

# BEYOND CLADISTICS: A Festschrift for Chris Humphries

## Abstracts

### **The Future of Systematics is Deeper than you Think**

Chris Humphries

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### **Early and late cladistic work on the Asteraceae-Anthemideae**

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### **Chris, Cycads, and Me**

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Cycads have been recognized as a group since the time of Linnaeus and all phylogenetic analyses have shown them to be monophyletic. The questions that have proven to be intractable have been the position of cycads in the tree of life and the relationships of genera and species within the cycads. This is true for analyses of morphological data only, molecular data only, and combined data sets. Moreover, none of the generic backbone topologies of the cycad generic trees can be rejected. Some of these disparities in molecular analyses can be explained by the presence of lab clades, i.e., clades that occur as a result from laboratories that have not provided voucher specimens. Some incongruities appear to be the result of analyses that are not based on parsimony and/or strict consensus trees but rather the use of neighbor joining, MrBayes, majority rule consensus trees, and an obsession with resolution and bogus support values. One consistent result of all analyses, both good and bad, has been the monophyly of all genera. Even though most current researchers seem to be concerned with producing trees, the time is coming when the trees will be used to produce monographs and other products of interest to a broader community. These are particularly germane because all cycads are endangered species and CITES protected. So the future lies in the use of trees and of course that also means the abuse of trees.

### **Humphries, Systematics and All That Jazz**

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Among the passions exhibited by Professor Chris Humphries are systematic biology and jazz music. Because Jazz music speaks so powerfully about the human condition and because systematic biology both benefits and suffers from the fact that it is guided by imperfect human beings, jazz opens a window on how and why systematists do what they do. Jazz lyrics are referenced to provide insight into the motivations of a great systematist, Professor Humphries, and reveal attributes of being human that help explain issues and trends in contemporary systematic biology.

## Rooted in cladistics: Chris Humphries, conservation – and beyond?

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Chris Humphries' commitment to understanding patterns, notably those revealed by cladistics and cladistic biogeography, enabled him to play a key role in the emergent notion of phylogenetic diversity. This, together with other new approaches to assessing priorities and setting targets, characterised some major changes in conservation biology during the 1990s. In this paper Chris Humphries' contributions to biological conservation are assessed, and placed in a context which has seen the focus of conservation shift from atomism and anthropocentrism, via representational and phylogenetic goals, to an increasingly integrated ecocentric approach to sustaining planetary biodiversity. These changes have been paralleled by shifts in perception from reductionism to holism in seeking a rational basis for developing a viable Human–Earth relationship. Conservation biology has, in the process, moved from being the preoccupation of self-selecting elites to an increasingly vital concern for all people, and is now going beyond science and conventional economics as it enters what may best be described as a “cultural phase”—in which the motivational values that guide human action, and the ways in which they can evolve, will play an increasingly important role.

## Homology and Organ Identity

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The fact that descriptive terminology is itself often interpretative represents a significant problem when making homology assessments. Indeed, the debate surrounding the origin of the angiosperm flower is frequently hampered by typological interpretations. The carpel is a good example of such interpretative concepts. It is difficult to reconcile homology among the diversity of carpels exhibited by early-divergent angiosperms, and harder still to homologize the carpel with female cone-bearing structures of any of the many gymnospermous groups. The term “identity” when applied to organs is itself challenged by proponents of continuum morphology. The monogeneric aquatic family Hydatellaceae (*Trithuria*) was recently transferred from from the monocot order Poales (e.g. grasses) to the early-divergent angiosperm order Nymphaeales (waterlilies), initially based on molecular data. This dramatic (and highly convincing) reassignment has prompted re-evaluation of the morphology and systematics of this unusual family, which possesses both monocot-like and dicot-like features. Some previous interpretations of organ morphology were at least partly dictated by presumed phylogenetic placement. For example, is the single cotyledon in *Trithuria* homologous with the two united cotyledons of water lilies (sometimes interpreted as a single cotyledon), or the single cotyledon of monocots? Furthermore, is each pistil of *Trithuria* a solitary carpel (as in many early-divergent angiosperms) or a pseudomonomerous gynoecium, i.e. a syncarpous ovary with a single functional carpel (as in many Poales)? Our data show that pistils develop as completely ascidiate structures in *Trithuria*, but ascidiate carpel development closely resembles pistil development in pseudomonomerous grasses. Previous placement of Hydatellaceae in Poales indicated pseudomonomery, an interpretation supported by the triquetrous fruit of *Trithuria*, which suggests a trimerous gynoecium, but the revised phylogenetic context means that each pistil is most parsimoniously interpreted as a solitary ascidiate carpel. Patterson's congruence test of homology – which depends on the precise equivalence of homology and synapomorphy – is not satisfied, because both ascidiate carpels and pseudomonomerous ovaries are widespread in extant angiosperms.

## **Homology of the daffodil corona**

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The trumpet like structure or corona of daffodil flowers has not been satisfactorily homologised with other floral organs. Within the flower, the corona is located between a whorl of perianth parts and a whorl of stamens and therefore positional criteria of homology are ambiguous about which floral whorl is modified to form the corona. One hypothesis is that the corona is an outgrowth of the perianth which comprises six petal-like parts. Circumstantial support for this is that the corona is petal-like in texture and often in colour. Alternately, the corona may be modified from stamens and in particular staminal filaments. Several other genera of Amaryllidaceae e.g. *Eucharis* have a staminal corona in which the anthers are located on top of the corona, indicating that the corona is formed from modified stamens. To distinguish between these two hypotheses B and C class floral organ identity genes have been cloned from *Narcissus bulbocodium*. Northern blots have been carried out to determine expression levels of B and C class genes of the perianth, corona, stamen and carpel tissue. In situ hybridization has been used to determine positional expression patterns of B and C class genes within the flower. Scanning electron microscopy has been utilized to determine the ontogenetic development of floral organs. These data are being explored relative to determining the homology of the daffodil corona.

## **The origin of leaves: evidence from the fossil record**

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Plants inherited much of their biochemistry from the green algae, but most of their morphology evolved on land. Understanding the origins of fundamental organs and tissue systems, currently the focus of much research in molecular developmental biology, therefore necessarily focuses on basal groups of bryophytes and vascular plants. The latter are characterised by two major clades, the morphologically conservative lycophytes (e.g., Lycopodaecaeae, Selaginellaceae, Isoetaceae) and the exceptionally diverse euphyllophytes (ferns, horsetails, seed plants). We argue that the leaf (megaphyll) (ferns and related plants) and the leaf plus axillary meristem (seed plants) are the keys to understanding euphyllophyte morphology. The Devonian fossil record presents unique insights into the early evolution of this organ system. Phylogenetic analyses that include fossils show that early lycophytes and euphyllophytes were leafless plants, and several different sorts of lateral appendage and branch systems have been implicated in the early stages of leaf evolution. The leaves of lycophytes are most likely derived either from modified trichome-like structures or spore-bearing organs, whereas in euphyllophytes their derivation from lateral branching systems is much more complex. Phylogenetic analysis indicates that leaves in euphyllophytes evolved through modification of several developmental systems at different levels in the hierarchy. Initiation of leaf primordium and basic leaf vascular patterning is most likely homologous among all crown group species. Leaf dimorphism (fertile/sterile) is an early feature, however the developmental history of spore and seed-bearings structures is complex, perhaps involving heterotopy. Bilateral symmetry in leaves (branching and vasculature) is not strictly homologous among crown euphyllophytes. The origin of dorsiventral patterning is still poorly understood, but information on this could be extracted from observations of dorsal and ventral surfaces of well preserved fossils. The far greater diversity of leaves in euphyllophytes as compared to those of lycophytes is a reflection of the much greater developmental complexity and flexibility inherent in their early development from shoot systems.

## **Evolution on a global scale: understanding the origin and diversification of the Compositae**

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One of every 10 flowering plant species is in the family Compositae. The family is monophyletic and the sub-familial classification and ideas about major patterns of evolution and diversification within the family remained largely unchanged from Bentham through Cronquist. The results of recent broad-scale molecular studies of the tribes were used to produce a meta-tree formed by linking the respective trees together on a known base tree. By examining the distribution of the terminal taxa a biogeographic pattern emerges. The extant lineages that are part of the basal grade are southern South American in origin followed by a subsequent radiation in Africa that gave rise to most of the tribes we know today. Nested in the African radiation are individual clades in Asia, Eurasia, Australia, the Americas, etc. Highly nested on the base tree there is a North American origin and diversification of the Heliantheae Alliance that involved repeated incursions into Mexico and South America. The South American radiation followed by the African explosion might suggest a Gondwanan origin for the family, but the few data that exist from pollen records and geology seem to indicate a more recent origin. The existence of the monotypic genus *Hecastocleis* inserts a North American taxon in between the South American basal grade and African radiations which might indicate long distance dispersal, or a North American or even an Asian presence. The sister-group to the western hemisphere clade Heliantheae Alliance is the small tribe Athroismeae, from eastern tropical Africa, leaving an unknown area, possibly Asia, between Africa and western North America. This global picture of the Compositae provides a framework for studies of characters such as pollen, corolla shape, chromosome number, phytochemistry, and many others. Today, we have a much better picture of the origin and evolution of the Compositae and the fun is just beginning.

## **Phylogeny of the Australian ‘monocalypts’, *Eucalyptus* subgenus *Eucalyptus* (Myrtaceae), reveals Paleogene history and east-west continental vicariance**

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*Eucalyptus* subgenus *Eucalyptus* (commonly called the ‘monocalypts’), is well-supported as a monophyletic group, with flowers characterised by a single petaline operculum, lack of free sepals, and anatropous ovules arranged in two rows per loculus. The group, with 111 species in a number of recognisable clades, includes some of Australia’s most important timber trees, such as *E. marginata* (jarrah) and *E. regnans* (mountain ash), the latter the tallest flowering plant in the world. The subgenus is distributed in both western and eastern Australia, ranging from tropical to cool temperate latitudes, and is most common in southern coastal and upland regions. A phylogenetic analysis of all taxa is presented based on published morphological analyses of individual clades, and new molecular analyses based on ITS and ETS nrDNA sequences. It is hypothesised that the subgenus was present in the Early Eocene across western and eastern Australia when conditions were warm and wet. The earliest lineages to differentiate are in the south-west of Western Australia, including tall wet forests trees on loamy soils and in river valleys (Jarrah forest bioregion); other clades occur today on lower nutrient soils on weathered lateritic plateau or sands of the Swan Plain. Mallee species are associated with granitic and quartzite hills, and south coast siliceous and calcareous sands of the Esperance Plains. Marine inundation during the Eocene and major climatic change at the Eocene/Oligocene boundary isolated these western lineages from

eastern populations, which form a monophyletic group. Humid conditions persisted in eastern Australia, associated with the elevated Great Dividing Range. The oldest, eastern lineages survive today in Queensland in a climate as warm as that of the Eocene, while more derived clades have evolved in the cooler south-east in a range of environments.

## **Floras to Phylogenies – Why Descriptive Taxonomy Matters**

Sandy Knapp and Bob Press

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Description is one of the three principal tasks of taxonomy (a.k.a. systematics), but has been characterized as “Cinderella science” and is often thought to be hypothesis-free or likened to stamp collecting. Here we explore descriptive taxonomy as practiced in floristics – the documentation of the plants of a particular area – and monography – the documentation of the plants of a particular taxonomic group, and link this to the role of description in creating further hypotheses about different aspects of plant diversity such as relationships or biogeography. Over the course of his career, Chris Humphries has engaged in all aspects of taxonomy – here we would like to use his output to show how a good knowledge of descriptive taxonomy can lead to more insightful hypotheses in other areas of the science. Descriptive taxonomy matters because it links cascades of ever-refined hypotheses about pattern and process in plant diversity.

## **Island Biodiversity Hotspots, the Challenge of Climate Change**

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Over 50,000 plant species are endemic to the world’s islands. This between one fifth and one eighth of the total flora of the planet depending on the estimate used in only about 5% of the total land surface. Recent estimates indicate that some 29% of the world’s biodiversity hotspots consist of islands or island groups and they are considered to be high priority conservation targets. Factors such as the small size of islands, their geographic isolation and often highly intensive land-use contrive to make their biodiversity face a wide range of threats including competition from alien invasive species, habitat destruction and now from the effects of global climate change. Islands, particularly in tropical and subtropical regions, with rich endemic floras are particularly vulnerable to the adverse effects of climate change with consequent biodiversity loss. Such a major challenge requires measures for mitigating and adapting to climate change. These will require approaches in both *in situ* and *ex situ* fields if we are to conserve both unique ecosystems and major centres of species diversity. Conservation policy for island hotspots should involve sustainable management, restoration and use of local biodiversity and ecosystems as well as measures for the long-term preservation of individual endemic species using modern *ex situ* conservation techniques.

## **Endemism and Evolution in Macaronesia**

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The Macaronesian region, comprising the volcanic, oceanic archipelagos of the Cape Verdes, Canaries, Selvagens, Madeira and Azores is located in the Atlantic Ocean between 15 and 30°N. The flora of the region includes many endemics, a high proportion of which are woody and there are several spectacular examples of island radiations (e.g. *Argyranthemum*, *Aeonium*, *Echium*). Macaronesia has long been an important focus for biogeographers and in a paper published in 1979, Chris Humphries described the patterns of diversity across the region and sought to explain why such a high degree of endemism occurs in such a small area. In the intervening 29 years, the continuing exploration of the region, new sources of data and methodological developments have all impacted on our understanding of the diversity and relationships of the region's endemic flora. In this talk we revisit some of the questions addressed by Chris in his 1979 paper in light of these developments. We review recent advances in our understanding of the relationships of island and continental taxa, re-examine patterns of endemic diversity across the region and evaluate hypotheses to explain the heterogeneous distribution of diversity both within and between islands.

## **Inferring Process from Pattern: The Biogeography of Wallacea**

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Wallacea is a biologically and geologically complex area of the Indo-Australian Archipelago that is bordered by Borneo to the west and New Guinea to the east. Its name honors Alfred Russel Wallace, legendary naturalist, biogeographer and co-proposer of the theory of evolution. Wallacea, along with concepts such as Wallace's Line and other lines used to separate biotic regions, are part of the descriptive and narrative phase of biogeography, as pointed out by Christopher J. Humphries in a 1990 review. The analytical phase of biogeography—proposing testable hypotheses of area relationships—has rarely been applied to the region. Wallacea lies between two major nodes in Léon Croizat's summary of major patterns of global distribution. Phylogenetic hypotheses and distribution patterns of taxa centered on Wallacea are used to interpret the biogeographic history of the region's biota within a hierarchical framework. Sympatry between western and eastern elements of the biota characterizes Wallacea. But, sympatry is not limited to Wallacea, nor may Wallacea necessarily be diagnosed as an area of endemism. Sympatry suggests that sister taxa had differentiated prior to modern formation of the Indo-Australian archipelago from Asian and Australian continental and island-arc components. Formation of composite land masses facilitated dispersal of sister taxa into the range of the other. Support for this hypothesis comes from identification of repeated areas of overlap or sympatry coincident in large part with geological sutures and faults throughout the archipelago and correspondence of modern distributions with ancient drainage patterns. Explanations of patterns are not sought in dispersal routes, centers of origin or lines. Vicariance (earth history) and biotic dispersal (overlap) may be used to interpret hierarchical distribution patterns.

## **The origin of fishes across the South Atlantic**

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How fishes are distributed in Britain today depends on ecology and history. How they are distributed through time depends on geology. How they are plotted in an atlas depends on phylogeny and geology. How they are distributed in real life depends on ecology, phylogeny and geology. This essay explores, through the eyes of fishes, how three disciplines interact with each

other to explain one of the most geologically and biologically significant events to shape our modern world.

## **Early British collectors and observers of the Macaronesian flora: from Chelsea to Kew**

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Macaronesia has long been a region of interest to systematists, biogeographers and conservationists, and one that has sustained Chris Humphries' interest from his early monographic work on *Argyranthemum*, through his broader biogeographical studies to a more recent study on diversity, rarity and the evolution and conservation of the endemic elements in the Canary Island flora. Several recent pieces of work have looked at different aspects of the history of the description of the Macaronesian flora, and a number of these are discussed, including the results of studies of the collections, chiefly from the Natural History Museum in London and the British Library, of James Cuninghame, Samuel Doody, Leonard Plukenet, and Francis Masson

## **Homology in classical and molecular biology – revisited**

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Despite being the most important concept in comparative biology, homology has remained an elusive concept. Every new biological discipline has tried to redefine or refine its use, and molecular systematics is certainly no exception. Even though, it is possible to make perfect correspondence between homology and its derived concepts in morphology and molecular biology, there appears to be one important exception – dynamic homology. Dynamic homology is used when sequences are aligned and the phylogeny is created simultaneously, but is dynamic homology something unique for molecular data or does it have parallels in morphology?

## **Beyond Belief: The Steady Resurrection of Phenetics**

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To most working systematists by the late 1970s phenetics, as a philosophy of systematics, was presumed to be dead or at least fatally wounded. Much discussion about methodology ensued and many different methods were proposed for discovering the relationships of organisms, such that some wanted to “consider all approaches as methods of statistical inference of phylogeny”. Even so, it was not expected that phenetics would rise from its own ashes. Yet that seems to be the case in certain areas of systematic endeavour. We will discuss some of these areas of activity and delve a bit further into the phenetics phenomenon.

## **Backing up into the Future – another look at monophyly**

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Monophyly is a central concept of phylogenetic systematics, or cladistics. As defined by Hennig (1966), monophyly is a relational concept. For a stem-species *A*, and its two descendants *B* and *C*, the relation *r* ('an immediate descendant of') marks out the monophyletic taxon *Tax* in terms of a set that includes two ordered pairs:  $Tax = r \{(A, B) (A, C)\}$ . The monophyletic taxon *Tax* thus includes the ancestor and all, and only, its descendants. Monophyletic taxa are inclusive concepts. This results in conceptual problems as the concept of monophyly is applied to species, and subspecific levels of biodiversity. These problems become apparent in a recent tendency to abandon the species category in favor of other concepts such as 'cladistically resolved unit', 'least inclusive taxonomic unit', 'evolutionary significant unit', or 'molecular operational taxonomic unit', as also in the requirement for 'Reciprocal Monophyly' deployed in phylogeography. It is argued that the application of the concept of monophyly to the species level and below results in a category mistake. The inclusive hierarchy of monophyletic taxa applies to levels above the species. At the levels of species and below, there applies a 'division hierarchy' which is not inclusive, but exclusive. This accords with the view of species as processual systems, and explains why ancestral species (and/or populations) are epistemically not accessible in terms of monophyly.

## **Whatever happened to chemical systematics?**

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## **Beyond Mayr: what is the minimum number of species concepts needed to maintain 21st century biology?**

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Richard Mayden used the Association's edited volume *Species: the units of diversity* (1997) to summarise species concepts of the 20th century. He was able to identify 24 apparently distinct concepts. In the subsequent decade, several further concepts, all rooted in genetic data, have been advanced. These many concepts are distributed in roughly equal numbers among three basic categories: reproductive isolation (gene exchange), similarity and monophyly. Conceptual debates among proponents of these three main schools greatly enlivened systematic biology during the second half of the 20th century, Moreover, they were fought alongside other, more explicitly phylogenetic but equally stimulating, duels (in chronological order: homology definition and recognition, phenetic vs cladistic analysis, phenotypic vs genotypic data, parsimony vs likelihood vs Bayesian tree-building). Thus far, conceptual debates of the 21st century have been much more muted, giving casual observers the (in my view erroneous) impression that those earlier conflicts eventually spawned clear and deserved winners. This period of relative conceptual quiescence may currently be 'politically' advantageous in promoting the myth that the systematics community has achieved consensus on these key issues. However, I view consensus as undesirable, since by definition it is a state incapable of generating meaningful intellectual stimulation. In any case, these key conceptual issues most definitely have *not* been resolved. The rapidly increasing diversity and complexity of the categories of data available to systematic biologists has, in practice, overwhelmed conceptual debates. Returning to concepts of species (and infraspecific ranks), these rightly remain the basic currency of systematic biology. However, even today, few systematists explicitly state which species concept(s) they are employing.

And few consider whether the (implicit) concepts used in their particular projects are a good fit to the data that have been gathered or to the hypotheses that are (hopefully) being tested. One undesirable downstream consequence has been the breakdown of the critical feedback loop between species delimitation and species identification, which has in turn encouraged decidedly unscientific aspirations for an unvarying unitary taxonomy. Against this surprisingly ambiguous background, I will explore which species concepts, and which sources of systematic data, could most usefully inform 21st century biology.

## **Ontogeny and Systematics revisited: developmental models and model organisms**

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This paper revisits a discussion of pollen and spore ontogeny that one of us (SB) presented at the symposium on "Ontogeny and Systematics" convened by Chris Humphries at the Third International Congress of Systematic and Evolutionary Biology in 1985. At that time there was considerable interest in the role of ontogenetic studies as a source of new characters and as a criterion from polarising character transformations. There was also an interest in predictive models based upon developmental studies. One such, presented at the 1985 Congress, was a model for the origin of pollen grains dispersed in permanent tetrads rather than as individual monads. Here we present electron microscope evidence in support of that model and show how, over thirty years later, it can be connected directly with evidence from molecular genetic studies of pollen development.