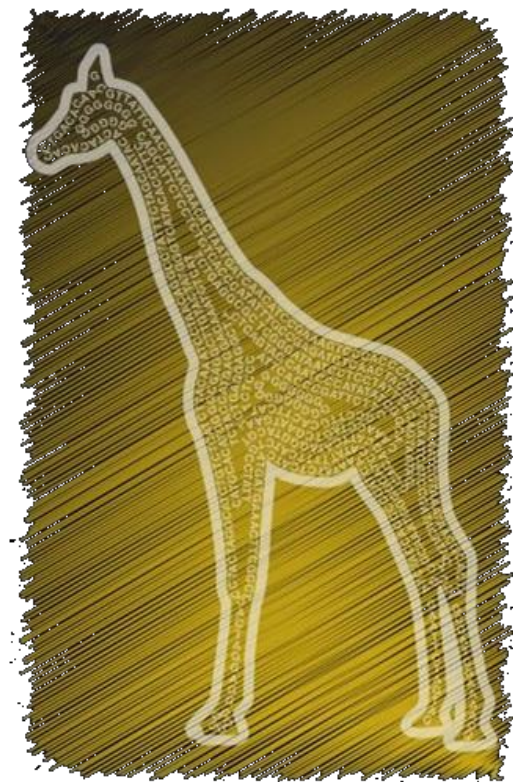


Abstract booklet




SYSTEMATICS

The Science that Underpins Biology

Museum of Natural History, University of Oxford

26-28 August 2015





Thank you for participating in the Systematics Association 2015 biennial conference from the 26-28th August at the Oxford University Museum of Natural History. This booklet, which is being sent to everyone who has registered, contains the latest programme details and abstracts for all talks and posters. We have two keynote speakers, four themed symposia (40 talks in total), over 80 contributed talks and 40 posters. A total of 120 talks and 40 poster contributions. Registration is currently 220, so 70% of all attendees are actively participating at the conference which is something our biennial meetings aim to promote and encourage. For the programme to work successfully and to coordinate with lunch and coffee breaks between three venues it is essential we keep to time. This means that the chair for each session will indicate to all speakers a few minutes from the end of the talk and will ask the speaker to stop after their allotted time which is 15 minutes including questions for contributed talks. So realistically a contributed talk is 12 minutes. The symposium talks are slightly longer and these will also be tightly kept to time. There will be a bell rung 5 minutes before each session is due to start. As you can see from the abstracts the content is broad and encompasses all aspects of contemporary systematics, so at any one time there should be something of interest for most people. Although we are attempting to keep printed paper to a minimum, we will be supplying a hard copy version of the programme at the conference.

Safe journey and very much looking forward to welcoming you to Oxford in a few days time.

Robert Scotland
President of the Systematics Association

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SUMMARY



Oxford University Museum of Natural History

Wednesday, 26th August

08:00 Registration opens

09:30 – 10:30 Keynote speaker: Michael Donoghue. MNH Lecture Theatre.

10:30 – 11:00 Coffee break

11:00 – 13:00

MNH Lecture Theatre. SYMPOSIUM: *The value of long term monitoring plots for plant systematics and ecology in the tropics*.

Pitt Rivers Lecture Theatre. Contributed talks.

13:00 – 14:00 Lunch break

14:00 – 15:30

MNH Lecture Theatre. SYMPOSIUM: *The value of long term monitoring plots for plant systematics and ecology in the tropics* [cont.].

Pitt Rivers Lecture Theatre. Contributed talks.

MNH Annexe. Contributed talks.

15:30 – 16:00 Coffee break

16:00 – 17:00

MNH Lecture Theatre. SYMPOSIUM: *The value of long term monitoring plots for plant systematics and ecology in the tropics* [cont.].

Pitt Rivers Lecture Theatre. Contributed talks.

MNH Annexe. Contributed talks.

18:00 Drinks reception at Oxford Museum of Natural History.

Thursday, 27th August

09:30 – 10:30 Keynote speaker: Peter Holland. MNH Lecture Theatre.

10:30 – 11:00 Coffee break

11:00 – 13:00

MNH Lecture Theatre. SYMPOSIUM: *Rooted in deep time. Palaeontological contributions to systematics*.

Pitt Rivers Lecture Theatre. Contributed talks.

MNH Annexe. Contributed talks.

13:00 – 14:00 Lunch break

14:00 – 15:30

MNH Lecture Theatre. SYMPOSIUM: *Rooted in deep time. Palaeontological contributions to systematics* [cont.].

Pitt Rivers Lecture Theatre. Contributed talks.

MNH Annexe. Contributed talks.

15:30 – 16:00 Coffee break

16:00 – 17:00

Main Lecture Theatre. SYMPOSIUM: *Rooted in deep time. Palaeontological contributions to systematics* [cont.].

Pitt Rivers Lecture Theatre. Contributed talks.

MNH Annexe. Contributed talks

19:00 Drinks reception and banquet (20:00) at Christ Church College.

Friday, 28th August

09:00 – 10:30

MNH Lecture Theatre. SYMPOSIUM: *Accelerating the pace of taxonomy*.

09:30 – 10:30

Pitt Rivers Lecture Theatre. Contributed talks.

10:30 – 11:00 Coffee break

11:00 – 13:00

MNH Lecture Theatre. SYMPOSIUM: *Accelerating the pace of taxonomy* [cont.]

Pitt Rivers Lecture Theatre. Contributed talks.

13:00 – 14:00 Lunch break

14:00 – 15:30

MNH Lecture Theatre. SYMPOSIUM: *Comparative approaches to the origin of biodiversity*.

Pitt Rivers Lecture Theatre. Contributed talks.

15:30 – 16:00 Coffee break

16:00 – 17:15

MNH Lecture Theatre. SYMPOSIUM: *Comparative approaches to the origin of biodiversity* [cont.].

Pitt Rivers Lecture Theatre. Contributed talks.

PROGRAMME



M. Friedman / Museo Civico di Storia Naturale, Verona (Italy)

Wednesday, 26th August

9:30-10:30

MICHAEL DONOGHUE

Yale University, USA

Systematics does underpin biology! Examples from *Viburnum*, a clade of flowering plants

10:30-11:00 — Coffee break

11:00-13:00

MNH LECTURE THEATRE

SYMPOSIUM. THE VALUE OF LONG TERM MONITORING PLOTS FOR PLANT SYSTEMATICS AND ECOLOGY IN THE TROPICS. R. TOBY PENNINGTON & TIM BAKER.

All legumes are not equal: understanding legume dominance in tropical biomes

Lehmann, C.E.R., A. Cabrelli, K. Dexter & R.T. Pennington.

Integrating ecological traits in the analysis of diversification of tropical trees

Baker, T., F. Coelho De Souza & R.T. Pennington.

Phylogeny, functional traits and community assembly on a long term forest plot in Malaysian Borneo

Kaye, M.E.

Using RAINFOR forest plots for estimating phylogenetic diversity of Amazonian tree communities

Honorio Coronado, E.N., K.G. Dexter, R.T. Pennington & RAINFOR Members.

PITT RIVERS LECTURE THEATRE

Missing data and topology in Total Evidence method

Guillerme, T.

The construction and delimitation of morphological characters

Rauhut, O.W.M.

The distribution of convergences on phylogenetic trees

Hughes, M.

4BaSAI – First insights on a new supertree method based on single quartet analyses and its performance with respect to different starting triplets

Kück, P. & C. Groß

Concatabominations: a priori identification of unstable taxa and ineffective overlap in phylogenetic and phylogenomic data.

Wilkinson, M., K. Siu-Ting, W.A. Akanni, D. Pisani & C.J. Creevey

Phylogenetic trees do not reliably predict feature diversity

Scotland, R.W.

13:00-14:00 — Lunch break

14:00-15:30

MNH LECTURE THEATRE

SYMPOSIUM. THE VALUE OF LONG TERM MONITORING PLOTS FOR PLANT SYSTEMATICS AND ECOLOGY IN THE TROPICS [CONT.]. R. TOBY PENNINGTON & TIM BAKER.

Using studies of phylogenetic diversity in tree plots across biomes to understand the general history of biome switching

Dexter, K.G., T. Baker & R.T. Pennington.

Tracking evolutionary diversity, phylogenetic structure, and species interactions across forest dynamics plots using plant DNA barcodes

Kress, W.J.

An Amazonian permanent plot network to quantify multi-trophic diversity across geographic and habitat gradients

Fine, P.V.A., C. Baraloto, G.P.A. Lamarre, I. Mesones & K.G. Peay.

PITT RIVERS LECTURE THEATRE

New inference tools for incorporating the effect of interspecific competition on trait evolution

Drury, J., J. Clavel & H. Morlon.

How should genes and taxa be sampled for phylogenomic analyses with missing data? An empirical study in iguanian lizards

Jeffrey W. Streicher, J.A. Schulte II & J.J. Wiens.

Morphological character analysis and the evolutionary change in development

Assis, L.C.S.

MNH ANNEXE

Phylogeny and evolutionary significance of Cambrian scalidophorans

Ma, X.

Reconstructing relationships of fossil jawless fish (Pteraspidoformes, Heterostraci)

Randle, E. & R. Sansom.

Fossils increase congruence between molecular and morphological hypotheses of spiny-rayed teleost (Acanthomorpha) phylogeny

Davesne, D., C. Gallut, V. Barriel, G. Lecointre, P. Janvier & O. Otero.

15:30-16:00 — Coffee break

16:00-17:00

MNH LECTURE THEATRE

SYMPOSIUM. *THE VALUE OF LONG TERM MONITORING PLOTS FOR PLANT SYSTEMATICS AND ECOLOGY IN THE TROPICS* [CONT.]. R. TOBY PENNINGTON & TIM BAKER.

Maximising synergy between systematics and ecology in the tropics via long-term monitoring plots

Pennington, R.T., T. Baker, E. Honorio Coronado & K. Dexter.

FINAL DISCUSSION

PITT RIVERS LECTURE THEATRE

The origin of annelids: reconciling morphology, fossils and molecules

Parry, L., G.D. Edgecombe & J. Vinther.

A total-evidence approach to dating with fossils

Klopfstein, S.

Experimental analysis of decay biases in the fossil record

Murdock, D.J.E., S.E. Gabbott & M.A. Purnell.

MNH ANNEXE

Evolutionary relationships of the Haplosclerida from Irish and Mediterranean waters

Longakit, M.B.A., J.M. Camacho Aguilar, M.V. Marra, O. Thomas, M. Aude & G. McCormack.

Are data from 18 genes enough to resolve bark and ambrosia beetle phylogeny?

Jordal, B.H., D. Pistone, S. Mugu & J. Gohli.

Species discovery and integrative taxonomy in jellyfishes (Cnidaria, Discomedusae)

Gómez Daglio, L. & M.N. Dawson.

Water mite speciation in Madeira

Valdecasas, A.G. & R. García-Jiménez.

18:00 — Drinks reception at Oxford Museum of Natural History

Thursday, 27th August

9:30-10:30

PETER HOLLAND

University of Oxford, UK

**From genomes to diversity: the prospects and problems of
evo-devo in reverse**

10:30-11:00 — Coffee break

11:00-13:00

MNH LECTURE THEATRE

**SYMPOSIUM. ROOTED IN DEEP TIME: PALAEONTOLOGICAL CONTRIBUTIONS TO
SYSTEMATICS.** ROGER BENSON, MATT FRIEDMAN & PAUL SMITH

Before roots, shoots, and leaves: the early fossil record of plants on land

Kenrick, P.

The tale of mollusc evolution would be fiction if there were no fossils to tell the story

Vinther, J.

The impact of fossils on arthropod phylogeny

Legg, D.A.

Problems and progress in terrestrial arthropod phylogeny

Garwood, R.J.

Palaeontological insights into the assembly of the echinoderm body plan

Rahman, I.A.

PITT RIVERS LECTURE THEATRE

Visual opsin gene evolution and the origin and diversification of snakes

Gower, D.J., B.F. Simões, F.L. Sampaio, N.S. Hart, D.M. Hunt & J.C. Partridge.

Viviparity stimulates diversification in an order of fish

Helmstetter, J.A., A.S.T. Papadopoulos, J. Igea, T.J.M. Van Dooren, A.M. Leroi & V. Savolainen.

Floral symmetry shifted 203 times in angiosperms

Reyes, E., H. Sauquet & S. Nadot.

Segmental allopolyploid origin in *Medicago arborea* (Fabaceae) revealed through next-generation sequencing and allele phasing

Eriksson, J.S.

Niche and trait evolutionary rates are correlated during the Proteaceae radiation

Onstein, R.E.

3D models of ant domatia and phylogenetics reveal how morphological evolution drove the recurrent specialization and dissolution of association in ant/plant symbioses

Chomicki, G. & S.S. Renner.

Testing developmental biology predictions with fossils – phylogeny, dental complexity and evolutionary rates of the Multituberculata

Corfe, I., L. Söilä & J. Jernvall.

Integrating fossils into the coral phylogenetic puzzle

Santodomingo, N., D. Huang, A. Budd & K. Johnson.

MNH ANNEXE

Integrated systematics finally gets a grip on a large genus – *Myrcia* (Myrtaceae)

Lucas, E.

Systematics of *Campylocentrum* (Angraecinae-Orchidaceae)

Pessoa, E.

The evolutionary history of *Cypella* (Iridaceae: Iridoideae) and allied genera: toward a taxonomic revision of Tigridieae based on leaf anatomy, floral morphology and molecular evidences

Chauveau, O., T. Pastori, L. Eggers, J.E.A. Mariath & T.T. Souza-Chies.

Rate heterogeneity and inconsistency of current models in molecular dating – the case of Annonaceae and Lentibulariaceae

Chatrou, L.W. & M.D. Pirie.

Phylogenetic backbone of Annonaceae (Magnoliidae) based on 29 whole-chloroplast sequences

Carrive, L., T. Couvreur, S. Little & H. Sauquet.

The evolutionary trends of genus *Hypochaeris* s.l. (lactuceae, asteraceae)

Ortiz, M.Á., K. Tremetsberger, C.F. Ruas, E. Urtubey, P. López-Sepúlveda, T.F. Stuessy & S. Talavera.

Accelerating integrative taxonomy in the genomics era: RADseq provides unprecedented species resolution in the genus *Lupinus* (Leguminosae)

Atchison, G.W., E. Bridges, S. Orzell, L. Deflorin, N. Contreras, S. Madriñán & C.E. Hughes.

13:00-14:00 — Lunch break

14:00-15:30

MNH LECTURE THEATRE

SYMPOSIUM. ROOTED IN DEEP TIME: PALAEONTOLOGICAL CONTRIBUTIONS TO SYSTEMATICS [CONT.]. ROGER BENSON, MATT FRIEDMAN & PAUL SMITH.

Neopterygii: the iceberg clade

López-Arbarello, A.

Fossils, ecomorphs, and the evolution of squamate reptiles

Müller, J.

The early evolution of Aves

O'Connor, J. & J. Choiniere.

PITT RIVERS LECTURE THEATRE

The taxonomy of endangered, endemic radiations: keeping the tradition alive through local teams and advanced technology

Attwood, S.W.

Drawers full of old, undescribed wasps: integrating curation with taxonomy and ecology

Broad, G.R.

A complementary role for old and new collections in revealing unsuspected species diversity in an endemic gastropod (*Paramelania*) from lake Tanganyika

Todd, J.A., J.D. Burgon & E. Michel.

Combining morphology, molecules, and morphometrics: revising closely related species in the genus *Araniella* (Araneae: Araneidae)

Spasojevic, T., C. Kropf, W. Nentwig & L. Lasut.

Untangling the molecular phylogeny of tapeworms

Waeschenbach, A., J.N. Caira, K. Jensen, J. Mariaux, B.B. Georgiev, T. Scholz, R. Kuchta, J. Brabec, V. Tkach, D.T.J. Littlewood & PBI Consortium.

Evolution of convergent functional systems in a speciose clade of parasitic wasps (Ichneumonidae, Cryptinae)

Santos, B.F.

MNH ANNEXE

Evolution of the leucobryoid morphology in Dicranidae (Bryophyta)

Bonfim, M. & M. Stech.

New ingredients for an old recipe: contribution of the Asian aubergines to a better understanding of the complex evolutionary history of Old World spiny solanums (subg. *Leptostemonum*)

Aubriot, X.

Genome skimming and phylogenomics of *Nicotiana* section *Suaveolentes* (Solanaceae)

Dodsworth, S.

Genetic patterns within the diploid-tetraploid *Arabidopsis arenosa* group

Kolář, F., E. Závěská, G. Fuxová, L. Hyklová, M. Lučanová, A.J. Nagano, H. Kudoh, S. Španiel & K. Marhold.

The recent discovery of four new, narrow endemic plant species within the well-studied *Plantago* genus shows the urgent need for taxonomic research in the Neotropics

Hassemer, G., H.M. Meudt & N. Rønsted.

Phylogenetic reassessment of subfamily Ajugoideae (Lamiaceae)

Moon, H.-K. & S.-P. Hong.

15:30-16:00 — Coffee break

16:00-17:00

MNH LECTURE THEATRE

SYMPOSIUM. ROOTED IN DEEP TIME: PALAEOLOGICAL CONTRIBUTIONS TO SYSTEMATICS [CONT.]. ROGER BENSON, MATT FRIEDMAN & PAUL SMITH.

Delusions in deep time: Is an accurate phylogeny fact or fiction in palaeontology?

Asher, R.

Clade-wide shifts in macroevolutionary dynamics and the role of fossil data

Slater, G.J.

Fossil biases and phylogeny

Sansom, R.S.

PITT RIVERS LECTURE THEATRE

What limits the morphological disparity of clades?

Oyston, J., M. Hughes, P. Wagner, S. Gerber & M. Wills.

Homoplasy and clade support across higher taxa and through research time

Mounce, R., G. Lloyd, M. Wilkinson & M. Wills.

How big is a genus?

Sigwart, J.D. K.D. Bennett, M. Sutton, A. Garbett & B. Picton.

Aphyly and Highly Diverse Organisms

Williams, D. & M. Ebach.

MNH ANNEXE

Joining up for digitisation – a pilot project between Kew and the Natural History Museum London

Phillips, S.W.

Scholarly publishing becomes a part of the research process: Data publication and re-use in the Biodiversity Data Journal

Penev, L., P. Stoev, T. Georgiev, J. Miller & V. Smith.

19:00 — Drinks reception and conference banquet (20:00) at Christ Church College

Friday, 28th August

9:00-10:30

MNH LECTURE THEATRE

SYMPOSIUM. ACCELERATING THE PACE OF TAXONOMY.

ROBERT W. SCOTLAND & QUENTIN WHEELER.

Widespread mistaken identity in tropical plant collections

Goodwin, Z., D.J. Harris, D. Filer, J.R.I. Wood & R.W. Scotland.

Accelerating the global systematic revision of scorpions: Improving accuracy and efficiency with integrative taxonomy, collaboration and cyberinfrastructure

Prendini, L.

The science of species and art of survival

Wheeler, Q.

A game of two halves? Taxonomy as a team sport.... take two.

Knapp, S.

PITT RIVERS LECTURE THEATRE

Areas of endemism under the semantic conception paradigm

Ung, V. & A. Grand.

The Gulf of Gabès (southern Tunisia): Center of Mediterranean endemism or ecophenotypic variations in extreme conditions?

Aissaoui, C., N. Puillandre, M. Oliverio & P. Bouchet.

Why do different oceanic archipelagos harbour contrasting levels of species diversity?

Jones, K., S. Pérez-Espona, A. Reyes-Betancort, D. Pattinson, Juli Caujapé-Castells, S. Hiscock & M. Carine.

Biogeography and the evolution of succulence in the Old World genus *Aloe* L. (Xanthorrhoeaceae)

Grace, O.M.

10:30-11:00 — Coffee break

11:00-13:00

MNH LECTURE THEATRE

SYMPOSIUM. ACCELERATING THE PACE OF TAXONOMY [CONT.].

ROBERT W. SCOTLAND & QUENTIN WHEELER.

Taxonomy on the fast track. Towards more sustainability in biodiversity research

Balke, M., T. von Rintelen & A. Riedel.

Accelerating the pace of taxonomy

Scotland, R.W. & J.R.I. Wood.

Searching for the silver bullet

Harris, D.

Developing a workflow for accelerating cumulative taxon descriptions, from fieldwork to publication.

Polaszek, A., L. Penev & S. Schmidt.

Nothing in taxonomy makes sense except in the light of Open Access

Agosti, D.

Mowing the lawn during an identity crisis: do well known groups need taxonomists?

Vorontsova, M.S.

PITT RIVERS LECTURE THEATRE

No ecological opportunity on a continental scale? Diversification and life-history evolution of African true toads (Anura: Bufonidae)

Liedtke, H.C.

Long-term decline in dinosaur speciation rates

Sakamoto, M., M. Benton & C. Venditti.

Testing for convergent evolution and adaptive radiations: the austral danthonioid grass radiations

Linder, H.P. & Y. Bouchenak-Khelladi.

Cryptic morphological characters and how they are changing the way we interpret plant taxonomy and evolution

Vasconcelos, T.N.C., E.J. Lucas & G. Prenner.

The effects of pollination and range shifts on the diversification of the tribe Antirrhineae

Ogutcen, E., J. Theriault, D.B. King & J.C. Vamosi.

Chameleons through time and space: extinction or adaptation?

Tolley, K.A.

Macroevolution of giant water scavenger beetles in the Cretaceous and Cenozoic

Toussaint, E.F.A.

The key role of systematics in conservation assessments of butterflies

Huertas, B.

13:00-14:00 — Lunch break

14:00-15:30

MNH LECTURE THEATRE

SYMPOSIUM. COMPARATIVE APPROACHES TO THE ORIGIN OF BIODIVERSITY.

COLIN E. HUGHES & MATT FRIEDMAN.

Competition and dispersal in clade diversification dynamics

Purvis, A. S. Echevarría-Londoño & T.H.G. Ezard.

New phylogenetic comparative methods and their application to our understanding of phenotypic evolution and diversification

Morlon, H.

Inferring island biogeography from phylogenetic data

Etienne, R.

Ecological release, perenniality and evolutionary plant radiations on island systems

Atchinson, G., N.M. Nürk & C.E. Hughes.

Scales of phenotypic diversification: exploring unconventional radiations in fishes

Friedman, M., J.T. Clarke & R.C. Harrington.

PITT RIVERS LECTURE THEATRE

Are coral reefs driving rates of diversification in jacks and allies (Carangoidei)?

Santini, F.

The shell beds of Lake Tanganyika: palaeoecology, patchy ecosystems and divergence in a rift lake

Michel, E., J.A. Todd, J. Tarrant & M.J. Soreghan.

A preliminary phylogeny for Upper Guinean angiosperms

Marshall, C.A.M.

Cave floras in SWChina: unexplored marginal biomes rich in diversity and undervalued for conservation

Monro, A., W. Yigang, F. Longfei & N. Bystrakova.

DNA barcoding and community structure assessment of a mixed dipterocarp forest in Brunei Darussalam

Heckenhauer, J., M. Barfuss, K. Abu Salim, O. Paun, M. Chase, T. Pennington & R. Samuel.

Edaphic determinism on tree community assemblages at a landscape scale in the tropical forests of South Cameroon

Vleminckx, J.

15:30-16:00 — Coffee break

16:00-17:15

MNH LECTURE THEATRE

SYMPOSIUM. COMPARATIVE APPROACHES TO THE ORIGIN OF BIODIVERSITY [CONT.].

COLIN E. HUGHES & MATT FRIEDMAN.

Did predation shape fish? Disentangling the complex drivers of fish body form diversity

Price, S.A.

Phylogenetic rates, adaptive evolution and evolutionary trends

Venditti, C.

Macroevolutionary divergence of bird bills

Thomas, G.H.

Extraordinary rates of evolution are common

Pagel, M.

PITT RIVERS LECTURE THEATRE

From medicinal use to phylogenetic prediction in drug discovery in the genus *Euphorbia* L.: classification of medicinal uses have major influence on data interpretation

Ernst, M., C.H. Saslis-Lagoudakis, O.M. Grace, N. Nilsson, H. Toft Simonsen, J.W. Horn & N. Rønsted.

The quest for Cinchona – a phylogenetic tale

Rønsted, N. C. Maldonado, C. Cornett, S.H. Hansen, C. Persson & A. Antonelli.

Traits involved in human selection of useful South American palms

Cámara-Leret, R., S. Fuarby, M.J. Macía, H. Balslev, B. Gödel, W.D. Kissling, N. Paniagua-Zambrana, N. Rønsted, J.-C. Svenning & C.H. Saslis-Lagoudakis.

Neotropikey – identification resources

Klitgaard, B., N. Biggs, J. Bishop, S. Edwards, S. Frisby, A. Haigh / W. Milliken.

KEYNOTE SPEAKERS



Oxford University Museum of Natural History

MICHAEL DONOGHUE

Department of Ecology and Evolutionary Biology, Yale University,
PO Box 208105 New Haven, CT 06520-8105 USA.

Systematics does underpin biology! Examples from *Viburnum*, a clade of flowering plants

Using real examples from our work on the flowering plant clade viburnum, I will highlight how a long-term commitment to understanding the systematics/phylogeny of a group of organisms can promote a wide range of down-stream analyses. Specifically, our improved knowledge of *Viburnum* has recently led to insights on (1) co-evolution, (2) leaf form in relation to phenology and biome shifting, (3) leaf anatomy in relation to photosynthesis and hydraulics, (4) biogeography and diversification, and, most recently, (5) replicated ecological speciation. I will briefly contrast this comprehensive "local" approach with the use of "global" megaphylogenies, arguing that studies based on deep knowledge of organisms will likely yield the more satisfying and lasting results.

PETER HOLLAND

Department of Zoology, University of Oxford, South Parks Road OX1 3PS Oxford, UK.

From genomes to diversity: the prospects and problems of evo-devo in reverse

The discovery of developmentally-important genes paved the way for a science in which embryonic development could be compared between divergent evolutionary lineages at the molecular level. This science, evolutionary developmental biology (evo-devo for short), aims to bridge the gap between molecular evolution and the evolution of body form. The traditional evo-devo approach focuses on a morphological or developmental character (such as segmentation, eyes, limbs, spines, colour patterns etc), and seeks to track down molecular changes that underpin evolutionary change to the character. In other words, it goes from phenotype to genotype.

There have been some impressive success stories. The 'reverse' evo-devo approach starts with molecular changes found by comparing genomes, and then asks whether they have contributed to phenotypic evolution. I will explore this approach using examples from homeobox genes and microRNAs, from Lepidoptera and other animals. The approach focuses attention on gene duplication, novelty and gene loss, as part of a suite of genetic changes that must ultimately contribute to organismal diversity.

SYMPOSIA

MUSEUM OF NATURAL HISTORY

LECTURE THEATRE

(In the programmed order)



Mark Waters

SYMPOSIUM — THE VALUE OF LONG TERM MONITORING PLOTS FOR PLANT SYSTEMATICS AND ECOLOGY IN THE TROPICS.

Ecologists have established a large number of permanent inventory plots across the tropics, focussed on understanding the controls of ecosystem structure and function, or maintenance of alpha diversity. These plots offer a great deal to systematists for completing the biotic inventory of the tropics, both in terms of species discovery and understanding distributions. Such links would also benefit ecologists, as once the organisms in these plots are described and identified consistently among sites, a wide range of other questions, such as the controls of beta diversity, can be addressed. Finally, a suite of new, interdisciplinary questions may emerge from such collaborations: on the soils, climate, and traits of plants, they represent fertile ground for studies of evolutionary ecology and biogeography.

All legumes are not equal: understanding legume dominance in tropical biomes

Caroline E.R. Lehmann¹, Abigail Cabrelli¹, Kyle Dexter^{1, 2} & R. Toby Pennington²

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Legumes (Leguminosae or Fabaceae), which evolved 60 million years ago, are one of the most diverse and ecologically successful families of flowering plants, and woody legumes are a particularly important component of many tropical biomes. Legumes are well known for an ability to fix nitrogen via root symbioses, a key innovation in plant function over the evolutionary history of plants thought to be fundamental in explaining their ecological success. However, not all legume species are able to nodulate and fix nitrogen. Further, legumes vary widely in their abundance and diversity across the tropics. Here, via a synthesis of data from 1304 plot inventories across forests and savannas of tropical Africa, Australia, Asia and South America we explore how N-fixation via nodulation is related to legume dominance across different biomes and environmental gradients. We examine dominance both in terms of species richness and biomass (using tree basal area as a proxy for woody biomass). On most continents, nodulating legumes are dominant in savanna ecosystems, especially arid savannas, whose woody plants communities are comprised almost entirely of nodulating legumes. Africa shows the highest dominance of both nodulating and nonnodulating legumes, although in general, continent is a more important predictor of dominance in non-nodulating legumes than in nodulating legumes. We suggest that the legacy of historical biogeography is more marked in the distribution of non-nodulating legumes, perhaps due to competitive exclusion by other, already established plant taxa in regions such as Australasia where Myrtaceae dominate. In contrast, we theorise that the functional innovation of nodulating legumes enables these taxa to dominate disturbance prone and arid systems where rapid rates of plant growth facilitate competitive success in stressful environments. In contrast to open

and arid savannas, nodulating legumes are less abundant in closed canopy forest environments, where legumes, while rich in species, do not show such pervasive dominance of biomass.

Integrating ecological traits in the analysis of diversification of tropical trees

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Permanent plots offer a range of ecological data concerning the distribution, abundance and size of tropical tree species that may be useful for understanding the evolutionary history of tropical biomes. However, a key advantage of long-term, re-censused plots is that they also yield data on how growth rates and survivorship vary among species. These demographic parameters may be particularly important for understanding why diversification rates vary among lineages and, as a result, why diversity varies among forests. We discuss the value of distributed plot networks for distinguishing the intrinsic, demographic traits of different species from the effect of environmental variation. These traits have significant phylogenetic signal and therefore the potential to influence the trajectory of diversification in different lineages. We demonstrate how demographic traits are related to the species richness and diversification rates of Amazonian clades of tropical trees, and discuss how an interaction between the intrinsic, ecological traits of different lineages and the particular geological context of western Amazonia may have created the hyperdiverse forests of this region.

Phylogeny, functional traits and community assembly on a long term forest plot in Malaysian Borneo

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Understanding the phylogenetic structure of an ecological community can be of great importance when trying to identify and understand the processes and mechanisms that drive community assembly. Niche assembly processes assume that species functional traits facilitate adaptation of species to local environments and determine the outcome of interactions among species. However these traits are an emergent consequence of the evolutionary history of a species and its close relatives, and so we predict that the phylogenetic structure of a community will influence, and be influenced by, the assembly mechanisms acting upon it. To test this we compared the phylogenetic structure of small communities with assemblages drawn at random from the meta-community of trees growing on the long-term CTFS Forest Dynamics

Plot at Danum Valley in Sabah, Malaysia. Using this approach we quantified phylogenetic overdispersion and clustering and then combined these results with functional trait data and environmental variables to infer the relative importance of contrasting community assembly processes. Community level studies in tropical rainforests are constrained by the high number and diversity of species, and the low resolution of taxonomic understanding in many lineages. In this study we demonstrate the value of a DNA bar-coding approach to developing a community scale phylogeny at a site where representation of the tree flora in herbaria was limited. Studies such as this emphasise the value of creating and maintaining long term forest plots, especially in high biodiversity areas.

Using RAINFOR forest plots for estimating phylogenetic diversity of Amazonian tree communities

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Phylogenetic diversity (PD) metrics are used to quantify the lineage diversity of communities and to provide information about the evolutionary history and conservation significance of sites. We examine variation in the PD of 283 ~1 ha Amazonian forest communities growing (i) on substrates of varying geological age; and (ii) in environments with varying ecophysiological barriers to growth. We evaluated PD as the total phylogenetic branch length across species in each plot (PDss), the mean pairwise phylogenetic distance between species (MPD), the mean nearest taxon distance (MNTD) and their equivalents standardised for species richness (ses.PDss, ses.MPD, ses.MNTD). Our results show that some PD metrics are positively (PDss) or negatively (MNTD) correlated with species richness (SR), while others (MPD and ses.MPD) are correlated with how evenly taxa are distributed among the three principal angiosperm clades. We find that the youngest (western Amazonia) and oldest substrates (Brazilian and Guiana Shields) have the greatest lineage diversity in communities indicated by the highest ses.PDss and ses.MNTD values, which is maybe related to differences in resource availability and substrate age. Meanwhile, forests on white-sands and seasonally dry tropical forests are dominated by close relatives from fewer lineages indicated by the lowest PD values, as evaluated by any metric, perhaps reflecting ecophysiological barriers that are difficult to surmount evolutionarily. Because MPD and ses.MPD do not reflect lineage diversity per se, we suggest that PDss, ses.PDss and ses.MNTD may be the most useful diversity metrics for setting large-scale conservation priorities.

Using studies of phylogenetic diversity in tree plots across biomes to understand the general history of biome switching

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Recent species-level phylogenetic studies have documented intriguing patterns of biome switching across tropical biomes. For example, many plant lineages found in wet forests and seasonally dry tropical forests (SDTFs) seem to have switched into savanna environments within the last 10 million years. Meanwhile, few lineages show switching into SDTFs during that time, i.e. most SDTF clades seem to be older. However, in the absence of well-resolved, species-level phylogenies covering all angiosperms, it is difficult to know the generality of this pattern. An alternative approach to elucidating general patterns of biome switching centres around evaluation of phylogenetic alpha diversity in communities across different biomes. As measures of phylogenetic alpha diversity are highly sensitive to sampling effects, standardised tree plots provide ideal data for its quantification. Here, we use tree plot data from across the three major biomes in lowland tropical South America (wet forest, SDTF, and savanna) to provide insights into the general history of biome switching.


Tracking evolutionary diversity, phylogenetic structure, and species interactions across forest dynamics plots using plant DNA barcodes

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Forest dynamics plots located in both primary and secondary forested zones provide natural laboratories for investigations of the ecological and evolutionary processes controlling species interactions and assembly into communities. DNA barcodes for both plants and animals are an essential aide in understanding these processes. A mega-phylogeny of 1,347 species of trees across 15 forest dynamics plots in the Smithsonian ForestGEO network was constructed using plant DNA barcode sequence data (rbcL, matK and psbA-trnH) to compare evolutionary structure in tree communities across latitudinal and longitudinal gradients. Three phylogenetic distance metrics that are commonly used to infer assembly processes were estimated for each plot (Phylogenetic Distance [PD], Mean Phylogenetic Distance [MPD], and Mean Nearest Taxon Distance [MNTD]). Overall, evolutionary relationships were highly resolved across the DNA barcode-based mega-phylogeny, and phylogenetic resolution for each community plot was improved when estimated within the context of the mega-phylogeny. The comparisons among plots based on the mega-phylogeny demonstrated that the communities in the ForestGEO plots in general appear to be assemblages of more



closely related species than expected by chance. In addition differentiation among communities is very low, which suggests a more substantial floristic connection among communities than previously thought. The use of DNA barcodes for estimating community phylogenies can also inform conservation priorities across habitats and landscapes. Moreover, intricate ecological interactions between plants and herbivores in these plots can be revealed with DNA barcode data for both partners. New investigations of insect and mammalian herbivores provide insights into the levels of specialization and generalization of these interactions.

An Amazonian permanent plot network to quantify multi-trophic diversity across geographic and habitat gradients

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Since 2007, we have installed 74 0.5-ha modified Gentry plots in Peru and French Guiana, and we are currently installing 27 more in Brazil. These 101 permanent plots from three geographic regions across 2500 km of Amazonia sample the three major habitats in each region (white-sand, terra firme clay, and seasonally-flooded forests). Plots representing each of the three habitats are sampled within replicated geographic blocks, allowing us to disentangle geographic and environmental drivers of forest composition from biotic interactions. To enable accurate comparison of plant communities across regions, we standardize botanical determinations of project type specimens from across regions by gathering together all vouchers at the Missouri Botanical Garden. Eleven lineages have also been DNA barcoded. Preliminary results from the existing 74 plots include more than 2200 tree species, and yet only 6% species overlap between Peru and French Guiana. In addition we find many divergent habitat specialists within many genera. Thus, we find strong patterns of plant beta-diversity across habitats and regions within Amazonia. In the same plots, we are quantifying arthropod and microbial diversity. We employ flight interception traps, aerial bait traps, light traps and both hand and net collecting which permits standardized sampling of the most important arthropod guilds. For microbes, we collect soil samples in all plots and conduct next-generation sequencing, focusing on fungal pathogens and oomycetes. We also collect roots from the 11 focal lineages to study mycorrhizal association. This work allows us to investigate the degree to which natural enemies are host specialists, the extent to which natural enemy diversity and host plant diversity is correlated, and whether relative abundance of host plants is related to natural enemy specialization or diversity. These data are critical to test hypotheses that relate natural enemy abundance and diversity to the evolution and maintenance of tropical tree diversity.

Maximising synergy between systematics and ecology in the tropics via long-term monitoring plots

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The premise of this symposium is that there is much to be gained by closer collaboration between ecologists and systematists working in tropical forests via mutual studies based around long-term permanent inventory plots. For systematics, we argue that permanent plots have a great deal to offer in terms of completing the biotic inventory of the tropics in terms of species discovery and understanding distributions. For ecology and evolutionary biology, we examine this premise critically, by asking which problems can only be solved by obtaining the accurate species identifications that taxonomic specialists can provide. For example, while estimates of diversity do not require accurate species names per se, estimating floristic similarity among sites and changes over time would greatly benefit from closer collaboration between ecologists and taxonomic specialists to confirm species identities amongst sites in taxonomically difficult groups. Accurate determinations are even more critical to link ecological plot data effectively with phylogenetic information or trait data which may have been collected at other sites. Other problems of evolutionary ecology such as studying diversification and speciation also require accurate identifications. Given the importance of naming species for many areas of 21st century ecology, and the benefits to taxonomy of working in permanent ecological plots, we explore practical issues of collaboration between systematists and ecologists. For example, should herbaria be archiving vouchers from permanent plots more actively, and can ecologists benefit from the experience of the systematics community in handling and mobilising specimen data online?

SYMPOSIUM — ROOTED IN DEEP TIME: PALEONTOLOGICAL CONTRIBUTIONS TO SYSTEMATICS

Palaeontology provides unique data with a bearing on the evolutionary history of biological lineages. This symposium will survey the Tree of Life, examining the impact that fossils make on hypothesized relationships, sequences of character change, and timings of major divergences in a series of major clades ranging from single-celled plankton to mammals. Specifically, this symposium sets out to examine: (i) the ways in which extreme variability of the fossil record across biological groups influences approaches to systematic questions in different clades; (ii) the way in which incomplete or biased preservation of biological structures might bias phylogenetic inference; (iii) the relevance of palaeontological data for exposing instances of homoplasy in extant groups that might otherwise lead to erroneous systematic hypotheses; (iv) the role of fossils in atomizing sequences of character change leading to modern clades. Apart from exploring these major themes, our symposium sets out to summarize relationships and evolutionary history for conspicuous branches of the Tree of Life in light of fossils, paralleling similar efforts completed largely or exclusively with recent data.

Before roots, shoots, and leaves: the early fossil record of plants on land

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Viridiplantae (green plants) is a clade containing possibly as many as 500,000 living species of green algae and land plants. Fossil evidence for the clade dates to at least 750 million years, but divergence time estimates based on molecular data hint at a true age that may exceed one billion years. As organisms, Viridiplantae vary enormously in size and complexity. In the context of phylogenetics, fossils contribute most in those clades which have evolved large and complex forms that are rich in morphology and robust in nature (e.g., calcareous green algae, land plants). Among the land plants, the fossil record is biased towards the larger vascular plants of lowland riparian habitats, and it is also heavily influenced by major changes in the rock record operating at a global scale. Because of their modular growth forms and their modes of dispersal and reproduction, plants fragment into numerous diverse parts presenting challenges to the systematist. Yet, exceptional preservation frequently encountered in permineralized fossils can yield information of a quality that outstrips that known for living relatives, frequently demanding parallel comparative studies of modern materials. The plant fossil record has been of greatest value in understanding the evolution of major organ systems in vascular plants during the Palaeozoic Era, including roots, shoots, leaves, vascular system and reproductive structures such as seeds. Here it is helping us to understand how key plant organs evolved from precursor structures, to disentangle homology from homoplasy, to better understand the evolution of the

plant life cycle, and to learn about the co-evolution of plants and their fungal symbionts.

The tale of mollusc evolution would be fiction if there were no fossils to tell the story

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Reconstructing evolution is founded on evolutionary trees, which help polarizing what is plesiomorphic, autapomorphic or convergent. Using comparative methods, it is even possible to predict the ancestral condition in parsimony or likelihood frameworks. These methods rely on using branch lengths and paraphyletic characters. However, more often than we prefer the morphology of extant organisms are so derived that it would be impossible to reliably detect homology. Molluscs are characterized by having a foot, radula, mantle and shell plates. However more often than desired these structures have been secondarily lost. Thus, no single extant group really represents the ancestral morphology for molluscs. Until recently it was thought that the vermiform aplacophorans were the most primitive members of molluscs due to their lack of shell plates and a foot. However, several discoveries show that they are in fact derived and secondarily simplified. A number of bizarre molluscan fossil discoveries help reconstruct the evolution of chitons and aplacophorans. Cephalopods are another classic example in which several fossils portray their evolution from shell bearing, slug-like nektonic forms to soft bodied and agile predators with jet propulsion and adaptive colouration.

Molluscs are therefore a classic example of why fossils matter. A clear picture of their evolution cannot be deduced from the extant diversity, and it can be argued that this would apply to any extant groups, which therefore raises concern for groups with a really poor fossil record.


The impact of fossils on arthropod phylogeny

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Arthropods constitute the most species rich phylum on Earth today. Constituting five main groups: the pycnogonids (sea spiders), euchelicerates (horseshoe crabs and arachnids), myriapods (centipedes and millipedes), hexapods (insects and their flightless kin), and crustaceans (crabs, barnacles, ostracods, etc.), their diversity and disparity is unrivalled by any other phylum. This great diversity, however, has made resolving the interrelationships of its constituent groups particularly difficult, with con-



flicting hypotheses commonly resolved using different methods. Whereas results produced using molecular data are tend to result congruent topologies, morphological data has produced widely conflicting results. One of the main reasons for such conflicting results is the difficulty in comparing extant taxa from widely disparate subgroups. The fossil record, and molecular clock analyses, indicate that the five main subgroups originated and diverged over 500 million years ago, allowing for a lot of time for ancestral characteristics to be overprinted by subsequent evolution. As a means of addressing this problem an extensive morphological data set composed primarily of fossil arthropods was constructed and analysed using general parsimony with implied character weighting. The inclusion of fossil was shown to increase congruence between those topologies produced using morphological and molecular techniques, thus emphasising the impact and importance of fossil for understanding relationships amongst deeply branching nodes in the tree of life.

Problems and progress in terrestrial arthropod phylogeny

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Terrestrial arthropods include the most abundant and species rich animal lineages. They represent the first known land animals, and have been an integral part of ecosystems on land since moving from aquatic environments. Building a consensus on the relationships between, and phylogeny of, myriapods, hexapods, and arachnids, has remained challenging. The enormous success of the groups, and concomitant morphological disparity, coupled with the convergent acquisition of numerous characters associated with a terrestrial mode of life, adds ambiguity to morphological analyses. Because terrestrial arthropod also represent ancient and rapid radiations, molecular analyses can struggle to build reliable phylogenies. This talk highlights these issues, and presents recent progress overcoming them. It provides an overview of the phylogeny within terrestrial arthropod groups, and underscore areas where no consensus exists. A key conclusion of the talk is that fossil evidence can provide key evidence for the resolution of these problematic nodes. Molecular clock estimates suggest terrestrialisation significantly predates the first body fossils of land animals. Renewed efforts in the search for terrestrial arthropods within Cambro-Ordovician deposits will provide morphologies closer to the deep events of cladogenesis. These could shed light on the earliest branching events in terrestrial arthropod trees, and also on evolutionary novelties such as insect wings and the production of silk in spiders.

Palaeontological insights into the assembly of the echinoderm body plan

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Echinoderms are a diverse and successful group of marine invertebrates, with around 10,000 extant species belonging to five major groups (including starfish and sea urchins), as well as a rich fossil history that dates back to around 520 million years ago. They are unique among bilaterians in exhibiting pentaradial (five-fold) symmetry as adults, having departed radically from the bilaterally symmetrical ancestral body plan. Deciphering the evolutionary emergence of echinoderms therefore requires a detailed understanding of their early fossil record, which documents some of the fundamental transitions in the assembly of the modern body plan. Reconstructing the phylogenetic relationships of key fossil taxa reveals that echinoderms passed through successive bilateral, asymmetrical, triradial and pentaradial stages. Moreover, the sequence of character changes leading to modern forms can be uncovered; an echinoderm-type water vascular system evolved after the acquisition of a stereom skeleton, but before radial symmetry.

Neopterygii: the iceberg clade

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Neopterygii is an ancient clade of vertebrates that has evolved through the Mesozoic and Cenozoic. It constitutes a very interesting case of an evolutionary radiation because of the tremendous asymmetry in the amount of living representatives of its main lineages: Holostei (Halecomorphi and Ginglymodi; 8 species), versus Teleostei (> 32,000 species). During the Triassic-Jurassic however, the diversity of holosteans largely exceeds that of teleosts.

In recent decades, there has been a significant focus on molecular studies in actinopterygian systematics, which led to new insights, but also to a considerable neglect of anatomical studies. Due to the paucity of detailed descriptions, the morphological variability of fossil neopterygians is rather poorly known and, thus, with a few exceptions, it has had little influence in systematics. Moreover, a few paradigms in neopterygian systematics have biased the study of fossils towards the search of a limited number of anatomical features that have been assumed to be apomorphic of a given clade, and the monophyly of the main neopterygean clades has never been thoroughly tested.

Luckily however, analysing the limited available anatomical information allows to postulate a few general hypotheses about the tempo and mode of the evolution-



ary radiation of the early representatives of this long lasting clade. It furthermore reveals great morphological variability and high levels of homoplasy among basal neopterygians, which remains hidden when only looking at the living forms, because, in addition to the huge bias in the amount of extant teleosts in respect to other living neopterygians, the few living holosteans are morphologically very derived when compared to the basal forms and are thus of limited value to understand morphological evolution at the base of Neopterygii.

Fossils, ecomorphs, and the evolution of squamate reptiles

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With more than 9000 living species, squamate reptiles constitute a significant component of today's vertebrate diversity. The phylogenetic relationships among the major clades have long remained contentious, and there is an especially strong conflict between the molecular and morphological hypotheses of squamate relationships. For example, molecular results favour a sister group relationship between geckos and most other squamates, whereas morphological studies propose iguanian lizards as sister to all remaining taxa. A major problem of morphological studies of squamate relationships is the high degree of homoplasy, which often obscures the phylogenetic signal. This is well evidenced by the many body-elongated and limb-reduced fossorial taxa, which seemingly evolved multiple times independently but have traditionally been difficult to place phylogenetically. Our own research has shown that fossil taxa can be important for the understanding of convergent squamate ecomorphologies, as they sometimes display "transitional" morphologies that no longer occur in the present. However, integrating fossil squamates into studies of extant forms is still hampered by the insufficient knowledge of extant squamate phenotypes. For many larger clades, only a few taxa have been studied in more detail, whereas the majority of species is lacking a detailed anatomical assessment. Also, there have been only a few studies that address the relationship between ecology, development, and phenotype at a larger macroevolutionary scale. Without such knowledge it will remain difficult to understand squamate (eco)morphological evolution and to compile reasonable morphological and fossil datasets that can be used in conjunction with, or complementary to, molecular data. For a better integration of past and present it is therefore necessary to increase our phenotypic knowledge of modern taxa, and investigate the different extant morphologies in closer relation to ecology and development.

The early evolution of Aves

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The Jehol Biota preserves the second-oldest and most diverse Mesozoic avifauna. The full phylogenetic spectrum of Early Cretaceous birds is represented, including long boney-tailed birds only more derived than Archaeopteryx, the basal-most pygostylians, and the oldest record of Enantiornithes (the dominant clade of Cretaceous birds) and their sister group, the Ornithuromorpha (containing crown birds). The volcano-lacustrine depositional environment of the Jehol represents a unique taphonomic window revealing more than just species richness, also recording aspects of reproduction and behavior, diet, integument, and other indicators of the biology of these early birds and their closest dinosaurian relatives. Fossils from the Jehol, as well as the Late Jurassic Yanliao Biota, have made it clear that volant activity did not evolve once, but multiple times within Maniraptora and that feathered forelimbs evolved initially for some purpose other than flight. The inter-relationships of avian clades are poorly resolved and their closest relative is unknown, obscured by the rampant homoplasy that characterizes avian origins. Previous phylogenetic analyses targeted at Mesozoic birds used 'Dromaeosauridae' as the outgroup and thus were unable to test alternative hypotheses regarding the avian sister taxon or the avian status of controversial taxa. Conversely, studies investigating maniraptoran relationships include a paltry number of stem birds and relevant character statements. The analysis presented here includes a nearly complete sample of Mesozoic bird taxa and a multilayered outgroup comprising several derived maniraptoran clades. Furthermore, our dataset outlines clear homology statements and ontologies between 'bird' characters and their non-avian theropod equivalents. It thus represents the most comprehensive attempt to resolve avian origins and relationships to date, and will enable more confident estimation of key parameters in the evolution of birds, such as disparity.

Delusions in deep time: is an accurate phylogeny fact or fiction in palaeontology?

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Modern vertebrate phylogeny is now better known than ever. The best and biggest datasets are generally available only for modern taxa; for fossils, we usually have little or no access to information beyond their bones and teeth. Since the processes

of decay are known to affect certain aspects of anatomy more than others, and if most species ever to have lived on Earth are preserved only as fossils, to what extent is it possible to have confidence in phylogenetic analyses that include fossils?

Here, I apply artificial extinction to test if palaeontological data accurately place species with known phylogenetic affinities. This method takes a living species (subject) and degrades its data to correspond to those for a given fossil (template). Subjects are extant, known for diverse data types, and have well-corroborated phylogenetic positions. Templates are extinct and may be known from a fraction of their overall anatomy. Artificial extinction retains the subject taxon's character states but distributes missing data according to the template. The extent to which characters from a template succeed in placing subjects in well-corroborated phylogenetic positions provides a heuristic, quantifiable basis upon which to assess the phylogenetic information content of fossils. Morphological characters available for primates, tenrecs, ruminants, and mammals generally recover more accurate trees than the same analyses using randomized character states, although smaller datasets and the least well-preserved fossils may overlap the 95% confidence intervals of trees generated using randomized states. Accuracy in these cases does not guarantee that of others, and any kind of small dataset prone to bias is potentially more misleading than most large datasets. However, these results suggest that palaeontological filters are neither ubiquitous nor overly pernicious in their effects on the mammalian Tree of Life.


Clade-wide shifts in macroevolutionary dynamics and the role of fossil data

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Understanding macroevolutionary dynamics through time is a common goal of palaeobiologists and neontologists. Both have long recognized the need to frame hypotheses in a phylogenetic context, and the past decade has witnessed tremendous growth in quantitative methods for studying macroevolutionary dynamics using timescaled trees. These methods have mostly been developed by neontologists, however, and are typically applied to molecular phylogenies of extant taxa. As a result, most studies have focused on testing whether macroevolutionary dynamics differ among clades or lineages evolving towards similar ecological regimes. The fossil record, in contrast, suggests that whole-clade dynamics may change through time based on intrinsic or extrinsic factors. Here, I investigate such dynamics using a phylogeny of living and fossil mysticete whales. In contrast with results from extant cetaceans, there is no evidence for declining rates of body size evolution through time. Furthermore, although body size shows some response to changes in average global ocean temperatures through time, phylogenetic inertia appears strong enough that the net effect is weak. In contrast strong support is found for an abrupt and substantial shift in macroevolutionary dynamics at the onset of the Pleistocene, 2.3 million years



ago. The inferred dynamics can be anticipated from geological, ecological and biomechanical perspectives, but are virtually undetectable using phylogenies of extant taxa. Complete understanding of evolutionary dynamics requires well-sampled phylogenies of fossil taxa. Such clades, where available, are model systems for 21st Century macroevolutionary biology.

Fossil biases and phylogeny

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In the era of molecular phylogenetics, fossils remain pivotal for understanding evolutionary history. Extinct taxa break up large gaps between the depauperate modern fauna, unlock sequences of anatomical change, and can be used to reconstruct evolutionary timescales, including calibration of molecular clocks. To make these inferences, it is necessary to include extinct taxa in phylogenetic frameworks. The large amount of missing data that afflicts fossils, even well preserved ones, is not generally seen as a problem for phylogenetic analyses. However, recent meta-analyses, lab-experiments and simulations have demonstrated widespread fossilization biases that systematically distort phylogenetic inference. Comparison of dental and osteological characters of mammals finds osteology to be a better fit with molecular trees than teeth are; that teeth are a poorer proxy for phylogeny accords with developmental data, but is unfortunate given their dominance of the fossil record. On a broader scale, removal of soft tissue characters from phylogenies of living vertebrates and invertebrates with hard skeletons results in individual taxa drifting down trees from their original position. This phenomenon of 'stem-ward slippage' was first observed in some entirely soft bodied organisms; the unexpected preferential loss of informative characters (synapomorphies) during decay can cause early fossil chordates to appear more primitive (plesiomorphic) than they were originally. Furthermore, study of empirical and simulated datasets reveals taxon placement to be extremely sensitive to accurate recognition of non-present characters as either phylogenetically absent or lost during preservation, which is highly problematic for all soft-bodied taxa. The implications of these combined findings are far reaching for palaeobiology and molecular clock studies. Nevertheless, it is hoped that identifying, quantifying and correcting for these problems will enable better practice for fossil phylogenies.

SYMPOSIUM — ACCELERATING THE PACE OF TAXONOMY

A major threat of the biodiversity crisis is that we will never learn everything we would wish to know about the origins, evolution, and organization of the biosphere. Some knowledge is key to understanding the functions of complex ecosystems. Other knowledge is key to piecing together the multi-billion-year history of life on our planet and making wise conservation decisions. Historically, a great deal of what we know of biodiversity has been captured through revisionary taxonomy and monography. The broadly comparative aspect of monographs means that they remain the most time-efficient and effective way to reassess existing data and add new data for large numbers of species. That said it is impossible to revise all taxa or address all gaps in knowledge at the same time. We must not only decide how to prioritize which taxa to monograph first, but also the sequence and relative emphasis to place on various categories of knowledge. The answer may be a mosaic of meeting various high priority objectives but this still requires difficult decisions regard priorities and distribution of limited resources. All of this would be challenging under any circumstance, but with the new reality of the biodiversity crisis knowledge of some species and information about them is literally a now or never proposition. While recent commentary on the global inventory of all species on Earth has largely focused on the size and extent of the remaining task in terms of numbers of species awaiting discovery and technological tools that aid in that discovery, a very real need exists to carefully examine the process of monography and to assure that what we are proceeding as effectively as possible. This includes identifying those aspects of traditional monographic work that are valuable and should be preserved as well as new approaches that add speed or quality to the work. This symposium will address how we can accelerate the pace of producing taxonomic revisions and monographs for species-rich clades.

Widespread mistaken identity in tropical plant collections


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Whole genome sequencing, digitization of natural history collections and database aggregators of specimen information are providing unique tools to study the natural world at unprecedented geographical and spatial scales to address major environmental issues including extinction, conservation and climate change. These 'big data' approaches to environmental science utilize the information provided on specimen labels and assume that each specimen has been correctly identified by an expert. Here we document the growth of herbaria and herbarium collections in museums and botanic garden plant collections worldwide. Using three independent methods we analyse the history of specimen identification and evaluate the accuracy of names used for four tropical taxa and one temperate taxon. Our data demonstrate that whilst the world's natural history collections of plants have doubled over



the past 40 years, on average more than 50% of tropical plant specimens do not have a correct name. This has serious implications for the uncritical use of specimen data from natural history collections.

Accelerating the global systematic revision of scorpions: improving accuracy and efficiency with integrative taxonomy, collaboration and cyberinfrastructure

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Scorpions are the fifth most diverse arachnid order, with more than 2,000 extant species in approximately 200 genera. Scorpion diversity is grossly underestimated, however. There may be as many as 7,000 scorpion species, for two reasons. First, scorpions are cryptic, seasonal, habitat-specific, and difficult to collect without appropriate methods, and most habitats where they occur have not been surveyed in appropriate seasons or with appropriate methods. Second, scorpion species are often difficult to delimit because, unlike many terrestrial arthropods, the genitalia provide few species-level characters in most families, hence taxonomists often resorted to subspecies for apportioning somatic variation, or recognized widespread polymorphs. Analyses of the variation in morphology, aided by reciprocal illumination from DNA sequences, have revealed that most scorpion subspecies are diagnosable species, many widespread polymorphs are complexes of range-restricted endemics, and up to half of all scorpion genera, as well as many suprageneric taxa, are paraphyletic. Unfortunately, the prevailing piecemeal approach to scorpion taxonomy, comprising single species descriptions, faunistic or regional treatments, rarely accompanied by phylogenetic analyses, is barely resolving the confusion, while a growing number of phylogeographical studies of DNA sequence data are decoupled from and largely uninformative for the revisionary process. The global inventory of these living fossils will be more accurately and more efficiently completed by integrative revisionary syntheses of monophyletic groups, especially if undertaken by teams of specialists, using advances in cyberinfrastructure, as illustrated by recent and ongoing revisions of speciose scorpion clades.

The science of species and art of survival

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Exploring, documenting, and understanding species and their adaptations to changing environments offer the best hopes for human prosperity in the face of a very uncertain environmental future. Biomimicry, however, is in its infancy and can only

fulfill its potential to the extent that taxonomy succeeds in completing an inventory, description, and phylogenetic classification of all species. Accelerating the rate of monographic and revisionary studies, completed to a high level of excellence and detail, is the next necessary step and an investment in the long term survival of humanity.

A game of two halves? Taxonomy as a team sport.... take two.

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For a decade or more taxonomists have been discussing and exploring how to speed up the work we do in order to relieve the so-called “taxonomic impediment”. Many different models and methods for doing this have been proposed – some work, some work for some people and some have had little effect. At the biennial in 2007 I showed that the commonly held vision of the lone taxonomist working alone in a corner and publishing single author papers versus the vision of large groups of physicists working and publishing together was false, and suggested that the concept of collections as infrastructure needed to be better shared. We have moved a long way since then. I will use examples from my work with Solanaceae – the nightshades – to discuss various ways in which we have tried to accelerate the basic taxonomic work in the family and the tools we have now that make this possible. I will also discuss some of the issues we now face in speeding up taxonomic work and how we might work together to overcome these. There is probably no one way to accelerate taxonomy perfectly – taxonomic groups differ, communities differ, but we really are in a new phase, thanks largely to new tools and ways of working. Last, but not least I want to explore what accelerating the pace of taxonomy really means and what some of the tradeoffs might be in the future.

Taxonomy on the fast track. Towards more sustainability in Biodiversity Research

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The term “turbo-taxonomy” was recently coined for an approach combining *cox1* sequences, concise morphological descriptions by an expert taxonomist, and high-resolution digital imaging to streamline the formal description of larger numbers of new species. We elaborated this approach and demonstrate the functionality of a



species-description pipeline by naming hundreds of new species of hyperdiverse Trigonopterus weevils in the open-access journal ZooKeys with content pushing into wiki-based species pages.

We conclude that this approach will not only increase speed, but also sustainability of global species inventories that usually suffer from near-complete lack of acceptable taxonomic foundation. It will be of great practical value to all the other disciplines that depend on a usable taxonomy and will change our perception of global biodiversity. While this approach is certainly not suitable for all taxa, it is the tool that will help to tackle many hyperdiverse groups and pave the road for more sustainable comparative studies.

Finally, we present a large-scale pilot study in Indonesia, and argue that fast track taxonomy and the BIN system will have to work hand in hand to provide objective, sustainable data in such a framework where it is hopeless to assume that traditional tools will be able to inform stakeholders about the contents of a given area. This approach offers multiple options for international cooperation, training and data analysis, requirements under new access and benefit sharing regulations.

Accelerating the pace of taxonomy

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The natural world is poorly understood and substantial taxonomic problems exist in many groups, especially the two most species-rich clades – insects and flowering plants. This fundamental lack of knowledge has serious implications for contemporary environmental science including compiling the encyclopedia of life, measuring extinction and conservation. Improving the taxonomy of a group of organisms of any size is non-trivial and has become more difficult due to the sheer volume of specimens, the amount of literature, and the multiplication of names associated with a group of any size. On the other-hand new technology in the form of digitization, DNA sequence data and online resources provides opportunities and access to information although these still have not led to an increase in either the number of taxonomic revisions nor the number of new species being described. This talk will describe an attempt to accelerate the pace of revising species-rich groups of plants with reference to the flowering plant genera *Convolvulus* and *Ipomoea*. In particular, the talk will explore different aspects of revisionary and monographic work as part of our role in providing reliable taxonomic information.

Searching for the silver bullet

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In order to find solutions to speeding up revisionary work aspects and methods of a recent taxonomic monograph are analysed. Article based citation metrics, h-index, changing career structures, management practices, e-taxonomy, DNA bar-coding, next generation sequencing, mass digitisation of herbarium specimens are all influences on present-day taxonomist that need to be considered when carrying out taxonomic revisions. A series of output and process related solutions are reviewed as part of a plan for a modern approach to taxonomic revisions.

Developing a workflow for accelerating cumulative taxon descriptions, from fieldwork to publication

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Across the living kingdoms, new taxa are described at a rate of about 15-20,000 a year. Given the maxim that species are becoming extinct more rapidly than they are being described, and accepting that the description of all life on earth is a worthwhile aim, it is imperative that we develop new tools and workflows to accelerate the rate of species description. We present here a workflow from field collection of specimens, through automated "non-destructive" DNA extraction, sequencing and analysis, specimen preparation and imaging, to online publication, using Microhymenoptera as an example. At each stage of the workflow, appropriate methods and tools, including software, are used to reduce specimen processing time, and hence accelerate publication of species descriptions. While the resulting published descriptions will serve mainly the purpose of making the new names available, the actual taxonomy and related information, including identification tools, will be universally freely available on the web in a central repository. Both the species descriptions and identification tools are matrix-based, and the latter are interactive and mainly visual. Advances in publication processes make virtually instant peer-reviewed publication possible. Most importantly, as new species are described, their associated data will be added to this central repository, achieving a cumulative, or iterative, taxonomy.

Nothing in taxonomy makes sense except in the light of open access

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Access to taxonomic data is the single most important factor that can accelerate the pace of taxonomic research. Access is a multifaceted concept and includes everything from finding taxonomic information, reusing it, and publishing it as widely as possible. However, without open access, access is meaningless and possibly discriminatory. Open access includes adoption of publishing business models, and focusing on the core concepts of taxonomic publication and dissemination of discoveries, not cross-financing other business or sustaining unfairly high profits. This may be achieved by pairing innovative methods in taxonomy with innovative business models. Open access means shared formats and standards so taxonomic articles can be read by humans or machines irrespective of domains. Open access means using machines to mine the rich content we produce, to be able to follow up links to cited external data, to produce the taxonomic knowledge-graph representing the information we seek. Though this seems very technical, the challenge is primarily social. Technical solutions already exist using semantically enhanced publishing derived from databases, such as Pensoft's publishing workflow based on the National Library of Medicine's Taxpub/Journal Archival Tag Suite allowing immediate post-publishing linking to these new treatments from Wikidata, GBIF, NCBI taxonomy linkout, EOL domain specific projects, etc. The Biodiversity Heritage Library and the Biodiversity Literature Repository infrastructure exist to make all taxonomic articles citable and accessible. Scientists have to abandon their attitude that scientific publishing ends with getting an article and that it is up to the next generation to discover, read and reuse the content. Scientific institutions need to return to their original mission of disseminating knowledge to the public. Funding agencies should require metrics on the usage of scientific results and data of their funded scientists and thus optimize their output per dollar spent.


Mowing the lawn during an identity crisis: do well known groups need taxonomists?

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If we need to describe all organisms as quickly as possible, why are all taxonomists not dedicated to knowledge gaps? Is there a contradiction between taxonomy as a question driven science, and taxonomy as a pragmatic species inventory service? Grasses are the most economically useful plant family including wheat, rice,



sugarcane, and bamboo. For this reason grasses are also the most thoroughly studied and best classified of all plant families. This talk will present grasses as a natural model system for the study of taxonomy. What should a grass taxonomist do to improve the taxonomy of the best known plant family? Should we all move to entomology?

SYMPOSIUM — COMPARATIVE APPROACHES TO THE ORIGIN OF BIODIVERSITY

Variation in the tempo of species and trait evolution through time and among lineages are striking and universal features of evolutionary diversification. The reasons why some lineages diversify rapidly and others not at all, why some clades are species-rich and others are not, and the underlying factors determining these differences, are fundamental to understanding how life became so diverse. Several recent developments are transforming our ability to understand the tempo of species and trait evolution and the overall evolutionary dynamics of species diversification: (i) the development of more sophisticated and powerful tools for modelling trajectories of diversification and for combining neontological and paleontological evidence; (ii) the proliferation of new molecular phylogenetic data, for many more clades spanning broader taxonomic, geographical and temporal levels; (iii) the assembly of more comprehensive species geographic distribution, functional and life history trait data sets. These developments are providing exciting new insights into rates of evolutionary diversification across time and space. This symposium will explore these questions and developments with contributions encompassing both methodological issues and empirical studies of large clades spanning the Tree of Life.

Competition and dispersal in clade diversification dynamics

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New phylogenetic comparative methods and their application to our understanding of phenotypic evolution and diversification

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Comparative phylogenetic methods, often based on stochastic evolutionary models, are fundamental to our understanding of phenotypic evolution and diversification. Abiotic changes and biotic interactions are thought to play a major role in these evolutionary processes, yet they haven't explicitly been accounted for in comparative phylogenetic models. I will present recent developments in my research group aimed at bridging this gap. In particular, I will present models that allow testing the role of abiotic variables on rates of speciation, extinction and phenotypic evolution, as well as models that allow testing the role of species interactions -- such as competitive, mutualistic, and antagonistic interactions -- on phenotypic evolution. I will then present applications of these new phylogenetic comparative methods to

empirical datasets. Our results suggest that climate played a major role in driving evolutionary rates, with faster phenotypic evolution in cool climates, and faster diversification in warm climates. They also point to the crucial role of competitive character displacement and biogeographic history in explaining the patterns of variation in phenotypic diversity that we observe today. I will end by discussing future directions in the development of phylogenetic comparative methods.

Inferring island biogeography from phylogenetic data

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Island biotas emerge from the interplay between colonisation, speciation and extinction and are often the scene of spectacular adaptive radiations. A common assumption is that insular diversity is at a dynamic equilibrium, but for remote islands, such as Hawaii or Galápagos, this idea remains untested. Here, we reconstruct the temporal accumulation of terrestrial bird species of the Galápagos using a novel phylogenetic method (DAISIE) that estimates rates of biota assembly for an entire community. We show that species richness on the archipelago is in an ascending phase and does not tend towards equilibrium. The majority of the avifauna diversifies at a slow rate, without detectable ecological limits. However, Darwin's finches form an exception: they rapidly reach a carrying capacity and subsequently follow a coalescent-like diversification process. Together, these results suggest that avian diversity of remote islands is rising, and challenge the mutual exclusivity of the non-equilibrium and equilibrium ecological paradigms.

Ecological release, perennality and evolutionary plant radiations on island systems


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Ecological release has long been considered to be the hallmark of adaptive island radiation and a key driver of species, trait and ecological diversification associated with evolutionary radiations in general. Despite the prominence of this phenomenon in evolutionary thinking, quantification and comparative analyses of ecological release across radiations has lagged behind, especially for plants. With the advent and rapid proliferation of methods to infer trajectories of diversification, it is surprising that there are very few, if any, studies that estimate rates of species, trait and niche evolution for island and island-like plant radiations in the broader comparative con-



text of their mainland relatives. At the same time, the striking parallels between radiations on oceanic islands and those on island-like mountains, and especially tropicalpine mountains, have intrigued evolutionary biologists ever since Carlquist's classical studies of island biology. While much emphasis has been placed on insular woodiness or montane perennality in island and tropicalpine plants, and how to explain these phenomena, little work has been done to document and understand the rapid appearance of diverse life forms associated with plant radiations in these systems. Here we present preliminary estimates of rates of species and life form diversification and the correlations between the two for a small set of classical plant radiations on oceanic islands and island-like tropicalpine habitats in the Andes, highlighting the spectacular parallels between these contrasting systems.

Scales of phenotypic diversification: exploring unconventional radiations in fishes

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Key concepts concerning the tempo and mode of evolution—including adaptive radiations and 'living fossils'—trace their intellectual roots to broad patterns of phenotypic change apparent over long timescales. However, modern studies of diversification in a comparative context overwhelmingly focus on a limited number of traits in small clades that have radiated recently in geologically ephemeral and geographically restricted environments. Although successful in the modern day, it is unclear how such groups might contribute to future diversity, or whether model 'microcosms' are appropriate for understanding the origin of variety in groups with ancient evolutionary roots and which diversified on wide spatial scales. Boasting a staggering variety of morphologies and ecologies, fishes present an attractive model system for the study of evolutionary diversification. In conjunction with the application of new genomic, comparative, and paleontological tools, we show how this remarkable variety can be harnessed in order to critically test hypotheses concerning the evolutionary origin of modern vertebrate diversity. Specifically, we focus on two examples that figure prominently in classic evolutionary debates: first, diversification of the earliest teleosts and its potential drivers, and second, the rate at which extreme morphological innovations arose in modern lineages of spiny-finned fishes.

Did predation shape fish? Disentangling the complex drivers of fish body form diversity

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One of the many challenges to understanding the origin of biodiversity is linking macroevolutionary patterns to ecological processes. For example, what drives the incredible diversity of body shapes across teleost fishes ranging from seahorses to pufferfish? At the microevolutionary scale it is well known that predators can induce morphological changes. Individual fish exposed to predation cues increase both relative body depth and relative fin spine length thereby enlarging the body dimensions that gape-limited predators must overcome. If similar adaptive plastic responses to predation facilitated evolutionary change over the history of teleosts, we would expect to find that fin spines and body dimensions evolve concomitantly at the macroevolutionary scale. Specifically, increases in body dimensions should parallel the orientation of the fin spines. Using a recently developed teleost phylogeny and morphological data from museum specimens we reveal results consistent with our predictions. Lineages with spines projecting in the horizontal plane (pectoral fin spines) have wider bodies, while those with spines on the vertical axis (dorsal, anal or pelvic fin spines) have deeper bodies. Moreover, there is a positive relationship between spine length and body dimension beyond the expected allometric relationship. Despite the diversity of factors that may influence shape evolution, we have identified macroevolutionary relationships that are consistent with the morphological changes induced by predators during intraspecific experiments. Thus potentially revealing a macroevolutionary signature of predation on the evolutionary dynamics of teleost body shape.

Phylogenetic rates, adaptive evolution and evolutionary trends

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There is a growing appreciation that phenotypic rates of evolution vary wildly among species. Such rates have the potential to provide a unique window in to historical periods of natural selection. To the extent that this is true, variation in phenotypic rates can be used to study macroevolutionary trends through time and highlight periods of exceptional evolutionary change. Here, I will talk about our recent work which uses a phylogenetic statistical approach that allows the rate of body size evolution to vary across a phylogeny to demonstrate a long-term directional bias toward increasing size in the mammals. These results are the first evidence from extant species that are compatible with Cope's rule: the pattern of body size increase through time observed in the mammalian fossil record. Our findings are not consistent with non-

adaptive explanations of size increase - highlighting the power of methods that detect variation in the rate of phenotypic evolution for studying adaptation.

Macroevolutionary divergence of bird bills

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Large-scale, continental to global, adaptive radiations contribute disproportionately to worldwide patterns of biodiversity. Phylogenetic studies have given new insight into the diversification dynamics of a number of exceptional radiations. However, a complete picture of the phenotypic diversity that underpins adaptive radiations has tended to focus on a few exemplar clades often geographically restricted to islands or island-like systems. Here, I use 3D morphometrics to describe the divergence and macroevolutionary pathways that generated the diversity of avian bill morphologies. The filling of avian bill morphospace is best described by gradual divergence interspersed with dramatic bursts of evolution. I propose that the extent and frequency of divergence to extreme morphologies implies a dynamic of regular breaking of ecological or developmental constraints opening up new ecological niches throughout avian evolutionary history.

Extraordinary rates of evolution are common

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I derive a simple equation to predict how much the rates of evolution should vary from branch to branch in a phylogeny that is derived from gene-sequence data assumed to be evolving according to a single common or homogeneous rate of change. When compared to phylogenetic trees derived from simulated sequence data, the expected and observed branch-to-branch variation match each other. Applied to phylogenies of real biological species, we observe significant numbers of departures, indicating that real adaptive change repeatedly introduces bursts of evolution at the molecular level, many of which represent substantial departures from the expected underlying rate. I muse on the relationship of these bursts to our finding from earlier work of punctuational evolutionary change in phylogenies, and on what these departures tell us about the ability of natural selection to sculpt evolutionary change. Our results also have a technical application to Bayesian phylogenetic inference, allowing researchers to adopt a rational prior belief about branch-to-branch variation in rates of change.

CONTRIBUTED TALKS

PITT RIVERS MUSEUM LECTURE THEATRE

(In the programmed order)



Mark Waters

Missing data and topology in Total Evidence method

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To understand macroevolutionary patterns and processes, we need to include extant and extinct species in our models. This requires phylogenetic trees with living and fossil taxa at the tips. One way to infer such phylogenies is the Total Evidence approach which uses molecular data from living taxa and morphological data from living and fossil taxa.

Although the Total Evidence approach is very promising, it requires a great deal of data that can be hard to collect. Therefore this method would likely suffer from missing data issues that may affect its ability to infer correct phylogenies.

We use simulations to assess the effects of missing data on tree topologies inferred from Total Evidence matrices. We investigate three factors that affect the completeness and the size of the morphological part of the matrix: the proportion of living taxa with no morphological data, the amount of missing data in the fossil record, and the overall number of morphological characters in the matrix. We infer phylogenies from complete matrices and from matrices with various amounts of missing data, and then compare missing data topologies to the “best” tree topology inferred using the complete matrix.

We find that the number of living taxa with morphological characters and the number of morphological characters in the matrix, are more important than the amount of missing data in the fossil record for recovering the “best” tree topology. We suggest that sampling effort should be focused on morphological data collection for living species to increase the accuracy of topological inference in a Total Evidence framework. Additionally, we find that Bayesian methods consistently outperform other tree inference methods. We recommend using Bayesian consensus trees to fix the tree topology prior to further analyses.

The construction and delimitation of morphological characters

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Morphological characters represent the empirical data in morphological phylogenetic analyses, yet often more emphasis is given to analytical procedures than to character construction and delimitation. Apart from the non-trivial issue that any character definition represents an abstraction of a single trait of an organism that logically represents an integrated biological entity, there are numerous problematic issues in the formulation of morphological characters. Some of these issues are explored using one of the best-studied clades of fossil vertebrates, non-avian theropod dinosaurs, as example.

A long known problem is the treatment of continuous (morphometric or meristic) characters, and a number of possible solutions have been proposed, ranging from gap coding to inclusion of absolute values. In gap-coding, the perceived gap between discrete sets of quantitative data often disappears with increased taxon sampling, which is to be expected if a more or less gradual evolution of morphological traits is assumed. The use of binned data (e.g. in percentual increments of the overall observed variability) suffers from the fact that any cutting point in continuous data is arbitrary. However, this method might have advantages over absolute values if exact values cannot be established, due to individual variation or incomplete preservation, which might result in disregarding available phylogenetic information. The matter is further complicated by the fact that, with increased taxon sampling, the distinction between qualitative and continuous characters often blurs, as seemingly discrete character states often also result from gradual changes.

Another problematic issue concerns ontogenetic or individually variable characters. Whereas one might argue to generally exclude such characters from phylogenetic analyses, this is problematic, as both individual and ontogenetic variation play important roles in evolutionary change.

The distribution of convergences on phylogenetic trees

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Homoplastic similarity is widely recognized as a fundamental potential problem for phylogenetic inference. Also fairly widespread is the notion that the likelihood of convergently evolved similarity between two taxa is not independent of how closely related these taxa are. For example, the idea that convergence or parallelism is more likely between two species of mammal, or between two species of fern than it is between a mammal and a fern seems like a reasonable proposition simply because ferns and mammals are so different from each other. They lack many homologous structural features that might form the basis of homoplastic similarities in more closely related and similar taxa. But to what extent does this sort of proposition, that the probability of convergence between two taxa A and B is positively correlated with the closeness of the phylogenetic relationships of A and B, hold across different scales of comparison? Does it represent an evolutionary law or at least a good rule of thumb? We present results of our ongoing attempts to address this question using parsimonious character optimization to identify the location on a phylogenetic tree of changes leading to homoplastic similarities between pairs of taxa and statistical approaches to determine if such homoplasy is non-randomly distributed on the tree.

4BaSAI -- first insights on a new supertree method based on single quartet analyses and its performance with respect to different starting triplets

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With 4BaSAI we present a new supertree reconstruction method for DNA and amino acid (AA) sequence data based on single quartet analyses. 4BaSAI is written in JULIA and combines various fast algorithms to build up complete topologies from a given sequence alignment and/or to evaluate and, if possible, improve the placement of individual taxa within a given topology. Single quartets are analysed either by Maximum Likelihood (DNA & AA data) or with new, long branch artefact reducing split search algorithms (DNA data). We are currently testing the success of our new approach on simulated sequences and on empirical data using different starting triplet combinations. We will describe the algorithmic structure of 4BaSAI and give a short introduction to our first results considering performance of 4BaSAI with respect to use of different starting triplets.

Concatabominations: a priori identification of unstable taxa and ineffective overlap in phylogenetic and phylogenomic data

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Individual taxa may be relatively phylogenetically unstable by virtue of limited data. An approach for diagnosing taxon instability due to missing data a priori termed safe taxonomic reduction (STR) identifies “rogue” taxa that can be removed from a dataset without impacting upon the interrelationships that will be inferred among the remaining taxa under parsimony and other criteria. This can reduce numbers of optimal trees and run times and yield better resolved consensus summaries. However, STR is not always effective. We present a simple heuristic method for identifying potentially unstable taxa that can be useful in cases where STR does not succeed. Additionally, applied to matrix representations of trees, the new approach can be used to help diagnose ineffective taxonomic overlap and identify taxa that are expected to be unstable in both supertree or supermatrix analyses of phylogenomic scale data. The



method uses compatibility to investigate whether combining data from incomplete taxa introduces additional conflict. Incomplete taxa that can be alternatively combined with many others without any apparent increase in the conflict in the data are identified as likely to be unstable. We illustrate the method these different contexts. Its main importance probably lies in experimental design given the truism that it is necessary to be able to recognize ineffective overlap in order to overcome it most efficiently.

Phylogenetic trees do not reliably predict feature diversity

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Phylogenetic trees provide a framework for understanding the evolution of features (properties, characters or traits) of species, where closely-related species share many common or similar features. This property of phylogenetic trees has practical use in applications such as bio-prospecting, where an optimal strategy exploits phylogenetic information to target closely related species to search for shared features of interest. The implicit corollary of this is that distantly related species share few features in common. This property of phylogenetic trees is thought to be useful for conservation evaluation in choosing sets of species that maximise the present utilitarian benefits of extant feature diversity (such as biologically active compounds or source systems for genetic engineering) as well as maximising the range of evolutionary trajectories into the future. Here I demonstrate that phylogenetic tree distance, both in real and simulated datasets, is correlated with feature similarity only for a short relative distance along the tree, such that there is no relationship for the majority of the length of most phylogenetic trees. In other words, close relatives share more features than distant relatives but beyond a certain threshold increasingly more distant relatives are not more divergent in phenotype. This means that measures of phylogenetic diversity based upon maximising phylogenetic distance may not maximize feature diversity.

New inference tools for incorporating the effect of interspecific competition on trait evolution

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Several classical evolutionary and ecological theories posit that competitive interactions between species in an evolving clade are important drivers of trait diversification. Adaptive radiation and character displacement theories, for example, assume that the mean value of a trait in one lineage is influenced by values of traits in other, competing lineages. Phylogenetic comparative methods, such as model-

fitting approaches to testing hypotheses about the tempo and mode of trait evolution, have become standard tools for evolutionary biologists using comparative approaches while accounting for shared ancestry among taxa. Few models of trait evolution, however, actually take into account interactions between species. The exceptions are diversity-dependent models of trait evolution, which model evolutionary rates as a function of the number of reconstructed lineages at a given time point in an evolutionary tree. Nevertheless, no currently available models treat trait evolution in one lineage as dependent on trait values in other evolving lineages. Here, we present a recent model of the evolution of a univariate, quantitative trait, which accounts for interspecific interactions. We develop a maximum-likelihood based approach to fit this model, which we refer to as the matching competition model, to combined phylogenetic and phenotypic data. We show using simulations that the approach accurately reconstructs the simulation parameters in a broad range of parameter space and has acceptable statistical properties (i.e., high power and low type-I error rates). Additionally, we describe a new method to incorporate data on biogeographical overlap between species into the matching competition and diversity-dependent trait models, since only species that have historically coexisted in sympatry have had the opportunity to interact. We then fit the matching competition model, diversity-dependence models, and other commonly used trait models these model to morphological data from Greater Antillean *Anolis* lizards, a classical example of an adaptive radiation. We found that models that incorporate both interspecific competition and biogeography fit the trait data better than models that do not. Until now, it has been difficult to test for a macroevolutionary signature of competitive interactions on contemporary trait values, and we hope that our statistical tools will provide new means for evolutionary biologists to test such hypotheses at macroevolutionary scales.

How should genes and taxa be sampled for phylogenomic analyses with missing data? An empirical study in iguanian lizards

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Targeted sequence capture is becoming a widespread tool for generating large phylogenomic datasets to address difficult phylogenetic problems. However, this methodology often generates datasets in which increasing the number of taxa and loci increases amounts of missing data. Thus, a fundamental question is whether sampling should be designed to maximize sampling of taxa or genes, or minimize missing data cells. Here, we explore this question for an ancient, rapid radiation of lizards, the pleurodont iguanians. Pleurodonts include many well-known clades (e.g. anoles, iguanas) but relationships among families have proven difficult to resolve strongly and

consistently using traditional sequencing approaches. We generated up to 4,921 ultraconserved elements with sampling strategies including 16, 29, and 44 taxa, from 1,179 to ~2.4 million characters, and ~30% to 60% total missing data. We then compared branch support for interfamilial relationships under these 15 different sampling strategies for both concatenated (maximum likelihood) and species tree (NJst) approaches. We found that both approaches had the highest support when including loci with up to 40–55% missing data overall. Thus, our results show that simply excluding all missing data may be highly problematic as the primary guiding principle for the inclusion or exclusion of taxa and genes.

Morphological character analysis and the evolutionary change in development

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Morphological character analysis is the most critical approach of comparative biology. With the rise of Willi Hennig's Phylogenetic Systematics, this approach gained a renewed attention, because of the impact of homology assessment in support of phylogenetic hypotheses and classifications. Now, with the emergence of Developmental Evolution (evo-devo), morphological character analysis received a second consideration, with focus on the understanding of ontogenetic, genetic, and environmental mechanisms involved in the understanding of phenotypic homology and evolution. In turn, the integration between phylogenetics and evo-devo is seen as a new exciting, awarding, and challenging issue for the agenda of comparative biologists. In line with this, the present work aims to integrate morphological character analysis in the context of phylogeny and development. I firstly describe the modes of evolutionary change in development, including: (a) heterochrony; (b) heterometry; (c) heterotopy; and (d) heterotypy. Subsequently, I provide a comprehensive synthesis between these modes of evolutionary change and Paul Sereno's view of neomorphic and transformational characters. Finally, I discuss the impact of this integration in the inference of character evolution and sister-groups diversification, and classifications as well.

The origin of annelids: reconciling morphology, fossils and molecules

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The phylogeny of annelids and the origin of their body plan are among the most controversial topics in the study of protostome evolution. While annelid body fossils are known from the early Cambrian Sirius Passet (~519Ma) and middle Cambrian Burgess Shale (505Ma), their relationship to living annelids has remained obscure.

We present a cladistic analysis of annelids, including a comprehensive sample of living taxa, fossils and outgroups. Previous morphological studies have been hampered by widespread multiple independent losses of key characters causing secondarily externally simple bodied taxa, such as the unsegmented Echiura and terrestrial clitellates, to be recovered as early branching taxa. We find that the inclusion of fossils recovers topologies that are congruent with molecular data, including clades of 'sedentary' and 'errant' polychaetes and a close relationship between echiurans, Capitellidae and Arenicolidae. The Cambrian body fossils are recovered as a grade in the annelid stem group under equal and implied weights parsimony and Bayesian inference under the mkv model. These taxa therefore place key constraints on the mode of life of the annelid ancestor and the sequential character transformations that lead to the origin of the annelid crown group.


A total-evidence approach to dating with fossils

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Phylogenies are usually dated by calibrating interior nodes against the fossil record ("node dating"). This relies on indirect ad hoc methods that, in the worst case, misrepresent the fossil information. Here, we compare standard node dating to an approach based on simultaneous analysis of fossil and extant taxa ("total-evidence dating") within a Bayesian context. As a test case, we focus on the early evolution of the Hymenoptera (Insecta). For node dating, we use nine calibration points derived from the fossil record, while total-evidence dating is based on 343 morphological characters scored for 45 fossil (4-20% complete) and 68 extant taxa. In both cases we used molecular data from five markers (about 5 kb) for the extant taxa. We use relaxed-clock models to accommodate rate variation across the tree but find it necessary to introduce a rooting constraint to avoid errors in tree topology. The order Hymenoptera is estimated by our approach to date back to the Carboniferous with



an approximate age of 309 My (291-347 My). Despite considerable uncertainty in the placement of most fossils, we find that they contribute significantly to the estimation of divergence times, as indicated by usually narrower posterior distributions that are less sensitive to prior assumptions when fossils are included as terminals. From a theoretical standpoint, total-evidence dating is preferable simply because it explicitly incorporates the fossil data instead of relying on secondary interpretation. Our results suggest that it can also improve the precision and accuracy of divergence time estimates.

Experimental analysis of decay biases in the fossil record

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If fossils are to realize their full potential in reconstructing the tree of life we must understand how our view of ancient organisms is obscured by taphonomic filters of decay and preservation. In most cases, processes of decay will leave behind either nothing or only the most decay resistant body parts, and even in those rare instances where soft tissues are fossilized we cannot assume that the resulting fossil, however exquisite, represents a faithful anatomical representation of the animal as it was in life. Recent experiments have shown that the biases introduced by decay can be far from random; in chordates, for example, the most phylogenetically informative characters are also the most decay-prone, resulting in 'stemward slippage'. But how widespread is this phenomenon, and are there other non-random biases linked to decay? Furthermore, to what extent can we use the results of decay experiments to inform the fossil record as a whole? Intuitively, we make assumptions about the likelihood of different kinds of characters to survive and be preserved, with knock-on effects for anatomical and phylogenetic interpretations. To what extent are these assumptions valid? From our experiments, and those of others, we have a growing database of patterns of character loss in a range of organisms across the tree of life. By combining these data we can predict the conditions under which stemward slippage is likely (or unlikely) to be significant, and identify other systematic biases introduced by decay. We also describe the decay trajectories of characters, or suites of characters, common to a range of taxa. These data are more widely applicable to the fossil record –allowing us to ground-truth some of the assumptions involved in describing exceptionally preserved fossil material.

Visual opsin gene evolution and the origin and diversification of snakes

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Debates about the origin of snakes over the last 150 years have revolved around two main interrelated aspects — the identity of their closest relatives (phylogeny) and the nature of the ancestral snake (ecology). The dominant hypothesis is that snakes diverged from 'lizard' ancestors and became snake-like as an adaptation to a burrowing phase in their early history. Support for this is found in the anatomical similarity of snakes and burrowing lizards, in the phylogenetic distribution of burrowing among extant snakes, and in plausible adaptive explanations for aspects of snake anatomy. Recently, the debate has been fuelled by new studies of fossil squamate reptiles, and new molecular phylogenetic evidence for living snakes. Given that the snake eye has played an important role in the burrowing ancestry hypothesis, we used ocular media transmittance, visual pigment microspectrophotometry and visual opsin sequencing to provide a fresh perspective on snake vision biology and what it might tell us about snake origins. Results suggest that the ancestral snake had three visual pigments, having lost two of those present in the ancestral vertebrate, consistent with some diminution of the visual system. However, the most fossorial extant snakes have only a single visual pigment, such that extreme fossoriality is unlikely to have characterized the ancestral snake, whatever the phylogenetic relationships of these extremely fossorial snakes. These results have implications for reconstructions of the ancestral snake but also for understanding the exceptional anatomical diversity of snake retinas, and what these can tell us about vertebrate visual evolution.

Viviparity stimulates diversification in an order of fish

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If fossils are to realize their full potential in reconstructing the tree of life we must understand how our view of ancient organisms is obscured by taphonomic filters of decay and preservation. In most cases, processes of decay will leave behind either nothing or only the most decay resistant body parts, and even in those rare instances where soft tissues are fossilized we cannot assume that the resulting fossil, however exquisite, represents a faithful anatomical representation of the animal as it was in life. Recent experiments have shown that the biases introduced by decay can be far from random; in chordates, for example, the most phylogenetically informative characters are also the most decay-prone, resulting in 'stemward slippage'. But how widespread

is this phenomenon, and are there other non-random biases linked to decay? Furthermore, to what extent can we use the results of decay experiments to inform the fossil record as a whole? Intuitively, we make assumptions about the likelihood of different kinds of characters to survive and be preserved, with knock-on effects for anatomical and phylogenetic interpretations. To what extent are these assumptions valid? From our experiments, and those of others, we have a growing database of patterns of character loss in a range of organisms across the tree of life. By combining these data we can predict the conditions under which stemward slippage is likely (or unlikely) to be significant, and identify other systematic biases introduced by decay. We also describe the decay trajectories of characters, or suites of characters, common to a range of taxa. These data are more widely applicable to the fossil record – allowing us to ground-truth some of the assumptions involved in describing exceptionally preserved fossil material.

Floral symmetry shifted 203 times in angiosperms

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The number of species in families of flowering plants ranges from 1 to more than 20,000; it is one of the symptoms of a highly uneven distribution of diversity in angiosperms. One of the commonly proposed factors in shaping this uneven distribution is the origin of key innovations. Clades possessing such an advantage are assumed to produce more species per unit of time. One generally accepted key innovation is floral zygomorphy (bilateral symmetry), which is considered advantageous over actinomorphy (radial symmetry) because zygomorphic flowers have more efficient pollen transfer via limiting pollinator approach angles. The presumed influence of zygomorphy on diversification rates has been argued mostly through the comparison of closely related clades with contrasting floral symmetry. This approach has ignored the broader picture in which many speciose angiosperm families are completely actinomorphic and the finer pattern of changes in floral symmetry. This observation has led us to question the extent to which floral zygomorphy can be considered a key innovation in angiosperms as a whole. To begin answering this question, we need to know where and how many times zygomorphy has originated in the angiosperm phylogeny. We recorded perianth symmetry from more than 700 species, selected to represent all 61 orders and 426 currently accepted families of angiosperms, and to include all presumed origins of perianth zygomorphy. We then reconstructed the evolution of perianth symmetry on a consensus backbone tree, using parsimony. We found perianth zygomorphy in 31 orders and 108 families. There was a minimum of 124 origins, almost the double of what was previously estimated, and 79 reversals to actinomorphy.

Segmental allopolyploid origin in *Medicago arborea* (Fabaceae) revealed through next-generation sequencing and allele phasing

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Polyploidization, the complete doubling of a genome, occurs in c. 15 % of all speciation events in angiosperms and twice as often in ferns, thus playing a central role in plant evolution. However, distinguishing between allo- (among species) and autopolyploidization (within species) remains challenging under standard laboratory techniques and phylogenetic analyses. Here we report a novel approach to use reads from next-generation sequencing to separate homoeologous alleles from their allelic variants, and demonstrate its application in the economically important legume genus *Medicago*. We demonstrated a complex reticulate evolutionary history, in which 80% of the genetic data (including a large number of unlinked nuclear loci) reflect an allopolyploid origin for *M. arborea* and *M. strasseri*, whereas the remainder of the data point towards an autopolyploid origin for those species. This pattern is likely derived from segmental allotetraploid hybridization, with a partial disomic segregation of the genome. Our results indicate that in *Medicago*, and probably many other polyploid plants, phylogenetic relationships can only be derived from substantial amounts of genetic information. This study demonstrates the potential of NGS data in revealing reticulate evolutionary stories. These findings have far-reaching implications in our understanding of morphological evolution, divergence times, and biogeographic history.

Niche and trait evolutionary rates are correlated during the Proteaceae radiation

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Ecologically-driven diversification can create spectacular diversity in both species numbers and form. However, the prediction that rates of change in intrinsic (e.g. functional trait) and extrinsic (e.g. climatic niche) variables are coupled during evolutionary radiation has not been critically tested, even though it is a central prediction of the model. Here, we test this hypothesis in the Southern Hemisphere angiosperm family Proteaceae, which occupies habitats ranging from tropical rainforests to deserts, shows spectacular radiations in open, Mediterranean shrublands in the Cape Floristic Region (CFR) and the Southwest Australian Floristic Region (SWAFR), and is remarkably variable in leaf morphology. We built a phylogeny for 337 Proteaceae species (21% of total), representing all main clades, climatic tolerances and

morphologies, and collected leaf functional trait data (blade area, sclerophylly, leaf shape) for 261 species and climatic niche data for 1645 species. We used phylogenetic generalized least squares regression, quantitative-trait evolutionary model testing and estimates of rates of functional trait and climatic niche evolution to show that divergent selection may have caused lineages in open vegetation types to evolve towards trait and climatic niche optima distinct from those from closed forest. Furthermore, we show that the macro-evolutionary rates of functional trait and climatic niche evolution are strongly correlated, and that these rates are particularly high in open vegetation clades, such as Banksia and Grevillea in the SWAFR, and the Proteaceae and Leucadendreae in the CFR, compared to rates in closed forest clades such as Macadamia and Roupalinae. We argue that exposure to variable climatic micro-environments in Mediterranean shrublands favours higher interspecific trait variability, and this may have facilitated the radiations in these systems.

3D models of ant domatia and phylogenetics reveal how morphological evolution drove the recurrent specialization and dissolution of association in ant/plant symbioses

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A central question in biology concerns the traits and ecological contexts that shape the assembly, specialization, and dissolution of mutualistic interactions. Symbioses between ants and plants, where plants provide housing to ants in exchange for defence or trophic payback, involve a mix of obligate and facultative mutualisms. To examine the role of plant morphology in ant/plant coevolution, we use the largest clade of ant domatium-bearing plants, tuberous epiphytic Rubiaceae in Australasia. We have generated a densely sampled phylogeny for the clade that includes the ant plants and use CT-scanning to reconstruct 3D models of the distinct domatium types. Our data reveal multiple losses of associations, all linked to changes in domatium morphology that coincide with range shifts outside the ants' ranges. Symbiosis loss is characterised by an increase in the size of domatium entrance holes, which then no longer filter out larger-bodied arthropods, small vertebrates, or water. Specialization in these symbioses led to a >100-fold increase in domatium internal surface, the joining of previously unlinked cavities, and the differentiation of distinct cavities types. To assess the ecological role of this architectural remodelling, we studied a subset of these symbioses in Fiji, where all types of domatium morphologies are found. The increase in domatium internal surface is mirrored by a proportional rise in ant colony size while increased domatium integration reduces the chance of colonization by non-mutualistic ants, two traits that positively feed back on the trophic mutualism. Overall, our study reveals that context-dependent selection on the morphology of the tuber mirrors the specialization and dissolution of ant/plant symbioses.

Testing developmental biology predictions with fossils – phylogeny, dental complexity and evolutionary rates of the Multituberculata

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The increase in maximum complexity of tooth morphology through the evolutionary history of mammals is marked. However, recent genetic and developmental studies suggest increases in morphological complexity are developmentally constrained and more difficult to achieve than reductions. Thus, over evolutionary time scales, we might expect increases in morphological complexity to occur less frequently than decreases. To address this hypothesis we studied patterns of change of tooth complexity in the extinct mammalian order Multituberculata, the most successful Mesozoic mammal clade and the longest-existing mammalian order known. We used diversification rate, phylogenetic comparative, and evolutionary rate analyses, allied with a novel multituberculate phylogeny and dataset recording functional parameters including toothrow dental complexity, tooth cusp number, and estimated body mass, to determine patterns and rates of morphological evolution and change in complexity. Dental complexity was quantified using 3D digital tooth models from laser-/CT-scanning lower toothrows and Orientation Patch Count, a measure of morphological complexity. Results show significantly more increases in dental complexity than decreases across Multituberculata, and more large increases than small, suggesting selection for higher complexity outweighed developmental constraints. However, within the only clade to acquire sufficient dental complexity to become predominantly herbivorous, equal decreases and increases in complexity occurred. It appears that once selection pressures for further complexity increases were relaxed, reassertion of developmental constraints balanced selection. Results from this fossil clade can be used to test developmental results and predictions regarding rates and direction of change of morphological complexity, and offer hope for bridging the gap between micro- and macroevolutionary studies.

Integrating fossils into the coral phylogenetic puzzle

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Calibration of molecular phylogenies has become commonplace as a tool for understanding the temporal correlation of biological and geological patterns, and in particular to develop models to help explain historical biogeographic patterns of diversity. In this study, for the first time we use new methodologies to explicitly incorporate coral fossils as non-contemporaneous terminal taxa into the phylogeny of the Merulinidae, one of the major reef coral groups in the Indo-Pacific. We benefit from a rigorous morphological framework, an integrated phylogenetic hypothesis for extant

taxa based on molecular and morphological characters, and well-preserved coral fossils from recently exposed outcrops of Miocene age in East Kalimantan (Indonesia). We found that fossils fit into the coral phylogenetic puzzle and their combined analysis with modern specimens resulted in older estimates of divergence times than using solely the calibration of nodes in a molecular tree. Our results provide unique insights into the times of origin and diversification of Merulinidae. Its origin dates from the Early Cretaceous, with the main clades diverging in the Paleocene/Eocene boundary, mid Eocene, and mid Miocene. We support the hypothesis of early diversification of Indo-Pacific lineages as high levels of cladogenesis are observed since the early Oligocene, reaching its maximum in the Middle Miocene. The Neogene is an interesting "optimum interval" to study phylogenetic relationships at species/genus/family level as work on fairly recent patterns can benefit from both numerous extant lineages and well-preserved fossils that can be placed into lineages with confidence. Our results emphasize the high potential of incorporating the fossil record into the construction of a robust phylogenetic hypothesis that better explains when, how, and where coral evolution had happened.

The taxonomy of endangered, endemic radiations: keeping the tradition alive through local teams and advanced technology

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The value of monography is exemplified by the faunal works of Rolf Brandt and George Davis, which have provided a foundation for studies of adaptive radiation, biodiversity, speciation, and medical parasitology. These monographs describe the freshwater snail family the Pomatiopsidae (Gastropoda: Rissooidea) of southern China and Southeast Asia. The Pomatiopsidae are best known through the Mekong fauna, which includes over 90 species of Triculinae (Rissooidea: Pomatiopsidae), 32 species of Stenothyra (Rissooidea: Stenothyridae), 42 Viviparidae (Rissooidea), and approximately 121 species of Buccinidae (Neogastropoda: Muricoidea). Among this fauna, the Triculinae are most noteworthy in that, with over 90 endemic species occurring within a single subfamily and along only a 300-km stretch of the Mekong River, they represent a unique freshwater molluscan biodiversity.

The talk will consider the potential of coordinating local researchers in addressing the problems currently covered by single-author monography, and the use of technology (RS-GIS, NGS and digital imaging) to facilitate monography within modern research management and funding systems. This talk will also outline the role of the monography of those like Brandt and Davis as essential to public health investigations into the identity of vectors of disease, and to the recognition and study of biodiversity. The likelihood of such work in the modern research funding framework will be considered, with Brandt having been a dedicated amateur and Davis a tenured researcher

free to focus an entire career on a single taxon. It is noteworthy that almost all taxonomic revision of the Pomatiopsidae is dated prior to 1996 and many species remain to be described.

Drawers full of old, undescribed wasps: integrating curation with taxonomy and ecology

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Parasitoid wasps are a case study in the 'taxonomic impediment'. Poorly known and mostly undescribed, parasitoid wasps are also exceedingly important in terrestrial ecosystems and massively species-rich. Interpreting their species-richness, biogeography and host-parasitoid associations is often only possible using museum collections. Unfortunately, collections are riddled with misidentifications, species-level taxonomy has proved to be unreliable and the literature is even worse. Specimens are not necessarily data, and use of a species name in the literature does not necessarily confer reliability. Misuse of junk data, from collections, observations and catalogues, is rife. Using examples from the family Ichneumonidae, I demonstrate the problems inherent in interpreting the literature and available collections then demonstrate the value that can be added through knowledgeable curation and demonstrate that much more effort needs to be directed towards specimen sorting and identification. Major collections of obscure organisms are rich in specimens that can be used to address all sorts of interesting questions, given appropriate investment.

A complementary role for old and new collections in revealing unsuspected species diversity in an endemic gastropod (*Paramelania*) from Lake Tanganyika

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Lake Tanganyika's endemic 'superflock' of cerithioideans is the most diverse (>100 spp.) and disparate (18 genera) gastropod radiation within today's Ancient Lakes. Species diversity is considered to be well known, excepting a single hyper-diverse genus. One iconic genus, *Paramelania*, has long been thought to comprise 2-5 morphologically variable species/forms. We undertook detailed re-examination of the following materials: a) 19th-early 20th C colls: Brussels, Tervuren & London (mostly shells only), b) 1980s-2000s: two research collections (shells, EtOH material), to assess the following:

- 1) Do shell-based 'species' coincide with molecular clades (COI, 16S)?
- 2) How does species composition of collections vary by date and collection method?
- 3) Are within-site collections of living and dead (shell) specimens comparable?

Robust molecular clades proved to be consistent with five, a priori, finely divided, shell-based species, permitting assessment of species diversity in the historic collections comprising shells only. Twenty-one species are separable using shell morphology (16 undescribed). Total collection size was 8395 shells from 147 locations, with marked differences in collection method, depth and substrata between historic and modern collections. High levels of sympatry were seen. Both wide-ranging species and short-ranged local endemics are present ($n=7$; undescribed) and evidence exists for extensive range shifts between dead and living populations. We conclude; 1) historic and modern collections give complementary views of diversity and distribution, capturing differences in geographic ranges and ecology; and 2) in systems with high local endemism, historic collections may contain undocumented diversity that is only revealed in a modern interpretive context.

Combining morphology, molecules, and morphometrics: revising closely related species in the genus *Araniella* (Araneae: Araneidae)

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The integration of independent data sets could solve problems in both traditional and DNA-based taxonomy. The aim of this study is to investigate the power of COI sequences and of morphometrics to distinguish closely related species in the genus *Araniella*. We put special emphasis on the species pair *A. cucurbitina* and *A. opisthographa* since the females are morphologically difficult to distinguish and often misidentified. A total of 216 sequences of eight *Araniella* species from seven European countries, North America and Asia were included in the molecular analysis. The results from both maximum likelihood and Bayesian phylogenetic inference indicate successful separation of six out of eight *Araniella* species, including *A. cucurbitina* and *A. opisthographa*. For the same six species, we detect no overlap of intra- and interspecific genetic divergence, leading to successful species identification with a threshold approach. In addition, morphometric analysis of the epigyna of *A. cucurbitina* and *A. opisthographa* supports species separation by two best explanatory ratios: receptacula length and distance between receptacula and copulatory ducts. Although a small overlap in the ratios still exists, the species identification rate increases when combining morphometric and molecular data, which demonstrates the efficiency of integrative approaches for distinguishing closely related species. However, none of the molecular approaches was able to separate closely related *A. alpica* and *A. in-*

conspicua due to shared CO1 haplotypes. Considering the clear morphological separation of the males and different habitat preferences, incomplete lineage sorting or introgressive hybridization could have led to identical CO1 sequences.

Untangling the molecular phylogeny of tapeworms

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The diversity of tapeworms reaches far beyond of what is typically known about this group from the few representatives of biomedical and veterinary importance (e.g. *Taenia* spp., *Diphyllbothrium* spp.). The large diversity of life cycles (typically involving crustacean intermediate hosts and vertebrate definitive hosts) means they have successfully established themselves throughout aquatic (both marine and freshwater) and terrestrial habitats, where the majority of the ~6000 known species are found parasitizing elasmobranch and tetrapod hosts. Over the past two decades, molecular data have produced an ever more stable and well-resolved backbone phylogeny, whilst increasing the number of orders from 12 to 19. In this talk, the recent contributions to the construction of the tapeworm backbone phylogeny will be recapped. Additionally, new molecular phylogenetic results will be presented that have been accumulated over the last 5 years from the NSF-funded Planetary Biodiversity Inventory project 'A survey of the tapeworms from vertebrate bowels of the earth'. This international collaborative project targeted previously unexplored hosts and/or geographic regions to increase the sampled diversity of tapeworms. The resultant phylogeny, based on two nuclear (18S and 28S rDNA) and two mitochondrial genes (16S rDNA and *cox1*), is composed of ~850 taxa, which represents the most significant contribution to tapeworm phylogeny, to date, allowing us to investigate the effects of host-use and phylogeography on the diversification patterns in this group.

Evolution of convergent functional systems in a speciose clade of parasitic wasps (Ichneumonidae, Cryptinae)

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With 241 genera and over 2,400 species worldwide, cryptine wasps are a dominant but poorly known group of insects that parasitize immature stages of moths, beetles and other insects. These hosts are usually concealed to various degrees, from leaf rolls and twigs to hard clay nests or wood. Therefore, several taxa developed morphological adaptations to find and assess deeply concealed hosts. Such features include a specialized antennal tip to tap hard substrates, producing pulses of sound; swollen

mechanoreceptor organs to detect vibrations; a stout, hardened ovipositor; and enlarged oviposition muscles. All these traits make cryptines ideal for studying the evolution of parasitism life strategies.

This work presents the first comprehensive phylogenetic analysis of Cryptini, often considered “taxonomically difficult” and “challenging” by researchers for their overwhelming diversity and intense morphological homoplasy. The ingroup includes 300 species belonging to 190 genera from all biogeographic regions. The dataset comprises molecular data from two mitochondrial and five nuclear loci, plus 162 phenotypic characters.

The resulting phylogeny shows little correspondence to the current supra-generic classification, highlighting the need for systematic revision in the tribe. It also demonstrates that host location adaptations evolved several times in the cryptine tree of life. The data are then used to investigate the hypothesis that host location characters are part of a complex morphofunctional system, and that the convergence of life strategies imposes constraints in the morphospace occupied by cryptine wasps. Statistical methods are used to (1) reconstruct ancestral states for the characters under investigation; (2) test hypotheses of correlation among life history traits and multiple phenotypic characters; and (3) assess the overlap in the morphospace occupied by convergent lineages.

What limits the morphological disparity of clades?

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Patterns of morphological and taxonomic diversity are often at odds. Specifically, there is a tendency for groups to reach maximum levels of morphological disparity relatively early in their evolutionary histories, even while species richness or diversity is comparatively low. Early high disparity is evident not only in a diverse range of animal clades but also major groups of vascular plants, suggesting it may represent a universal evolutionary phenomenon. The shapes of disparity profiles through time can be quantified in terms of their centre of gravity, with bottom heaviness ($CG < 0.50$) being typical of extinct clades that do not terminate at a mass extinction. It is widely supposed that increasing developmental constraints or ecological restrictions limit the range of morphologies that can evolve within a clade; consistent with an observed decrease in the rate of origination of novel bodyplans and higher taxa through time. It has also been demonstrated that the rate of evolution of new character states decreases through time, although the relationship between this ‘character exhaustion’ and overall disparity has hitherto been untested. Here, we quantify the rate of character exhaustion in 93 published phylogenies of extinct animal clades, and test for a

relationship with disparity profile centre of gravity. We find no significant correlation, and conclude that patterns of early high disparity are not shaped by exhaustion of the state space in any straightforward manner.

Homoplasy and clade support across higher taxa and through research time

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We quantify the levels of homoplasy in over 1,200 morphological character matrices of animals using parsimony, and investigate its distribution across taxa and throughout research time. No index of homoplasy is entirely satisfactory, and we explore the empirical relationship between the ensemble consistency index (CI), the ensemble retention index (strictly an index of retained synapomorphy), and the homoplasy excess ratio (HER). We propose a refinement to the latter; specifically controlling for the distribution of missing entries. We also investigate whether levels of homoplasy predict levels of tree support; specifically mean non-parametric bootstrap support, total support index (TSI) and proportional support index (PSI). Surprisingly, the relationship is not especially strong. Lastly, we model the extent to which all homoplasy and support indices are biased by data matrix dimensions, complementing the theoretical work of Hoyal-Cuthill and colleagues. We find the expected inverse relationship between the number of taxa and the CI, but also between the number of characters and CI. The CI is therefore a poor measure of homoplasy between data sets. The RI and modified HER are much less biased by dataset parameters, and yield similar results, although we prefer the scaling of the latter. We demonstrate a significant decline in the CI inferred for data sets over the last 30 years of research time, but this is largely attributable to an increase in data set dimensions over the same period. Residual CI and modified HER show no such trends. There are also significant differences in homoplasy and branch support between higher taxa, which remain after modeling out data set dimensions.

How big is a genus?

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Genera are units that contain variable numbers of species, from one (monotypic) to several thousand. The frequency of genera with differing species richness is

a strongly skewed distribution; the largest proportion of genera, usually around 30%, contain only a single species and a very small proportion contain large number of species. Past observations of this phenomenon have invoked taxonomic 'splitting', and implied this skew distribution is in conflict with strict tree-thinking or true phylogenetic systematics. Yet we show the predominance of monotypic genera is a strongly consistent pattern across Metazoa, so empirical evidence suggests it may be a 'real' result of speciation processes. To address this question, we compared genus-size frequency distributions from empirical data (real taxonomy of real organisms) with simulations that provide omniscient or ideal genus-size frequencies (simulated taxonomic sorting on simulated trees). We generated hypothetical trees using birth-death models with known and constant probabilities of speciation (birth) or extinction (death) at each generation. We imposed a taxonomic sorting on the set of species that were non-extinct after 500 generations, based on phylogenetic topology and/or character attributes for each surviving lineage generated during the simulation. These explored both character-similarity and relative distances of tips, with and without imposed monophyly. Thus we show that observed taxonomic patterns of living animals in fact closely match an idealised hypothetical taxonomy of monophyletic species-groups, especially when defined by character similarities. Monotypic genera are, as should be expected, very frequent, and large genera very rare (splitters 1, lumpers 0).

Aphyly and highly diverse organisms

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Many of the names in any recent classification may represent groups that have yet to be demonstrated as monophyletic. That is, many named taxa in use today are of unknown phyletic status. In an earlier paper it was suggested that these unknown groups might best be referred to as aphyletic, "meaning that they require taxonomic revision" (Ebach & Williams 2010). These groups have no status with respect to any phylogenetic interpretation. In our view, application of this terminology would avoid the often made assumption that when a monophyletic group is discovered (diagnosed, recognised) from within a group of species in an already known and named genus, then the species left behind are rendered paraphyletic and explanations for paraphyly are then discussed. In fact, in our view, most groups of species left behind after describing a monophyletic group are aphyletic: we do not know what their status is relative to the data to hand. Since we described the term aphyly we discovered another term meaning roughly the same, 'merophyly', introduced over 30 years ago by Nelson Bernardi (1981) and that Hennig used the term "restkörper" (which might be translated as 'the bits left over', or more simply 'remainder') before he introduced the term paraphyly. We discuss the term aphyly and give examples from two highly diverse groups of diatoms.

Areas of endemism under the semantic conception paradigm

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Historical biogeography consists of looking for relationships between areas of endemism. Since its inception, many authors have debated upon the “nature” of these areas of endemism. What are they? How to define them?

According to Axelius (1991), an area of endemism is a specific combination of at least two (or more) endemic species; this is the most common definition used nowadays by biogeographers. Many others also defined areas this way (e.g. Harold and Moï 1994). Others like Rieppel (2007) or Crother and Murray (2011, 2013) defend the theory that areas are individuals simply because species are individuals. We would like to give, through an ontological reasoning, a different point of view, under the semantic conception paradigm. This philosophical approach formalizes theories as models, i.e. sets of objects and relations with logical constraints. We present an alternative evolutionary model accounting for areas. We demonstrate the relevance of this model considering the ontology it provides, the interdisciplinarity it accounts for (i.e. reduction of historical biogeography, phylogenetic systematics and temporal dimension to the same model), and its faithfulness of the “adequacy to reality” protocol.

The Gulf of Gabès (southern Tunisia): center of Mediterranean endemism or ecophenotypic variations in extreme conditions?

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Although, the present Mediterranean marine fauna is the result of a history going back to the Messinian Salinity Crisis, current biogeographical patterns mostly reflect Quaternary to modern oceanographic conditions. The Gulf of Gabès, in southern Tunisia, is remarkable for its extreme ecological characteristics (major tidal amplitude, shallow depth, high insulation, high temperature) that demark it from “ambient” Mediterranean conditions. Starting with the work of malacologists at the turn of the 19th-20th centuries, the molluscs of the Gulf of Gabès have been recognized to exhibit a number of morphological characters that set them apart from the “typical forms” that occur in the rest of their Mediterranean. To date, 33 species (6% of the total Gulf of Gabès mollusc fauna) are treated as valid local endemics. Using an integrative taxonomy approach, combining molecular (COI and 28S genes) and morphological

data, the objective of the study is to re-evaluate the status of these Gulf of Gabès "local forms": are they valid, endemic species? or do they represent ecophenotypic variation? Given the young geological age (6-8 ka) of the Gulf, where would local endemics have originated? The gastropod genera *Jujubinus* (Trochidae), *Diodora* (Fissurellidae), *Ocenebrina* (Muricidae) and *Aplus* (formerly *Polia*; Buccinidae) all have in common non-planktotrophic larval development. They are represented in the Gulf by, respectively, 3, 6, 9 and 2 species, of which 2, 1, 5 and none are considered endemic. Our molecular results analysed with ABGD and coupled morphological data confirm the validity of some of the endemic taxa - but also infirms it in other cases; molecular data also reveal unsuspected cryptic lineages inside and outside the Gulf, underlining the weakness of current, morphology-based, taxonomy of many Mediterranean molluscs.

Why do different oceanic archipelagos harbour contrasting levels of species diversity?

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In a letter to Joseph Hooker dated Christmas Day, 1844, Charles Darwin commented on a recent enumeration of the Azores flora and noted: Watson's Paper on [the] Azores has surprised me much; do you not think it odd, the fewness of peculiar species? More than 160 years later, the distinctiveness of the Azorean flora – specifically the low number of single island endemics (SIEs) and limited intra-archipelago diversification in comparison with other archipelagos in Macaronesia - remains to be satisfactorily explained. This study investigates diversity and diversification of *Pericallis*, a Macaronesian endemic genus which exemplifies the distinctiveness of the Azorean flora: one species (with two subspecies) is recognised in the Azores (and both subspecies are multi-island endemics) whereas the Canarian members of the genus are more numerous and are largely SIEs. Integrating morphometric, genetic and bioclimatic data for Azorean and Canarian lineages we show that contrary to earlier suggestions, neither (i) differences in the taxonomic treatment of the morphological variation, nor (ii) the perceived ecological homogeneity of the Azores, can explain the differences observed. Genetic data demonstrate a stronger geographical signal in the Azores than the Canaries, reflecting the greater isolation of islands. From a genetic level, the Azores do not seem so 'odd', even if this is not reflected in morphology.

Biogeography and the evolution of succulence in the Old World genus *Aloe* L. (Xanthorrhoeaceae)

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Succulence in plants is an ecophysiological and morphological syndrome characterised by the presence of water-storing tissues and drought tolerance. The succulent syndrome is phylogenetically and geographically scattered in the plant kingdom, and has evolved repeatedly among angiosperms in particular. The genus *Aloe* L. (Xanthorrhoeaceae subfamily Asphodeloideae) is one of the most speciose of African succulent plant groups, with approximately 500 *Aloe* species on the African continent, Madagascar and the Arabian Peninsula. *Aloe* is charismatic and benefits from considerable taxonomic attention, yet the biogeography of this diverse group has been neglected. Recent molecular systematic studies of *Aloe* have afforded an opportunity to address this gap. A Bayesian consensus tree inferred for 184 *Aloe* species, using seven DNA regions (ITS, matK, rps16, psbA, rbcL and the trnL-F intron and spacer), was used to develop a biogeographic scenario for the genus. Divergence times were estimated using a penalised likelihood approach and ancestral area reconstructions were based on checklist distribution data for *Aloe*. The results indicate that *Aloe* originated in southern Africa around the mid-Miocene, and has a complex evolutionary history. Two major radiations, driven by different speciation processes (firstly, isolations and vicariance around ~10Mya, and subsequently by dispersal events), gave rise to the contemporary diversity of *Aloe*. Ancestral trait analyses suggest that, unusually, leaf succulence may have been almost completely lost repeatedly in *Aloe*.

No ecological opportunity on a continental scale? Diversification and life-history evolution of African true toads (Anura: Bufonidae)

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The niche-filling process predicted by the Ecological Opportunity hypothesis has been accredited as being a key mechanism for generating exceptional diversity in island colonizers. Whether the same process governs the lineage accumulation and trait disparity and evolution of continental colonization events is less clear. Here we test this prediction by investigating the rate dynamics and trait disparity of one of Africa's most prolific amphibian colonizers, the true toads (Bufonidae). By reconstructing the most complete, multi-locus molecular phylogeny of African Bufonidae to date

(comprising ca. 70% of all currently recognized species and uncovering an unexpectedly high number of cryptic taxa), we find that the diversification of lineages on the African continent has been relatively constant throughout time and across clades, with no evidence for an early burst or a diversity-dependent slowdown. Body, clutch and egg size evolution, traits often under strong selection pressures, have also been more or less constant throughout history and across clades, with relative subclade disparity decreasing more or less as a function of time (Brownian motion). Furthermore we show that habitat generalists have persisted in most extant subclades and speculate that their lower speciation rates may have buffered the proliferation of lineages. Due to the inherent dispersal ability or broad habitat tolerance of large-scale colonizers, the geographic size, ecological complexity and age of continents, we argue that the Ecological Opportunity model may not be the most suitable model for predicting the diversification history of continent-wide radiations.

Long-term decline in dinosaur speciation rates

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Whether the extinction of Mesozoic dinosaurs at the end of the Cretaceous Period 66 million years ago (Ma) was sudden and catastrophic or prolonged and gradual has been much debated. Previous studies have focused intensively on dinosaurian taxic diversity (raw or bias-corrected numbers of unique taxa) through time, or have been restricted in time to the last 10-20 million years of the Cretaceous, while speciation dynamics, e.g., patterns of speciation and extinction, remain largely unexplored. Speciation dynamics is key to understanding the evolutionary history and eventual extinction of dinosaurs. Using a Bayesian phylogenetic approach we found that in the three dinosaurian clades, Ornithischia, Sauropodomorpha and Theropoda, speciation slowed down, and after c. 100 Ma extinction rate actually surpassed speciation rate with Mesozoic dinosaurs on average seeing a reduction in their capacity to replace extinct species with new ones, making them vulnerable to extinction. Thus, dinosaurs were in a long-term decline prior to the Chicxulub impact and unable to respond quickly to and recover from the catastrophic event. We also found a significantly positive relationship between speciation and eustatic sea level, indicating geographical controls on speciation dynamics. While speciation slowdowns are widely observed, distinctions between various slowdown patterns such as saturation or declines have previously not been made, because the latter can only be detected in trees where taxa are sampled through time, e.g. Mesozoic dinosaurs. The methodology we use has the potential to address speciation dynamics in other groups, especially in elucidating the patterns and mechanisms of speciation slowdowns.

Testing for convergent evolution and adaptive radiations: the austral danthonioid grass radiations

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Parallel adaptive radiation to the same climate change should result from convergent morphological changes. These morphological changes may function as modulators, very variable traits which stimulate the diversification rate. We develop a protocol to test for convergent evolution, and also to locate modulator traits. We test our protocol on the parallel, late Miocene-Pliocene radiations of the austral danthonioid grasses: one radiation occurred in the African genus *Pentameris*, and other in the American-Australasian genus *Rytidosperma*. The two clades show a greater variance in plant height and leaf anatomy than the rest of the subfamily (tested using BAMM), thus exploring a greater morphological space than the rest of the (non-radiating) subfamily. These morphological changes could be interpreted as convergence to a more seasonal climate, and so a more open vegetation, reducing the advantage of long-lived, sclerophyllous leaves and tall plants which can persist in a dense shrubby vegetation. This explains the radiation of the danthonioid grasses in the late Neogene.

Cryptic morphological characters and how they are changing the way we interpret plant taxonomy and evolution

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In the last 20 years, plant systematics has experienced a change in focus, more commonly using molecular rather than morphological characters to elucidate natural relationships among taxa. As a result it is common to see cases of taxon polyphyly or clades that “don't make sense” in the light of morphological characters traditionally used to classify these taxa. The next step, where much effort is currently being applied by systematists and evolutionary biologists, is the careful search for “true” synapomorphies that support a given phylogeny and any consequent taxonomical changes and can explain the evolutionary history of the group. This work examines how micro-morphological traits and characters based on development – also sometimes called “cryptic” characters – are changing the way plant taxonomy and evolution are interpreted using examples from Myrtaceae. The potential for cryptic characters to explain systematics in Myrtaceae is currently being explored, with micro and ontogenetic characters (e.g. stamen development, nature of anthers, papillae and vascular system) found in some cases to be more consistent than traditionally used characters (e.g. calyx fusion, number of calyx lobes, seed and fruit type). These traditional characters while useful at some level, often present high homoplasy indices

at the genus or species level and are less useful for phylogenetic interpretation. Understanding of cryptic characters not only provides better support for systematics studies, but also allows a less biased interpretation of plant evolution and the phenotypic response of a group to its environmental pressures, ultimately leading to lineage diversification.

The effects of pollination and range shifts on the diversification of the tribe Antirrhineae

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Range shifts are considered an important precursor to evolutionary divergence because they place populations in different environments that favour different characters. Long-distance dispersal promotes an expansion in niche breadth in terms of pollination syndromes in angiosperms, potentially explaining a wide variety of pollination syndromes. Antirrhineae, a tribe under Plantaginaceae, is a useful group for studying the interplay between dispersal and pollination in macroevolution because it has members in the Old World and the New World, and exhibits numerous transitions in major pollinating groups.

By integrating predictive modeling and range reconstructions with phylogenetic analysis, we aim to: i) reconstruct where major range shifts have occurred within Antirrhineae; ii) determine whether range overlap increases or decreases with time since divergence within the tribe; and iii) examine whether shifts in geographic distribution and pollination syndromes are associated with differences in speciation rates in Antirrhineae.

We find that Old World had higher speciation rates than the New World in Antirrhineae, but the pollination mode did not have any effect on the diversification of the tribe. However, interaction of these two characters has a significant effect on speciation rates in Antirrhineae. Our age-range correlation analysis also suggest that sympatric speciation is predominant in the tribe, with a trend towards young nodes having more range overlap than older nodes in the phylogeny.

Chameleons through time and space: extinction or adaptation?

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Biogeographic patterns can be influenced by shifting distributions as a response to environmental conditions to which species are adapted, but alternatively can be explained by adaptation of organisms in situ to changing environments over time. To examine this hypothesis in chameleons, ca. 90% of described species in the family were examined in a dated phylogenetic framework. Most genera radiated in the Oligocene, and recent radiations are scarce, resulting in numerous paleo-endemic lineages, explained by the reduction of the Pan African forest coupled to the increase in open habitats since the Oligocene. Geographic regions (Eastern Arc, Madagascar) that contain fragments of ancient forest have higher phylogenetic diversity (PD) due to retention of paleo-endemic lineages. PD was lower than expected by chance in all areas, suggesting the phylogeny is over-dispersed, possibly as a result of extinction filtering. Recent radiation (e.g. Pliocene) is uncommon, and occurs primarily within only two genera. This suggests that these lineages were able to take advantage of fine-structure microhabitats (e.g. grasses, fynbos) within the open vegetation that emerged since the Pliocene. This is supported by morphological (i.e. small body size, limb lengthening, hand/feet reduction, and ornamentation reduction) and performance traits (bite force, gripping, sprinting) adapted to fine-structure habitats. In contrast, paleo-endemic lineages have not radiated substantially since the Oligocene-Miocene, and these lineages retain morphological features that are adaptive in forest habitats. This work suggests that biogeographic patterns for chameleons can be explained primarily by lineage loss that corresponds with forest habitat reduction since the Oligocene, but that certain lineages in this family have adaptively radiated to new habitats since the Pliocene.

Macroevolution of giant water scavenger beetles in the Cretaceous and Cenozoic

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Giant water scavenger beetles of the tribe Hydrophilini represent about 200 species spread on all continents but Antarctica. The systematics of this group has been investigated using morphological characters but no exhaustive molecular phylogenetic hypothesis presently exists. Here we sampled 81 species of this group for which we sequenced four gene fragments (CO1, Arginine kinase, 18S and 28S). We inferred

the phylogenetic relationships among Hydrophilini using Bayesian Inference and Maximum Likelihood. We also inferred the biogeographical history of Hydrophilini scavenger beetles across their entire range of distribution using a multimodel approach. Finally, we studied diversification dynamics to understand the impact of abiotic factors on speciation and extinction rates throughout the evolution of the group. Our results support the monophyly of all extant genera with the exception of *Hydrochara* in which *Brownephilus* is nested. We recover an origin of the tribe in the mid-Cretaceous in a Gondwanan setting. The early evolution of the group seems to have been shaped by vicariant events whereas more recent biogeographical patterns are likely the results of dispersal in particular toward the Nearctic region. We also recover heterogeneous evolutionary rates during the Cenozoic that could have resulted from climatic disruptions. Using giant scavenger beetles as a case study, we show that likelihood-based methods are an efficient tool to unveil the evolutionary histories of widespread clades and identify the triggers of their rise and fall.

The key role of systematics in conservation assessments of butterflies

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The hyper-diverse tropical regions present the biggest challenge for taxonomists, conservationists and ecologists, as abundance and distributional data necessary for thorough analysis is unavailable for many species. Accelerated rates of deforestation in the tropical forests make them a priority for more information and detailed studies on threatened species and future areas for conservation. One case study (among many) of how well-resolved taxonomies are critical to conservation is presented, following the systematic study of the poorly-known group ringlet butterflies, currently placed in the genus *Splendeuptychia* Forster, 1964 (Nymphalidae: Satyrinae). This genus was revised using morphological characters based on data from more than 1000 specimens and 30 collections around the world, data from fieldwork, online sources, and literature and in light of recent results from molecular studies. This research examines the feasibility of assessing the threat status of tropical butterflies following the current IUCN categories and criteria. Using collections data as the primary source and using an accessible methodology I attempt to deal with the challenges of working with poorly known butterfly groups, as they may be over-lumped and many have undescribed species yet, usually with small distributions. Once unnamed taxa and several cryptic species were recognised, the number of species-level taxa in this group increased significantly, as did the number of threatened species because species with restricted ranges were taxonomically overlooked. This study highlights the importance of detailed systematic research to achieve effective biodiversity conservation. Unless further resources are invested in core areas such as taxonomic studies, threat assessments on hyper diverse faunas and regions may be biased or inaccurate.

Are coral reefs driving rates of diversification in jacks and allies (Carangoidei)?

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Several studies have suggested that coral-reefs can drive diversification within a number of fish groups (e.g., wrasses and parrotfishes, pufferfishes and allies, damselfishes, butterflyfishes, and requiem sharks). With the exception of requiem sharks, however, all these groups include mostly herbivores, planktivores or species that feed on invertebrates. The major groups of reef-affiliated piscivorous fishes such as jacks, barracudas, snappers and groupers, have not yet been investigated. We generated the largest time-calibrated phylogeny for jacks, pompanos and allies, a major group of predatory fishes in coastal environments worldwide. This group exhibits great morphological and a rich fossil record dating back to the Eocene. Our phylogeny includes ~85% of the extant diversity and shows a late Cretaceous origin and post-KPg radiation of jacks. We reconstructed the morphospace of both extant and fossil jacks by digitizing 383 photographs for 114 extant and 31 fossil species using 16 landmarks and 31 semi landmarks, and used this to compare the levels of disparity between groups on the basis of habitat (reef vs non-reef) and diet (piscivores vs non-piscivores). Finally, we used BiSSE to test if shifts of habitat (reef vs non reef) and diet (piscivory vs non-piscivory) induced variation of the tempo of lineage diversification. Our results show a reduction in the morphospace occupied by the extant groups when compared to the Eocene taxa. On the other hand, extant groups living in the open water environment show higher disparity than extant groups living in association with reefs. Furthermore, piscivory, but not coral reefs association, leads to higher rates of diversification in jacks and allies.

The shell beds of Lake Tanganyika: Palaeoecology, patchy ecosystems and divergence in a rift lake

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Shell beds are full-circle, biologically generated habitats for living organisms and key windows on past environments in fossil outcrops and cores. Lake Tanganyika (LT), Africa, has huge carpets of shell beds; up to 30% of shallow soft substrate consists of densely packed shelly substrates dominated by dead shells of a single gastropod species (*Neothauma tanganyicense*). Like other biogenic habitats such as reefs, LT shell

beds host a rich, endemic fauna of sponges, fish, molluscs, crabs and other organisms. Some of these appear not only to be specialised on this unique substrate, but to have speciated *in situ*.

We are assessing this geologic-biologic system to determine how origin and persistence of the shell beds relates to population and evolutionary history of shell bed organisms and to ecosystem structure. Our multi-disciplinary project includes a range of approaches, from genetics of *Neothauma* to structural and sedimentological geology of the depositional systems. COI sequences reveal significant population structuring among living *Neothauma*, implying restricted gene flow even in this ubiquitous species. Understanding the mechanism of formation and age of these shell beds is critical for a range of issues from rates of divergence to interpretations of paleoclimates.

These shell beds are impacted by increasing rates of sedimentation caused by anthropogenic land-use changes. Preliminary data indicate that modern sediment blankets on the shell beds are thick and extensive enough to 1) preclude sponge growth, 2) remove cryptic habitats and 3) fragment these ecosystems into isolated patches.

A preliminary phylogeny for Upper Guinean angiosperms

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The Upper Guinean forests run along the West African coast from Sierra Leone in the west to Ghana in the east. They hold c. 2800 species, of which c. 25% are endemic to the region. Within the region are a number of 'hotspots': small geographic areas (e.g. south west Ghana) where high concentrations of globally rare species occur together. The Upper Guinean flora is relatively well described, compared with many parts of the tropics, although there is no consensus on the processes that have generated the diversity and distributions of these species. Here, I present a preliminary dated phylogeny for Upper Guinean angiosperms using the chloroplast barcode genes *rbcl* and *matK*. Around 40% of Upper Guinean angiosperms have been sampled, and their putative sister species (congenerics from elsewhere in Africa) have been included where sequences were available. Preliminary findings are presented regarding the timing, tempo and evolutionary processes involved in the diversification of Upper Guinean angiosperms. In particular, differences in the timing and tempo of the evolution of globally rare versus globally widespread species are considered, in order to understand Upper Guinean hotspot assembly. Understanding the evolution of hotspots in Upper Guinea can benefit interpretations of other hotspots to build a global understanding of how biodiversity came to be distributed the way it is.

Cave floras in SWChina: unexplored marginal biomes rich in diversity and undervalued for conservation

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China has ca 100k caves, an unknown proportion of which contain plants. These caves are associated with the karst and limestone landscape that stretches from southern China to Vietnam, Laos, Myanmar and into Thailand and Peninsular Malaysia. Whilst known to contain endemic species of priority for conservation in China this flora remains undocumented. We sought to address this by documenting the vascular plant diversity of 63 caves between 2009 and 2014 making 898 taxon observations of 424 species from 190 genera and 90 families. Of the species observed over ¼ are endemic to caves and could be considered cave specialists. In addition, over ¼ of the species observed were endemics to their respective Chinese Province (Guangxi, Guizhou or Yunnan). Over ¾ are endemic to China. We suggest therefore that caves are important for the conservation of species diversity for China. We also suggest that caves represent a distinct habitat for plants, characterised by low levels of photosynthetically active radiation (PAR), relatively constant humidity and temperature and soils with low levels of organic material.

We sought to identify factors influencing cave species community composition using multivariate and regression analyses and to make an estimate of the flora's species richness using non-parametric prediction (species area curves). Multivariate and regression analyses suggest that cave community species composition is influenced by precipitation, surface area, PAR, orientation, cave width and geographical distance. A species accumulation curve suggests that the cave flora could include 503 to 905 species (depending on permutation technique).

We discuss our findings in the context of current threats and conservation actions to karst landscapes and the caves they include and suggest that caves be the focus of dedicated conservation planning. We also believe that cave floras can be of value to explore broader questions in evolutionary biology: 1) the role of dispersal, population size, breeding system in speciation, 2) relict floras from a previous climate, and 3) adaptations to very low light and very stable environments.

DNA Barcoding and Community Structure Assessment of a mixed Dipterocarp forest in Brunei Darussalam

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Maintaining wide genetic diversity is essential for forest health, as it allows for adaption of species and conservation of ecosystem function. A clear understanding of how forest communities are structured is important for protection and restoration of ecosystems and their services that sustain human population. DNA Barcoding is a fast and reliable tool to assess and monitor biodiversity. As a DNA based method it can be used to identify species even when morphological characters (i.e. flowers) are not available, as well as to detect undescribed and cryptic species. Here, we assess biodiversity and phylogenetic community structures of a 25 ha mixed dipterocarps forest at Kuala Belalong (Brunei Darussalam) which is set up by the Centre of Tropical Forest Science (CTFS). Considering different ecological niches, all individuals of woody plants (> 1 cm diameter at breast height) were sampled from 38 subplots (10x10 m) leading to a total number of 2040 specimens. Samples were barcoded with the standard plant barcoding markers *rbcL* and *matK*. Initial investigations with the *rbcL* marker revealed 56 families which belong to 21 different orders. The available *rbcL* sequences were used to reconstruct phylogenetic relationships to get an insight into evolutionary processes responsible for species diversity. Phylogenetic analysis of the sequence data was consistent with the APG III phylogeny. To achieve higher resolution at species level *matK* barcode sequences will be included into the existing matrix of the *rbcL* sequences.

Edaphic determinism on tree community assemblages at a landscape scale in the tropical forests of South Cameroon

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Species distributions are often spatially structured within tropical forest tree communities. Such distributions are partly induced by the filtering of spatially structured environmental conditions, but also by seed dispersal limitation. In the present study, we aimed at disentangling the relative contributions of each process, using tree species abundances and detailed environmental data from 203 tropical forest plots (of 0.2 ha each) located in South Cameroon, at spatial scales ranging from 250 m to 100 km. To do so, we used a method combining Moran's eigenvector maps, variation partitioning and torus-translations to test the fraction of species abundance variation explained by spatially structured environmental variation (while discarding the effect of dispersal limitation), a fraction that is usually not testable when using advanced spatial models like MEM.

At the community level, 6.4% of the overall species abundance variation was significantly explained by spatially structured soil properties (essentially the soil texture and aluminium toxicity), while only a minority of species represented by min. 30 individuals (12%) were significantly distributed according to these properties. However, a higher proportion of the abundance variation (> 25%), at the community or population level, was attributed to dispersal limitation alone.

Our results provide further evidence that tree species assemblages are partly shaped by spatially structured habitat heterogeneity but that dispersal limitation also play a major role, a poorly documented subject in central African forests. We also highlight the usefulness of the torus-translation test to correctly interpret the spatially structured environmental effect (which always accounted for the most important part of the environmental contribution), as this effect was sometimes important but nearly or not significant.

From medicinal use to phylogenetic prediction in drug discovery in the genus *Euphorbia* L.: Classification of medicinal uses have major influence on data interpretation

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The urgent need of meeting medical needs combined with the alarming rate of biodiversity loss, and the lack of systematic approaches to plant-based drug discovery have fostered growing interest in phylogeny-guided approaches to plant-based drug discovery. Based on the hypothesis that plant-derived specialized metabolites form a mirror image of evolutionary relationships of the plants producing them, studies employ reports of medicinal uses as a proxy for bioactivity and through phylogeny predictions about unstudied species are made. As best practice, medicinal uses are classified into disease categories following standardized methods, which however, have limited ability to reflect unique pharmacological properties. In the present study we propose an alternative classification system of medicinal uses based on molecular disease mechanisms, which we argue are more closely related to the chemical nature and thus bioactivity of the plants metabolites. Using documented medicinal uses of the extremely species-rich (~2000) and near-cosmopolitan genus *Euphorbia*, known for its pro-inflammatory metabolites, including the recently released drug ingenol mebutate, we document the impact different classification systems have on subsequent data interpretation.

The Quest for *Cinchona* - a Phylogenetic Tale

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The quest for *Cinchona* or Jesuits' bark for the treatment of malaria is one of the most exciting tales in human history. *Cinchona* bark is probably the one remedy that has saved more lives and relieved more human suffering than any other remedy in history since its discovery in Peru in the early part of the 17th century. Imperial history, botanical confusion, and great variety in the quantity and composition of about 30 different *Cinchona* alkaloids among some 25 species in the genus *Cinchona* L. (Rubiaceae: Cinchonoideae) and among populations from different areas and habitats of the Northern and Central Andes complicated the search for the best quality of *Cinchona* bark. Is it possible that the plant hunters never found the best species or variety for quinine production?

In this talk we use phylogeny, chemical profiles, and environmental traits of over 100 samples representing about 25 species (20% of the tribe) and 8 of 9 genera from across the Andean mountain range to revisit the quest for *Cinchona*. Our results highlight the skills of the Native Americans to find the best medicinal plants and suggest that chemical diversity within species is primarily correlated with altitude. The methodologies developed through this project could pave the way for a theoretical as well as practical use of phylogenies as biochemical and medicinal predictors in plants.

Traits involved in human selection of useful South American palms

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There are more than 50,000 plant species used by local human communities around the world. How have humans selected these species? Morphological and ecological traits may be involved in that selection, however assessing the correlation between species' usefulness and their intrinsic traits is problematic due to phylogenetic autocorrelation: values of morphological and ecological traits do not vary randomly across species, but are constrained by phylogenetic relationships. Here, we focus on the palm family (Arecaceae), one of the most species-rich and economically important families in the tropics. For 210 palm species in northwest South America, we compile ethnobotanical information from 1,200 interviews across 20 localities in the region, along with a database of species' morphological traits and information on species' ranges and local abundance. Using the most up-to-date phylogeny available for South American palms, we perform a phylogenetically corrected exploration of potential morphological and ecological traits involved in plant human selection. Understanding the principles underlying this process can help us understand how humans explore biodiversity, but it can also provide leads to further explorations of useful biodiversity.


Neotropikey - identification resources

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Developed by the Royal Botanic gardens, Kew Neotropikey includes free, online identification resources to Neotropical Angiosperms. A family-level key to the 318 Angiosperm families present in the Neotropics was first launched in 2010 and is regularly updated. Whilst Neotropikey is an important identification resource for people with little access to botanical literature, a CD version of the 1st edition was published for use in places without internet access, like tropical field stations. 260 of the 318 families are accompanied by a family webpage containing highly illustrated family synopses with: Description, Notes on delimitation, Distribution, Distinguishing characters, References to important species-level identification literature, etc. About 100 of the family webpages contain dichotomous keys to genera. An illustrated glossary links particular terms directly to the family webpages. From 2011 onwards, an additional six genus-level matrix keys were developed to Latin American Malvaceae s.s. (plus a Scratchpad to the 78 Neotropical genera), Thymelaeaceae, Lauraceae, Plantaginaceae, Orobanchaceae, and Scrophulariaceae. And, currently the team is developing a 1st species-level matrix key to the large (c. 280 spp.), economically important legume genus *Inga*, endemic to the Neotropics. The keys are developed in Lucid 3.5 and the family webpages in Factsheet-Fusion (<http://www.lucidcentral.com/>); and the classification largely follows the APG II for the Dicot families, and the APG III the Monocots. While core-funding for Kew's Americas team provides staff time for development, co-ordination, and editing, more than 100 taxonomists: 45 in Latin America, 30 international, and 25 from Kew contribute their specialist families. Next steps will be to



develop a much-requested application for smart phone, and more genus- and species-level matrix keys and Scratchpads. (<http://www.kew.org/science/tropamerica/neotropikey.htm>).

CONTRIBUTED TALKS
MUSEUM OF NATURAL HISTORY
ANNEXE
(In the programmed order)



Mark Waters

Phylogeny and Evolutionary Significance of Cambrian Scalidophorans

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Scalidophora (priapulids, loriciferans, and kinorhynchs) and Nematoida (nematodes and nematomorphs) form the ecdysozoan clade Cycloneuralia, which is the sister group to panarthropods. Scalidophorans today belong to three relatively insignificant phyla, but their fossil record can be traced to the earliest Cambrian period where they played a much more important role in marine ecosystems. Morphological and phylogenetic studies show that scalidophoran morphologies have been conserved throughout evolutionary history, and thus the exceptionally preserved Cambrian species provide crucial information for illuminating the early evolution of Cycloneuralia and Ecdysozoa. However, due to the limits of preservation and the preliminary status of existing research, the morphological details, classification, systematic position, and phylogenetic relationships of these Cambrian worms are still sources of considerable debate, so a thorough systematic review of this Cambrian group of animals is overdue. Most Cambrian scalidophorans are priapulid-like, and phylogenetic analysis has assigned most of them to variable positions within the priapulid stem group or even more deeply within the ancestry of Scalidophora or Cycloneuralia as a whole, whereas a few taxa have even been resolved as crown group priapulids. The recently published new priapulid *Eximipriapulus globocaudatus* from the Chengjiang Lagerstätte (Yunnan, China) shows exceptionally preserved anatomical details that allow direct comparison with extant priapulids. The animal is inferred to have been an active burrower using a double-anchor strategy. Inclusion of *Eximipriapulus* in the most recent character matrix for cladistic analysis of fossil and recent priapulids resolves the new genus within the priapulid crown group.

Reconstructing relationships of fossil jawless fish (Pteraspidoformes, Heterostraci)

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Inter and intra-evolutionary relationships are fundamental to our understanding of small and large scale patterns of vertebrate evolution. Key amongst these are the ostracoderms: a polyphyletic group of jawless fishes comprising the jawed vertebrate stem. Only a handful of these clades have robust phylogenies in place, hindering our interpretation of early vertebrate histories. A new phylogeny is proposed for the Pter-

aspidiformes – the largest and most studied clade of heterostracan ostracoderms. Difficulties such as large amounts of missing data and the limited morphological variability within the group has led to an exploration of many different coding strategies. Using a combination of observations of museum specimens and data from published literature, unique characters have been constructed and cladistic analysis applied using Mesquite and TNT. Different coding strategies include an analysis with discrete characters only, a combination of discrete and continuous characters and gap coding strategies (transforming the continuous into discrete characters). All described Pteraspidiformes genera (43) are included along with two outgroup taxa (*Anglaspis* and *Nahanniaspis*). Two representatives of the Psammosteidae (*Drepanaspis* and *Psammosteus*) were then added to the analysis to elucidate their inclusiveness within the Pteraspidiformes. Here we show that many 'classic' Pteraspidiformes clades hold true under our analysis, with discrete and discrete and continuous datasets giving very similar topologies. The Psammosteidae are found to belong in a derived position within the protaspid Pteraspidiformes. Gap coding datasets, however, result in vastly disparate tree topologies to all other coding methods perhaps due to the method being highly sensitive to missing data.

Fossils increase congruence between molecular and morphological hypotheses of spiny-rayed teleost (Acanthomorpha) phylogeny

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With about 17 000 extant species (almost one third of vertebrates), Acanthomorpha is a large group of teleosts, characterised by spines on their unpaired fins. Since the 2000's, numerous large-scale molecular phylogenies have restructured the acanthomorph evolutionary tree by challenging previous, anatomy-based relationships. However, major uncertainties remain, in particular for the first dichotomies of the tree. In this study, we established an osteological database covering the base of the acanthomorph tree, in order to test the phylogenetic hypotheses proposed by molecular data with an independent character set. The taxonomic coverage included all relevant extant taxa, but also Upper Cretaceous fossils (amongst the oldest acanthomorphs known), which was not the case in previous anatomical studies. Our results showed that:

1. A congruence with molecular results is observed on most points, providing independent corroboration and morphological synapomorphies for the 'molecular' clades

2. Fossil taxa play a key role in achieving this congruence: when they are excluded from the dataset a different topology, highly different from the others, is found.

We emit the hypothesis that previous anatomical workers failed to uncover the relationships supported today, not because of a bad interpretation of characters, but because of an incomplete taxon sampling. We conclude that, in order to obtain consensual phylogenetic hypotheses, a dialogue between anatomical and molecular results, but also the inclusion of fossil taxa when possible, are critical points that should be addressed in more future studies.

Evolutionary relationships of the Haplosclerida from Irish and Mediterranean waters

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Previous work has shown clearly that systematic revision is necessary for members of the sponge Order Haplosclerida. Previously considered to have few described members of a single genus, Haliclona, we show that Ireland is host to many distantly related species across the major clades in what is now also considered to be a large and very diverse group, the marine Haplosclerida. We will discuss evolutionary relationships between Atlantic and Mediterranean species and, using a multidisciplinary approach including morphological, molecular, cytological and chemical approaches, discuss new synapomorphies to support clades. Part of our systematic approach includes the description of new taxa and the erection of old and abandoned taxon names.

Are data from 18 genes enough to resolve bark and ambrosia beetle phylogeny?

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Bark and ambrosia beetles are snoutless weevils that live and feed on phloem under bark in branches and tree trunks, or in the pith of twigs or in the endocarp of seeds, or deep in the heartwood where they cultivate fungi as food for the larvae. In addition to variable feeding modes, there is a tremendous variation in reproductive systems, including monogyny, bigamy or harem polygamy, and parthenogenesis or permanent inbreeding associated with haplodiploidy or paternal genome elimination. A largely resolved phylogeny will therefore provide an extraordinary powerful tool

in testing hypotheses on the origin of evolutionary novelties and species diversification in this group of weevils. Previous phylogenies were largely unresolved at deeper nodes and were ambiguous with respect to the monophyly of Scolytinae and its position among other weevil subfamilies, particularly the relationship to Platypodinae. This presentation summarizes phylogenetic results based on nucleotide and amino acid data from 18 gene fragments. A brief overview of major problems in the gene screening process is given and compared to NGS methods. Resolution at deeper weevil nodes was problematic although our data revealed that Platypodinae is clearly not related to Scolytinae and occurred as one of the early diverging lineages in Curculionidae, near Dryophthorinae (-idae). Considerable progress was made in the resolution of Scolytinae and now enables reconstruction of key evolutionary traits and their influence on speciation rates.

Species discovery and integrative taxonomy in jellyfishes (Cnidaria, Discomedusae)

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Marine species richness is estimated at ~226,000; another ~0.5-0.7 million species may be undescribed. Imprecision in these estimates is ascribed to the so-called taxonomic impediment, a penurious understanding of taxonomy as a scientific discipline, and undersampling in high diversity areas [e.g. tropics—Tropical Eastern Pacific (TEP)]. Here we describe diversity of a taxon—Scyphozoa—that is common in all oceans and is largely neglected, despite being economically and ecologically important. While scyphozoan systematics and taxonomy have been enriched by descriptions of new species, compilations, and monographs during the 19th and early-mid 20th centuries, the classification of ~140 spp. proposed in 1961 is essentially still in use today. The problem of accurately estimating the taxonomic richness persists because although molecular techniques resulted in transformational publications that promised a renaissance in the taxonomy and systematics of the group, those techniques have been only partially adopted (only 5% of the publications [between 2000-2014] integrative molecular and morphological approaches). To estimate the species richness of this taxon, we explored a poorly sampled area (TEP), used quantitative morphological approaches, and a robust molecular phylogeny to delimit and identify species; we discovered 19 new species, increasing the species richness for Discomedusae by 16%. This study will provide the foundations for ecological and biogeographical hypotheses, which are necessary to contextualize the evolutionary patterns of marine taxa.

Water mite speciation in Madeira

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In 1942, O. Lundblad, after extensive sampling in parts of Europe, published a study on Madeiran water mites. In his work he found 25 species, 24 of them new to Science, belonging to 12 different genus. Ten species belong to the genus *Torrenticola*, and eight of those *Torrenticola* species were found together in the same sampling point. To the untrained eye, *Torrenticola* species look very similar. This fact, together with the popular suspicion that taxonomists propose new species 'out of the blue' based on minimum differences, could give rise to the idea that those species were just 'figments of Lundblad's imagination'.

Attracted by the idea that some biologically interesting process was taking place with these taxa in Madeira, we decided to carry out a research program along the following lines: a) Study Lundblad's Madeira *Torrenticola* collection, available in the Stockholm Natural History Museum; b) Sample the original locations for fresh material, to further the morphological and molecular study.

Our communication reviews our present results, aimed at answering the following questions: 1) Are Madeira Lundblad's *Torrenticola* real species? 2) If so, which main phenotypic character allows them to coexist? 3) Are they the product of individual dispersion or are they the product of 'dispersal plus speciation' events in Madeira waters?

Integrated systematics finally gets a grip on a large genus – *Myrcia* (Myrtaceae)

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Case studies of the positive feedback loop between an integrated systematic approach, taxonomy, monography and classification in a mega-diverse 'nightmare' genus are described. Neotropical Myrtaceae are emerging from a period of taxonomic turmoil. Myrtaceae is one of the most taxonomically difficult families in south America due to 1) high levels of morphological similarity and plasticity, 2) the existence of two very large genera: *Eugenia* and *Myrcia* s.l. (ca. 1000 and 700 species respectively). *Myrcia* s.l. encompasses three other traditionally accepted genera, many species of which are gradually being transferred to *Myrcia*. *Myrcia* s.l. is of immense ecological importance in the Atlantic forests and cerrado savanna of Eastern Brazil and is diverse in other threatened tropical rainforest biomes such as in the Amazon and Caribbean. A monograph of the group is long overdue and will be supported by a new sub-generic classification currently in preparation. Under this scheme, *Myrcia* s.l. is divided into nine morphologically cohesive clades. Before a new classification of the group is published, these clades are tested using morphological and phylogenetic data to show that they are diagnosable natural groups. To test these groups, multiple, multi-disciplinary studies are underway. Clade by clade, researchers are increasing the sample of species included in DNA-based phylogenies, testing for monophyly and identifying species relationships. Clade by clade, (often) the same

researchers are monographing the species, providing descriptions, stabilising the nomenclature and generating baseline distribution data upon which other studies relating the taxonomic work to ecology and evolution can be built. These subsequent morphological, anatomical, biogeographical, evolutionary and ecological investigations then feedback into *Myrcia* s.l. systematics and have brought taxonomic control and a user friendly classification tantalisingly close.

Systematics of *Campylocentrum* (Angraecinae-Orchidaceae)

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Campylocentrum is a Neotropical genus with about 70 species belonging to the mostly Afro-Madagascan subtribe Angraecinae (Orchidaceae). Its monophyly is supported by molecular analyses that also indicated *Dendrophylax* Rchb.f. as its sister. Half of the species grow in Brazil, and one-third is endemic to the Atlantic Forest, which is cited as its center of diversity. A relevant taxonomic study of *Campylocentrum* is the *Flora Brasiliensis*, where an infrageneric classification was proposed including three sections. The characteristic tiny flowers, combined to the similarity among the species and the lack of updated taxonomic review, make difficult the taxonomic identification of the taxa. Mistakes are common, and they compromise, for example, the use of the information for phylogenetic analyses, conservation and biogeographical studies. Specimens from 70 herbaria were analyzed, and fieldwork was carried out, especially in Brazilian Atlantic Forest and the Amazon Basin. An accurate morphological analysis allowed us to recognize that the present classification is not natural, and several transfers of species are needed. Anatomical structure of the velamen, presence/absence of leaves, kind of leaves and number of parts in the viscidium are the main characters useful in distinguishing the sections. *Campylocentrum* sect. *Dendrophylopsis* comprises 15 leafless species with reduced stems and a viscidium of only one part, whereas *C.* sect. *Pseudocampylocentrum* includes seven species with granulose roots, terete leaves and elongate stems and a viscidium with two parts. The largest section with about 48 species, *C.* sect. *Campylocentrum*, is distinguished by smooth roots, conduplicate leaves, elongate stems and a viscidium with two parts. The conclusions of this study are preliminary, and the status of these groups will be further evaluated by a phylogenetic analysis based on molecular data.

The evolutionary history of *Cypella* (Iridaceae: Iridoideae) and allied genera: toward a taxonomic revision of Tigridieae based on leaf anatomy, floral morphology and molecular evidences

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Tigridieae is a New World tribe encompassing 16 genera and about 160 species of bulbous perennials in Iridaceae and forms a monophyletic lineage defined by molecular and morphological synapomorphies, however the current systematics of the tribe remains poorly understood. Results of previous studies have shown that the circumscription of the subtribes Cipurinae and Tigridiinae, as well as the generic delimitations based on minor floral variations, should be revised to maintain the principle of monophyly in Tigridieae. Analyses based on nine molecular markers were conducted to investigate the phylogenetic relationships among 64 species of *Cypella* and 12 allied genera placed in Cipurinae. The phylogenetic framework was used to assess the evolution of leaf anatomy and floral morphology among Tigridieae. The observations showed that foliated leaves with subepidermal marginal sclerenchyma are only found among species of six genera, which constitute one of the two major lineages of the tribe. This result strongly suggests a new delimitation of the subtribes based on leaf anatomy and molecular evidences. The pattern of evolution of floral morphology among *Cypella* and closely related genera shows that the generic circumscriptions should be best evaluated in the light of a multivariate continuum rather than a series of discrete categories, this continuum of morphological variations reflecting presumably different levels of adaptations to different pollination strategies. This evolutionary pattern is consistent with the adaptive radiations observed among the African genera of Iridaceae and their current taxonomic treatment.

Rate heterogeneity and inconsistency of current models in molecular dating – the case of Annonaceae and Lentibulariaceae

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Age estimates within Annonaceae, particularly for the two major clades (subfamilies Annonoideae and Malmeoideae) that comprise most of the species, have been disputed for some time. The average branch length from the crown node to the tips in Annonoideae is twice that of Malmeoideae. These differences translate into contrasting age estimates depending on the assumed pattern in change of molecular evolutionary rate. The pattern of sister clades with contrasting average branch

lengths is not uncommon in angiosperms. In Lentibulariaceae, Pinguicula is a clade with shorter branches that is sister to clade with longer branches, comprising the genera *Utricularia* and *Genlisea*.

We set out to critically test two commonly used Bayesian dating methods that apply different models of substitution rate variation: the relaxed-clock and random local clock model. For both families, we varied the ratio of 'long branch clade' and 'short branch clade' species represented, and used no calibration points other than fixing the age of the root node. We found that the analyses using both models are sensitive to sampling bias. In the analyses using the relaxed clock model, the proportion of 'long branch clade' species influences the estimated age of the 'short branch clade' crown node: when the fraction of 'long branch clade' species is below a certain threshold, the age of short branch clade crown node increases. The analyses using the random local clock model did not converge on a single, but on two different distributions of ages and substitution rates.

Phylogenetic backbone of Annonaceae (Magnoliidae) based on 29 whole-chloroplast sequences

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Annonaceae are a species rich magnoliid family (~2400 species, 109 genera) that probably originated in the Upper Cretaceous. They are globally distributed in tropical rainforests and have a relatively consistent habit (mainly trees and some lianas). Although general floral structure is stable and conserved across the family (three whorls of three tepals, numerous stamens and carpels), they display high floral morphological diversity in characters putatively related to pollination strategies, such as perianth shape and differentiation. These traits make Annonaceae an ideal model family to investigate diversification, floral evolution, and their possible links. To address the question of diversification rates and morphological evolution, a well-resolved phylogeny is crucial. The current phylogenetic framework of this family is comprehensive, but some key nodes are still unresolved, mainly in subfamily Malmeoideae. Thus far, only a limited number of plastid markers have been the main source of molecular characters in plant phylogeny, including Annonaceae. With Next Generation Sequencing, a substantially expanded molecular dataset can be used to help us resolve the remaining uncertainty in the phylogeny of Annonaceae. Here we present a new phylogenetic backbone of the family based on 29 new whole chloroplast genomes (24 Annonaceae, 5 outgroups). Following a "genome skimming" approach, whole-genomic DNA was sequenced as a whole on an Illumina HiSeq2000 platform, with only the chloroplast genomes assembled. Several assembly strategies were used and compared. We show this approach to be efficient for *de novo* assembly of plastid genomes from non-model plants, consistent with recent pilot studies on other plant

taxa. Phylogenetic analyses were conducted with standard reconstruction methods (Maximum Parsimony, Maximum Likelihood and Bayesian Inferences). The tree produced here is a first step towards a more comprehensive phylogeny of Annonaceae where each genus will be sampled and the same methods and sequencing strategies used.

The evolutionary trends of genus *Hypochaeris* s.l. (Lctuceae, Asteraceae)

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The genus *Hypochaeris* L. s. l. includes c. 60 species, which could be grouped in five phylogenetic groups. Four groups distributed by the Old World with c. 15 species, most of them Mediterranean-Macaronesian, and the last one, larger, with c. 45 species, is the results of a fast adaptative radiation in South America, as consequence of a single colonization event, from North Africa, as far as we know. *Hypochaeris* includes annual and perennial herbs, with usually only basal leaves, homomorphic or dimorphic achenes, and $x = 3, 4, 5$ and 6 as a basic chromosome number. As many Asteraceae, *Hypochaeris* exhibits sporophytic homomorphic incompatibility system, with self-incompatible, self-compatible species and taxa with SI and SC populations. The aim of the present study is a comparative analysis of character evolution: incompatibility system, annuality and chromosome number, along the phylogeny of the genus. The preliminary results showed that self-compatibility and annuality were the most derived characters.

Accelerating integrative taxonomy in the genomics era: RADseq provides unprecedented species resolution in the genus *Lupinus* (Leguminosae)

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A species designation is a critical hypothesis that serves as the foundation for a wide range of disciplines across biology. Without a rigorous approach to species delimitation and designation of new species, we risk basing downstream analyses and findings on unstable ground. Integrative taxonomy combining multiple types of data (morphological, molecular, geographical & ecological) to test species hypotheses can provide a more robust approach than traditional herbarium-specimen based morphology alone. Recent advances in species delimitation methods and the availability of genome-wide DNA sequence data sets via NGS have generated renewed interest in integrative taxonomy, but its uptake within botany has remained slow. Species delimitation and phylogenetic resolution remain pervasive problems across the genus *Lupinus*, especially for recently evolved clades where species boundaries remain poorly defined and species relationships unresolved. These difficulties present significant problems for documenting taxonomic diversity across the genus. To address these problems we are assembling densely sampled (all species and multiple accessions of species) phylogenies using genome-wide DNA sequence data generated using nextRAD (SNPsaurus, Oregon, U.S.A). These new phylogenies are interpreted in conjunction with detailed morphological, geographical and ecological evidence to refine species delimitation, detect cryptic species and infer robust hypotheses of species relationships. We have generated nextRAD data for 475 accessions for three clades (Florida, Old World and Andes). These data have unprecedented power to resolve species limits and relationships on a large scale.

Evolution of the leucobryoid morphology in Dicranidae (Bryophyta)

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Haplolepidaceous mosses (subclass Dicranidae) form the second largest lineage of mosses with c. 4000 species. A peculiar morphology within Dicranidae is called leucobryoid, comprising species with a whitish-green color due to a particular leaf costa structure. When first described, these plants were grouped in the family Leucobryaceae. Later taxonomical studies reviewed that classification, and ultimately it was redefined based on preliminary molecular phylogenetic reconstructions. Although nowadays it is known that leucobryoid species occur in different families together with non-leucobryoid species (Calymperaceae, Dicranaceae, Leucobryaceae), their exact phylogenetic relationships are yet insufficiently resolved. This study aims to improve our knowledge on the origin and evolution of the leucobryoid morphology. One important question concerns relationships of the leucobryoid genus *Octoblepharum*, which was placed either in Leucobryaceae, Calymperaceae or in an own monogeneric family. A previous molecular study resolved *Octoblepharum* as sister to Calymperaceae, thus supporting the latter treatment. However, Octoblepharaceae did not gain wide acceptance. Based on a broader marker and taxon sampling, our results confirm the molecular divergence between *Octoblepharum* and Calymperaceae, and validate the status of Octoblepharaceae. They corroborate that the leucobryoid

morphology appeared at least four times in Dicranidae, indicating that a detailed morphological study is needed to compare the leucobryoid morphology in these lineages. Our results also corroborate marked differences in evolutionary rates in Leucobryaceae and Calymperaceae, being much faster in the latter. These differences may be related to the more tropical distribution of Calymperaceae, since in habitats with higher energy the evolutionary rates tend also to be higher.

New ingredients for an old recipe: contribution of the Asian aubergines to a better understanding of the complex evolutionary history of Old World spiny solanums (subg. *Leptostemonum*)

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A giant among the flowering plants, *Solanum* L. (c. 1500 species) has a cosmopolitan distribution and numerous plants of global agricultural importance (e.g., potato, tomato, aubergine). Within *Solanum*, the spiny *Solanum* clade forms the most species-rich major lineage (c. 450 species). In contrast to their New World relatives, Old World spiny *Solanum* have received little attention. The Asian taxa in particular have never been revised in their entirety and have been sparsely sampled in all phylogenetic analyses to date. This has significantly impeded understanding of *Solanum*'s evolutionary history. Based on sampling from Africa and Australia Old World taxa have been characterized as a monophyletic group. To test this hypothesis, we are clarifying Asian spiny *Solanum* species delimitation and building broad molecular sampling. Our preliminary results show that these taxa do not all resolve with other Old World taxa, some being instead members of New World clades. Our data refute the monophyly of Old World spiny *Solanum* and suggest at least three independent introductions from the New World, thus shedding new light on biogeography of spiny *Solanum*. We are now enlarging sampling in order to further clarify these patterns and fill this major gap in knowledge of *Solanum* phylogeny.

Genome skimming and phylogenomics of *Nicotiana* section *Suaveolentes* (Solanaceae)

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Genome skimming involves shotgun high-throughput sequencing of genomic DNA at low-coverage. Traditional uses of such datasets focus on plastid genome assembly; however a large proportion of genomic information, particularly repetitive elements, is usually ignored. These repeats were recently shown to have useful phylogenetic signal when their abundance is considered as a phylogenetic character in closely related species or clades. Utilizing comparative graph-based clustering of high throughput sequence reads, which results in abundance estimates of different

classes of genomic repeats, phylogenetic trees are then inferred based on the genome-wide abundance of different repeat types treated as continuously varying characters. Here we present results of phylogenomic analyses using this approach, along with analyses of plastomes in order to infer the systematic relationships in *Nicotiana* sect. *Suaveolentes*, a group for which there is little genetic differentiation in standard phylogenetic markers. Aside from important phylogenetic results for this recently diverged section of the genus, perspectives are given more generally for the use of this methodology in systematics and DNA barcoding.

Genetic patterns within the diploid-tetraploid *Arabidopsis arenosa* group

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The *Arabidopsis arenosa* group is a diploid-autotetraploid complex unique within the entire genus by co-occurrence of both diploid and their polyploid derivatives. As a close relative of *Arabidopsis thaliana* it is, together with other wild relatives of this important model plant, moving into focus of plant evolutionary biology and experimental botany. In order to elucidate relationships within *A. arenosa*, we conducted a population-level field sampling across its whole range and evaluated patterns of cytotype and genetic diversity of 140 populations using flow cytometry, RAD sequencing, and nuclear microsatellites. We detected a parapatric distribution of the diploid (mainly SE Europe) and tetraploid (mainly NW Europe) cytotypes forming contact zones in south-eastern Alpine forelands and in the Carpathians. Despite close cytotype contact at the landscape scale we found only negligible proportion of within-population cytotype mixtures. The diploid cytotype split into five genetically distinct groups that are geographically segregated but do not reflect the obvious morphological differentiation between lowland and alpine areas. Ecological preferences differ partly among the main diploid lineages but do not contribute to segregation of the cytotypes.

The presence of marked internal ploidy-level, morphological, ecological and hitherto largely unknown genetic variation highlights *A. arenosa* as very promising model for addressing various evolutionary questions on origins and consequences of plant genome duplication.

The recent discovery of four new, narrow endemic plant species within the well-studied *Plantago* genus shows the urgent need for taxonomic research in the Neotropics

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The Neotropics harbour around 90,000–110,000 species of seed plants, about 37% of the world's species, and encompass widely known hotspots for conservation priorities. However, many plant species in this area are threatened by habitat destruction, overexploitation, and biological invasions. Most dramatic is, however, the fact that numerous still undescribed, narrow endemic species may become extinct before they are discovered and described. *Plantago* (Plantaginaceae) is a cosmopolitan genus including over 250 species, concentrated in temperate and high-elevation tropical regions. Most *Plantago* species have comparatively restricted geographic distributions, including many extremely narrow endemics. This genus is comparatively well-studied taxonomically, as it has been subject to taxonomic treatments by many notable botanists, including Joseph Decaisne (1807–1882), Robert Pilger (1876–1953) and Knud Rahn (1928–2013). Nevertheless, since 2011 four new *Plantago* species have been discovered in South America: *P. corvensis* Hassemer, *P. pyrophila* Villarroel & J.R.I.Wood, *P. rahniana* Hassemer & R.Trevis., and another new *Plantago* species currently being described. All four species are narrow endemics, classified as Endangered or Critically Endangered according to the IUCN criteria. These discoveries highlight the fact that even for well-studied genera, there are still considerable knowledge gaps which thwart the implementation of effective policies and measures for the conservation of biodiversity in the Neotropics. For some other less-studied plant groups, the knowledge gaps are likely to be even greater. To address this urgent problem, further taxonomic research focusing on Neotropical plant groups is both fundamental and essential, and should include field work, revision of herbarium material, and state-of-the-art molecular phylogenetic analyses. Unless such research is prioritised, current trends of diminishing funding available for taxonomic research and diminishing numbers of skilled taxonomists will continue to hinder the discovery and conservation of the world's biodiversity.

Phylogenetic reassessment of subfamily Ajugoideae (Lamiaceae)

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Family Lamiaceae are well known plant group by their beauty and economic importance, but the reliable phylogeny of family as a whole is still lacking to date. In

particular, the phylogeny of subfamily Ajugoideae has been changed dramatically based on molecular sequence data, in which, for example, genera *Caryopteris* and *Clerodendrum* were transferred from Verbenaceae, and *Discretitheca*, *Ovieda*, and *Tripora* are newly proposed or resurrected monotypic genera. However, the entire phylogeny of Ajugoideae was never suggested after these changes of subfamily delimitation. To retrace the evolutionary history of Ajugoideae, we conducted phylogenetic analyses using available sequence data on nuclear *ITS*, plastid *trnL-F*, *rbcL*, *matK*, and *ndhF* of Ajugoideae. Multiple approaches were adopted such that analyses were conducted on the single and various combination of each marker. Furthermore, we evaluated discriminative power of each marker and calculated the genetic divergence at the various taxonomic level. The significance of reconstructed phylogeny and application of those markers for the study of entire Lamiaceae will be discussed.

Joining up for digitisation – a pilot project between Kew and the Natural History Museum London

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European herbaria have traditionally had divergent practices: different paper sizes, different curatorial techniques and different management systems. For centuries we have lived with our differences, but this year Kew and the NHM-London decided that in order to move forward digitisation of our joint holdings of plant diversity efficiently, we would do a pilot to the same standards—an experiment to see if we could overcome our historical differences to leverage the power of working together to make our collections digitally accessible. Efforts were focussed on several groups of economic plants, *Solanum*, *Hypericum* and Dioscoreaceae. Over 70,000 specimens have been imaged using Picturae's 'digistreet' method. A 'digistreet' is essentially a purpose-built conveyor belt that minimises manual handling of fragile herbarium specimens and captures high resolution images. After the herbarium specimen images had been through quality control they were then sent to a data capture team in Suriname, where the label information was transcribed. A number of different digitisation models were tested to discover the most optimum workflow. We will discuss the challenges we faced, the problems we overcame, the lessons learnt and our experience of how this coming together across London worked.

Scholarly publishing becomes a part of the research process: Data publication and re-use in the Biodiversity Data Journal

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One of the biggest and increasingly worrying impediments in biodiversity science is the currently dominating publication model in non-machine-readable formats, e.g. PDF and the need of additional effort to mark-up, extract and database the information from them, so that to allow re-use. The Biodiversity Data Journal (BDJ) and associated Authoring Tool (PWT) build on the experience of ZooKeys and PhytoKeys do a few steps more. BDJ is the first work flow ever to support the full life cycle of a manuscript, from writing through community peer-review, publication and dissemination within a single, online collaborative platform.

The PWT provides a set of pre-defined, but flexible, article templates, and import function from external databases based on community accepted standards (Darwin Core, TaxPub), including track change and comments tools, review history, online collaboration between authors and external contributors. Submission to the journal is simply at the click of a button.

All data can be downloaded in tabular format (CSV) straight from the article text and re-used by anyone, given that the original source is cited. Upon publications, occurrence data and taxon descriptions are also automatically exported in machine-readable Darwin Core Archives to be harvested and indexed by aggregators (GBIF, EOL, Plazi, etc.). Occurrences are published as a separate dataset in GBIF bearing the BDJ article DOI, which increases the visibility and citation probability of both the article and the data.

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Ecology of ectomycorrhizal fungi associated with Dipterocarp trees in Malaysia

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The family Dipterocarpaceae are dominant components of tropical forests in SE Asia, both in terms of species richness and importance as timber trees. All members of the family are known to form ectomycorrhizal (ECM) associations with a wide, but currently unknown diversity of fungi. Little is also known about the degree of specificity between the trees and fungi. The current project will address both these issues. A preliminary compilation of ECM fungi found fruiting with Malaysian dipterocarps contains 208 species representing nineteen families, but recent molecular work characterising fungal communities directly on the host roots strongly suggests a much higher number of potential ECM fungi including many undescribed species. However, molecular identification is currently constrained by a lack of reference DNA barcodes. My proposed work therefore initially involves producing reference data from ECM fungal herbarium collections housed at Royal Botanical Garden Edinburgh. A total of 308 collections from Malaysia have been sampled and are being sequenced. Based on morphological and sequence data, potential species richness is much higher than currently believed with the Boletaceae and Russulaceae being the most species rich families. Commonly, collections with European names have been erroneously identified and represent undescribed species.

Are the Coastal Forests of Eastern Africa sources of species diversity?

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The Coastal Forests of Eastern Africa (CFEA) are one of the most threatened biodiversity hotspots in the world. The distribution of biodiversity and how it accumulated in this hotspot is poorly known. In particular, it is unclear whether the present distribution of diversity is mainly: a) The result of recent colonisation from adjoining refugial areas (Eastern Afromontane Region) due to habitat instability and inundation of the CFEA, or b) the result of radiations from relicts within CFEA which have persisted in suitable climatically stable environments. To test these questions we are using next generation sequencing (NGS) methods and Species Distribution Models (SDMs) on amphibians. Preliminary results suggest that diversity is heterogeneously distributed and that this often corresponds to habitats that have been climatically stable in the CFEA. The phylogenetic diversity within the CFEA indicates substantial variation among sites – and not that the adjoining Eastern Afromontane Region is necessarily a source area of diversity. Various lines of evidence (e.g. narrowly distributed species, numbers of endemics, phylogenetic analyses, and SDMs) now support the idea that the coastal region is, at least partially, a source area of diversity.

Eco-ethology of bees visitors on *Vicia faba* L. var. *major* (Fabaceae) in Algeria

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Due to their ecological key position and diversity, plant-bee relationships constitute excellent models to understand the processes of food specialisation. The purpose of this study is to define and identify the most important species of bees foraging broadbean flowers, we estimated morphological, phonological and behavioural features. We discuss the results by considering the food specialisation level of the visitor. In the studied populations (Algiers, Algeria), visiting bees belong to four different genus: *Apis*, *Andrena*, *Eucera* and *Xylocopa*. *Eucera* is foraging broad beans flowers during months of April, May. The genus *Andrena* and *Xylocopa* were found on weeds after the flowering period of beans. The two species have not a preferred type of vegetation compared to *Eucera*. The main pollinators were generalist bees such as *Apis mellifera* L. and *Xylocopa pubescens* Spinola (Apidae), and specialist bees such *Eucera numida* Lep. (Apidae). The results show that no one of the studied species, neither the specialist, nor the generalist ones, share adaptative morphological or behavioural features that may improve foraging on *Vicia faba*. However, there is a narrow synchronisation between the daily and yearly phenologies of *E. numida* and those of *V. faba*. This could be an adaptation of the specialist bee to its host plant. Thus, the food specialisation of *E. numida*, as for most specialist bees, would be more linked to its adapted phenology than to an adapted morphology.

Developing an identification key for the economically important genus *Inga*

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Inga is a neotropical genus of c. 280 tree legume species, and a common feature in lowland and montane rainforest from Mexico, throughout Central and South America to Uruguay. *Inga* is notorious for its morphological uniformity. All species are trees with paripinnate leaves and characteristic foliar nectaries. It has been cultivated for more than 2,000 years for the sweet, white tissue surrounding the seeds. More recently, *Inga* species are being used as multi-purpose trees as shade trees for coffee and cacao, in agroforestry systems, as sources of fuelwood and timber, and as soil improvers, as *Inga* species produce nitrogen-fixing root nodules, which improves

growth and yield. As a sandwich student working in the Americas team at Kew since August 2014, I have spent the past year helping to develop the web-based Neotropikey using Lucid 3.5 software. Since January 2015, I have been creating an electronic identification key to the c. 280 species of *Inga*, using a combination of Pennington's monograph (1997), and the vast *Inga* collections held at Kew. In consultation with Dr. Pennington, a list of morphological characters important for species identification was created for scoring. Images for all species including their diagnostic characters were sourced. This key is important, because Pennington's (1997) monograph provides no key to *Inga* sections, as the character overlap between species and sections makes preparation of a dichotomous sectional key impossible. Thus, only users with species level knowledge will know which sectional sub-key to use in his monograph. When completed, my new key will provide a quick, reliable and accessible tool for identifying *Inga* species, and it will be incorporated into the Neotropikey web-site.

Sharing one of the world's largest microscope slide collections: digitisation at the Natural History Museum

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Microscope slide collections are a typically under-utilised resource in museums. The slide digitisation pilot project at the Natural History Museum aims to capture data from 100,000 slides in ten months. Research grade images will be generated for 20% of the material in the pilot using an off-the-shelf automated histology scanner (Zeiss Axioscan z1). Due to the variety of slide sizes, specimen conditions and mounts, additional instrumentation (SatScan, Zeiss AxioZoom v16) has to be used and protocols and must be developed. The poster presents digitisation workflow, the progress the pilot has made so far and highlights the challenges inherent in digitising these historical collections.

Introducing Involucraoideae and its importance to understanding the evolutionary history of figs and their close relatives Castilleae (Moraceae)

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Figs and fig wasps have long been a textbook example of coevolution, and to this end much research has been dedicated to understanding this interaction from

ecological and evolutionary perspectives. Figs, comprising 800 species are among some of the larger genera of angiosperms. Recent studies of the mulberry family, Moraceae, to which figs belong have identified the sister lineage of figs, the Castilleae. This is a small group of approximately 60 species, which help us see figs not only as a large lineage, but also one that likely experienced increased rates of diversification throughout its history. Little work has been done on Castilleae, and we argue that a better understanding of the clade, hereafter Involucraoideae, to which both figs and Castilleae belong, provides a better vantage point for studying the evolutionary history of the figs. In this study, we define Involucraoideae and provide a phylogenetic framework for its members making use of the most comprehensive fig and Castilleae phylogenies currently available, including more than 300 accessions for six nuclear markers (ITS, ETS, *G3pdh*, *Waxy*, *At103* and *nucpGS*). Finally we propose clade names within Involucraoideae to provide a common framework for understanding the origin and evolution of pollination and diversification patterns within the group.

Phylogeography of western Mediterranean *Cymbalaria* and systematic implications

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Cymbalaria is a monophyletic genus composed of 17 taxa endemic to the northern shore of the Mediterranean Sea. The westernmost species form a monophyletic group of four species that grow in the islands Corsica and Sardinia, and some of the Balearic Islands (Mallorca, Menorca and Cabrera). Here we performed molecular (AFLPs and chloroplast DNA sequencing) and morphological analyses of 43 populations of this group in order to infer its phylogeography and to propose a congruent taxonomic classification. AFLPs support four monophyletic species mostly congruent with current taxonomy and the morphological analyses. *Cymbalaria aequitriloba* is a morphologically variable species distributed in Corsica, Sardinia, Mallorca and Menorca. *Cymbalaria fragilis* was previously considered an endemism of Menorca allegedly characterized by its smooth seeds, but here we demonstrate that alveolate seed populations from Cabrera and Menorca, previously considered to belong to *C. aequitriloba*, also belong to *C. fragilis*. *Cymbalaria muelleri* and *Cymbalaria hepaticifolia* are shown as two monophyletic species endemic to Sardinia and Corsica respectively. Both AFLPs and sequencing results suggest that the common ancestor of the group originated in Corsica-Sardinia. Two long distance colonization events to the Balearic Islands are inferred. The first dispersal event was linked to speciation and originated *C. fragilis*. In the second, *C. aequitriloba* expanded its range from NW Sardinia to the Balearic Islands. Further range expansions of these two species within the Balearic Islands would have been facilitated by land bridges during Pleistocene glaciations. Results also suggest a latter colonization of Corsica by *C. aequitriloba*, after the

unsuitable climatic conditions during glaciations. Incongruities between AFLPs and sequence data suggest a mostly effective reproductive isolation of the species at present, but a history marked by hybridization.

Cryptic diversity of skeneiform gastropods in the hydrothermal vent fields of Okinawa Trough, Japan

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Iheyaspira lequios Okutani, Sasaki & Tsuchida, 2000 discovered and described from the Iheya North Knoll hydrothermal vent field has long been considered the only skeneiform gastropod in the Okinawa Trough vents. During the last decade such gastropods of a similar size (~8mm) and form have been found across many vents the Okinawa Trough, and have all been identified as *I. lequios*. Recently, these gastropods were barcoded and found to comprise of four distinct lineages with consistent differences in the cytochrome c oxidase I (COI) gene. In the present study, the phylogenetic relationship of these four lineages within Gastropoda was analysed using a multi-gene Bayesian analysis using COI, 16S rRNA, and 12S rRNA. The resulting consensus tree revealed that three lineages belongs to Skeneidae including *I. lequios* and two undescribed *Iheyaspira* species but the forth lineage surprisingly represented a neomphaline gastropod. Solid morphological differences especially in radula characteristics were found between the skeneids and the neomphaline, confirming their systematic position. This is the first record of Neomphalina from hydrothermal vent sites in Japanese waters, although one species *Retiskenea diploura* Warén & Bouchet, 2001 is known from seeps of Japan Trench. In addition, the genus *Iheyaspira* was found to be paraphyletic and *I. bathycodon* Nye, Copley, Linse & Plouviez, 2013 from vents of Cayman Trough may need to be housed in a new genus. These results highlight the need to better explore and understand the true diversity of small vent gastropods, which have been much overlooked in many parts of the world in the previous years.

Systematics of *Calydorea* Herb. (Iridaceae) in Southern Brazil: taxonomic review and range extensions

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Although revised in the past 25 years, the South American genus *Calydorea* Herb. (Iridoideae: Tigridieae) remains inadequately understood within Iridaceae. Kew World Checklist of Monocots considers that nine species occur in Brazil, eight of them

distributed in the Southern region. This study aims to review taxonomy and spatial distribution of the genus in South Brazil. Data were provided by continuing botanical exploration, as well as national and international herbaria reviews. Vegetative and reproductive traits were examined, measured and compared with protologs and types. A synoptic treatment of the genus is presented for Southern Brazil, that includes nomenclatural review, updated descriptions, revised key for identification, phylogenetic relationships, illustrations and comments on distribution data. Six species are recognized for Southern Brazil (*Calydorea approximate* R.C. Foster, *C. basaltica* Ravenna, *C. campestris* (Klatt) Baker, *C. crocoides* Ravenna, *C. luteola* (Klatt) Baker and *C. nuda* (Herb.) Baker) and four species, *C. alba* Roitman & A. Castillo, *C. charuana* Deble, *C. longipes* Ravenna, *C. riograndensis* Deble, are reduced to synonymy. The southern Brazilian species show two distinct distribution patterns, encompassing the Pampa Biome on the one hand and the high altitude areas of the Atlantic Forest Biome on the other hand. Phylogenetic relationships reveal that the species studied are organized into two clades, and form distinct geographical clusters.

Shedding light on the adaptive evolution of a dominant and wide-spread plant lineage in the Neotropics

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Although studies based on network databases have enhanced our understanding on the floristic and community structure of the Amazon forest, very few have committed to face the systematic challenges and improve the taxonomic treatment of tropical plant lineages, especially those with high morphological incongruence. This is the case for *Protium heptaphyllum* (Aubl.) Marchand, a species complex classified as one of most hyperdominant trees across the Amazon Basin. My study aims to disentangle the evolutionary history of this dominant and widespread tree and check if what have been recently classified as a single hyperdominant species actually represents more than one monophyletic lineage. We used an integrative approach based on morphology, population genetics, and functional ecology to test this assumption and to understand the role of habitat heterogeneity in promoting adaptive divergence in Neotropical plant lineages. *P. heptaphyllum* populations have been sampled at research tree-plots across many different tropical habitats (e.g. Rain Forests, Savannas, Swamp Forests, Seasonal Dry Forests and Grasslands). This group exhibited a remarkable leaf shape, flower and fruit trait variation and very few characters are informative to resolve its taxonomic delimitation. Preliminary phylogenetic analysis based on multiple nuclear genes showed that *P. heptaphyllum* populations are polyphyletic and this taxon should not be classified as a single hyperdominant species. According to the phylogenetic species concept, this clade could be divided into five

different diverged plant lineages. Although we have not yet achieved a desired phylogenetic resolution, our results suggest that conclusions made upon the hyperdominance phenomenon in the Amazon should be more cautious and conservative, because there is a great chance of hyperdominant species representing multiple incipient diverged lineages. We strongly encourage tropical systematists to perform a consistent taxonomic and phylogenetic review of hyperdominant trees sampled by the Amazon Tree Diversity Network and the Amazon Forest Inventory Network.

Diversity of jellyfishes

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Scyphomedusae are important pelagic predators at the center of concerns about a 'rise of gelatinous zooplankton' and the degradation of coastal ecosystems. Yet knowledge of the scyphomedusae is largely incomplete: 40-50% of species are unknown, and approximately half of these are uncollected. Moreover, journal papers and newspaper press about the causes of changes in the frequency or intensity of 'jellyfish blooms' have referenced only a small portion (in fact <10%) of known species indicating general under-appreciation of jellyfish diversity and its implications. While current taxonomic publications describe a little over 200 valid species of Scyphozoa molecular analyses, quantitative morphological analyses, and examination of existing collections suggest there are at least 30 known cryptic species, 38-80 species in existing collections that are new to science yet undescribed, and ~80 species of Scyphozoa remaining to be discovered. We estimate total ~340-380 species in Scyphozoa. Novel diversity includes representatives of new families and new genera in known families from poorly surveyed regions.

Explosive diversification of *Solanum* L (Solanaceae) in the old world

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Solanum L. (Solanaceae) is one of the largest genera of angiosperms with great economic importance. The variety of traits and occupied niches makes this genus an interesting case study to understand the diversification dynamics in angiosperms. Using a time-calibrated phylogeny and BAMM, a Bayesian framework to detect heterogeneity in evolutionary rates, we identified shifts of diversification among main clades and estimated the distribution of present-day diversification rates for 1170 species of *Solanum* L. We found differences in distribution of rates between new world and old world taxa. This variation is associated with an explosive diversification that

coincides with an inferred dispersal from South America to the old world. Further studies are needed to reveal the effect of traits and environment on diversification of this intriguing genus.

The impact of taxonomic rank on measuring biodiversity

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Biodiversity is often measured by species richness; alternatively, higher taxa such as genera are used as a 'surrogate' especially in the fossil record. However a 'genus' could represent a single species, or a thousand. Our aims were to quantitatively address how genetic diversity varies among genera, using several relevant larger clades. We gathered sequence data from comprehensive databases (GenBank, Barcode of Life Database) combining all available published COI sequences for species in five clades of hard-shelled marine invertebrates: chitons (Neoloricata n=1607 sequences), ark clams (Arcoidea n=707), bryozoans (Cheilostomatida n=1331) barnacles (Sessilia n=6120) and brittlestars (Ophiurida n=3330). We then quantified genetic variance within each taxonomically-defined genus. The main metric of interest was genetic pairwise distances, calculated from sequence alignments independent of any phylogenetic framework. The observed distances represent the percentage of nucleotide positions with differing basepairs between sequences; the minimum genetic 'size' of a genus represents the maximum pairwise distance among the group. In each of the 5 clades (216 genera, 13,095 sequences, 684 species) at least one genus had an intrageneric pairwise distance of >20%. The genetic sizes of genera are highly variable, chiton genera range from distances of 1% (*Rhyssoplax*) to 37.5% (*Leptochiton*). The number of sequences sampled does not impact genus 'size'. Genetic 'size' is positively correlated to the number of species sampled ($r(26)=0.61, p<0.01$). In fact, the effect of genus systematic species richness is a stronger effect in chitons ($F(1,26)=12.56, p=0.0015$). The total species diversity of the genus impacts measured genetic 'size' even when that diversity is not fully sampled. Examining genus level diversity in a diverse sample of appropriate organisms will ultimately help quantify the error introduced through taxonomic surrogacy.

Testing the utility of museum specimens for DNA barcoding and phylogenetics of the Colorado potato beetle genus, *Leptinotarsa* (Coleoptera)

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The beetle genus *Leptinotarsa* Stal, 1858 is a genus originating in Mexico with a geographical spread south into Central America and north into North America as far as Canada. Some species are considered pests, most notably the Colorado potato

beetle, *L. decemlineata*, is a serious pest of potato and has spread to parts of Asia and Europe via its association with the potato *Solanum tuberosum* L. In order to assess the utility of specimens in the collections of the Natural History Museum, London (NHM), for molecular analysis, we initially selected species with reasonably large numbers of specimens and a range of specimen ages. Specimen age ranged from 184 years old to 5 years old, with the bulk of the specimens collected during the 1930s-1950s. Where possible, we used the most recently collected material, but the museum collection is relatively specimen poor for some taxa, obliging us to experiment with older material. We used a 'non-destructive' protocol and found that DNA extraction and subsequent sequencing success was greater using whole individuals incubated for 15-17 hours. Age of specimens did not determine sequencing success overall, suggesting that specimen preservation and storage is more influential. The mitochondrial gene region *cytB* was successfully sequenced for most species. Future goals include collaboration with researchers on a more comprehensive phylogeny using multiple gene regions, and investigating species distributions and host ranges over time using data generated from NHM collections digitisation.

Towards a taxonomical revision of *Calendula* L. (Asteraceae) in the Iberian Peninsula

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Calendula L. is a circum-Mediterranean genus that comprises 10 to 25 species, depending on the taxonomic concept adopted. Several partial taxonomic revisions have been done, but none included the entire genus, and no agreement has been reached on its infrageneric classification. The inconsistent taxonomic concepts preconized by the different authors is a consequence of the large morphological variability of the genus (including the still not very well understood phenomenon of heterocarpy), of the occurrence of intermediate forms and of a large cytological variability ($2n = 14$ to 88 chromosomes, genome sizes and ploidy levels). To contribute to a better classification and understanding of the evolutionary relationships of the taxa of this genus, morphometric analysis, karyology and flow cytometry were used in plants extensively collected in the field, complemented with herbarium vouchers and plants obtained through seeds. The results obtained so far enabled us to delimit four species: *C. arvensis*, *C. tripterocarpa*, *C. officinalis* and *C. suffruticosa*. In the latter we included nine subspecies, including the formerly recognized species *C. incana*. As *C. incana* shares the same chromosome number and genome size as *C. suffruticosa*, the former species was considered a subspecies of *C. suffruticosa* and not a distinct species. This was further reinforced by the results of molecular analysis (O. Plume, pers. com.) which also do not support the segregation in two groups. In this work we present

a summary of the data that led us to propose this classification of the genus for the Iberian Peninsula.

Low phylogenetic beta diversity and geographic neo-endemism in Amazonian white-sand forests

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Over the past three decades, many small-scale floristic studies of white-sand forests across the Amazon basin have been published. Nonetheless, a basin-wide description of both taxonomic and phylogenetic alpha and beta diversity at regional scales has never been achieved. We present a complete floristic analysis of white-sand forests across the Amazon basin including both taxonomic and phylogenetic diversity. We found strong regional differences in the signal of phylogenetic community structure with both overall and regional Net Relatedness Index and Nearest Taxon Index values found to be significantly positive leading to a pattern of phylogenetic clustering. Additionally, we found high taxonomic dissimilarity but low phylogenetic

dissimilarity in pairwise community comparisons. These results suggest that recent diversification has played an important role in the assembly of white-sand forests causing geographic neo-endemism patterns at the regional scale.

Taxonomy and evolution in the clades "*Inula bifrons*" and "*Inula montana*" (*Inula* L.; Asteraceae): Taxonomic position and phylogenetic affinities of the Iberian endemism *Inula langeana* Beck.

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The clades "*Inula bifrons*" and "*Inula montana*" (*Inula* L.; Asteraceae) comprise five species mainly distributed in Eurasia, some of them endemic to the Western Mediterranean. Previous morphological and genetic data suggest that polyploidy and hybridization may have played an important role in the evolution of both clades. Particularly, a hybrid origin of the Iberian endemic *I. langeana* has been traditionally proposed. We have analysed the genetic and morphological variation of these clades using AFLPs markers and a morphometric study to address questions on species delimitation and phylogenetic relationships within these two clades. Our data show that reticulate evolution (probably ancient hybridization or incomplete lineage sorting) has played an important role in the evolution of the clades, which has obscured the traditional taxonomic interpretation of the whole group. Based on newly generated data, we provide a taxonomic framework for the members of the clades "*Inula bifrons*" and "*Inula montana*", as well as a key to the species involved.

SkyIslands Database: Effective management of biodiversity data

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Tools are increasingly required to manage and access the burgeoning amount and types of biological data being generated. We have developed an integrated data management system for taxonomic data that allows subsequent dissemination of taxonomic knowledge. Our "SkyIslands" database focuses on amphibians found in the Eastern Afromontane Region of Africa – an area designated as a biodiversity hotspot, poorly understood with a large undescribed cryptic diversity and highly threatened. Biological data has been obtained from over 20 years of fieldwork and previous historical collections. The database is based on FileMaker, MySQL, and Java. It allows the storage of different types of data including genetic, morphological, distribution records, acoustic, and images. All data can be queried and searched for and subsequently exported in a range of formats.

One important aspect is the implementation of BLAST in the database that allows the querying of genetic data against GenBank and other new unpublished genetic

data simultaneously (including genetic similarity scores and adjustable cut-off %). This allows rapid and comprehensive barcoding of new and unknown samples including easy data extraction for making phylogenetic trees. The query system we developed provides a best summary of all available genetic data – and therefore species identification and phylogenetic relationships. These user-friendly processes in the “Skylslands” database lead to rapid identification of samples towards short or long term biodiversity studies in the region. We plan an online platform to be available for various types of users. Overall, the database aims to provide an impetus for increasing knowledge on the biodiversity and its conservation. In addition we want to make this extended BLAST service available to the scientific community: www.graviton.ch/blast.

Systematic implications of the vascular supply to the gynoecium in the tribe Myrteae (Myrtaceae).

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A diagnostic character of Myrtaceae is the presence of an inferior ovary. The evolutionary origin of the inferior ovary in Myrtaceae is much debated by floral morphologists. Myrteae is the largest tribe of Myrtaceae, it has a principally neotropical distribution with some species tolerant of colder, drier biomes. The two scenarios of ovary origin in Myrteae are appendicular (resulting from the fusion of the base of the hypanthium) or receptacular (resulting from fusion with the floral receptacle); a mixed scenario is also possible. Studies related to the vascularisation of the gynoecium allow the different ovarian origins to be elucidated; complementary information is also available from the vascular supply to the ovules, number of carpels and nature of placentation, little studied characters relevant to the analysis and understanding of evolutionary relationships and systematics of tribe Myrteae (Myrtaceae). The aim of this study was to map structural features related to the vascularisation of flower buds of 20 species of Myrtaceae to elucidate differences in ovarian origin. Standard anatomical analyses techniques were used to visualise selected characters and their evolutionary history was traced using Mesquite (v. 2.71). Results indicate that most species are bicarpelate, pluriovulate with an appendicular origin of the ovary. Most species have ten monocyclic vascular bundles in the floral tube and trans-septal vascularisation of the placenta. Morphological character optimisation over the most recent phylogenetic hypothesis of relationships in Myrteae suggests that the Myrteae ancestor had receptacular inferior ovaries with multiple ovules per locule. Results are interpreted in light of ecological changes throughout the evolutionary history of the tribe.

Systematics and evolutionary history of the *Helichrysum pendulum* complex (Compositae) in the Mediterranean basin

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The geological and climatic history of the Mediterranean basin over the last 6 million years has been determinant in shaping current geographic pattern of genetic variation in organisms. The evolutionary history of the *Helichrysum pendulum* complex, distributed in several islands and isolated continental localities of the Western-Central Mediterranean basin, makes an ideal case of study. Chloroplast and nuclear DNA were sequenced and multivariate morphometric analyses were performed for representatives of 44 populations, covering the whole range of the complex. Our results suggest that the complex originated in northern Africa and colonized several islands and continental areas of the northern basin through the Gibraltar and Sicilian straits using land connections during phases of low sea level, but also through long distance dispersal events. While nuclear sequences suggest a model of isolation by distance and show a strong genetic barrier between populations of Western and Central Mediterranean areas, chloroplast data reveal the existence of two divergent and not geographically structured haplotype groups within the complex. Ancient hybridization among distantly related lineages is suggested as the most plausible cause for the pattern of haplotypes, while evidences of current hybridization between *H. pendulum* and several species out of the complex are detected with nuclear data. Considering together morphological and molecular data, a new taxonomic treatment is provided, where six species are recognized, three of them of hybrid origin.

How does above- and below-ground carbon storage change with forest age?

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Tropical forests store more carbon than any other terrestrial ecosystem. Globally there is now a greater area of secondary forest than old-growth (primary) forest. These secondary forest systems are critical for carbon sequestration and storage; however, total carbon budgets of secondary forests are little understood. We currently lack knowledge of how total carbon stocks within secondary forests change with forest age, and the relationships between different carbon pools. Using a network long-term study plots in continuous forest, and across a chronosequence of forest ages, we aim to produce detailed estimates of above- and belowground carbon and identify the

relative contribution of different carbon pools to total carbon stocks. To achieve these estimates, we will measure belowground carbon within soil and roots, and above-ground carbon within living and dead biomass. We will integrate these detailed plot-level estimates with existing canopy height data and LiDAR imagery, to extrapolate carbon estimates to the landscape-scale. Results from this study will improve our understanding of carbon stock dynamics within secondary forests, enabling us to plan effective conservation to achieve policy goals such as REDD+.

Morphological studies of a new genus of Polytrichaceae with two disjunct species in East Africa and the Himalaya

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The family Polytrichaceae comprises a large number of structurally complex mosses, as well as others that are structurally less complex and have been recognised historically in the polyphyletic genus *Oligotrichum* s.l., a group with many southern and northern hemisphere members. Recent molecular analyses combined with a rigorous morphological and anatomical study using the compound light microscope (LM) and scanning electron microscope (SEM) support the recognition of *O. glaciale* and *O. cavalli* under a new genus that is more closely related to *Psilopilum*, *Steereobryon* and *Atrichum* than to other members of *Oligotrichum*. Capsules of *O. glaciale* were discovered for the first time from the type locality, while identification of new localities for the species in the Sino-Himalaya amongst recent collections leads to a great extension of its known range. The species concepts of these two species were reassessed with the aid of thorough morphological observations. Here we detail the morphological characters supporting the new taxonomy. The degree of development of leaf lamellae, differentiation of the leaf margin, and the size, shape and habit of the leaves were studied. Sporophytic characters were also examined with special emphasis on capsule morphology, including peristome architecture and the distribution of stomata in the apophysis in both dry and wet states. Although the two species are mutually highly distinct, a thick apophysis with cryptopore stomata in the dry state is synapomorphic for the new genus.

AlyBase – database of names, chromosome numbers and ploidy levels of Alyseae

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The Alysseae represents the third largest tribe of the family Brassicaceae. Its native range is in Eurasia and North Africa and the centre of diversity lies in the Mediterranean and Irano-Turanian regions. Phylogenetic relationships in the Alysseae have been poorly explored until recently when a series of molecular studies were published and the traditional morphology-based taxonomic concept of the tribe was proven to be artificial. In order to summarise current knowledge on the tribe and to facilitate further studies we created a research infrastructure for the Alysseae taxa consisting of the database of accepted names and their synonyms and published chromosome number/ploidy level data. Based on available evidence, we provide an updated generic concept of the tribe and suggest recognizing 24 genera within Alysseae. All chromosome number and ploidy level data were checked in primary sources and taxonomic revision was done, based either on voucher specimens or on the localities of origin. Production version of entire project uses database platform PostgreSQL 8.3 deployed on Debian Linux. Client side uses CakePHP framework with XHTML, CSS, and JavaScript. GoogleMaps API serves for geographic data visualisation.

Mega-complex typification in a mega-diverse group: the case of *Myrcia guianensis* and allied species (Myrtaceae)

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Myrcia s.l. comprises three genera, *Myrcia*, *Marlierea* and *Calypttranthes*, and has about 700 species. Nowadays, this large group is divided into nine monophyletic informal groups, each in the process of monography, with a subgeneric classification in preparation. Aside from the complex descriptive taxonomy required, a major challenge facing revisionary work is typification. After more than 150 years of taxonomic uncertainty, one informal group, the 'Guianensis group' can be confidently studied as a 'whole', since it is certainly monophyletic. The 'Guianensis group' is distributed throughout the Neotropics, mainly in the Cerrado and Atlantic Forest biomes of Brazil. Within *Myrcia* s.l., an already nomenclaturally chaotic group, the 'Guianensis group' is one of the most confused. As a result of immense morphological plasticity at the species level, the number of existing names greatly outnumbers that of accepted species. The Guianensis group currently includes 36 species based on 365 names, most of these described by Berg in *Flora Brasiliensis* (1857-1859). Large-scale reassignment of types to names is now necessary as a result of specimen destruction during WWII or when two or more collections have been designated as types. Lectotypification or

neotypification is necessary for respectively 92 and 5 names, and is a painstaking process requiring location, identification and justification of 19th century names in multiple collections. Taxonomic revision, even of a relatively low number of accepted names, is seriously slowed if the underlying typification is 'mega-complex'.

Exploring the generic boundaries in *Psammopyrum* (Triticeae, Poaceae)

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The internal classification of the tribe Triticeae has undergone profound reorganizations since cytotaxonomic techniques proved useful in the classification of the group. The European species traditionally included in *Elymus* s.l. were later distributed in four genera based on their genomic constitutions: *Elymus* L., *Thinopyrum* Á.Löve, *Trichopyrum* Á.Löve and *Psammopyrum* Á.Löve.

Psammopyrum includes three species, one of them with two subspecies: *Psammopyrum athericum* (Link) Á.Löve from W and S Europe, and *Ps. fontqueri* (Melderis) Á.Löve, *Ps. pungens* (Pers.) Á.Löve subsp. *pungens* and *Ps. pungens* subsp. *campestre* (Gren. & Godr.) Á.Löve from the Balearic Islands and the Iberian Peninsula (the latter present also in NW France). The genomic constitution that characterizes the genus *Psammopyrum* was first established based on the chromosomal behaviour of artificial hybrids. However, further cytogenetic data obtained using *in situ* hybridization techniques for *Ps. athericum* and *Ps. pungens* questioned the genomic constitution initially proposed for the genus. The present study aims at revising the generic boundaries of *Psammopyrum* from a cytogenetic viewpoint and provides new data of *Ps. fontqueri* using GISH and FISH techniques. Furthermore, leaf anatomy is studied for this species, as well as for others from closely related genera, all of them previously included in *Elymus* s.l. A new genomic constitution is proposed for *Ps. fontqueri*, which is similar to that of *Ps. athericum* and *Ps. pungens*. Besides it is demonstrated that the anatomical characters may be highly useful in the delimitation of the genus *Psammopyrum*.

Pterocarpus rohrii s.l. (Leguminosae: Papilionoideae: Dalbergieae) one or ten species? Morphometric re-evaluation and revision of this polyphyletic species complex

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Recent phylogenetic analyses suggest that the neotropical timber species *Pterocarpus rohrii* s.l. is polyphyletic (Saslis-Lagodakis et al., 2011; Klitgaard et al., 2013). Species limits for *P. rohrii* s.l. are tested here, in light of the conflict between the phylogeny and Rojo's (1972) broad species circumscription which is causing headaches throughout the Neotropics to botanists, foresters, and conservationists needing to identify this economically important species. Specimens were selected for morphological study to include all the morphologic and geographic variation within this species complex, and all names currently synonymized under *P. rohrii* s.l. Species limits were tested using morphometric analyses of 34 characters recorded from 171 herbarium specimens including the type specimens of all the synonymized names. Principal coordinate analyses revealed morphologically similar but distinct species. Qualitative characters with diagnostic potential were identified to justify the recognition of these species, though quantitative characters had limited diagnostic value. Nine taxa previously synonymized under *P. rohrii* s.l. are here reinstated, including eight species (*P. floribundus*, *P. hayesii*, *P. reticulatus*, *P. rufescens*, *P. steinbachianus*, *P. villosus*, *P. violaceus*, and *P. zehntneri*), and one variety (*P. violaceus* Vahl var. *angustifolius* Benth.) is recognised as a species new to science, *P. angustifolius* Mansfield-Williams & Klitgaard. Our study shows that for taxonomically complex and confused groups, revisionary and phylogenetic studies are iterative processes. The phylogenies have highlighted taxonomic challenges in what was known to be a difficult group and were used to direct the morphological studies.

Amazonian forests in Pando, Bolivia: floristic diversity and composition

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We describe two types of forests in western Pando, terra firme (dry ground) and varzea (seasonally inundated). We installed five permanent one hectare plots, three in terra firme and two in varzea, and tagged, measured and identified all trees with d.b.h. ≥ 10 cm. In total 2854 individual trees, 366 species, 188 genera y 54 families were recorded. Diversity at family, genus and species level is relatively similar in the two forest types. Varzea averaged 673 individuals with d.b.h. ≥ 10 cm/ha, 117 species/ha, 89 genera/ha, 37 families/ha, and a Shanon-Wiener diversity index of 3.73; and terra firme 503 individuals with d.b.h. ≥ 10 cm/ha, 117 species/ha, 83 genera/ha, 37 families/ha, and a Shanon-Wiener diversity index of 3.89. On the other hand, the expressed forest similarity (Sørensen) is 30.6% (species level), 56.5 (genus level), and 81.3 % (family level), demonstrating that these forests are floristically distinct. The most ecologically important species in varzea are *Theobroma cacao*, *Socratea exorrhiza*, *Virola pavanis*, *Astrocaryum murumuru*, *Attalea phalerata*, *Brosimum lactescens*, and *Sorocea briquetii*. *Pentaplaris davidsmithii* and *Otoba parvifolia* are restricted to varzea forests

of the preandian zone, whilst *Manilkara bidentata* and *Virola pavonis* are restricted to the varzeas of the study area in Pando. This is coupled with a particularly low abundance of *Iriartea deltoidea* in the varzeas of Pando, while this species is dominant in preandian varzeas. The most ecologically important species in terra firme are *Tetragastris altissima*, *Pseudolmedia laevis*, *Bertholletia excelsa*, *Cecropia sciadophylla*, *Phenakospermum guyanense*, *Alseis reticulata*, *Pausandra trianae*, *Oenocarpus batata* and *Poecilanthe effusa*.

Frugivory, functional traits and the diversification of a tropical angiosperm family: Annonaceae (Magnoliales)

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Frugivory (i.e. fruit-eating and seed dispersal by animals) is ubiquitous in tropical ecosystems, but the role that frugivores have played in the macroevolution of species-rich tropical plant families remains largely unexplored. This project will investigate how plant traits relevant to frugivory (e.g. fruit size, fruit colour, fruit shape, understory/canopy growth form, etc.) are distributed within the angiosperm family of custard apples (Annonaceae), how this relates to diversification rates, and whether and how it coincides with the global biogeographic distribution of vertebrate frugivores (birds, bats, primates, other frugivorous mammals) and their ecological traits (e.g. diet specialization, body size, flight ability, etc.). Annonaceae are particularly suitable because they are well studied, species-rich (ca. 2400 species), characteristic in all tropical rainforests, and dispersed by most groups of vertebrate seed dispersers. Using a phylogenetic framework and functional trait and species distribution data we will test (i) how fruit trait variability relates to phylogeny and other aspects of plant morphology (e.g. leaf size, plant height, growth form, floral traits) and animal dispersers and their traits, (ii) to what extent interaction-relevant plant traits are related to diversification rates, and (iii) whether geographic variability in fruit traits correlates with the biogeographic distribution of animal dispersers and their traits.

Wallace's Line and the biogeography of *Aglaia* (Meliaceae)

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Southeast Asia has one of the most diverse terrestrial biota on our planet. Despite increasing scientific interest, the Indo-Australian Archipelago, geologically highly complex and hosting an outstanding level of endemism, remains only partly understood biogeographically. We present an updated and resolved phylogenetic tree for

the woody genus *Aglaia* (Meliaceae), and investigate its geographic origin and dispersal history. The two distinct *Aglaia* fruit types in Sundaland, one with seeds dispersed by primates and the other by birds, are also found in Australasia, but the dispersers east of Wallacea are different. Previous biogeographical analysis of *Aglaia* demonstrated that the faunal boundary, Lydekker's Line, represented a dividing line for *Aglaia* and that relatively few species had a distribution that included Sundaland, Wallacea and Australasia. Most of those that did were complex or variable species, each consisting of several entities. Our latest biogeographical analysis (BEAST, SDIVA, DEC), based on DNA sequences of 157 accessions of *Aglaia*, representing 102 species and all phylogenetic entities, shows that the directionality of dispersal events to or across Wallacea was predominantly eastwards, following the expansion of wet tropical forest across Wallace's Line and beyond. *Aglaia* had a Sundanian origin and started to disperse eastwards during the Miocene, with limited dispersal across Lydekker's Line. The comparison of the age of clades with the proposed age of their areas of distribution shows good temporal agreement.

Phylogeny and biogeography of *Ceiba* Mill. (Malvaceae: Bombacoideae) using next-generation, targeted enrichment sequencing

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Ceiba Mill. (Malvaceae: Bombacoideae) comprises 18 mostly Neotropical species and is one of the most conspicuous elements of neotropical Seasonally Dry Tropical Forests (SDTF), which represent some of the most threatened and least studied forests in the world. *Ceiba* has a historically complex taxonomy and some problems of species delimitation remain unresolved. Previous Bayesian analyses of sequence data from ITS and ETS for 14 species recovered *Ceiba* as monophyletic and as sister to *Pseudobombax* and "*Pachira quinata*". *Ceiba* comprises three main clades that are geographically and ecologically structured: (i) a humid forest clade including *C. samauma* and *C. pentandra*, sister to the remaining species, though with weak support; (ii) a clade composed of *C. schottii* and *C. aesculifolia*, from Central American and Mexican SDTF, and (iii) a South American SDTF clade including 10 species. Furthermore, data did not support monophyly of the '*insignis*' morphological complex or the two sections of the genus that are based on pollen and staminal appendages characters. To investigate interspecific relationships further and to assess biogeographic history of the genus, we are using molecular phylogenetic approaches based on next-generation sequencing techniques, specifically using targeted enrichment. This technique enables the sequencing of hundreds of independent nuclear loci, as well as loci from the chloroplast genome, which together can provide many phylogenetically informative characters. With a robust and detailed phylogeny, we can

integrate molecular, morphological, and ecological data to contribute to species delimitation in *Ceiba* and use the biogeographic history of the genus to gain insights into the evolution of Neotropical SDTF.

Phylogenetic relationships and evolutionary dynamics of relevant morphological characters in *Odontites* and related genera (tribe Rhinanthaeae, Orobanchaceae)

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Parasitic plants represent an attractive study group due to its special life style, physiology and ecology. Although the position of some families and genera of parasitic plants within the global Angiosperm phylogeny remains unclear, the monophyletic tribe Rhinanthaeae —traditionally included in the family Scrophulariaceae— was transferred to the Orobanchaceae based on the analysis of DNA sequence data. The phylogenetic relationships between the genera included in the Rhinanthaeae are more or less well known, but the species level relationships are only studied for a few genera (i.e., *Euphrasia*, *Bartsia* and related genera, *Phtheirospermum* and related genera). Here, we present a phylogeny of *Odontites* s.l. based on the analysis of nDNA (ITS) and cpDNA (*rps16* y *trnK*) sequences. We compare the species groups obtained with two different taxonomic treatments based on morphological data. Furthermore, the variation and evolutionary dynamics of some selected morphological characters traditionally considered relevant for the intraspecific classification of *Odontites* is studied using RASP software.

Floristic consistency of the main forest vegetation types occurring in the Cono Sur of South America through analysis of more than 3500 tree species

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The biogeographic history of southern South America led to a markedly distinct flora within the frame of the Neotropics, which is also particularly heterogeneous in terms of eco-geographic distribution. This environmental complexity is at the base of the many and controversial classification systems proposed for the vegetation of the so-called Conosur (Paraguay, Chile, Argentina, Uruguay and parts of Brazil and Bolivia). In this study, we aimed at assessing the floristic consistency of main vegetation types occurring in the region. Our dataset consisted of 221039 occurrence records of 3571 species of shrubs and tree in 1254 sampling sites spread over six countries and eight phytogeographic domains: Atlantic Forest, Pampa, Gran Chaco, Patagonia, Southern Andean, Mediterranean Chile, Temperate Pacific and Pacific Islands. This dataset was extracted from NeoTropTree, a database with species composition of

sites distributed across the whole Neotropics. We performed a cluster analysis and NMDS ordination of this dataset followed by partial analysis of variance (ANOVA) and then obtained the taxonomic distinction and indicator species. Our results showed a consistent differentiation among 25 main vegetation types. The greater differentiation took place among the phytogeographic domains and leaf flush regimes (evergreen, deciduous and semideciduous) though there was also a remarkable latitudinal gradient. Our analyses showed that the pre-defined vegetation types were consistent in terms of woody flora composition and have a considerable number of indicators, many of which endemic. Any conservation initiative in the regions should consider these peculiarities.

Around the world in 146 dogs: A new global fossil canid phylogeny and the historical phylobiogeography of Caninae

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The phylogenetic relationships of North American fossil Canidae have been subject to many recent studies but canids from other continents have received less attention. We present the results of the first ever combined evidence analysis (molecular and morphological characters) of global Canidae, with additional fossil taxa included either *a priori* or *a posteriori* based on expert opinion. We used Beast 2.1.3 and the R package BEASTmaster to conduct a Bayesian total evidence analyses (tip-dating) with our combined evidence matrix and fossil occurrence dates for a dated phylogeny of extant and extinct Canidae. Our analysis includes 237 Canidae (65 in subfamily Borophaginae, 26 in subfamily Hesperocyoninae, and 146 in subfamily Caninae). Our results are moderately consistent with previous studies but the inclusion over 50 fossil taxa previously excluded resulted in differences both in the clade topology and timings. We also conducted a historical biogeographical analysis of subfamily Caninae using our tipdated phylogeny, and distribution data from fossil databases. We used the R package BioGeoBEARS to perform inference of biogeographic history on phylogenies and statistical model choice to compare the fit of many different models of biogeography that may evolve on a phylogeny. Models that include “founder-event speciation” (speciation coincident with dispersal to a new region) appear to dominate, gaining over 99% of the AIC model weight. Newly developed BioGeoBEARS features allowed us to estimate whether an absence of a fossil taxon from a certain region is a ‘true absence’ or just ‘absence of evidence’ based on the completeness of the fossil record, resulting in more robust biogeographical models.

Molecular phylogenetic insights into the diversification and historical biogeography of the Sun orchids (*Thelymitra*, Orchidaceae)

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Thelymitra (c. 120 species) is a characteristic component of the Australian terrestrial orchid flora, and has a recent history of rapid diversification and hybridization. The Sun orchids display a striking morphological diversity often difficult to interpret and our knowledge on how this fascinating diversity has been shaped over the time is still limited.

Here we present a multi-locus phylogeny of *Thelymitra* based on nuclear (ITS) and plastid markers (*matK*, *psbJ-petA*, *ycf1*) based on a broad taxonomic sampling which identifies major clades within the genus and provides first insights into infrageneric relationships. We reconstructed the evolution of key floral characters to assess their taxonomic value, and compared previous taxonomic treatments with the molecular phylogenetic results. We estimated divergence times and examined biogeographical patterns of species divergence using time-calibrated phylogenies in order to elucidate the effect of past climatic oscillations, dispersal and geography on the diversification of this charismatic group.

Systematics of the genera *Pleurastrum* and *Chlorococcum* (Chlorophyta), with the detection of a new polar taxon

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The genus *Pleurastrum* Chodat (Chlorophyta) is present in soils, freshwater habitats, and as lichen symbiont and it includes species that can undergo different growth forms (coccoid, sarcinoid, and filamentous) depending on field and culture conditions. Because of its high polymorphism, the taxonomic history of this genus is confusing, with many authors questioning its monophyly and several taxonomic revisions during years. Currently, only two species are confirmed under this genus: the type species *Pleurastrum insigne* and *P. photoheterotrophicum*.

Many more species are recognized under the genus *Chlorococcum* Meneghini (Chlorophyta), whose type species is *Chlorococcum infusionum*. This group of coccoid green microalgae is ubiquitous, since it is found in soil, freshwater, and marine environments, and it is reported from such diverse habitats like hot springs and Antarctica. The simple morphology and the lacking of unambiguous diagnostic characters make the identification of members of this genus very difficult.

This research was started in order to characterize two coccoid green algal strains isolated from Terra Nova Bay, Victoria Land (Antarctica). Morphological, ultrastructural and molecular analyses were carried out on the two isolates, as well as on *Pleurastrum* and *Chlorococcum* strains got from International culture collections for comparison. The molecular analyses were based on the *rbcL* and *tufA* genes and on the ITS region, with a focus on the ITS2 structure.

Our results allow us to attribute the two isolated strains, together with two of the comparison strains, to a new polar taxon and to further circumscribe the genera *Pleurastrum* and *Chlorococcum*, with the synonymization of different species.

Phylogenetic signal of Amazonian tree traits associated with carbon processing and storage

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Understanding how evolutionary relationships affect current ecological processes depends on the link between phylogenetic relatedness and ecological similarity. This relationship can be measured by the extent of phylogenetic signal: when phylogenetic signal is high, species relatedness may provide useful understanding about species ecologies. This link is potentially particularly important in tropical forests due to their high tree diversity where measuring intra- and inter-specific variation in traits is difficult. Here, we quantified phylogenetic signal of traits associated with carbon processing and storage in tropical trees, including both "hard" traits (e.g. demographic traits, potential tree size) that are integrated measures of tree performance and more closely related to fitness, and "soft" traits (e.g. leaf mass per area, leaf nitrogen) that reflect specific aspects of plant function. We used a genus-level phylogeny, including 497 tree and palm genera generated from DNA sequences of *rbcL* and *matK*, and trait data from a large network of plots distributed across the whole Amazon. Overall, we found significant, though intermediate levels of phylogenetic signal, across all traits. Our findings are consistent with coordinated, genetic control over carbon storage and processing over evolutionary time and may suggest convergent evolution in different lineages associated with adaptations to vertical and horizontal light gradients in tropical forests. The magnitude of phylogenetic signal for key traits associated with carbon processing and storage suggests the potential to use the evolutionary relatedness of species as a proxy for ecosystem structure and function, and their response to environmental change.

Crop wild relatives of the brinjal eggplant (*Solanum melongena* L.: Solanaceae): Evaluating gaps in global germplasm collections and identifying priority collecting areas

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Crop wild relatives (CWR) provide important traits in breeding efforts, including pathogen resistance and abiotic stress traits, and are essential for maintaining food security. Despite their importance, current global genebank collections represent only a small fraction of CWR diversity. Here we study the gaps in the global germplasm collections of the brinjal eggplant (*Solanum melongena* L.) and its wild genepool that include species mostly from the Old World. Following the previously established gap analysis methodology, we collate all publicly available global germplasm records for the brinjal eggplant and its CWR. Collections available in seed banks are then compared to records available in global herbaria to study how much of the wild diversity is currently represented in germplasm collections. We find that most eggplant CWR have either no accessions or are represented by a small number of accessions in seed banks compared to their native natural ranges. We identify that c. 20% of the eggplant CWR are under severe risk of extinction due to their small geographic ranges and ongoing habitat degradation in tropical East Africa and Asia. Priority areas are identified where targeted collections should be made to strengthen global resources for eggplant breeding in the future. These include Eastern Africa, particularly the Kenya-Tanzania border, where several CWR co-occur but where no previous germplasm collections exist. The traditional genepool concept is discussed in relation to the brinjal eggplant and the large genus *Solanum* L., and a new genepool concept for the crop is provided. We emphasize the importance considering the wild relatives outside of the genepool concept by including phylogenetic relationships as well as extinction risk when targeting localities for CWR collection.

A taxonomic review to *Biscutella* sect. *Biscutella* (Brassicaceae)

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The genus *Biscutella* L. (Brassicaceae) is renowned by its taxonomic difficulty, mainly caused by the lack of reliability of most morphological characters. It includes

about 50-70 taxa easy to recognise based on their typically flattened didymous silicles.

Biscutella sect. *Biscutella* (*B. ser. Lyratae* Malin.), which comprises most of the annual □rarely perennial□ species of the genera, has received many diverse taxonomic treatments according to different available revisions.

On the framework of a phylogenetic study of *B. sect. Biscutella*, which combines morphological and molecular data and brings new insights in the taxonomy of the group, a new taxonomic arrangement is presented here for that section.

As a result, the distribution of some taxa □*B. lyrata*, *B. didyma* or *B. maritima*□ is modified. Some other typically accepted taxa have been relegated to infraspecific ranks (mostly varieties), whereas others are better treated in synonymy of widely distributed biological entities. For each accepted taxa, the principal synonyms are shown, as well as morphological and distributional diagnostic data.

A phylogenetic approach to *Biscutella* sect. *Biscutella* (Brassicaceae)

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The genus *Biscutella* L. (Brassicaceae) includes about 50-70 taxa easy to recognise based on their typically flattened didymous silicles. However, the relative uniformity of most vegetative characters and the lack of reliability of those traditionally used for taxa differentiation result in much of taxonomic confusion for which the genus is renowned.

Taxa in *B. section Biscutella* (*B. ser. Lyratae* Malin.) are annuals or rarely perennials, with petals gradually attenuate at the base, not auriculate, and lateral intrastaminal nectaries. They occur mostly in the Mediterranean basin, and are distributed in southern Europe (including Corsica, Sardinia and Sicily), northern Africa and the Middle East.

Recent treatments admit six species in this section, *B. lyrata* L., *B. baetica* Boiss. & Reut., *B. maritima* Ten., *B. morisiana* Raffaelli, *B. didyma* L. and *B. raphanifolia* Poir. However, the arrangement of taxa in the section usually differs among the regional floras and many other infraspecific taxa have been described based on morphological variation of leaves and silicles. In the present contribution, morphological and molecular data based on nuclear (ITS) and plastid (rpl32-trnL) regions were combined to generate a phylogeny of *B. sect. Biscutella*. Phylogenetic molecular trees are fully congruent with morphological and biogeographical data, and bring new insights in the taxonomy of the group.

Systematic of *Rumex bucephalophorus* L. (Polygonaceae) based on nuclear microsatellite markers

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Rumex bucephalophorus L. (Polygonaceae) is a Mediterranean-Macaronesian species which shows an enormous morphological diversity. Mainly based on diaspore morphology, previous systematic studies encompassed its variability in four subspecies within it (subsp. *canariensis*, *gallicus*, *hispanicus* and *bucephalophorus*). Two of them, subsp. *gallicus* and subsp. *hispanicus*, are not clearly distinguished neither by morphology nor through molecular markers (AFLP and ITS sequences). We have characterized 16 nuclear microsatellite loci for this species in order to test previous classifications and to analyze its genetic structure focusing on the distinctiveness of both subsp. *gallicus* and *hispanicus* based on bayesian and genetic-distance approaches. Our analyses revealed moderate to high levels of genetic diversity in *R. bucephalophorus* populations (A: 3.35-5.38; HO: 0.32-0.63; HE: 0.38-0.64). Our genetic structure analyses are congruent with the classic taxonomy of this taxon. A bayesian approach (STRUCTURE) determined the existence of three genetic groups: a first group constituted by Macaronesian populations (subsp. *canariensis*), a second group by subsp. *bucephalophorus*, and a third mixed genetic group formed by subsp. *gallicus* and *hispanicus*. However, hierarchical analysis of the molecular variance (AMOVA) and neighbor-joining trees based on genetic distances also showed the split among the previously undistinguished subsp. *gallicus* and *hispanicus*. In conclusion, the robustness of morphologic taxonomy of *Rumex bucephalophorus* is supported by highly polymorphic microsatellite markers.

Myrtle: how many species and subspecies?


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The genus *Myrtus*, described by Linnaeus in 1753, is known and cultivated since ancient times as an ornamental plant in gardens and parks. It is characterized by high morphological variability that, during the last 150 years, raised several doubts about the number and the validity of species and subspecies belonging to the genus. At present, *Myrtus* counts only two recognized species: *Myrtus communis*, widespread in the Mediterranean basin, and *M. nivellei*, endemic to the central Saharan mountains. Moreover two subspecies are currently accepted: *M. communis* subsp. *communis*, which corresponds to the plants growing naturally, and the subsp. *tarentina*, which is currently the most frequently cultivated myrtle in European gardens.

In 2010, in Granada (Spain) gardens, Casares *et al.* rediscovered a very rare type of *Myrtus*, *M. baetica*, whose morphology resembles that of the main type used during



the Middle Ages in the Islamic gardens of the Iberian Peninsula and whose knowledge was lost in Europe since the Renaissance. However it seems to be still cultivated with the name of 'Moorish myrtle' in the U.S.A. and Morocco and there are some historical evidences that specimens of this type of myrtle can be present in some English Botanic Gardens, like Kew, with the denominations of "orange myrtle", "Jewish myrtle" or "twisted myrtle".

Here we show a preliminary molecular study to define the taxonomic position of specimens of *M. baetica* in relation to *M. communis* subsp. *communis* and *M. communis* subsp. *tarentina* plants, using the plastid *rbcL* and *matK* markers and the intergenic spacers *psbA-trnH* and *rpl2-trnH*. Moreover the validity of *M. nivellei* as distinct species is investigated.