. The key here is reciprocity – if you're always asking for help you'll soon be ignored. But

if you can give as well as receive help you'll generate a healthy respect. Twitter convention has it that questions are often marked with the #lazyweb hashtag – use this to indicate you have a question that you want answered. Similarly if you need a PDF you don't have subscription access to, try supplying the URL link to the paper + your email address + #icanhazpdf in a tweet. @BoraZ created this convention and it's now rather popular with many requests every day appearing on Twitter for PDFs. This facilitates quick and easy access to the literature, enabling thorough scholarship, by-passing the often tedious and slow inter-library loans procedure.

The Systematics Association, like other societies, e.g. @SVP_vertpaleo, @GeolSoc, @LinneanSociety, and journals, e.g. @systbiol, @MethodsEcolEvol, @BiolJLinnSoc and @ecologyletters, have had a presence on Twitter since 2011: @SystAssn.

Want to talk about systematics? Tweet us at @SystAssn. Happy tweeting tweeps :)

References

Sakaki T, Okazaki M and Matsuo Y. 2010. Earthquake shakes Twitter users: real-time event detection by social sensors. In *Proceedings of the 19th international conference on World wide web, WWW '10*, New York, USA: 851-860. ACM. Available at <http://dx.doi.org/10.1145/1772690.1772777>.

Culotta A. 2010. Towards detecting influenza epidemics by analyzing Twitter messages. *KDD Workshop on Social Media Analytics*. Available at <http://arxiv.org/abs/1007.4748>.

Tumasjan A, Sprenger TO, Sandner PG and Weppe IM. 2010. Predicting elections with Twitter: what 140 characters reveal about political sentiment. In *Proceedings of the Fourth International AAAI Conference on Weblogs and Social Media*: 178–185. Available at <http://www.aaai.org/ocs/index.php/ICWSM/ICWSM10/paper/viewFile/1441/1852>.

Asur S and Huberman BA. 2010. *Proceedings of the IEEE/WIC/ACM conference on web intelligence and intelligent agent technology 1*: 492–499. Available at <http://www.hpl.hp.com/research/sci/papers/socialmedia/socialmedia.pdf>.

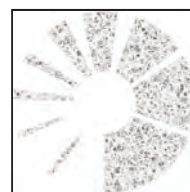
A list of relevant accounts on Twitter to follow:

@David_Hillis (University of Texas)
 @kcranstn Karen Cranston (Open Tree of Life)
 @rdmpage (Professor of Taxonomy at Glasgow University)
 @cydparr (EOL)
 @phylofoundation (updates from The Phyloinformatics Research Foundation)
 @phylogenomics (Prof. Jonathan Eisen, UC Davis)
 @Dr_Bik (marine genomics, UC Davis)

@JChrisPires (plant genomics)
 @k8hert (Kate Hertweck, NESCent)
 @TRyanGregory (University of Guelph)
 @pedrobeltrao (bioinformatics, UCSF)
 @ewanbirney (associate director at the EBI)
 @caseybergman (University of Manchester)
 @ianholmes (computational biologist)
 @lukejharmon (University of Idaho)
 @cboettig (theoretical ecology & evolution)
 @tomezard (University of Surrey)
 @eperlste (evolutionary pharmacologist, Princeton University)
 @RosieRedfield (UBC)
 @NYCuratrix (Susan Perkins, AMNH)
 @theleechguy (Mark Siddall, AMNH)
 @AndyFarke (vertebrate paleontologist)
 @TomHoltzPaleo (paleobiologist)

At the Natural History Museum London:

@nhm_london (official NHM London account)
 @edwbaker (biodiversity informatics)
 @DavidMyWilliams (diatomist)
 @vsmithuk (cybertaxonomist)
 @Coleopterist (Max Barclay)
 @SandyKnapp (Solanaceae taxonomist)
 @NHMdinolab (updates from Paul Barrett's lab)
 @gna-phylo (updates from Thomas Richards' lab)



One species or three? The Azorean butterfly-orchids

Richard Bateman

Jodrell Laboratory, Royal Botanic Gardens, Kew
r.bateman@kew.org

Our SRF proposal entitled *Cladogenesis versus anagenesis in Macaronesian plants: Azorean butterfly orchids* concluded with the phrase ‘all laboratory work will be completed by the end of 2010.’ Oh well, even the best-laid plans ... the initial fieldwork in the Azores finally took place in June 2011! However, taking the extra time to better align our ducks has proven advantageous – a mere two months later, much progress could already be reported.

To summarise the challenge being addressed: Orchids have justifiably gained reputations for enthusiastically undergoing rapid radiations at the drop of a hat, and for being able to migrate over long distances by means of their air-borne dust-seeds. Indeed, no fewer than 12 orchid lineages have established themselves on the Macaronesian islands: seven on the Canaries, five on the Madeiras and three on the most remote archipelago, the Azores. Most of the resulting island endemics differ only subtly from their mainland sister species



The best remaining natural vegetation on Faial persists in the nature reserve occupying this 350 m-deep caldera; naturally, the orchids live near the bottom! (image: Paula Rudall).



Platantthera azorica on Pico; this controversial endemic species has been estimated to be represented in the Azores by as few as 500–1000 individuals; our data suggest that this figure is only a modest under-estimate (image: Richard Bateman).

morphologically, whereas molecularly the difference is in some cases more substantial, suggesting a significant period of isolation and independent evolutionary history in such cases. But remarkably, the majority of these lineages have undergone only anagenetic speciation; they have deviated away from their mainland relatives, but they have not undergone further splits since their arrival on the islands.

The one apparent exception to the remarkable dominance of anagenesis in Macaronesia is the butterfly-orchids of the genus *Platantthera*. This lineage similarly differs morphologically from its closest mainland relatives, but it also appears to have undergone a single cladogenetic speciation event subsequent to its arrival on the Azores. However, little is known about the two supposed Azorean species of *Platantthera*, whose taxonomic status remains contentious; indeed, the recently completed IUCN Red List treatment recognised only one. This multi-faceted SRF-funded project is seeking to infer the evolutionary

origin(s) of these species (pictured).

The SRF grant partially funded a field trip by the author and Paula Rudall that encompassed three Azorean islands, located in two of the three clusters that together constitute this volcanogenic archipelago: Sao Miguel, Pico and nearby Faial. The remaining six islands were surveyed by our Azorean collaborator, Mónica Moura, a feat achieved largely during her 2011 sabbatical. Data acquired in 2011 encouraged Bateman and Rudall to return to the islands in 2012, aided by a small grant from the Botanical Research Fund and targeting the islands of Santa Maria, Pico and, most importantly, Sao Jorge. The most immediate result of this determined and combined assault was to expand knowledge of the occurrence of the orchids across the islands; we now know that the more widespread and locally frequent of the two species, *P. micrantha*, occurs on all nine islands and the rarer and putatively endangered *P. azorica* is absent only from the less altitudinous island, Graciosa.

The SRF proposal promised to conduct non-destructive sampling on six populations of each species, some mixed and others single-species. In fact, we now find ourselves blessed with at least some data from every island, encompassing 30 Azorean populations and 216 individuals; these plants can be compared with similar numbers of *Platantthera* scored from mainland Europe during our previous research project and Morocco in May 2012. We remain ignorant of pollinator spectra on the Azores, though small moths are implicated. Preliminary analyses of each of the datasets collected – morphometrics, electron micrographs of flowers, population genetics of the plants (by Sal Cozzolino at Naples), population genetics of the mycorrhizal partners (by Martin Bidartondo at RBG Kew) – all reinforce the circumscription of these superficially similar plants into not one but two cohesive species, and suggest that the rarity of *P. azorica* relative to *P. micrantha* may reflect narrower ecological tolerances. More startling discoveries made this summer apparently shed much light on this intriguing orchid ‘mini-radiation’, not least revealing a species new to science and suggesting strongly contrasting approaches to forming mycorrhizal partnerships. However, detailing these revelations should on balance await the full synthesis of our data that is now under way.

To end on a more general note, one insight gained during preparation for the trip was the high proportion of my colleagues who had considered visiting the Azores and the tiny proportion who had actually done so. Paula and I returned energised, with a vivid impression of an exceptional laboratory for natural history studies. The rugged landscapes offer marvellous opportunities for comparative studies of volcanic geomorphology; the islands differ considerably in age and altitudinal range,



Native vegetation in the foreground offsets the iconic (and still slightly smouldering) volcanic peak of Pico (2351 m); the author is paying homage to the serendipitous discovery of arguably the only Azorean orchid other than *Platanthera* – *Serapias* 'atlantica' (image: Paula Rudall).

which is at least partly dictated by whether the peaks remain or have been shed to generate spectacular calderas – features that maintain their own microclimates (compare the pictures of Pico and Faial). Biotas are of modest diversity but rich in presumed endemics, which form some unintuitive communities. And what appears from the air to be a re-creation of the Somme on the island of Pico turns out on closer inspection to be a World Heritage Site composed of unique vineyards. Each resilient vine is inserted directly into a lava flow and surrounded by a protective cylinder of basalt blocks (essential, given the Hebridean-style weather systems), ultimately generating local wines of excellent value. However, ranged against these major positives are major negatives, notably the devastation caused by misguided EU funding of subsistence dairying and the most impressive cases I have seen of the annihilation of native communities by pretty but hyper-invasive exotics (gingers and tree-ferns, anyone?). Few places in the world can be more deserving of increased conservation activity.

Book Reviews

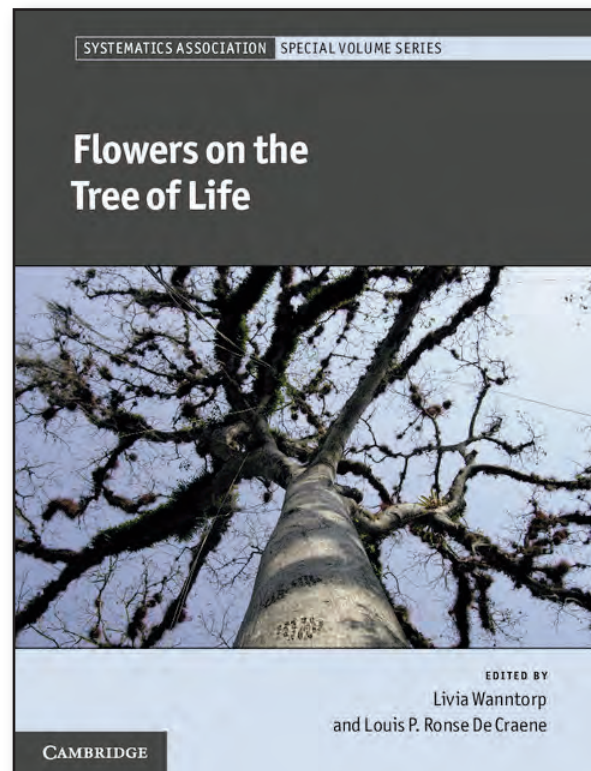
Flowers on the tree of life.

Wanntorp, L. & Ronse de Craene L.P. 2011. Systematics Association special volume 80. Cambridge University Press, Cambridge, U.K. hardback. 310 pages

Maarten J. M. Christenhusz

How did flowers evolve? How did they change during their evolutionary history? Where on the tree of life do fossil flowers fit in? Is morphology of flowers at odds with molecular findings? These and other questions are addressed in a dozen chapters authored by researchers on the evolution of flowers, who came together during a symposium organised by the Systematics Association and the Federation of European Biological Systematic Societies in Leiden, the Netherlands during August 2009. In the introduction, the role of morphology in plant systematics in past and present is discussed. It is stated that, in spite of the currently domineering molecular approach in botany, morphology as a synthetic science - building from multiple sources - should again be on the centre-stage in botany. Morphology complements the findings of molecular data in phylogenetic and evolutionary studies and with the need for discovering synapomorphies when new unexpected relationships are found in molecular studies, it seems likely that morphological approaches will be unavoidable. This comprehensive introductory chapter is followed by five chapters addressing the early evolution and diversification of flowers and six chapters addressing more specialised topics.

The first chapter, 'Spatial separation and developmental divergence of male and female reproductive units in gymnosperms, and their relevance to the origin of the angiosperm flower', addresses the development of bisexual flowers in angiosperms from unisexual ancestors in gymnosperms from a historical and developmental perspective. This chapter concludes that processes controlling gender can only be studied in extant species, whereas there are wholly extinct groups in which gender expression is ambiguous, but important



due to their phylogenetic positions. Most current knowledge on gender expression relates to angiosperms. In conifers Pinaceae have been the most preferred study group, prompted by its economic importance rather than its phylogenetic position. Conifers are phylogenetically divergent and have the most structurally divergent male and female reproductive organs of any seed plant group. The authors state that we will therefore learn more about the gymnosperm ancestor of angiosperms by studying extant taxa that show similarity in male and female developmental programming such as Ginkgoaceae, Cycadaceae and Zamiaceae, the 'living pteridosperms'. Phytohormones and transcription factors are suggested as causes of the gradational nature of gender control in gymnosperms. Therefore they suggest revitalising phytohormone focussed physiology, which went out of fashion by the end of the 20th century, but they also stress the importance of fossils to bridge the morphological gap between extant angiosperms and gymnosperms.

This elaborate chapter is followed by 'New flowers of Laurales from the Early Cretaceous of eastern North America', in which the diversity of fossil flowers is assessed. Among these fossil Laurales, characters of extant members of that order are represented.

The chapter 'Tracing the early evolutionary diversification of the angiosperm flower', morphological characters are mapped on a molecular phylogeny to reconstruct the origin and early evolution of flowers. In this chapter the authors conclude that the ancestral flower had many tepals and stamens and several carpels with a single ovule, although it is not certain if the tepals were spirally arranged or in whorls of three. The authors improved the picture of floral development and provided a general framework which can be applied in other disciplines of botany.

This subject is continued in chapters five, 'Changing views of flower evolution and new questions', and six, 'Centrifugal stamens in a modern phylogenetic context', in which the importance of morphological characters for phylogenetic reconstruction of the tree of life are

A 'must read' for any botanist
studying the classification of
flowering plants

analysed. Chapter five in particular, addresses the usefulness of morphological characters in understanding phylogenies, especially with regard to fossil evidence, in which the role of morphological data becomes increasingly important. Chapter six explores characters of importance at early branches in the tree of life, and the significance of centrifugal stamen development is addressed in that respect.

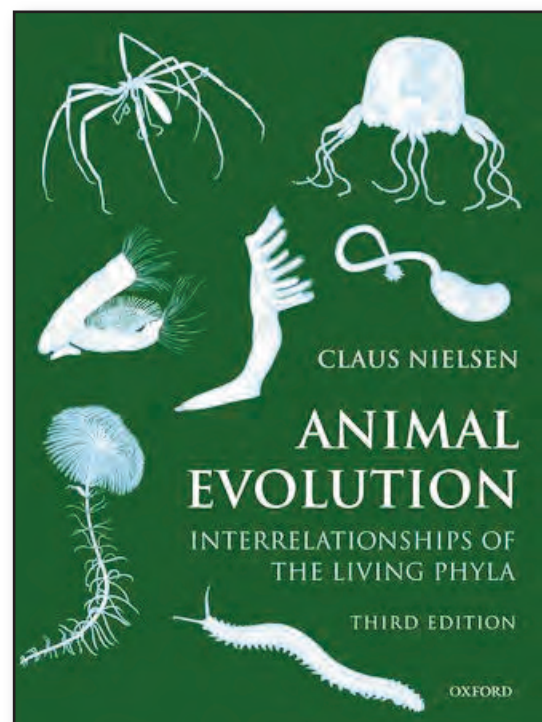
After these more general studies there are six more specialised chapters addressing families where

morphological systematics is of particular importance. Chapter seven discusses the androecium of palms – which is incredibly diverse compared to other monocots – in a phylogenetic context, especially with regard to polyandry and its evolutionary significance. Chapter eight discusses the systematic implications of floral development in the newly defined Nitrariaceae. This study shows that molecular evidence placing groups together that previously were not thought to be related, has shed new light on the evolution of flowers in these lineages. Chapter nine studies the multiplication of flower parts in *Conostegia* (Melastomataceae). Chapter ten discusses the diversification of the elaborate pollination mechanism of Marantaceae. Chapter eleven studies the ontogeny of flowers of an oddball species of *Acacia* (Fabaceae). This study shows that even though *Acacia* flowers are superficially uniform, they show a wide range of ontogenetic patterns. In the final chapter the development of the complex flowers of *Napoleonaea* (Lecythidaceae) is unveiled.

This volume provides a broad introduction to modern flower systematics. It discusses the current state of understanding of the evolution of flowers and it is a 'must read' for any botanist studying the classification of flowering plants. It will be a great help for students and researchers that want to engage in the fascinating field of the evolution of flowers.

Animal Evolution Interrelationships of the Living Phyla

Nielsen, C., 2011.



Oxford University Press, Oxford, UK.
Hardback and paperback, 416 pages.

Gordon Paterson

Far out in the uncharted backwaters of the unfashionable end of the Tree of Life lies a small unregarded clade, the opisthokonts, within which there is an insignificant branch, the Holozoa, or to those of us with digital watches—the animals and their nearest protist relatives. Your guide to the amazing morphological diversity to be found in this clade is *Animal Evolution* by Claus Nielsen, now in its third edition.

In approaching this review I have to confess that I come from an ecological background and therefore my knowledge of the minutiae and issues associated with advances in our understanding of animal evolution is rather hazy. Why I am doing this review comes down to rifts in the continuum and making the mistake of dropping into my colleague Ronald Jenner's room, picking up this book and uttering the words 'this looks interesting. I really must read that...'

So I thought that this book would provide a good guide to the state of the art in this particular field of endeavour. I also thought it would be interesting to see how far our understanding has advanced since the last time I had to consider the animals and their evolution (not quite as far back as Haeckel but it has been a while). So how does this edition fair as a guide to the animals and how has it changed since the last guide some eleven years ago?

It does not take long to realise that there have been considerable advances in our understanding of the relationships within the animals. Back in the 1970s and early 80s research into animal evolution had almost hit the buffers. Embryology and many of the sciences which underpinned evolutionary hypotheses had reached a plateau and, despite the rise of cladistics and methods of phylogenetic analyses, the reliance on morphology and embryology did not radically advance our understanding. The arguments may have been fun but ultimately the advances gained were not substantial. This is partly because many of the organisms themselves were difficult to place. These were small, often featureless or nearly featureless taxa such as Myxozoa and simple, worm-like *Xenoturbella*. Determining homologies based around absences was and remains problematical. And yet, there was progress, discovery of new classes and the redefinition of phyla continued as important discoveries in cellular and larval organisation were made. You only have to compare the range of groups within *Animal Evolution* with any of the zoology textbooks of that time to realise just how much has changed.

Nielsen's book summarises the state of the art and attempts to provide the reader with a synthesis. Each chapter deals with a different branch of the animal tree summarising the characters, some of the biology and listing gaps and needs for future research. In this regard the format and layout of this edition will be familiar to those who have read previous ones. For me one of the interesting aspects of this book is the history of advance and the development of the morphological character set. I found it fascinating to dip into the book to read about some of the more unusual new phyla or to find out what

new developments there were in some of the groups of which I have more knowledge. However, what is also clear is the rise and utility to be found in molecular analyses and characters.

The main difference between this volume and the previous one is that it is no longer possible to ignore the molecular evidence. So many of the relationships we are now able to hypothesise have come about because of an increasing sophistication in interpretation of molecular characters. This has led to some surprising results. For example the 'sponges' are not a monophyletic group! Who saw that coming? The animal cake always had a sponge base. Similarly, continued gene and taxon sampling has seen some members of the tree bounce around the animal clade changing position as each new analysis is published, the relationship between *Xenoturbella* and the other main clades is an example. In the previous edition of *Animal Evolution* it was confidently placed in the molluscs, it had previously been considered a deuterostome somewhere near echinoderms. Nielsen, in the third edition, bows to the molecular evidence and now this taxon is considered to be in a new clade called the Acoelomorpha and at the base of Eubilateria, at least for the moment.

So a major difference between the second and third volumes of Nielsen's book is the incorporation of molecular evidence on a par with the morphology. But in many respects this is the main strength of the book - it tries to link morphological and molecular evidence, to provide some sensible stability during a period of the continued production of molecular-based phylogenies, each suggesting something new and frequently unresolved in the arrangement. The latest RNA based trees of Mallet et al. (2012. *Molecular Phylogenetics and Evolution*, 64:603–617) are just the most recent case in point, where many taxa find themselves realigned in some frankly unlikely relationships (by the authors' own admission and because the morphological evidence does not agree), but which are nevertheless published because it provides an incremental advance in some other part of the tree!

Another difference between Nielsen's latest edition and previous ones is the overall phylogeny itself. There are new groupings for which new terms and names have to be established, always a contentious act. Since the last volume there have been ten new groups proposed at various levels on the tree. Some are even well defined. Much of the rearrangement reflects the cut and thrust in the research over the last ten years since the last edition. The separation of the 'sponge' clades at the base of the tree has resulted in two new groupings. Also there is a recognition of groupings such as the Ecdysozoa, which had previously been unadopted because the molecular data were not sufficient.

Thankfully there does appear to be some consensus, if I may use that term in this context. There are other areas where new evidence appears to support older groupings, such as the Polyzoa bringing together the Bryozoa, Cycliophora and entoprocts. The hemichordates are back having been separated previously into pterobranchs and

enteropneusts. The clades Protostomia and Deuterostomia are fairly consistent, both in the phyla that they comprise and in their relation to one another; groups that I remember from my early zoological days. The same cannot be said of the relationships within each. And interestingly this where the limitations of morphology often shows. The protostomes in particular have few morphological apomorphies but are consistently identified by several molecular studies. Within these apparently well-defined groupings, relationships are still problematical, for example, how are the platyhelminths related to the other lophotrochozoans? So, despite our progress, much still remains to be done. This is made clear in the relevant sections, where Nielsen indicates the gaps and presents the issues to be resolved.

So what did I learn? For a start that there has possibly never been a more exciting time to study animal evolution. The new approaches that molecular analyses bring are really testing assumptions and providing truly unexpected results. But tempered with this is the fact that morphology is still at the heart of this endeavour because as Nielsen says 'it is the history of morphological change we wish to explain'.

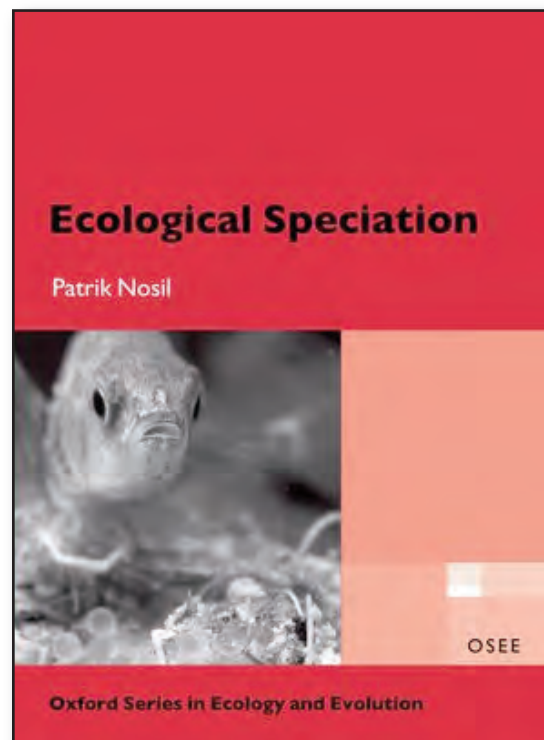
Animal Evolution is a wonderful guide to this diverse, often bizarre, part of the tree of life and, like all guides, much of it is useful (where are the good restaurants? Or in this case, what are the characters underpinning the classifications? Where are the limitations? Here is a potted summary of the group), some parts are likely to be disputed (this restaurant was actually lousy!). Molecular data in many instances do not agree with the morphology and some may by now be out of date (that restaurant closed years ago!). Well, each reader can find their own examples depending on their standpoint. But it is one of the few books I have come across which tries to provide a comprehensive summary of all the evidence available; with references which are the basis for future searches in the web so you can follow where the latest research is taking us now. Finally, the book itself is well laid out and illustrated and the little vignettes of a representative from each group are one of the book's charms. Given the continued flux in the study of this branch of life, all it needs on the back cover is a friendly 'Don't Panic (there will be another classification along in a minute)' and the guide would be perfect!

Ecological Speciation

Nosil, P., 2012.
Oxford University Press, Oxford, UK.
Hardback and paperback, 280 pages.

David L. Hawksworth

Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense de Madrid, Madrid; and Department of Life Sciences, The Natural History Museum, London; d.hawksworth@nhm.ac.uk



Adaptation to different ecological situations, either habitats or host organisms, the consequent or subsequent development of barriers to gene exchange, and often supplemented over time by other distinguishing features by molecular drive, are amongst the most fundamental processes of speciation. Here Patrik Nosil, of the Department of Ecology and Evolutionary Biology of the University of Colorado at Boulder, defines 'ecological speciation' as "the process by which barriers to gene flow evolve between populations as a result of ecologically based divergent selection between environments" (p. 7). He sees speciation as a continuum, and does not dwell on species concepts as "they generally share the characteristic of having stages of divergence along a continuum" (p. 3). Nevertheless, as much of his personal research has been concerned with walking-stick insects of the genus *Timema*, it is perhaps not surprising that it is evident from the examples he discusses that his species concepts are biological rather than phylogenetic. Organisms that do not reproduce sexually are not covered, and the cases discussed are predominantly from insects. I was surprised to see coevolution almost summarily dismissed without any substantive discussion (p. 68), and the only example of an 'arms race' mentioned to be of crossbills and pine (p. 83); perhaps he should have consulted the Systematics Association's Special Volume no. 32 on *Coevolution and Systematics* (1986) which has examples from mutualistic and parasitic symbioses.

On the positive side, there is a chapter on tests of ecological speciation, and here phylogenetic methods have a half-page and are acknowledged of value where experimental data are not available. Hybrids also attracted his attention, especially in relation to *Helianthus* and *Mimulus*. Another aspect that surprised

me was how short the chapter on genomic aspects was, at just 20 pages, where there is much that could have been added from studies in, for example, fungi and the possible role of horizontal gene transfer. One section I did enjoy, however, was that dealing with the geographical dimension, including allopatry, parapatry, and sympatry. The final chapter is especially challenging to workers in experimental ecology in relation to speciation, with a list of 25 “major, yet unresolved, questions” (pp. 216-218), and nine “unresolved hypotheses” (pp. 219-220).

Having had great expectations from the title, I must admit to being rather disappointed by this book

Overall, having had great expectations from the title, I must admit to being rather disappointed by this book. I had hoped it might inspire fresh hypotheses over some cases that my research group in Madrid are currently addressing by molecular systematic methods, but that was not the case. However, the target audience is stated to be graduate level students, academics, and researchers in “ecology, evolutionary biology, and genetics” (back cover), rather than those working in systematics, so perhaps my expectations were unjustified. If a fresh edition is contemplated in the future, however, it would be valuable if the scope could be expanded to increase the size of the audience it would appeal to.

Biogeography of Microscopic Organisms Is Everything Small Everywhere?

Diego Fontaneto, D. (ed.), 201.
Systematics Association Special Volume 79
Cambridge University Press, Cambridge, UK.
Hardback, 384 pages.

Blanca Pérez-Uz

Dept. Microbiología III. Fac. Ciencias Biológicas.
Universidad Complutense de Madrid.

I was (misled by the cover with a nice picture of the ciliate *Stentor*) expecting this book to deal only with protists, and was surprised when I found out that it included all types of prokaryotic and eukaryotic microscopic organisms and all those organisms having microscopic dispersal mechanisms. The common theme is whether small organisms, especially those below 1–2 mm, have a biogeography compared to macroscopic organisms.

This edited book from the Special Volume Series of the Systematics Association is the result of discussions brought up from the symposium on “The importance of

being small: does size matter in biogeography?” held in Leiden last August 2009. It includes chapters dealing with organisms ranging from bacteria to yeasts, protists, fungi, mosses, ferns and micrometazoans, providing a thorough review of the literature on biogeography which I found really useful for teaching purposes, especially at postgraduate levels.

My original expectations were based on the fact that a great deal of controversy and debate has been going on between two different lines of thought on protist diversity and biogeography. Some of these views are based on the old statement “everything is everywhere; the environment selects” (Baas-Becking, 1934; De Wit & Bouvier, 2006), which is referred to in the book as the EiE hypothesis or the cosmopolitan and worldwide distribution model (Fenchel & Finlay, 2006), versus the moderate endemism model as sustained by Foissner (2009), who holds the view that more than half of the protists are still undescribed and defines this as one of the main problems to interpret biogeographic patterns for these organisms (Foissner, 2006). I was, however, puzzled not to find any chapter from Fenchel or Finlay supporting the first hypothesis, at least for unicellular eukaryotes. Although I must admit that some chapters initially seemed to refute the EiE hypothesis, these finally turned out not to embrace either hypothesis, but to consider both hypotheses as possible explanations of the biogeographies of different organisms.

The book is organized in five sections including: the theoretical framework, prokaryotes, unicellular eukaryotes, pluricellular eukaryotes, and processes. I found the repeated description of the EiE hypothesis in most chapters a little bit redundant since this was the focal point of the book. However, different points of view about how the biogeography of microscopic organisms should be approached are shown for the different organisms considered in every chapter. Some chapters also provide new questions or alternative hypotheses to be tested, which I found encouraging for the development of this type of work.

The theoretical framework is established in the first section in two chapters. Chapter 1 (Fontaneto & Brodie) addresses the question: *why biogeography of microorganisms?* In other words, whether microorganisms really do have a biogeography when comparing their distribution patterns to macroscopic organisms. As a summary of what is to be found in the book, a concise review of the following chapters is included, pointing out the different views used for or against the cosmopolitanism model. Special attention is paid to the definition of taxonomic units, niche and spatial patterns. Size is explored in this chapter as a determinant characteristic for microorganisms distribution. However, alternatives are proposed, such as the high potential for dispersal, and the other distribution patterns that can influence their biogeography.

David M. Williams (Chapter 2) critically discusses the EiE proposal from an historical perspective. A specific example of biogeography and evolution of diatoms supporting the endemism model is described later. The conclusion is that, at least in some cases, geological

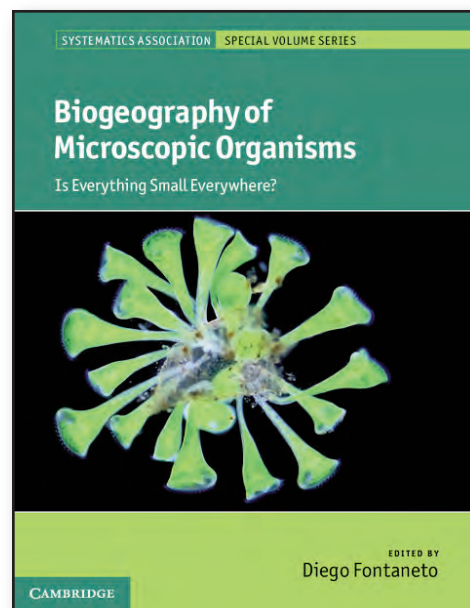
changes might be more important than ecological ones in the distribution patterns of the groups presented. Size, shape and dispersal abilities are considered irrelevant.

The prokaryote biogeographic evidence is included in the second section, in two chapters (Chapters 3 and 4).

Although originally most lines of research suggested a cosmopolitan distribution of prokaryotes (Ramette & Tiedje, 2007), some studies using genetic markers indicate examples of dispersal limitation (Martiny et al., 2011) and some degree of endemism (Bell, 2010). Lacap et al. (Chapter 3) briefly review these methodologies and the actual landscape of prokaryotic biogeography. The starting point is defining the species concept in prokaryotes and the challenges associated with the chosen definition. Although the phylogenetic species concept places limitations on the type of biogeographical interpretations that can be reached, nowadays most ecological studies of prokaryotes are based on rDNA marker analysis, and the advantages or disadvantages of the molecular tools used to estimate prokaryotic diversity are pointed out. The authors also include a summary of literature which shows evidence of non-random environmental distribution in prokaryotic biogeography, indicating taxa-area relationships, environmental heterogeneity patterns, distance-decay patterns and the influence of temporal scales on prokaryotic diversity. Possible lines of biogeographic research are finally outlined proposing different questions for future research.

An example of the biogeography of supposedly niche-restricted extremophiles is described in Chapter 4 (Marchant et al.). This work describes thermophilic bacteria of the genus *Geobacillus*, which have been found in cool environments, also describing possible functional aspects in these environments. Four possible alternative biogeographic hypotheses are tested: random spatial distribution, effects of environmental conditions or the cosmopolitanism hypothesis (EiE), historical influence, and both historical events and recent environmental conditions. They conclude that size alone cannot account for spatial distribution. Other specific attributes are considered, such as tolerance to extreme conditions experienced during passive transport. These might explain a world-wide distribution due to high stress resistance of these species.

The third section on unicellular eukaryotes is treated in 4 chapters, three dealing with protists (Chapters 5, 6 and 7) and a final one with yeasts (Chapter 8). Foissner's chapter (Chapter 5) includes nice examples of protist dispersal mechanisms to support his moderate endemism model. Several plausible explanations are considered: early geological events (not treated in this chapter), differential structure and physiology of resistance stages, and human introductions. Putative percentages are assigned to several dispersal routes for both cosmopolitan and/or restricted distribution. The size of the organism is, however, not considered as an important factor in these processes.



Chapter 6 (Bass & Boenigk) discusses how historical biogeographic structures can vary depending on the methodologies and concepts used to study them. It gives an overview of the main problems in evaluating biogeographical patterns in protists. The authors argue that difficulties are mainly due to the lack of definition of morphospecies and SSU genotyping or any other type of marker used to define taxonomic units. Depending on these, different conclusions about cosmopolitanism or more restricted distributions can be reached. For instance, increasing endemism can be concluded with an increasing phylogenetic resolution. Several suggestions are proposed to overcome these problems, including the adoption of more experimental approaches to test specific ecological hypothesis such as autoecological and dispersal mechanisms in cosmopolitan lineages which might provide information about their dispersal rates and therefore their colonization rates.

Chapter 7 (Heger et al.) considers the diversity and distribution of protists within testate amoebae, with an example in Arcellinida, which shows species with both cosmopolitan and restricted distribution patterns. The authors conclude in this case that molecular tools are increasing the knowledge of diversity, where morphological resolution cannot. However, other factors are considered important in explaining the biogeographic patterns encountered. The type of dispersal, survival mechanisms during transportation and the capacity to develop new populations are some of them. In this case, the presence of hard structures that are well preserved allows biogeographic information to be obtained from palaeoecological data, which is not possible in other microorganisms.

Other eukaryotic microorganisms are treated in Chapter 8 (Ganter), this time dedicated to a group of cactophilic yeasts associated with necrotic tissues of cacti as an example of microorganisms with a restricted distribution and with a high level of endemism. It is argued that the

characteristic distribution pattern is in part maintained by their type of dispersal mechanism (active animal vectoring). Therefore this chapter is a clear example that the EiE hypothesis cannot be considered a universal theory of microbial distribution, although some examples of ubiquitous cactophilic yeasts are also cited.

Pluricellular eukaryotes are treated in section IV, organized in six chapters (9–14). These consider fungi, lichen fungi and lichen photobionts, mosses, ferns and two final chapters on micrometazoans.

Chapter 9 (Gelm) on Fungi uses comparative phylogeographic analysis to estimate intraspecific genetic diversity, genetic population structures and long-distance gene flow in arctic and boreal fungi. The ultimate goal of the author was to evaluate intercontinental migration between arctic-alpine and boreal-temperate fungi and to detect possible biogeographic patterns due to dispersal mechanisms in these groups. The author describes high genetic diversity and efficient long distance dispersal capabilities (especially wind dispersal, sea ice and migratory animals) in arctic species which allow them to track potential niches in these extreme environments.

In the case of lichen fungi and their photobionts treated by Werth in Chapter 10, propagules are the microscopic dispersion mechanisms, providing a high dispersal capability and a characteristically high stress tolerance. Unlike examples in other chapters, lichens show distinct distribution patterns which are favoured by their high dispersal capabilities. Lichen fungi and their photobiont biogeographies and phylogeographies are treated in separate sections. In the case of lichen fungi, the author concludes that both the EiE and vicariance hypotheses have been supported, and it seems that biogeographic history is species-specific. However, in the case of lichen photobionts the geographic patterns are less clear due to taxonomic uncertainties and also to the fact that photobionts can associate with different fungal species.

it provides a way out of the heated
biogeography debate

Some photobionts seem to be ubiquitous while others have restricted distribution patterns, and the lichen symbiosis appears to be associated with environmental gradients.

Chapter 11 (Medina et al.) deals with bryophytes which show a high level of diversity and these are proposed as possible candidates to corroborate the EiE hypothesis due to their wide distribution ranges. The approaches used to test the proposal in this case are both morphological and phylogeographic data. Results shown indicate that bryophytes show both extensive and narrow distribution ranges, although low levels of endemism have been found. Their biogeographies can be explained through long-distance dispersal by wind, continental drift, stepping-stone migration and anthropogenic dispersal, all

processes similar to those affecting flowering plants.

Fern cases are reviewed by Schaefer in Chapter 12. A summary of different studies on phylogenies, distribution ranges and available habitats is presented. As in the case of mosses, ferns are widespread, and seem to fit well with the EiE hypothesis. However, some data indicate dispersal barriers to spore dissemination that could be the important limitations in this group. These are described, to explain rare and localised species distributions.

Chapter 13 (Artois et al.) on microscopic animals is organized into short sections by different authors, each explaining the biogeography of a different group. Many problems in these groups arise from taxonomic uncertainties in their identifications. Gastrotrichs show specific patterns of diversity and distribution, but it is indicated that further molecular studies are necessary to confirm widespread distributions. Rotifers have dormant stages for passive dispersal, and both cosmopolitan and restricted distributions are found in this group. This chapter shows that tardigrades, although generally considered cosmopolitan, show low levels of endemism. A relatively high level of endemism is, however, found at species level without parthenogenesis, or with latent stages (cryptobiosis) that may have a paleogeographic origin.

Other groups, such as micrognathozoans, cycliophorans, loriciferans, kinorhynchs and gnathostomulids, neither support nor reject the EiE hypothesis (cosmopolitanism). The problems in these groups are that taxonomic status and presence of species complexes are still under investigation. All are considered to be undersampled; this is a common problem for the detection of biogeographic patterns.

Nematodes have, however, evident geographic patterns, but it is not clear if dispersion or vicariance is the cause of these. Flatworms also have too few data to infer patterns of distribution. It is possible that cosmopolitan species could represent complexes of sibling species, so molecular work, together with morphology-based taxonomy, is suggested as a way of detecting distribution patterns.

Finally, Chapter 14 (Guil) reviews the available data on micrometazoan molecular information within the EiE framework. Data on tardigrades are used as an example of, at least in this case, both alternatives being feasible; neither can be definitely rejected or accepted.

The last part (V) of the book is dedicated to biogeographic processes and includes three chapters. Chapter 15 (Jenkins et al.) evaluates three factors involved in biogeographic principles for both macro- and microscopic organisms. These factors include abundance, body size and distribution and, finally, effects of niche on spatial distribution and phylogeographies. Conclusions indicate that in fact cosmopolitanism has pointed to new research directions, but at the moment few data allow the evaluation of relationships between abundance, body size and distribution for microbes. Niche constraint is discussed as a fact in microbes, and phylogeographic analysis does not seem to support

microbes not having biogeography.

Chapter 16 (De Meester) approaches the topic from a metacommunity analysis perspective to phylo- and biogeography, indicating in this case that there must be differences between biogeography of macro- and microorganisms related to their dispersal mechanisms and fast population development, especially during asexual reproductive cycles.

The last chapter, 17, focuses on spatial distribution, arguing that there is not much difference between large and small organisms with respect to their biogeography. The differences found are ascribed to their large dispersal potential and their affinity for microhabitats, suggesting new questions for research.

Finally, I have to indicate that from my original expectations, I found this book interesting and enriching since it provides a way out of the heated biogeography debate. Views from different organisms show the same kinds of problem afflicting biogeographic studies in microorganisms, but provide alternative perspectives that might be a starting point for testing different hypotheses that were not considered previously. The reader, however, is led from most discussions to the fact that sampling efforts and analysis of both biotic and abiotic data would be necessary to understand biogeographical patterns. As other research results have pointed out (Foissner, 2006; Finlay & Esteban, 2007; Martiny et al., 2011), both spatial and temporal scales are key for investigating the distribution of microbial biodiversity. I would recommend this book to all those interested in the topic since it presents a thorough review of the literature, which is very useful as a guiding line for future research.

References

- Baas Becking LGM. 1934. *Geobiologie of inleiding tot de milieukunde*. The Hague: W.P. Van Stockum & Zoon.
- Bell T. 2010. Experimental tests of the bacterial distance-decay relationship. *The ISME Journal* 4, 1357-1365.
- De Wit R and Bouvier T. 2006. "Everything is everywhere, but the environment selects"; what did Baas Becking and Beijerinck really say? *Environmental Microbiology* 8 (4): 755-758.
- Fenchel T and Finlay BJ. 2006. The diversity of microbes: resurgence of the phenotype. *Philosophical Transactions of the Royal Society B – Biological Sciences* 361: 1965-1973.
- Finlay BJ and Esteban GF. 2007. Body size and Biogeography. In Hildrew AG, Raffaelli DG and Edmonds-Brown R (eds.), *Body size: the structure and function of aquatic ecosystems*. Cambridge University Press.
- Foissner W. 2006. Biogeography and dispersal of microorganisms: a review emphasizing protists. *Acta Protozoologica* 45: 111-136.
- Foissner W. 2009. Protist diversity and distribution: some basic considerations. In Foissner W and Hawksworth DL (eds.), *Protist Diversity and Geographical Distribution. Topics in Biodiversity and Conservation Series*. Springer.
- Martiny JBH, Eisen J, Penn K, Allison SD and Horner-Devine MC. 2011. Drivers of bacterial β -diversity depend on spatial scale. *Proceedings of the National Academy of Sciences of the United States of America* 108 (19): 7850-7854.
- Ramette A and Tiedje JM. 2007. Biogeography: an emerging cornerstone for understanding prokaryotic diversity, ecology, and evolution. *Microbial Ecology* 53: 197-207.

Inspirations

An interview with Anne Yoder

How would you summarise yourself in the form of a title of a scientific paper?

"Too many datasets, too little time: the irreducible challenge of the 24-hour day"

When did you decide to follow the career path you are on now?

It was the combination of first seeing the amazing diversity of lemurs at the Duke University Primate Center (now, the Duke Lemur Center, which I direct) when I was an undergraduate, and the experience of being a technician at the Smithsonian's Museum of Natural History. The lemurs inspired the organismal focus, and the Smithsonian showed me the day-in day-out work life of a professional evolutionary biologist. Together, the mix was a pretty powerful incentive to go to graduate school for my Ph.D. and to study the evolutionary biology of lemurs.

What are the main goals of your research, and what is your future ambition?

I want to know when lemurs arrived in Madagascar, how they got there, and what they have been doing ever since. I also want to understand their fundamental biology, all the way from genotype to phenotype. This has led me into scientific disciplines such as phylogenetics, divergence time estimation, biogeography, population genetics, ecological niche modelling, disease ecology, and genomics — just to name a few. I am a jack of all trades, and master of none. My ambition is to master at least one of these trades. Right now, that is genomics.

What organisms have you worked on, and which are your favourite organisms and why?

As you may have detected from the above, lemurs are my favourite organisms. To me, the fascination lies in their incredible diversity, as well as in their innate charisma. They really are magnificent.

How many hours per week do you work?

That really depends upon what is going on. When I am trying to stay on top of all three of my work arenas (research, administration, and teaching), it feels like 100, but realistically, it's probably around 60-70 hours per week. I'd like to spend all of it on research.

What percentage of time do you spend on each of your different responsibilities: reading, writing, lab work, field work, teaching, administration, etc.?

That is an impossible question to answer. It changes day to day and week to week. I can tell you that I don't get nearly enough time for reading. Reading papers and analysing data are the two things that I like best about being a professional scientist.

How many students, postdocs, and technicians are in your lab?

At this moment, I have four postdocs and four graduate students in the lab. We'll probably be taking on a couple of undergraduates for the spring term.

What gives you the most satisfaction and frustration in your job?

My greatest satisfaction is being curious about some phenomenon, articulating the questions in such a way that they can be answered, determining the proper type of data and analyses to answer the questions, analysis of the data, seeing the patterns in the data, and then writing a super cool paper to summarise the answers to the questions. This process nearly always leads to more questions, and the process is repeated.



My greatest frustration is not having enough time to do these things.

Could you say something about the importance of international collaborations for your research?

My research programme would never have succeeded without my international collaborations. I have very active collaborations with scholars in the U.K., Germany, Spain, and of course, Madagascar. My Malagasy collaborators are fundamental to everything that I do as a scientist, and as a conservation biologist.

What kind of field work do you do and where has it taken you so far?

I don't do as much fieldwork now as I used to, but all of my fieldwork has occurred in Madagascar. All together, I have spent more than a year of my life in Madagascar.

Have any memorable incidents happened during field collecting?

Every single moment in Madagascar is memorable. It is an incredibly vivid place. When in the forests, you see plants and animals that are almost beyond imagining, and when in the cities and villages, you see poverty that will absolutely break your heart. It can be challenging to emotionally synthesize these contrasts. But all that said, some of the happiest and most peaceful hours and days of my life have been spent in a tent in the wilds of Madagascar.

Oh; I just now thought of a rather fun anecdote: On one expedition, we had to make a river crossing in our jeep, but there was no bridge. A very enterprising local villager had devised a TINY pontoon raft to transport vehicles across the river. The raft was exactly large enough to accommodate one vehicle. Our pilot used two planks of wood, aligned just so, to allow the jeep to drive up onto the raft. It was a very shaky situation, to say the least. As the pilot polled us across the river, he struck up a lively conversation with my Malagasy colleagues. I could tell by the tones of alarm in their voices that the topic was very exciting (the conversation was held, needless to say, in Malagasy, of which I speak very little). When we landed safely on the other side of the river, I asked my colleagues what they had been discussing. In replying, they explained that on the previous day, several local villagers had been attacked and killed by a crocodile. Accordingly, the return trip back across the river on the following day was more than a little harrowing. It is hard to convey just how precarious was the placement of the jeep on that tiny little raft!

Is there any paper or book that has been very influential for your thinking?

I think that I knew that there was no turning back after I read Jane Goodall's book, *In the Shadow of Man*. I read it the second time through instantly after reading it the

first time. I was absolutely enthralled by the idea of being deep in the forest, observing animals that had never before been studied. This was when I was a junior in college. Later, as a graduate student, I couldn't get enough of phylogenetics. I mean seriously; I became completely obsessed with phylogenies and how we estimate them. I guess that Hillis and Moritz (1990) would have been the most influential book of my graduate student years.

Who was the most important mentor in your career?

I have two: my thesis advisor, Kathleen Smith, and my colleague, Michael Donoghue. My career would not have been the same - at all - without their friendship and guidance.

What is the best advice you have ever received?

When studying (and obsessing!) about my qualifying exams, a fellow graduate student (who had successfully passed his) told me: "Anne, if someone asks you a question that you don't know the answer to, say 'I don't know'". That little phrase has come in handy more than a few times!

How many scientific publications do you have at the moment?

68 (including a few that are in review).

Could you nominate any of your discoveries or papers as the most important one, or the one (or several) that you personally like best? Why should people not working on your organisms care about your work?

My two favourite "discoveries", if you can call them that, are that lemurs colonised Madagascar only once, and that there are dozens (and counting) species of mouse lemurs. I think that my work has relevance to fields as disparate as biogeography and Darwinian medicine, not because of anything that I have accomplished in particular, but because of the extraordinary diversity of these primates and the remarkable island on which they have evolved.

You have a lot of papers with co-authors. Is there a particular contribution you generally bring to these papers?

I like to think that I am pretty good at "connecting the dots" by finding the themes among and general implications of discrete observations.

What skills do you think a successful researcher in your discipline must possess?

Determination, passion, creativity, curiosity, persistence, patience, and the ability to accept criticism and use it to improve one's work. A good bottle of wine helps a lot too!

Do you have any tips for students aspiring to a career like yours?

Here is a direct quotation from an email that I sent to my lab group while I was on sabbatical at University College London last spring. This was in response to an advice blog about professional networking that I sharply disagreed with; I wanted to offer an alternative view:

"1) Choose a project that you are really passionate about; otherwise, you will burn out. Graduate school and the years beyond can be arduous and thankless, with rewards coming few and far between at times. If you don't really care about your research, you may well want to give up.

2) Have good and original ideas (yes; this is one of the hardest parts!) When you formulate an idea that you are really excited about, don't just let it sit. Immediately start looking into the literature to see what is known about your idea/project, and what remains to be done. Once you have determined the "what still needs to be done" part, start doing it!! Of course, you'll want to run your ideas past your advisor (while a graduate student), your mentor and peers (while a postdoc), and your colleagues (when a junior faculty member). But assuming that you don't receive outright discouragement, go for it!

3) Write lots of grant proposals once your ideas have gelled, even a little bit. It is good practice, and may even bring in some money! They also make great CV stuffers.

4) WRITE THINGS UP AS YOU GO. I think that you've all heard me say, "until it is published, it is not science".

5) Be generous with your peers and colleagues, and with those who are more junior than you. Do not be jealous and protective of your ideas. As long as you follow the steps above, having good ideas, collecting the data necessary to answer the questions involved, and you write up the results promptly, you will be successful — even if someone else is working on virtually the same thing. By being graceful, generous, and good at what you do, you will come out ahead.

6) The advice offered about avoiding book chapters, etc. is actually quite good. CVs are judged on a number of criteria, and journal quality is definitely a very important one. The others are INDEPENDENCE (as judged by the number of papers on which you are either first or corresponding author, as well as by the distinctiveness of what you are doing) and PRODUCTIVITY (the old "publish early and often").

Anyway, I hope that this is at least a little helpful. To sum it up: have good original ideas, follow up on them, work your ass off, be a good colleague, and get your work published. If you do all of these things, you WILL get a job in academia. The networking, politicking, and developing of strategies will only help you if you have first followed the steps above. Otherwise, they are a complete waste of time."

What do you think are currently the greatest impediments to achieving a successful career in your field, and how could you go about dealing with these?

There simply aren't enough good jobs. There's not much that an individual can do about that other than be the best and most productive scientist that they can possibly be, no matter what is their professional situation. And be sure to have fun along the way! That last point is incredibly important!

New editor for The Systematist

It is with some sadness (and also, perhaps, a sense of relief) that Dr Ronald Jenner is relinquishing the post of Newsletter editor to me. Ronald has been a great inspiration and has produced many high-quality and entertaining editions of the Systematist in the eight years he has held this post.

I am a post-doctoral plant taxonomist at the Royal Botanic Garden Edinburgh. My project involves the systematics and biogeography of the genus *Amomum* Roxb. (Zingiberaceae), a moderately species-rich genus of Southeast Asian gingers. This is my first attempt at editing a magazine and I hope I can maintain the high standards and interesting content that have become the norm for this newsletter under Ronald's editorship!

The Newsletter has changed in appearance over time, but has always remained true to its roots and is driven by the interests and enthusiasm of the members of the Systematics Association. Please do not hesitate to contact me if you have a piece that you think might be interesting to our readers, or if you have comments on any of the articles in the previous edition.

Jane, editor.

Royal Botanic Garden Edinburgh
j.droop@rbge.ac.uk

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

Upcoming lecture

Integrated mediators in domestic and wild species

Julian Hosking

18th April 2013

The 6th Annual Biodiversity Policy Lecture

Linnean Society and Systematics Association

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 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.

For information on membership, contact the Membership Secretary, Dr Jon Bennett (membership@systass.org), St Pauls School, Lonsdale Road, London SW13 9JT, U.K.

The Systematist (ISSN 1744-5701) is the Newsletter of the Systematics Association.

Editors

Dr Ronald Jenner
Department of Zoology
The Natural History Museum
Cromwell Road
London SW7 5BD, UK
(r.jenner@nhm.ac.uk)

Dr Jane Droop
Royal Botanic Garden Edinburgh,
20A Inverleith Row,
Edinburgh EH3 5LR
(j.droop@rbge.ac.uk)

The Systematics Association is Registered Charity Number 270429.

