Foreword

The pedigree of plant collections for scientific research extends to at least the European Renaissance when herbaria first became fundamental botanical tools. Herbaria record the physical evidence of the diversity and spatial and temporal distribution of the planet’s plant life. Today, herbarium specimens, prepared using sixteenth-century technology, are being used to investigate twenty-first-century problems.

Traditionally, morphological and anatomical investigations of herbarium specimens have been used to answer fundamental botanical questions. Today, investigations using DNA and pollen isolated from herbarium specimens have become commonplace. Researchers, take advantage of the often difficult fieldwork undertaken by others, now have access to extinct species, or species difficult to collect for political, conservation, social or financial reasons. However, confirmation of specimen identification remains; a task that is usually underestimated, especially by researchers working in areas replete with high-quality fieldguides.

As access to herbaria and the manipulation of large datasets has become easier, researchers from many disciplines, even if they have no direct interest in taxonomy, have recognised that the vast quantities of data filed in herbarium cabinets cannot be ignored. Herbarium data, amalgamated into international databases, are used to model processes of species introduction or changes in species’ ranges due to climate change and even the provision of ecosystem services. Herbaria have risen to the self-evident challenge of digitising herbarium specimens and abstracting data. However, challenges with amalgamated data sets remain including collector and curator biases and the ever-present concern with specimen identification.

The articles in this edition demonstrate the fundamental role of herbaria in botanical research, whether it is the description of new species (p. 11), monography and Flora writing (pp. 5-7), investigating global patterns of conifer diversity (pp. 10-11), surveying botanical diversity in a hotspot (p. 12) or investigating the homology of the daffodil corona (pp. 8-9).

Stephen A. Harris
Curator of Oxford University Herbaria

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Front cover image:
Narcissus bulbocodium (Hoop Petticoat Daffodil) growing on a slope at Castelejo in the Algarve region of Southern Portugal - see article on pages 8-9. Photographs by Timothy Walker.

Typesetting and layout of this issue of OPS by Serena Marner

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we were delighted Sir David Attenborough visited Oxford University Herbaria and the Sherardian Library of Plant Taxonomy on the 16th February 2012 to view the Fauna Graeca. The Fauna Graeca is an unpublished collection of folio-sized animal watercolours made by the artist Ferdinand Bauer when he accompanied John Sibthorp, third Sherardian Professor of Botany at Oxford, on his tour of the eastern Mediterranean in 1786-87. Images of the Fauna Graeca can be viewed at http://www.bodleian.ox.ac.uk/science/resources/sherardian-library/flora_graeaca, together with images of the Flora Graeca which comprise 966 watercolours of the plants of the eastern Mediterranean, also made by Bauer on the same expedition.

John R.I. Wood, Research Associate in the Department of Plant Sciences, has been identified as one of the ‘superstars of botany’. His plant collecting activities and the importance of his work were reported in a news feature in Nature in April 2012. This followed a report of research published in the Proceedings of the Royal Society B: Biological Sciences, which was led by Dr Robert Scotland of Plant Sciences and Dr Dan Bebbet of Earthwatch, plus other colleagues from around the world.

John Wood has found and collected more than 100 new plant species during his career (so far) and collected over 28,000 plant specimens which are deposited in herbaria. Bebbet et al. established that more than 50% of the world’s plant species have been discovered by just 2% of plant collectors, for example by botanical explorers such as Sir Joseph Banks. There are fewer ‘great plant hunters’ in modern times, but John is an example of an individual whose experience and skills in the field enables him to make a ‘disproportionate contribution to the discovery of new plant species’; similar to those of the great plant hunters of past centuries. Today, few institutions employ plant collectors but with an estimated 15-30% of the world’s flowering plants yet to be discovered, finding and recording new plant species is vital to understanding global biodiversity.

William Dampier’s collections in Oxford University Herbaria
An article about the preserved plants, collected by the privateer and circum-navigator in 1699 from New Holland (Australia), appeared in the Western Daily Press on 24 November 2012. William Dampier was born in the village of East Coker in Somerset where there is a plaque in the village church commemorating him as the first Englishman to explore Australia. Even today people pay tribute to Dampier in the guest book at the church. The house where he was born still stands nearby.

William Hawthorne and Cicely Marshall continued their work in northern Nimba County, Liberia, with a winter 2012 trip supported by Euronimba. They have used the sample coverage to produce an ecological base map, which maps the extent of each vegetation type across the area. The base map contributes to an atlas produced by URS, which displays the distributions of the globally rarest (Black star) plant species of the area. The data from the Liberian work have also been written into a guide book called ‘Important plants of northern Nimba County, Liberia’, a draft of which was produced in 2012 with support from ArcelorMittal Liberia. The final print is forthcoming, and features a full annotated checklist for the region, as well as illustrations of about 250 species with high global conservation value, local use value or ecological dominance.

Expeditions and visits
During 2012, Caroline Pannell spent one month, with a Fellowship from the Singapore Botanic Garden, determining the SING holdings of Aglaia (3000 specimens). She gave an informal lecture on the taxonomy and biology of Aglaia. Caroline spent April in Xishuangbanna Botanical Garden, Yunnan, China, visited several field sites, attended the Association for Tropical Biology and Conservation Asia Pacific Chapter Meeting and a training course, entitled ‘The Plants of Tropical Asia – Field Botany Course’, which focused on tree identification using vegetative characters. In July and August, she held a Fellowship at the Forest Research Institute of Malaysia. During this visit, Caroline wrote a draft of family accounts for the Salicaceae and Achariaceae for the Flora of Peninsular Malaysia and carried out fieldwork in Langkawi, Br Lagon and Ulu Gombak in Peninsular Malaysia. She gave a lecture on the dispersal biology and biogeography of Aglaia. During the fieldwork and field botany course she also gathered information from living plants for an interactive key to genera of Peninsular Malaysian plants, which will be based on vegetative characters.

Caroline is most grateful to the botanists at FRIM, SING and XTBG for the help and enthusiastic support they gave her during all of these visits.

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News items

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Publications 2012


of tolerance of metalliferous soils. *Alyssum* (Brassicaceae) is the largest known hyperaccumulator genus, comprising approximately 188 species distributed throughout the Mediterranean region and south-west Asia. Approximately one-quarter of these are largely restricted to areas of serpentine soils and have the ability to accumulate nickel to high concentrations in shoot tissue. This genus provides a good example in which to study the origins of a complex physiological trait, but its phylogeny is currently poorly understood.

To produce a well-resolved phylogenetic tree to investigate the number and timing of origins of nickel hyperaccumulation within *Alyssum*, DNA sequence data have been generated for four chloroplast regions (*matK*, *rps16-trnK*, *trnD–T* and *trnL–F*) from 170 of the 255 species of the Alyssaeae. Additional sequencing has been carried out for the chloroplast genes *ndH* and *rbcL* and the nuclear gene *PHYA*. A Bayesian analysis employing a relaxed uncorrelated lognormal molecular clock and multiple fossil-age calibration points was carried out using BEAST to reconstruct a time-calibrated phylogeny of the tribe.

Optimization of the nickel hyper-accumulation trait onto the Alyssaeae tree suggests that nickel hyperaccumulation arose twice in this tribe in the late Miocene/early Pliocene: 3.3–8.3 Mya in *Alyssum* and 6.3–8.8 Mya in *Bornmuellera*. The single origin in *Alyssum* is strongly associated with a significant acceleration in species diversification rate, suggesting the ability to hyperaccumulate nickel could have provided a key evolutionary innovation facilitating rapid range expansion and subsequent species diversification. The scattered distribution of nickel hyper-accumulators across small island-like patches of serpentine soil suggests that allopatric speciation may have driven rapid diversification in this clade.


Abstract of systematics thesis submitted in 2012

The following D.Phil. thesis was submitted and successfully defended in 2012:

**Evolution of Nickel Hyperaccumulation in *Alyssum* L.**

**Tom Flynn**

Linacre College

Supervisors: Professor Andrew Smith (Oxford), Dr Stephen Harris (Oxford) and Dr Colin Hughes (Institute for Systematic Botany, University of Zurich).

Phylogenetic studies are providing powerful new insights into the evolution of complex traits. Metal hyperaccumulation is an unusual and complex physiological trait found in about 500 plant species and is associated with an exceptionally high degree of tolerance of metalliferous soils. *Alyssum* (Brassicaceae) is the largest known hyperaccumulator genus, comprising approximately 188 species distributed throughout the Mediterranean region and south-west Asia. Approximately one-quarter of these are largely restricted to areas of serpentine soils and have the ability to accumulate nickel to high concentrations in shoot tissue. This genus provides a good example in which to study the origins of a complex physiological trait, but its phylogeny is currently poorly understood.

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This strategy has revealed clear geographic structuring of genetic variation within *C. hirsuta* with congruent patterns between chloroplast and nuclear markers. Climate suitability modelling has revealed that Pleistocene glacial dynamics can explain some of these patterns. Currently, the closest relatives of *C. hirsuta* are uncertain due to the lack of phylogenetic resolution and taxon sampling within *Cardamine*, a large genus of some 200 species.

**Student reports**

**Elizabeth Cooke** (D.Phil., 4th year) **Systematics and Phylogeography of *Cardamine hirsuta* L.**

Supervised by Dr Robert Scotland (University of Oxford), Dr Mark Carine (Natural History Museum, London) and Professor Miltsos Tsiantis (University of Oxford and Max Planck Institute for Plant Breeding Research, Köln). BBSRC funded.

*Cardamine hirsuta* L. (Brassicaceae) is an emerging model system for studies into the evolution of development. It was developed by Professor Miltsos Tsiantis and colleagues in Oxford and is proving useful for investigating the genetic basis of morphological traits (e.g., Hay and Tsiantis, 2006; Kougioumoutzi et al., 2012). My D.Phil. attempts to put this model organism in a systematic and phylogeographic context. The specific aims of this project are to: a) describe the geographic and phylogenetic structure of molecular variation in *C. hirsuta*, in order to construct a phylogeographic hypothesis for *C. hirsuta* in its native range; and b) identify the closest relatives of *C. hirsuta*.

*Cardamine hirsuta* is a common winter-annual weed native to Europe, the Middle East, North Africa and the East African High Mountains. Humans, particularly through the horticultural trade in recent times, have accidentally assisted *C. hirsuta* in expanding its range so that it is now found across much of the temperate world. Anthropogenic dispersal has also moved *C. hirsuta* about within its native range, making it the reconstruction of its phylogeographic history a challenging prospect.

Individual sampling for this study has predominantly come from herbarium specimens, plus my own collections from a few targeted field trips, providing excellent coverage of *C. hirsuta*'s native range. Sanger sequencing of multiple chloroplast and nuclear regions has been used to describe the phylogenetic structure within *C. hirsuta*. Pilot studies were used to test established chloroplast markers from Shaw et al. (2007) and new single copy nuclear regions developed for this project for suitable levels of infraspecific variation. This strategy has revealed clear geographic structuring of genetic variation within *C. hirsuta* with congruent patterns between chloroplast and nuclear markers. Climate suitability modelling has revealed that Pleistocene glacial dynamics can explain some of these patterns. Currently, the closest relatives of *C. hirsuta* are uncertain due to the lack of phylogenetic resolution and taxon sampling within *Cardamine*, a large genus of some 200 species.

**References**


Zoë Goodwin (D.Phil. 2nd year)
Revision of Drypetes Vahl and the history of species discovery in Aframomum

Supervised by Dr Robert Scotland (University of Oxford) and Dr David Harris (Royal Botanic Garden Edinburgh). NERC-funded studentship. Synthesis-funded trip to the National Herbarium Nederland at Wageningen, April 2012.

During a successful first year of my D.Phil. at Oxford I have begun to get to grips with my revision of Drypetes and I have started an interesting analysis of the history of species discovery in the genus Aframomum. The highlight of the year was the opportunity to visit some fantastic herbaria across the UK and Europe as part of my work on Drypetes.

Drypetes is a large, pantropical genus of small trees in the Putranjivaceae, notable for the presence of mustard oils (also found independently in the Brassicaceae) and infamously difficult to identify in the field. The Putranjivaceae is a recently created APG family also containing the much smaller genera Putranjiva from Asia and Sibangea from Africa.

Drypetes is characterised by stipules and simple, alternate, distichous, often coriaceous leaves with an asymmetric leaf blade base, and toothed, occasionally entire margin. The genus is dioecious with flowers fasciculate in the leaf axils or on old branches, occasionally cauliflorous. The flowers have an intrastaminal, nectiferous disk and are apetalous, the drupaceous fruit usually possess a pair of distinctive, persistent, flattened stigmas.

Currently there is considered to be just over 200 species worldwide, with about 115 species in Asia and the Pacific, 77 species in Africa and 18 species in the Neotropics. Centres of diversity of the genus seem to be located in Central Africa and South East Asia. For pragmatic purposes I have decided to focus my studies primarily on the African species of Drypetes. As part of my thesis I need to confirm whether or not the African species are fully monophyletic as suggested by initial investigations, and whether or not to include the species currently assigned to Sibangea.

During my first year I spent a significant amount of time examining herbarium material at the Department of Plant Sciences in Oxford (FHO), Royal Botanic Garden Edinburgh (E), Royal Botanic Gardens, Kew (K) and a very successful two-week trip in April to the National Herbarium Nederland at Wageningen (WAG, Syntheses-funded) combined with a three-day visit to the National Botanic Garden of Belgium (BR) just outside Brussels. I have also spent a significant amount of time testing and modifying primers to barcode the genus. This molecular work will allow me to test fully the monophyly of the African species and also hopefully contribute iteratively and informatively to the revisionary aspect of my project.

The second part of my project focuses on Aframomum, a genus in the ginger family (Zingiberaceae) from Africa. The first species of Aframomum were described as early as 1753 in the genus Anomum, before being split into a new genus Aframomum in 1904, which has been recently revised by David Harris and Alexandra Wortley. Initial analyses of specimens and species names indicate that Aframomum appears to demonstrate very pronounced patterns in specimen collection, specimen identification and species discovery. I hope that the completion of my analysis of the history of Aframomum will allow us insights into how we conduct taxonomy on land plants and how we can refine this process to allow us to identify rapidly the remaining undiscovered species.

The Florilégium Project

In the spring of 2012 we launched the Oxford Botanic Garden and Harcourt Arboretum Florilégium Society, which will be run in conjunction with the Department of Plant Sciences.

A dozen or so enthusiastic artists were invited to join, all with considerable experience of botanical illustration. Drs. Alison Foster and Stephen Harris compiled the initial list of plants to be illustrated and prepared an instruction sheet with details of page size, style and emphasised the need for complete accuracy. Once a year the artists will submit their finished artwork and a selected panel will accept pieces which are considered to be of a suitable standard. These will be stored in Plant Sciences and become a unique collection of illustrations for archival purposes.

We meet once a month in the garden through spring, summer and autumn, select our plants and make a start on the paintings. The aim is to be as comprehensive as possible, portraying both flowering and fruiting habits and enlargements, where necessary. Additional workshops have been held in Plant Sciences, giving instruction in dissection, composition and techniques of drawing from herbarium specimens. Every few years the Botanic Garden will host an exhibition of artwork.

The Garden is the oldest of its kind in this country, having been established in 1621. Jacob Bobart was appointed as the first superintendent and in 1648 published a catalogue listing 1600 plants that were then established in the garden. A number of these species are still there, including Buxus sempervirens, Cyclamen hederifolium, Epimedium alpinum and Tradescantia virginiana. These, and six others, comprise the first of our three themes for drawing or painting.

The second theme features plants that have a special connection with Oxford. No one wanted to choose Oxford Ragwort, Senecio squalidus, last year! I had no idea that Ivy-leaved Toadflax, Corydalis muralis, was also called “Oxford Weed” and was thought to have been introduced on statues brought over from Italy. Several painted parts of the Black Pine, Pinus nigra, under which J.R.R. Tolkien loved to sit and pronounced as his favourite tree. Two other plants have a particular association with the herbarium, Geranium oxonianum “Claridge Druce” and the blue-flowered water lily, Nymphea x daubenyana, which arose in the Garden.

Our third - and much larger theme - is to make a start on the medicinal plants. I am hoping a few more illustrators will be tempted to join us.

Rosemary Wise
Botanical Artist

Integration of molecular data in the context of a Foundation Monograph

Concerns over biodiversity loss have accelerated the need for a working list of plant species to aid conservation and document diversity before it disappears (Paton et al., 2008). However there is currently great uncertainty surrounding the number of flowering plant species, with estimates ranging between 230,000 and 420,000 species, largely due to the high level of synonymy (Scotland & Wortley, 2003). This is coupled with a further estimated 70,000 undescribed species (Joppa et al., 2011). A major impediment to the completion of an accurate plant species list is the lack of any global treatment for many species-rich plant groups. These large genera are often considered too daunting, too large and/or too widespread to be tackled from a global monographic perspective (Frodin, 2004).

The Foundation Monograph is proposed as an innovative and pragmatic approach for overhauling the taxonomy of species-rich, widespread, taxonomically neglected groups of plants in a short time frame. This approach, similar to traditional monographs, recognises that the most accurate way to delimit species – and therefore accurately account for synonyms – is via a critical examination of specimens across the entire geographical distribution of the group. However, the Foundation Monograph approach also recognises the enormity of the task of completing the global inventory.
given current taxonomic practice and therefore limits the aims of the monograph by prioritising the delimitation of species. Crucial to this approach’s methodology is the integration of molecular data to test species’ limits, establish species’ relationships and provide novel identification tools. The species hypotheses are established primarily on morphological analyses and then later corroborated, or refuted, using DNA barcodes and a phylogenetic approach based on monophyly. 

Convulvulus was selected for the pilot study as it is a reasonably large, species-rich genus, estimated to contain 150-200 species. The genus has an almost worldwide temperate distribution, with its main centre of diversity in the Mediterranean and Western Asia. Although Sa’ad (1967) revised the taxa in this region, it has not been monographed as a whole since the work of Choisy (1845). Since then molecular techniques have provided further insights suggesting a comprehensive treatment of the genus, including molecular data, would be valuable.

To develop the method for the integration of molecular data in the context of a Foundation Monograph this study included 312 specimens covering a total of 174 species of Convulvulus and Calystegia (a suspected segregate genus). Ninety-two per cent of the specimens were from herbarium material sourced from eight herbaria. The sequencing success for the barcoding markers matK (49%) and rbcl (74%) and the nuclear ITS region (65%) varied due to DNA degradation of herbarium specimens. Phylogenetic analysis on this more comprehensive sample of species confirmed that Convulvulus is paraphyletic with Calystegia nested within as a monophyletic clade. Polymersia was confirmed as the sister group. The phylogenetic analyses refuted and corroborated the species hypotheses for a number of species groups.

Outlined below are two specific examples: Convulvulus capensis and C. althaeoides are highly variable species that are morphologically indistinguishable, suggesting to some that they might possibly be the same species. However, the two species have very disjunct distributions, with C. capensis distributed in South Africa and C. althaeoides distributed in the Mediterranean. The phylogenetic analyses confirmed that the two species were separate species and together did not form a monophyletic group.

Convulvulus chinensis has previously been considered part of C. arvensis due to shared morphological features. However, the phylogenetic analysis revealed that C. chinensis cannot be included in a clade with C. arvensis without also including C. durandoi. Using Convulvulus durandoi is morphologically very distinct from both C. chinensis and C. arvensis. Its inclusion in the clade suggests that C. chinensis and C. arvensis, despite morphological similarities, should be considered separate species.

The next stage of the project is to prepare a Foundation Monograph of Ipomoea. Ipomoea is the largest genus in Convulvulaceae containing approximately 600-800 species. It is widespread, and distributed in both tropical and subtropical regions of the world. As with many large widespread genera, the last global treatment was from the 19th century. Major challenges in producing the Foundation Monograph are expected to be the geographical distribution of material and the burden of the extensive historical and contemporary literature.

Key References


Bethany Williams
Research Associate

Salicaceae and Achariaceae for Flora Peninsular Malaysia

Previous Floras for the SE Asian region have included the family Flacourtiaceae. However, when Chase et al. (2002), reported on their molecular investigation of this enigmatic family, they formally transferred all genera from the Flacourtiaceae to other families and removed the family from modern angiosperm classification (APG II & III). Most former Flacourtiaceae genera now belong to two pre-existing families: first the Salicaceae, previously a well-defined, mainly north temperate, family with only two genera, Salix and Populus; second the Achariaceae, formerly a South African family with three monospecific genera of climbing and acaulescent herbs and subherbaceous subshrubs. Alford (2007) is exploring whether Casearia, Osmeia and all other genera of the tribe Samydeae should be recognised as a separate family, the Samydeae, distinct from Salicaceae.

Most genera in the former Flacourtiaceae have a superior, unilocular ovary with parietal placentation. The ovary is semi- inferior in Homalium, Byrsanthus and Bembicia and it is modified to an apparently multi-locular ovary in Flacourtia. The fruit is either a berry or capsule with 2-8 valves. These characters are also found in many other families and the Flacourtiaceae had a reputation for being confusing and largely unrecognizable in the field (Sluemer, 1954). Characters such as polyandry, apetal and a glandular floral disc are found in different combinations in different genera or tribes, but in many genera the flowers are too small to examine easily even with a hand lens. This made it difficult to distinguish Flacourtiaceae from other small-flowered families, especially Euphorbiaceae and Celastraceae and resulted in the family being treated as a ‘dustbin’ for plants not obviously belonging elsewhere. Williams (1965) summed up the situation with the words “If in doubt, put it in the Flacourtiaceae”. The Salicaceae and Achariaceae belong to the clade Malpighiales, first identified by Chase et al. (1993). Further investigation of the phylogenetics of the Malpighiales (Wurdack & Davis, 2009) united 10 families (Achariaceae, Groupiaceae, Lacistemataceae, Malesherbiaceae, Passifloraceae, Salicaceae, Samydeae, Scypostegiaceae, Tumeraceae and Violaceae) into a strongly supported clade in which placentation is parietal.

I am preparing treatments of the families Salicaceae and Achariaceae for the Flora of Peninsular Malaysia. With the exception of Salix tetrasperma, all the genera and species included in these accounts used to belong to the Flacourtiaceae. In addition to one species of Salix, the genus of Salicaceae found in Peninsular Malaysia are Flacourtia (1 or 2 species and 2 cultivated), Casearia (8 species), Osmeia (1 or 2 species), Homalium (8 species), Scoparia (3 species) and Nemesciolaepia (1 species). The genera belonging to Achariaceae are Ryparosa (8 species), Hydrocaryus (13 species), Spathocalyx (1 species), Pangium (1 species, wild and cultivated) and Erythropspermum (1 species). During field work in 2011 and 2012, I saw representatives of all genera either in the wild or in cultivation, made herbarium specimens, and collected leaf samples into silica gel for DNA extraction. I have consulted the herbarium collections at BM, FHO, K, KEP, L, NY and SING and written new descriptions for each species using fresh, dried and spirit material. Fieldwork
was complicated by the similarity of these genera to the many other families with alternate, simple leaves. The most productive approach was to target sites where species of Salicaceae and Achariaceae were known to occur. This resulted in recording and collecting new information on fruits and flowers, distribution of male, female and bisexual flowers within and between trees, habit, habitat, architecture, population structure and some phenological information.

One of the earliest families to be published in *Flora Malesiana* was Sleumer’s 1954 account of the Flacourtiaceae and this has provided an excellent starting point for the *Flora of Peninsular Malaysia* account. Some modifications of Sleumer’s species delimitations are necessary, especially in *Ryparosa*, *Hydnocarpus* and *Casearia*, but these should be seen as refinements rather than substantial changes to his treatment of the family for the region. He consulted and annotated a large number of herbarium specimens from most of the herbaria cited above. Several other research groups are currently involved with revisions or treatments of the family in SE Asia. Bob Harwood (Bangkok and Australia) is writing an account for the *Flora of Thailand*, Bruce Webber and Ed Tsen (University of Western Australia) are preparing a revision of

### References


Caroline Pannell
Research Associate

Caroline in FRIM non-Dipterocarp Arboretum
Photograph by Yao Tze Leong (FRIM)
Homology of the daffodil corona

Several years ago I came back from our annual undergraduate field trip to the Algarve in Portugal puzzled by the identity of the daffodil corona, the crown-like structure in the middle of daffodil flowers. I had examined the flower of the hoop petticoat daffodil - *Narcissus bulbocodium* - (front cover and back page) in the context of organ identity (Figure 1) and was none the wiser about what part of the flower was modified to form the corona. On my return I consulted with two colleagues (Paula Rudall at Kew and Peter Endress in Zurich) and read some literature [1,2,3,4] to learn that the exact identity of the daffodil corona had remained a mystery throughout the history of botany. As the corona is located between the tepals and the stamens, it had been previously hypothesised that the corona was a modification of the stamens [3] or the tepals [1]. A related issue, often discussed relative to the identity of the daffodil corona is that many other genera, e.g. *Eucharis, Hymenocallis, Pancratium*, from the same family as daffodils (Amaryllidaceae) also have a corona. In these other genera it has been interpreted that the corona are formed from the staminal filaments as the anthers (pollen bearing part of the stamen) are usually located at the apex of the corona. Specifically this type of corona is termed a staminal corona. The difference from this type of corona compared with that of the daffodil is that the staminal filaments of the daffodil are often located at the base of the flower and do not form part of the corona. Genera that have a corona within Amaryllidaceae are variously related to other genera that do not have a corona and therefore the corona has evolved multiple times with this family. With regard to the daffodil corona, one question is whether the independent evolution of this trait is variation on the same theme (parallelism) throughout the family or represents different ways to evolve a similar structure (convergence).

One difficulty in understanding the development of young daffodil flowers is obtaining enough material as the flowers are very small (a few millimetres) and develop inside the bulbs in the summer before they emerge from the ground the following spring (Figure 2). Therefore identifying when exactly in the summer the flowers develop is not trivial and dissecting out these early stage minute flowers is also very difficult and demands time and patience. Over several years we dissected more than 2000 individual daffodil bulbs.

We examined the early stages of flower development and were able to take advantage of the fact that developmental geneticists have identified those genes that specify the identity of the various floral organs [5,6,7]. Crucially with respect to the daffodil problem, so-called B & C class genes variously specify the identity of tepals (B genes), stamens (B & C genes) and carpels (C genes). Therefore the experimental design adopted was to clone these genes from the daffodil and examine which of the genes were being expressed in the corona and in that way gain some insight into what organ was being modified to form the corona.

Our results demonstrated that the corona initiates as six separate groups of developing cells (Figure 3) from hypanthial tissue between the stamens and perianth. Scanning electron microscopy images and serial sections demonstrated that corona initiation occurs late in development (Figure 4). Therefore identifying the floral organs of the daffodil can be a challenging and time-consuming process.
4), after the other floral whorls are fully developed. To define more precisely the identity of the floral structures, daffodil orthologues of the BC floral organ identity genes were isolated and expression patterns were examined in perianth, stamens, carpel, hypanthial tube and corona tissue. Coupled with in situ hybridization experiments, these analyses showed that the expression pattern of the C-class gene NbAGAMOUS in the corona is more similar to that of the stamens than that of the tepals. In combination our results demonstrate that the corona of the daffodil Narcissus bulbocodium exhibits stamen-like identity, develops independently from the orthodox floral whorls, and is best interpreted as a late elaboration of the region between the petals and stamens associated with epigyny and the hypanthium (Figures 3 & 4)[8].

References


Robert Scotland
*Reader in Systematic Botany*

Figure 3: Schematic view of corona development in Narcissus bulbocodium relative to the other floral organs. (a) The major whorls of the floral ground plan are established before any evidence of the corona is visible. (b) The corona develops late between the tepals (T) and stamens (St) on the hypanthium. (c) Floral diagram showing the arrangement of tepals (red), stamens (green) and carpels (blue) prior to coronal initiation. (d) The corona (yellow) first emerges at six separate locations outside of, but interdigitated with, the stamens. The corona subsequently extends vertically, developing into a coherent ring of tissue between the stamens and tepals (e). Image from Waters et al. (2013).

Figure 4: Developmental progression of flowers of Narcissus bulbocodium. (a) Young flower at the stage at which the floral ground plan is well established but there is no corona present. (b) Same flower as in (c) with stamens and tepals removed showing absence of the corona. (c) More mature flower at the stage when the corona has begun to initiate. (d) More mature flower with the tepals removed showing the emerging corona. Arrowheads point to coronal high points that coincide with regions between the stamens. Abbreviations: B, bract; H, hypanthium; T1, whorl 1 tepals; T2, whorl 2 tepals; St, stamens; C, carpel. Scale bars: 500 µm (a and d), 100 µm (b), 1 mm (c). Image from Waters et al. (2013).
A diversity of conifers

Globally, there are 615 species of conifer in 70 genera and eight families. Although associated by most with the extensive forests of pines and spruces in the northern parts of America and Eurasia, conifer diversity lies elsewhere. Only a handful of species have a distribution that extends over more than one continent, the most widespread of these being *Juniperus communis*. Seven of the 70 conifer genera have a wide and trans-continental distribution. All but one, *Podocarpus*, are (virtually) confined to the Northern Hemisphere; these are *Abies*, *Larix*, *Picea*, *Pinus*, *Juniperus* and *Taxus*. Some 200 species are confined to the Tropics and the islands of Borneo (large) and New Caledonia (small) each contain more native species of conifers than all of Europe.

In the north, a belt of boreal coniferous forest dominated by a small number of species encircles the globe. Elsewhere, conifer species are most abundant in major mountain systems, e.g., in western North America, Mexico, Central America and in the Andes of southern Chile; in Europe from Spain to Greece; in the Himalayas, China and Japan; and in New Guinea and New Zealand. Other areas of abundance are perhaps less expected, such as the Atlantic side of the USA and SE China where forests tend to be dominated by angiosperms. Less densely populated but equally surprising are parts of Australia and parts of Malesia other than New Guinea, where angiosperms are once again the dominant trees of forest. Some small islands are rich in conifers, most notably New Caledonia, Taiwan and Tasmania.

Apart from regions such as Antarctica, the High Arctic and major tundra zones, steppes and deserts, there are some very large areas devoid of conifers. In South America these are the Amazon Basin and Mato Grosso; in Africa, the Congo Basin and West Africa; in Asia, the Indian subcontinent and most of the Tibetan Plateau. The greatest enigma of all is the near absence of conifers in the Indian subcontinent. All but one species of conifer in India are confined to the Himalaya or to the hills in the far north east of the country and these nearly all belong to the Pinaceae, the subfamily Cupressoideae in Cupressaceae, and the Taxaceae.

There are also disparities in taxonomic diversity in those regions where conifers occur. All eight families, over 80% of the genera, and slightly over half of all conifer species occur in fourteen centres of diversity around the Pacific Ocean. The centres of conifer diversity around the Pacific Rim are all mountainous, often islands and have oceanic climates with moderate temperatures and high precipitation. Separation and
The great age of the Pacific as an ocean basin, going back to the origin of the oldest extant families, also played a role. Continuous movement of its plates towards shifting land masses, creating subduction zones where they contacted, causing volcanism, island forming and mountain building, provided suitable habitats during the entire length of the evolution of modern conifers.

Other major centres of conifer diversity are in China (especially Sichuan and Yunnan Provinces) and along the Himalayan Range from the east, with species diversity receding further west but generic diversity remaining high. On the Atlantic Ocean coasts, only the north east of the USA scores high in generic diversity but not in species numbers. Scattered degree cells with high diversity are also present in western Malesia (Sundaland) more distant from the Pacific Rim, and in Europe. The diversity in Europe is a remnant of much greater diversity before the Pleistocene extinctions that decimated the tree flora of that continent.

These, together with other facts and figures on conifer biogeography, diversity and conservation status, have now been brought together to create a global atlas of conifers. The atlas presents maps of all families, genera and species (and many varieties) based on the data of some 37,000 verified herbarium specimens. Maps that analyze the distribution of conifer biodiversity are also presented showing hotspots and areas of endemism. An Atlas of the world’s conifers: an analysis of their distribution, biogeography, biodiversity and conservation status will be published by Brill in Autumn 2013.

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The sad history of a Bolivian Butterwort

Butterworts belong to the genus Pinguicula in the family Lentibulariaceae. They are of characteristic appearance with leaves arranged in a basal rosette from which arise one or more scapes usually bearing a single flower. They are insectivorous plants whose leaves function as fly papers to catch and absorb small insects. Until recently only a single species, Pinguicula involuta Ruiz & Pavon, was known from Bolivia. Here follows the history of the second species, which involves botanical rivalry and the perils of development.

1995: In July of this year a single population of another Pinguicula species was found near the village of Nuevo Mundo in the south-central Andes of Bolivia by a group of botanists led by Michael Kessler, then of Göttingen University. Quite independently I found the same population in November of the same year. Some 30 or more plants were growing on a damp vertical sandstone rock above a river gorge lying close to the road to the village. I visited the area frequently over the next few years but never found any plants anywhere else in the area although similar habitats were not uncommon.

2007-8: Two publications appeared close together describing this species as new. The most comprehensive was a joint Bolivian and German paper (Beck et al. 2008), which named the plant Pinguicula chuquisacensis. S. Beck, A. Fleischm. & Borsch and gave a detailed account of its relationship with other Pinguicula species based on molecular studies, discussed its ecology and assessed it as “Critically Endangered”. It cited various collections and summarised the history of its discovery. However, it was not the earliest publication. A group of what can only be described as “botanical cowboys” from the Czech Republic visited the area in 2007 and described it under the name Pinguicula jarmilae J.I. Halda & M. Malina (Halda et al. 2007), which has priority as the accepted name under the botanical code. Their paper compares it with the not very closely related Spanish species Pinguicula mundi, and provides an epithet with no obvious meaning to a Bolivian. It gives a description and illustration but provides only minimal information on habitat location. Nothing more was possible, of course because the authors were unaware of the wider context and acted independently from Bolivian institutions and probably illegally within Bolivian environmental laws. Actions of this sort, of course, create resentment in many biodiverse-rich countries and create problems for bona-fide researchers.

2013: I visited Nuevo Mundo again this year looking for Ipomoea species and wanted to show my companions the Pinguicula. However, a new road bridge had been built over the site and not a single Pinguicula could be found.

The Future: It is, of course, possible that Pinguicula jarmilae will be found elsewhere in the region at some future date but, for the moment, it must be considered extinct in the wild. However, that is not quite the end of the story. Halda and his colleagues took seeds from the plant and it is now in cultivation in various countries, see http://www.cpukforum.com/forum/index.php?showtopic=30251&t=20 for pictures and further information. Perhaps some good has come from this not very honourable story and I have to admit that the new bridge is a lot more secure and easy to negotiate than the old wooden log construction. Even though a bit of good has emerged from this, the ethics of biopiracy, if that is what it was, and the consequences of development for biodiversity remain relevant issues for ongoing debate.

References


John R.I. Wood
Research Associate
The Japan Hotspot

Tom Price (left) and Ben Jones (right) in Japan recording site data for seed collections. The information will be incorporated into the BRAHMS database, ensuring field data remains associated with each individual collection. The associated information adds great value to the collected material.

The Botanic Garden and Harcourt Arboretum (OGBHA) has recently undertaken a project to collect and document seed of the native flora of Japan. This project has been developed in collaboration with the Department of Plant Sciences (DPS) and builds on research conducted by Dr. Nodoka Nakamura into the Japan hotspot: see the website http://herbaria.plants.ox.ac.uk/bol/florajapan

The objective is to cultivate plants of wild origin at both the Botanic Garden and Harcourt Arboretum, showcasing the unique flora of Japan and interpreting biodiversity research conducted by the DPS to the wider public. Supporting herbarium specimens will be accessioned into the Fielding-Druce Herbarium, with duplicates retained by partner institutions in Japan and the University of Bonn Botanic Garden.

OGBHA has recently conducted collection audits, assessing the fitness for purpose of the collections in line with the core activities of the department. These audits highlighted the need to both develop our geographic collections and to focus on sourcing new material of known origin. The opportunity to work closely with the DPS, linking the need for development with ground-breaking biodiversity research, presented a unique and exciting way of improving the collections held at OBGHA.

Using bioquality hotspot maps formulated by Dr. Nakamura’s research, areas of high biodiversity within Japan could be identified. These areas provided a focus for selecting sites for the collection of seed across the archipelago. In order to plan the logistics for such collections a reconnaissance trip was required. Consequently Ben Jones (Arboretum Curator) and I visited Japan for four weeks during November 2012. Contacts were established at Botanic Gardens across the country, from Hokkaido in the north to Shikoku in the south, and field sites visited and investigated for potential seed collection activities. We were met with interest and support for the project from our Japanese colleagues, with offers of assistance with planning, permit applications and field work. The project will run over three years, focusing on northern, central and southern Japan consecutively. We hope to work closely with the Japan Association of Botanical Gardens and the Ministry of the Environment, building relationships for longer-term collaborative working.

To complement the collection of both seed and herbarium specimens the team will conduct Rapid Botanical Surveys at selected sites, providing data to ground truth the bioquality hotspot map produced by Dr. Nakamura and contributing to ongoing research in the field of biodiversity science. Collaborations have been established with the University of Bonn Botanic Garden and the Millennium Seed Bank Partnership, Kew (MSB) to facilitate the project. Bonn has an interest in developing their collection of Japanese plants to celebrate their association with Phillip Franz von Siebold (1796-1866). There are also active research interests in taxa native to Japan at both Bonn and Oxford, requiring well-documented wild material.

The collaboration with the MSB offers several exciting opportunities, including the banking of collected seed, which will allow the project to contribute to ex situ conservation targets. Training in seed collecting, post harvest handling and seed conservation techniques have also been made available as well as assistance with shipping, import and plant health. The MSB are very keen to extend their activities into Japan. Colleagues from the MSB have been invited to participate in the collection trips, the hope being that this project will help to help facilitate this objective.

The Japan hotspot project not only provides the opportunity for staff at OBGHA to acquire new skills and knowledge, but also promotes the work of the university at an international level and further enhances the links between OBGHA and the DPS.

Tom Price
Gardens’ Curator,
Oxford Botanic Garden

Voucher herbarium specimens were prepared for each seed collection. These will be accessioned into the Fielding Druce Herbarium, Department of Plant Sciences, Oxford.

Alnus sieboldiana – ‘our first black star-rated species collection’. This is a species named after the German physician Phillip von Siebold who studied the flora and fauna of Japan.
Mark Catesby's collections in Oxford

In the early eighteenth-century, North America was part of the burgeoning Empire attracting the attention of naturalists in Britain. All manner of novel natural history treasures were being returned to British shores, contributing to understanding the natural world. One of these colonial explorers was the Englishman Mark Catesby (1682-1749; Frick & Stearns, 1961; Meyers & Pritchard, 1998). Catesby first visited North America in 1712 and 1715. During this three-year visit, his collections convinced a group of gentlemen to sponsor his subsequent North American explorations between 1722 and 1726. Catesby is best known for the illustrations, which resulted from these explorations, in his two-volume Natural History of Carolina, Florida and the Bahama Islands (1729, 1747). Catesby's supporters included the Royal physician Sir Hans Sloane (1660-1753), whose collection eventually founded the British Museum, the diplomat William Sherard (1659-1728) and Charles Du Bois (1656-1740), Treasurer of the East India Company. In return for their financial support, Catesby sent them specimens to add to their herbaria. Today, the Sloane Herbarium is housed in the Natural History Museum, London (McMillan et al., 2013), whilst the herbaria of Sherard and Du Bois are housed in Oxford University Herbaria.

Following a search of all the pre-1796 herbaria housed in Oxford (c. 60,000 specimens), all specimens bearing Catesby's name or likely to have been collected by him have been imaged and gathered into a single database.

In Oxford University Herbaria, Catesby specimens are spread across three pre-1796 herbaria. The Sherard Herbarium was amassed by Sherard and bequeathed to the University in 1728. The herbarium was part of Sherard's grand plan, the Pinax, to publish a list of all of the world's known plants (Sherard, unpublished). Over the next century it continued to grow as the Sherardian Professors of Botany added material. Today, the Sherard Herbarium comprises about 21,000 specimens. Numerous collectors, including John Bartram (1669-1777), John Clayton (1668-1773), William Clerk (fl. 1710-1734), William Houston (1695-1733), John Mitchell (d. 1768), Thomas More (fl. 1700-1730) and Michel Sarrazin (1659-1734), contributed North American specimens.

However, Catesby made the largest single contribution. Three hundred and forty eight specimens bear his name and are localised to: Virginia (2, possibly 3, specimens); Carolina (65, possibly 66, specimens); South Carolina (178 specimens); and Providence (30 specimens). Seventy one specimens are unlocalised. Associated with a specimen of Nelumbo lutea Pers. (Nelumboaceae; Sher-1090-10) a pen and ink drawing by Catesby was rediscovered, which clearly revealed Catesby was using the drawing as a substitute for a flower which he 'could not preserve'. The Herbarium also contains specimens of cultivated plants, usually raised at Eltham Palace, the home of Sherard's brother, James (1666-1737), from seeds collected by Catesby. The German-American botanist Friedrich Traugott Pursh (1774-1820) visited Oxford as he was completing his magnum opus Flora Americae Septentrionalis; or, a systematic arrangement of the plants of North America (1814). He considered Sherard's herbarium 'the most complete collection of North American plants now extant' (Pursh, 1814: xviii) and specifically cited 11 Catesby specimens.

Part of the Dillenian Herbarium was separated from the Sherard Herbarium in the late-nineteenth century by George Claridge Druce (1850-1932). Druce separated those specimens he considered to have been grown at Eltham Palace and used in the production of the plates for Johann Dillenius's (1684-1747) Hortus Elthamensis (1732). However, the decisions Druce made were flawed since wild-collected specimens were included, and some specimens were collected much earlier than the publication date of the Hortus. Thirty four specimens in the Dillenian Herbarium are associated with Catesby, or places he could have collected.

The Du Bois Herbarium was created by Charles Du Bois and apparently given to the University during Humphrey Sibthorpe's (1712-1797) tenure as Professor. The herbarium comprises some 13,000 specimens, and was originally bound in 74 elephant folio volumes and arranged according to John Ray's (1627-1705) Historia Plantarum (1686, 1688, 1704). The Du Bois Herbarium was unbound, remounted and organised into its present form by Druce on the orders of Isaac Bayley Ballour (1853-1922) in the 1880s. The main collectors who contributed North American specimens were David Krieg (d.1713) and William Vernon (fl. 1688-1711), who collected in Maryland, and an unknown person who collected around Hudson Bay. Four hundred and fifty eight specimens bearing Catesby's name are localised as: Virginia (32 specimens); Carolina (3 specimens); and South Carolina (412 specimens). Eleven specimens bearing Catesby's name are unlocalised. Some of the American collections have been studied but generally the Du Bois's Herbarium has been the subject of little research. Pursh makes no mention of the Du Bois Herbarium when he visited England (1811-1815), despite the collection being in Oxford.

Interpretation of the Catesby specimens in Oxford University Herbaria is confused by Sherard's apparent habit of relabeling specimens in his own hand and discarding original labels. Furthermore, the original specimen order and much of the contextual information was lost when the Du Bois Herbarium was unbound. Despite these issues, labels in Catesby's hand are associated with 70 specimens found in Oxford University Herbaria and the Sloane Herbarium.

A website of the Catesby specimens in Oxford University Herbaria is available at http://herbaria.plants.ox.ac.uk/bol/catesby.

Specimen from the Sherardian Herbarium of Nelumbo lutea Pers. (Nelumboaceae; Sher-1090-10) collected by Mark Catesby from Carolina in 1722.
References


Stephen A. Harris
Druce Curator of Oxford University Herbaria

Druce Archive

The Druce Archive project, documented in Oxford Plant Systematics 18, has been completed. The archive consists of around 160 boxes of correspondence, ephemera, photos and glass slides once owned by George Claridge Druce and housed in the Sherardian Library of Plant Taxonomy. The archive contents are recorded on the Plant Taxonomy LibGuide:
http://libguides.bodleian.ox.ac.uk/content.php?pid=229816&sid=1901222

Rowan MacGregor
Graduate Library Trainee
News from the Herbaria

During 2012 work continued on all herbarium activities in the form of databasing, digitisation of material, sending and receiving loans, returning loans after completion of studies by research staff, plus adding new accessions. The incorporation of material, either new or having been re-determined, often required re-organizing collections and replacing folders. In the summer months we had the help of three students, Katie Anders, Libby McGowan and Hanna Sundall, who were temporarily employed to mount specimens.

2012 was again a busy year in terms of visitors. 145 people visited and a number of groups were given tours with particular interests as detailed below.

Fielding-Druce (OXF) and Daubeny (FHO)

A group of ten trainee Oxford Green Badge Guides came to see the historic herbaria and the Sherardian Library in order for them to be able to observe and then promote the University’s rich collections with remarkable histories. A group of Bodleian Library Sconal trainees were also given a tour and shown links/associations between the collections of herbarium specimens and books from the 17th century to the present day. Dr Mark Spencer, Senior Curator of the British and Irish Herbarium, Natural History Museum, London brought six volunteers from BM to be shown examples from different collections. It was interesting to discuss similarities and difficulties which the two herbaria share. In June, Michael Pirie, Head Gardener of Green Templeton College, who was teaching a course on Gardens of the University of Oxford, brought a group of 12 students. They were shown a number of 17th century specimens, books and manuscripts relating to the Oxford Botanic Garden from the collections of Jacob Bobart and Robert Morison. Professor Eloise Carter from Oxford College of Emory University, Georgia USA brought seven visiting American students studying a Plants and Society course. After an introduction to the herbarium, they were shown selected historical specimens and books from the 17th century to the present day. Dr Stephen Harris also showed a group from the ‘Friends of the Oxford Botanic Garden’ around the herbaria. The theme of this visit was to put the activities of the Botanic Garden into the wider context of plant sciences over the last 400 years.

A number of artists also visited to draw inspiration from seeing examples of Ferdinand Bauer’s watercolours and sketches from the Flora Graeca, plus associated herbarium specimens. A group of Chinese Brush painters were introduced to the herbarium and were delighted to see 18th century watercolours of Japanese plants held in the Library as well as the Flora Graeca. Many other researchers visited to study particular genera and determined much material. Paul Harris and Jessica Turner continued to make a number of day visits to carry on with their search for plants collected in Sussex.

For one week in July, Dr Aleck Yang, from the National Museum of Natural Science in Taichung, Taiwan, visited with three other researchers from TNM Herbarium, the Botanical Garden and the Taiwan Forestry Research Institute Herbarium (see photo above). They made a thorough search through OXF for botanical specimens collected by Richard Oldham (1837-1864) in Taiwan and Japan during 1864. They located in the region of 300 specimens of which approximately 10% were types. This information will be added to their collections database in Taiwan and will be made available to other Taiwanese researchers studying the Flora of Taiwan and Japan. They listed and digitally photographed the sheets, leaving copies in OXF which will be incorporated into the BRAHMS database. They were very impressed with the quantity of material located in OXF and found the week extremely useful.

A special loan of historic material consisting of nine specimens collected by the privetare William Dampier in 1699 was borrowed by the Übersee-Museum in Bremen, Germany, for display in an exhibition entitled “Adventurers, Explorers, Researchers” to run from October 2012 to April 2013. The aim of the exhibition was to portray the dynamics of adventure, discovery and research by presenting collections from known and pioneering individuals. About 300 additional specimens were sent out on loan from FHO during 2012 included 117 specimens. Another batch of 69 mixed specimens were types. Another batch of 69 mixed specimens sent from the University of Waterloo, Ontario, Canada and collected by the late Professor John Morton in Sierra Leone and Ghana were mounted. An isoneotype specimen of Malus pumila from the RBG was also received and accessed.

Material received on loan for research included specimens of Aglaia (Meliaceae) for determination by Caroline Fennell from the Sarawak Biodiversity Centre. Several small loans of Convolvulaceae and Ipomoea were received for study by John Wood and Beth Williams. Specimens returned from loan after completion of studies included Amicia and Mimoso (Fabaceae), Tecoma (Bignoniaceae), Chazalia (Rubiaiceae), Ruellia (Acanthaceae), Senecio (Asteraceae) and specimens collected in Trinidad and Tobago. 160 duplicates, mostly Fabaceae from Brazil and Mexico, collected by a former D.Phil. student Marcelo Simon, were sent as a gift to UB (Brasilia) and this included four type specimens. Material sent out on loan to FHO during 2012 included sheets of Monanthotaxis (Annonaceae), Neopelonea (Lecythidaceae), Strophanthus (Apocynaceae) and Uapaca (Euphorbiaceae). Amongst material returned to FHO from loan, was a holotype specimen of a newly described species, Gilbertiodendron tonkolili. The specimen had been collected by William Hawthorne et al. from the Northern Region of Sierra Leone in 2006. The species is endemic to the region and on the ‘critically endangered’ list.

Serena Marner
Herbarium Manager
Painting and drawings of various stages of development of *Narcissus bulbocodium* by Rosemary Wise. See article on pages 8-9.