



The Sturt pea through 300 years of Australian botanical exploration

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Abstract: The Sturt pea, *Swainsona formosa* (G.Don) J. Thompson, was one of the first Australian plants collected by a European; during Dampier's 1699 voyage. The botanical study of the species reflects the story of Australian botany itself. Starting from the earliest explorers, the Sturt pea has been the subject of scientific study, which has continued to the present day. In fact, the flower has long been a part of Aboriginal culture, with many local names and myths attributed to it. The Adnyamathanha word for the species, *ngarapanha*, can be translated as 'little liar', as it was thought to deceive locals into thinking there was water nearby. This name is fitting in a botanical sense as well, as the Sturt pea is quite distinct from its closest relatives and has often deceived botanists. Its large, striking red flowers are very different from the other species in the genus *Swainsona* Salisb.

In this paper we endeavour to review the botanical and evolutionary study of the species and its relatives, including our ongoing research at the State Herbarium of South Australia, where we have used the latest molecular approaches to study the genus. Our research seems to have resolved some of the competing taxonomic hypotheses, but challenges remain. Looking forward, it will take a combination of all the scientific evidence to tell the story of the Sturt pea, which continues to fascinate modern explorers just as it has throughout its colourful history.

Keywords: Legumes, molecular phylogeny, genomics, botanical history, Australian explorers

Introduction

*Such savage and scarlet as no green hills dare
Springs in that waste, some spirit which escapes
The learned doubt, the chatter of cultured apes
Which is called civilisation over there*

from the poem *Australia*
A.D. Hope (1943, p. 42)

William Dampier was looking for water. He and his men had rowed ashore near what is now Broome, Western Australia, in the spring of 1699, armed with weapons as well as shovels and pickaxes to dig wells. Soon after landing they spotted some natives at a distance, who were "menacing and threatening of us." Despite his many "signs of peace and friendship" (Dampier 1729, p. 208) the "New Hollanders" kept their distance, so Dampier and his men attempted to capture one of them in hopes of learning where to get fresh water. In the inevitable clash that followed, Dampier shot one of the natives and one of his own men was hit by a lance.

Nine days before this encounter, further south, again looking for water, Dampier collected the first plant specimens in Australia by a European. One of these was "of a deep red colour, looking very beautiful" (Dampier 1729, p. 200). This turned out to be the Sturt pea (*Swainsona formosa* (G.Don) J. Thompson) and along with other specimens, was taken by him back to England, where they are still held today in the Oxford University Herbarium (Fig. 1). It is no coincidence that Dampier would have collected the Sturt pea; as Symon & Jusaitis (2007) point out, he was not a botanist and likely picked plants that stood out from the others. Ever since, the species has attracted the attention of explorers and botanists who have ventured into the Outback, drawn to its dark red flowers with their unusual shape. It is no surprise that the Sturt pea would be amongst the first plants collected by anyone new to the Outback, botanist or otherwise.

More humble relatives in the genus *Swainsona* Salisb. (Salisbury 1806: t. 28) did not receive as much attention as the Sturt pea. In contrast to the big, showy petals of *S. formosa*, the other members of the genus have much

smaller flowers, with softer colours of white, yellow and pink. The larger flowers and brighter colours of Sturt pea are likely the result of the shift to bird pollination, from primarily insect-pollinated flowers of its relatives (Symon 2000). This shift may also have been a factor in the Sturt pea's range expansion, compared to its closest relatives in Western Australia, east across the arid lands of Australia (Fig. 2). These sometimes-dramatic shifts in morphology creating distinct (and often bizarre) forms are a common theme in the Australian flora (Barlow et al., 1981).

Sturt pea's very distinctive appearance (Fig. 3) relative to other members of the genus and the early inaccessibility of the inner arid lands of Australia made it difficult to put the species in its proper taxonomic place. Over the centuries, as both the Outback and the genus have been explored more extensively, the taxonomic status of the Sturt pea and the evolutionary relationships in the genus *Swainsona* are now much better known. The age of molecular genetics has provided new tools for the taxonomist and has allowed for confirmation of taxonomic hypotheses and more fine-scale determination of relationships that are independent of



Fig. 1. Image of the historical specimen of Sturt pea in the Oxford Fielding Herbarium, collected by William Dampier, 22 Aug. 1699. Photo provided by Oxford University Herbaria.

the sometimes-misleading convergent morphological adaptations in otherwise more distantly related species. With the advent of genomics, we have even greater tools to study plant evolution. In this new age of 'omics' research, we have the capacity to explore the depths of the plant genome for all fields of research. For the taxonomist, these latest tools not only provide enhanced ability to reconstruct the evolution of their target species, but soon it will be commonplace to examine the changes in the very genes responsible for the morphological traits underlying their taxonomic distinction within the genus.

Dampier's voyages set the tone for European explorers in the centuries to follow: clashes with natives, struggles just to stay alive, a panoply of strange and exotic animals and plants. The Australian Outback, both beautiful and terrifying, has long held the fascination of many an explorer. In the pages that follow we offer a brief overview of the botanical exploration of the Sturt pea and the genus *Swainsona*, and follow it through the age of exploration to its recent revision with modern floristic methods and on to its reassessment with molecular genetic techniques. With increasing advances in genomic research and next-generation sequencing we are discovering ever more startling aspects of the

plant genome and its associated microbiome, revealing surprising biodiversity. As we explore further into the genome of the Sturt pea, we find that, like the Outback, there are still many secrets waiting to be discovered.

History

A veil hung over Central Australia that could neither be pierced or raised.

Charles Sturt (1849, p. 260)

The centre of Australia has long been a source of mystery. The last frontier of the continent, the interior arid lands at the same time repelled settlement and encouraged explorers, naturalists, and adventurers of every sort. In the early years of settlement, newly arriving Europeans stayed to the peripheries, close to the coasts. The interior gave up its secrets reluctantly and only after much effort and hardship of the early explorers.

One of the greatest obstacles to travel in the Red Centre is lack of water and the journals of the early explorers are filled with references to endlessly, sometimes desperately, searching for the next water source.

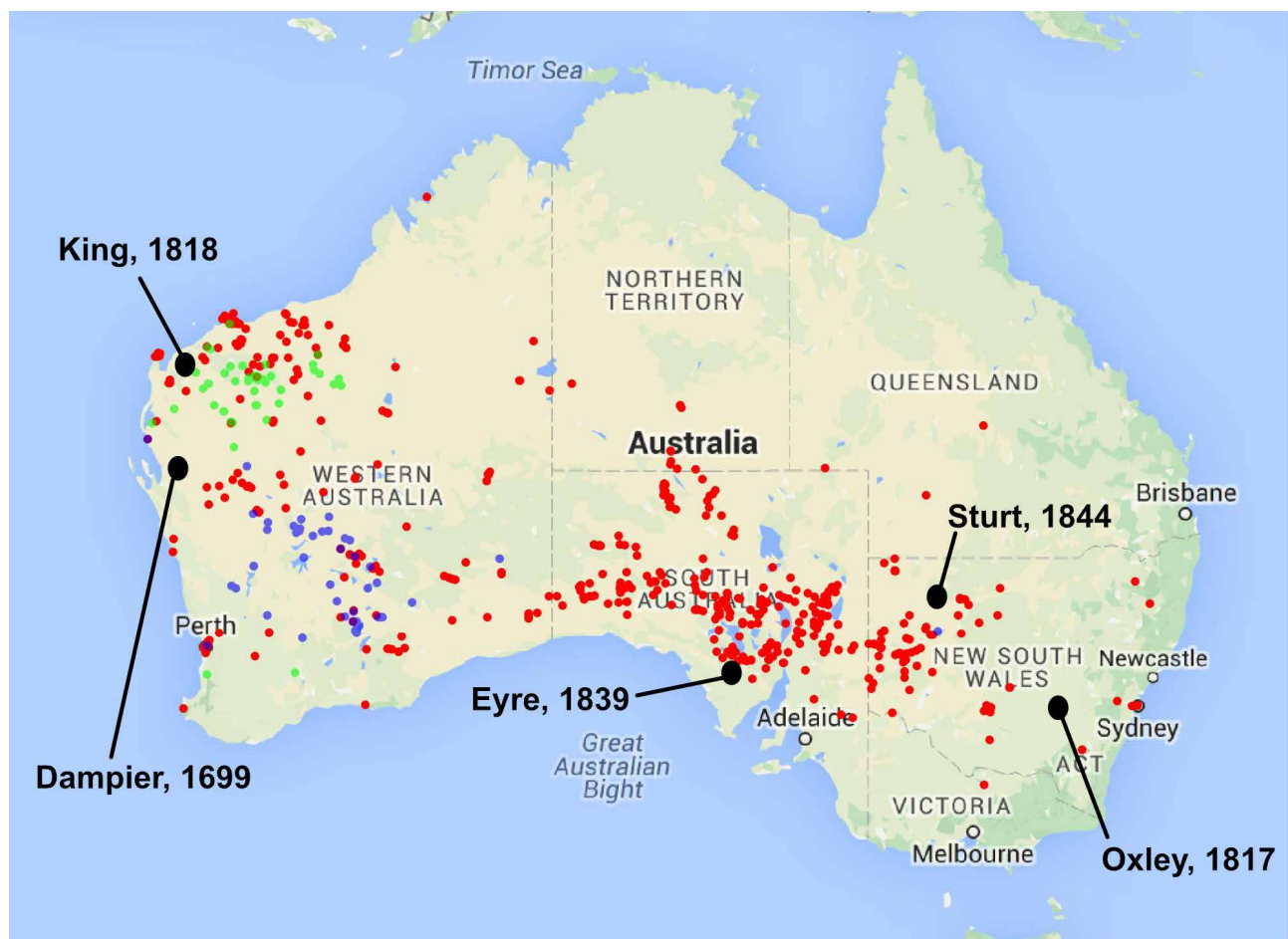


Fig. 2. Distribution map of Sturt pea (*Swainsona formosa*: red circles) and close relatives (*S. maccullochiana*: green circles, *S. beasleyana*: blue circles). Collections by early explorers are also indicated. (Distribution data from the Australasian Virtual Herbarium; base map by Google).

Often specimens of the Sturt pea (along with many other species) were found while looking for water, as was the case for Dampier's first collection. In fact, an overarching motivation for exploration into the interior was to find the fabled 'inland sea' that many believed to cover much of the centre of Australia. Finding such a water source would of course have allowed settlement much further inland and as such was a prime motive for early exploration into the Outback (Oxley 1820; Sturt 1833, 1849). This was a main driver for the first recorded collection of the Sturt pea in the early 19th century. John Oxley, who was following the Lachlan and Macquarie rivers in New South Wales for the elusive inland sea, came across a specimen that Cunningham named *Kennedyya speciosa* A.Cunn. (Oxley 1820; Orchard 2017).

About a year later, on the opposite side of Australia, along the coast of Western Australia, during Lt. Phillip King's survey of the intertropical coastline, a few plants of Sturt pea were collected along the Ashburton River (King 1827; Brown 1849). The botanist who accompanied King was Allan Cunningham, who also had been with Oxley the previous year. Upon examination of the two collections, Lindley decided (Lindley 1835) that not only did they belong to a different genus, but also they were different enough to be two separate species, *Clianthus oxleyi* A.Cunn. ex. Lindl. for the eastern specimen and *C. dampieri* A.Cunn. ex. Lindl. for the western. The fact that they were found on opposite sides of the continent (and

their distribution) was probably a factor in his decision (Symon & Jusaitis 2007).

One of the biggest believers in the existence of an Australian inland sea was the explorer Charles Sturt. Sturt knew both Oxley and Cunningham and took up their quest with vigour. The journals of both his early (1828–30) and later (1844–45) expeditions have many references to an inland sea and his party was always either "rapidly approaching" (p. 84), "in the immediate vicinity" (p. 112) (Sturt 1833), "within a tangible distance," (p. 184) or not very "far from the outskirts" (p. 241) (Sturt 1849) of the mythical great water body. After his last and furthest expedition into Central Australia, Sturt conceded that there was no sea in the heart of the country and admits he never had imagined a desert of "such boundless extent" (Sturt 1849, p. 324).

Yet, Sturt's expeditions were not completely futile. As with the other explorers, Sturt brought along naturalists to record and collect the animals and plants along the way, many new to science. Some specimens of Sturt pea were collected, in circumstances that are by now familiar: searching for fresh water for themselves and their horses amid nervous dealings with sometimes unfriendly natives. Sturt was becoming frustrated with an Aboriginal guide who he felt was deliberately leading them away from good water. He was leading his men back towards an earlier camp, when some Sturt pea plants were spotted along a small creek (Sturt 1849). A couple of days later, along a creek, another specimen



Fig. 3. Sturt pea in flower. (Photo: Tony Robinson).

was found. This one was in the bed of the creek, a place where Sturt “certainly did not expect to find that splendid creeper growing” (Sturt 1849, p.138).

It is no coincidence that the Sturt pea was so often found by explorers searching for water, or along waterways, as the species is most commonly found in soils subject to periodic flooding, often along waterways and watering holes (Cunningham *et al.* 1981; Symon & Jusaitis 2007). Despite growing in and being associated predominantly with the arid interior (and often called “Sturt’s desert pea”), the species, as with many members of the genus, depends on above average rainfall seasons, occurring sporadically or not at all during drought years (Symon & Jusaitis 2007).

The distinct morphology of the Sturt pea set it apart from any other Australian legume species and early taxonomists found it difficult to place. The name given to Dampier’s collection in part was *Colutea Novae Hollandiae* in John Ray’s *Historia Plantarum* (1704). Botanists in the 19th century did not use this name as it was pre-Linnaean and had no standing, and the plant went through several name changes, starting with George Don, who named it as two species, *D. formosa* and *D. speciosa*, in a new genus, *Donia* G. Don (named for his father) and remarked on its horticultural potential (Don 1832). Lindley transferred these species to the New Zealand genus *Clianthus* Sol. ex Lindl., based on similarities of flower shape and colour (Lindley 1835). (See comments in paragraph above.)

It was the botanist Robert Brown who sorted out the taxonomy of the many specimens found across Australia. In London, Brown had the benefit of access to more specimens than those of Cunningham, including John Eyre’s 1839 collection in the Gawler Ranges, additional specimens collected along the north-western coast on Darwin’s Beagle voyage (collected by Bynoe), the collections from Sturt’s expedition, as well as Dampier’s original collection that he had seen at Oxford. After comparing all known specimens of Sturt pea to that time, Brown concluded that all the collections belonged to the same species, which he called *Clianthus dampieri* Cunn. ex Lindl. (Brown 1849). (For more details on the complex taxonomic history of the Sturt pea, see Orchard 2017 and George 2018.)

Although the Sturt pea flower looks remarkably like the New Zealand genus *Clianthus* (“Kakabeaks”), Brown suspected that this alliance would not last and that the Sturt pea would again become a distinct genus. He based this on fruit characters from one specimen, though he lacked sufficient ripe pods to confirm his observation. This anticipated work 150 years later that showed the fruit anatomy between *C. puniceus* (G. Don) Sol. ex Lindl. and a New Zealand species of *Swainsona* was distinct (Heenan 1997). Despite these suspicions, the generic name *Clianthus* remained with the Sturt pea for a long time, although there was disagreement regarding the correct name for the species (Ascherson & Graebner 1907; Ford & Vickery 1950).

The apparent similarities between Kakabeaks and the Sturt pea are likely based on a parallel evolutionary shift to bird pollination.

But if the Sturt pea was not in the genus *Clianthus*, then where did it belong? In 1990, Joy Thompson, of the National Herbarium of New South Wales, transferred it to the genus *Swainsona* as *S. formosa* (Thompson 1990). With the benefit of having available many more specimens from ‘previously little-known areas’, Thompson (1993) could assess the relationships of Sturt pea with other legumes more thoroughly and determined that the closest relatives to the Sturt pea were species of *Swainsona* in Western Australia, especially *S. beasleyana* F. Muell. (Thompson 1990). Despite its smaller flower size, *S. beasleyana* shares with the Sturt pea aspects such as leaflet number and shape, stipule lobes, similar peduncles and flower shape (Thompson 1993). Nevertheless, as Symon & Jusaitis (2007) point out, Thompson gave more reasons to take the Sturt pea out of *Clianthus* than to put it into *Swainsona*. The separation from *Clianthus* was based on several characters, including differences in the inflorescence, calyx, fruit pods, stipules and habit (Thompson 1990). In a later full revision of the genus, *S. formosa* and *S. beasleyana*, along with five other species of *Swainsona* in Western Australia, were placed in a ‘Group 3’, based on diagnostic characters, including large stipules not forming an abaxial ridge and a slender un-stiffened style (Thompson 1993, p. 445).

However, not everyone was convinced with the Sturt pea’s new taxonomic home. George (1999) thought that the differences between Sturt pea and *Swainsona* merited raising a new genus, *Willdampia* A.S. George, with a single species *W. formosa* (G. Don) A.S. George, citing as evidence the large flowers, the colour and orientation of the standard and the acute keel (George 1999). Symon (2000) countered that these characteristics were all adaptations to bird pollination and that a range of pollination mechanisms within one genus is widely accepted. Symon further argued that the pods of the Sturt pea fall well within the range of *Swainsona* (Symon 1990) and later (Symon & Jusaitis 2007, p.28) added that the “cotyledons, leaves, pods, seeds, stipules, inflorescence, hairiness and plant form,” as well as its ecology and distribution, all place it comfortably within *Swainsona*.

Furthermore, Symon (2000; and Symon & Jusaitis 2007) contended that *S. maccullochiana* F. Muell., endemic to the Pilbarra, is the closest relative of the Sturt pea. This was based on similar vegetative parts (e.g. racemes, stipules, flower keel) and seeds that are almost identical. The one main difference between these two species is the habit: the Sturt pea is prostrate while *S. maccullochiana* is erect, growing to 2 m tall. It is interesting that this is also one of the characters that led Thompson to separate the Sturt pea from *Clianthus* (Thompson 1990).

Molecular phylogenetics

Living in your genome is the history of our species

Barry Schuler (2009)

The confusion and debate around the placement of the Sturt pea and the identity of its closest relatives, is emblematic of one of the biggest challenges in plant taxonomy. With a species as distinct as the Sturt pea and as different as it is from other legume species in the Outback, it can be difficult to determine which characters signify a shared evolutionary history (homologies), and those which are the result of convergent adaptations (homoplasies). When there have been dramatic changes such as occur with a shift from insect to bird pollination (e.g. increasing flower size and shape, colour to brighter red), as is the case in *Swainsona*, sorting out the taxonomy can be even more daunting. Advances in molecular genetics over the last three decades have provided much more data

for plant systematics, including many ‘neutral’ markers, so called because the mutations in these DNA regions are essentially neutral with regard to morphological changes due to natural selection. Molecular systematics has become an important tool for reconstructing evolutionary history and sorting out homologous from plastic characters.

However, genetic markers are not without their pitfalls and in some cases, can even be misleading, for a host of reasons. Often gene regions become copied over the course of evolution and the different copies may have evolved separately. Other parts of the genome may have been introduced through hybridization with related species; or in general, others may have histories that differ from the species history (e.g. incomplete lineage sorting). Nevertheless, molecular systematic data do allow for a reconstruction of species history that is independent of (sometimes homoplasious) character evolution.

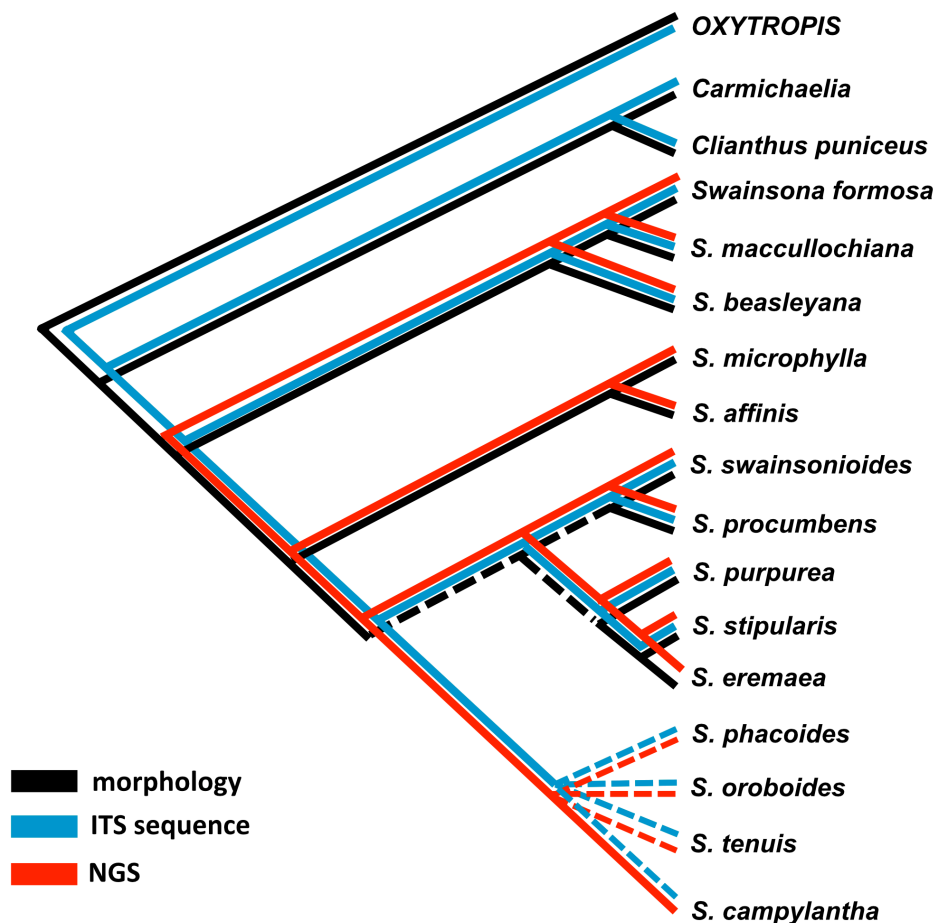


Fig. 4. Composite phylogeny of selected species of *Swainsona* and related genera (*Oxytropis* as outgroup). Branch colours indicate data type that supports each relationship: morphology (largely considering most recent taxonomy, e.g. Thompson 1993, Symon 2000) = black branches; traditional DNA sequencing (so-called Sanger sequencing) = blue; and next-generation sequencing (NGS) = red. For the most part, there is good agreement amongst the data sources. In some cases, gaps are filled in by other data sets. The Sturt pea is firmly within *Swainsona* and its closest allies are *S. maccullochiana* and *S. beasleyana*. Other groupings are confirmed as well. The

species *S. affinis* was considered close to *S. microphylla*, from which it can be difficult to distinguish. The widespread species *S. purpurea* was thought to be a subspecies of *S. stipularis*, but appears to be distinct (Moore 2005). The South Australian species *S. eremaea*, on the other hand, could be part of a *S. stipularis* complex (data not shown). Another clade, including *S. phacoides*, *S. oroboides*, *S. tenuis*, and *S. campylantha*, form a tangle that will require further study. Full results of our study will be published in a forthcoming paper (Cross *et al.*, in prep.). ITS sequences and analysis according to Wagstaff *et al.* (1999), NGS techniques following Cross *et al.* (2016).

The first DNA sequence data applied to the genus *Swainsona* utilised the nuclear ribosomal Internal Transcribed Spacer region (nrITS); this region is one of the most common markers for plant systematics as it lies within a housekeeping gene region of the genome (i.e. it is not under selection) and it is a more variable, non-coding spacer region between conserved ribosomal genes. Using this marker, Wagstaff *et al.* (1999) confirmed Thompson's and Symon's contention that the Sturt pea belonged to *Swainsona* and was distinct from *Clianthus* (Fig. 4). However, *Swainsona* was paraphyletic (meaning the clade in the phylogenetic tree contains other taxa besides *Swainsona*) with respect to the New Zealand genera *Carmichaelia* R.Br. and *Clianthus* (Wagstaff *et al.* 1999). The statistical support (in the form of bootstrapping) for the generic relationships was weak, but this research seemed to resolve some questions (placement of *S. formosa*), while raising others (possible paraphyly of *Swainsona*).

At the State Herbarium of South Australia, we have begun a project on the phylogeny and taxonomy of *Swainsona*. In the first phase, we re-examined the findings of Wagstaff *et al.* (1999), using DNA sequences (of the same nrITS region as Wagstaff *et al.* (1999) used) of many additional species of *Swainsona* from our extensive herbarium collections. Our preliminary results (Fig. 4) indicate that *Swainsona* is monophyletic, distinct from *Carmichaelia* and *Clianthus* and the Sturt pea remains in *Swainsona*. Further, by including specimens of the purported closest relatives of the Sturt pea, our results supported Symon's (2000) theory that *S. maccullochiana* was the closest relative to *S. formosa* and that *S. beasleyana* was also closely related (as per Thompson 1990, 1993).

The last few years have seen incredible advances in molecular genetics, enabling breakthrough discoveries in plant biology and giving rise to a new sub-field in biology, termed 'genomics' (in fact just about every field of molecular biology has joined in by adding the suffix '-omics', e.g. proteomics, metabolomics, etc.). Thanks to new DNA sequencing technologies, collectively called next-generation sequencing (NGS) (or also high-throughput sequencing: HTS), the amount of genetic information produced has increased several orders of magnitude just over the past decade (Mardis 2011) and dropped just as dramatically in price. Entire plant genomes can be sequenced in a matter of weeks, which would have taken months/years only a decade ago. These new advances have begun to be applied to plant systematics (being called—you guessed it—phylogenomics).

Although the costs of sequencing a plant genome have dropped, for a large genus it is still impractical to obtain complete genomes for all the species. Fortunately, several techniques have been developed to subsample the genomes of many samples and then compare putative homologous regions to reconstruct phylogeny (McCormack *et al.* 2013). We developed one of these methods to make it flexible and economically efficient

for a wide range of evolutionary questions (Cross *et al.* 2016) and utilized this on several species of *Swainsona*, to determine its efficacy for a large, diverse genus. The preliminary results show (see Fig. 4) good correspondence with taxonomic work as well as the earlier DNA sequence data. One advantage of this kind of NGS data is that it consists of many short DNA regions scattered throughout the genome, providing essentially a consensus of all the plant's genes. This nullifies the effect of alternative gene histories (e.g. incomplete lineage sorting, hybridization) that can distort the true species tree. However, unforeseen problems also appear; for example, sometimes extensive paralogy that has been found in plant genomes.

Here at the dawn of the genomic age, it is tempting to disregard previous work and put all our faith in the coming data blitz whose sheer volume will swamp everything that came before it. Indeed, this is only the beginning and in coming years the amount and quality of data will continue to increase exponentially. By combining systematics with other techniques, such as RNA gene expression, we stand at the brink of realizing the holy grail of phylogenetics: discovering the very genes responsible for the phenotypic characters used to define the taxonomy of a genus and unravelling the genetic mechanisms that lead to such dramatic morphological shifts in genera such as *Swainsona*. For example, regarding the shift to bird pollination, as seen in the Sturt pea, many of the central genes responsible for the morphological changes have already been discovered (Cronk & Ojeda 2008; Clare *et al.* 2013).

Nevertheless, Robert Brown did not need an Illumina HiSeq machine to distinguish the Sturt pea from New Zealand *Clianthus* and David Symon correctly determined the closest relative with nothing more than his keen eye and extraordinary taxonomic knowledge. As the early explorers searched deeper into the Outback, they provided more and more specimens that enabled botanists to further resolve the many taxonomic puzzles of the Australian flora. The new molecular genetic tools are only a continuation of the story of Australian botanical exploration. Now, as we search deeper into the genomes of *Swainsona* and other Australian taxa, we will build on the work of Brown, Thompson, Symon and others, to determine more deeply how the taxa are related and discover the path through which the Australian flora evolved to its present wondrous—and often bizarre—state.

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