

An integrated approach to studying tropical plant diversity – Taxonomic monographs, herbarium specimens and the sweet potato (*Ipomoea batatas*)

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Recent decades have witnessed a massive increase in data accumulation, but our knowledge of the world's biodiversity is still fragmentary: data accumulation has not been matched by a parallel taxonomic effort, and many groups of organisms have never been comprehensively studied. In the current context of climate change and biodiversity loss, we need to accelerate taxonomy and species discovery. This, however, requires a good taxonomic and phylogenetic framework, which is lacking for most groups of tropical plants.

This contribution discusses the role of botanical monographs in accelerating taxonomy. We argue that the increasingly easier access to data in the world's herbaria and the availability of DNA sequence data place botanists in an unparalleled position to produce taxonomic monographs, the forefront of taxonomic research.

We illustrate the discussion with the results of a monographic study of the genus *Ipomoea* (Convolvulaceae). We integrated herbarium-based morphological studies with techniques of phylogenetic and genomic analysis of thousands of specimens to develop more robust species delimitation hypotheses and a comprehensive phylogenetic framework. Monographs such as ours have implications for other disciplines beyond taxonomy. We specifically show how it enabled important discoveries related to the origin of sweet potato, a worldwide staple crop.

Keywords

Crop wild relatives, Natural history collections, Plant diversity, Species discovery, Taxonomy

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Accepted

13. 6. 2023

DOI

<https://doi.org/10.12685/bauhinia.1353>

Charles Darwin travelled across the world on board the *Beagle* from 1831 to 1836. Observations during that trip and back home in England inspired what would later become a seminal work in biology. However, The „Origin of Species“ was not Darwin's first relevant contribution to science. Darwin's most important work until then and, in fact, the work that established his reputation as a zoologist was a monograph of barnacles. His interest in barnacles began with the collection of a specimen off the coast of Chile in 1835 during the voyage of the *Beagle*; it then took him eight years of intense work (1846–1854) to complete his monograph (Darwin 1851, 1854). Darwin's monograph includes a detailed account of the world's barnacles known at the time, both living and fossil, descriptions of new species, first-time observations on barnacle biology and the confirmation that cirripeds are not molluscs but crustaceans (Richmond 2007).

At the start of his work on barnacles, Darwin realised barnacle taxonomy was in much need of study¹. Undaunted, his initial confusion was soon replaced by excitement for the task². Finally, towards the end of his work, he felt exhausted³. Luckily, Darwin finished his monograph, and the rest is history. The work made Darwin's reputation among his contemporaries and in 1853 the Royal Society presented him with a Royal Medal „For his work entitled Geological observations on coral reefs, volcanic islands, and on South America, and his work, Fos-

¹ „Literally not one species is properly defined: not one naturalist has ever taken the trouble to open the shell of any species to describe it scientifically, & yet all the genera have ½ a dozen synonyms. [...] The subject is heart breaking.“ (Darwin 1849a).

² „How I shall enjoy getting back to Down with renovated health, if such is to be my good fortune, & resuming the beloved Barnacles.“ (Darwin 1849b).

³ „I am at work on the second vol. of the Cirripedia, of which creatures I am wonderfully tired: I hate a barnacle as no man ever did before, not even a Sailor in a slow-sailing ship.“ (Letter to W.D. Fox 1852).

sil Cirripedia of Great Britain, Section Lepadidae, Monograph of the Cirripedia” (Hooker 1853, Jackson 2014). The address delivered by the then President of the Royal Society, William Parsons, 3rd Earl of Rosse, speaks about the merit and contribution of Darwin’s monograph to science⁴. Since its publication, Darwin’s monograph has accumulated thousands of citations (cf. Google Scholar), and, 170 years on, it is still relevant to researchers working on Cirripedia (e.g., Buckeridge et al. 2018, Simon-Blecher et al. 2021). More importantly, Darwin learnt new methods and arguments through his monographic work and built a global view of biology that was of utmost importance to his later works.

The past and present of botanical monographs

A taxonomic monograph is a compendium of all existing systematic knowledge about a group of organisms, ideally a clade (i.e., a monophyletic group; Box 1), and its importance and uses far exceed taxonomy, as we show later in this paper. In botany, the first so-called „taxonomic monograph” was Robert Morison’s *Plantarum Umbelliferarum Distributio Nova*, published in Oxford in 1672 (two-hundred years before Darwin’s monograph of *Cirripedia*). Morison was followed by others in the 17th and 18th centuries, and monographs were most common in the 19th century and the first half of the 20th century, during the so-called Golden Age of Botany. Alongside some of the most ambitious global botanical works, such as de Candolle’s *Prodromus* (de Candolle and de Candolle 1824) or Engler’s *Das Pflanzenreich* (Engler 1900), this period witnessed the publication of many botanical monographs, such as those on *Geranium* Tourn. ex L. (Andrews 1805), *Paonia* L. (Anderson 1818), *Dianthus* L. (Williams 1893), *Mimulus* L. (Grant 1924), and *Heuchera* L. (Rosendahl et al. 1936), to name just a few.

Since around the 1950s, taxonomic monographs have focused on small to medium-sized genera (e.g., Harris and Wortley 2018, Boza Espinoza and Kessler 2022) or genera geographically restricted to one country (Martins and Almeda 2017; Cardona-Cruz et al. 2021). Large, mega-diverse genera are rarely monographed as a whole; instead, work normally focusses on specific subgenera or sections within them (e.g., Bohs 2001, Lucreño et al. 2021).

A monograph of *Ipomoea*

In 2013 we set out to monograph *Ipomoea* L., a megadiverse genus in the Convolvulaceae Juss. family with c. 800 species and a pantropical distribution. Within just seven years, we published sixteen papers on the genus, one of them a monograph of all 425 species in the American continent (Wood et al. 2020). To date, we have described 70 species new to science; identified and re-organised synonyms in the genus to a 69% synonymy rate (i.e., 7 out of every 10 names published in relation to *Ipomoea* are synonyms); designated almost 300 lectotypes; and published over 400 species

Box 1. Content of a monograph

A taxonomic monograph is the systematic study of a group of organisms (normally an order, family, or genus) at a global scale and combining morphological, ecological and, at the present time, molecular data. Comprehensive Monographs include a range of information for every species, including:

- > Nomenclature and types
- > Descriptions
- > Distribution, habitat, ecology
- > Conservation status
- > Uses
- > Reference specimens
- > Photographs, maps, illustrations
- > Identification keys
- > Cytology, micromorphology
- > DNA and phylogenies

⁴ „In your Monograph of the Pedunculated Cirripeds, you have treated generally of the structure, economy and zoological relations of these animals, and given a systematic arrangement and description of the different species. In the accomplishment of your task, you have not only made use of previously existing materials with sound and enlightened criticism, but, by the discovery of new facts and the promulgation of original views, contributed most materially to advance the department of knowledge to which your researches more immediately belong, and rendered valuable service to physiological science in general.” (Earl of Rosse 1854, pp 355–356)

descriptions, distribution maps, phylogenies, and identification keys (Muñoz-Rodríguez et al. 2019, Wood et al. 2020). We also investigated the relationship between *Ipomoea* and other formerly recognised genera in the tribe Ipomoeae (*Argyria* Lour., *Rivea* Choisy, etc.), showing that they were all nested in *Ipomoea* and proposing the recognition of an expanded, monophyletic *Ipomoea* (Muñoz-Rodríguez et al. 2019, 2023). We have provided extensive detail on the taxonomic results of our monographic work (description of new species, synonymy rates, extensive lectotypification, etc.) in different publications (Wood et al. 2015, 2017, 2020, Wood and Scotland 2017a; b; Muñoz-Rodríguez et al. 2019, 2023).

Importantly, this monographic work not only overhauled the generic and species-level taxonomy of *Ipomoea* but provided insight on a range of topics, including trans-oceanic contact theory (Muñoz-Rodríguez et al. 2018), evolutionary radiations and biogeography (Muñoz-Rodríguez et al. 2019; Carruthers et al. 2020), the extent of specimen mis-identification in natural history collections (Goodwin et al. 2015, 2020), and the origin and evolution of a crop species – the sweet potato (Muñoz-Rodríguez et al. 2018). This reflects the value of overhauling the taxonomy of a group in a phylogenetically informed way, which in turn acts as a springboard for insight into a range of topics.

In the rest of this paper, we discuss how a taxonomic monograph of *Ipomoea* enabled the study of the origin and evolution of the sweet potato, including the identification of its closest wild relatives and the living species that are most likely direct descendants of its progenitors.

Sweet potato knowledge

Sweet potato, *Ipomoea batatas* (L.) Lam., is the most well-known and economically important member of the genus *Ipomoea*. Cultivated in all tropical and subtropical regions of the world for its edible storage roots, it is among the ten most consumed crops worldwide (Food and Agriculture Organization of the United Nations, 2022). Orange-fleshed sweet potato varieties are rich in β -carotene, a vitamin A precursor, and their consumption helps to alleviate vitamin A deficiencies which affect millions of children worldwide (Kurabachew 2015).

In 2013, at the start of our project, many aspects of sweet potato evolution remained poorly understood. It was not known, for example, whether the sweet potato had a single origin or multiple origins, as there were papers supporting both conflicting views (Muñoz-Rodríguez et al. 2018). In addition, it was not known whether *Ipomoea batatas*, a hexaploid species, originated by direct autopolyploidization from a wild ancestor – or which ancestor species it was – or whether it was the result of hybridisation between different species. Studies aiming to clarify the relationship between the sweet potato and its wild relatives were numerous, but knowledge about the species closely related to the crop species was generally inadequate. Among other prob-



Fig. 1, A–D. Sweet potato wild relatives are morphologically very similar.

A *Ipomoea batatas*

B *Ipomoea grandifolia*

C *Ipomoea ramosissima* and

D *Ipomoea triloba*

Photographs: J.R.I. Wood / R.Scotland

lems, evolutionary studies were often based on wrongly identified specimens (e.g., Jones 1967, Muñoz-Rodríguez et al. 2019). A consequence of the lack of a sound taxonomic framework was that different authors had proposed almost all species in the sweet potato group as possible progenitors of the crop, mostly with little evidence.

In summary, at the beginning of our study, species boundaries in the sweet potato group were ill-defined; misidentified specimens were common in herbaria and the literature; and the phylogenetic relationship between wild relative species and the crop was uncertain.

Sweet potato studies in the context of a taxonomic monograph

The basis for our work on sweet potato was the study of *Ipomoea* herbarium specimens. During this project, we studied thousands of herbarium collections; our specimen database currently includes c. 14 000 collections (c. 22 600 specimens) from around 100 herbaria and virtual herbaria worldwide, and many other specimens have been studied but not databased. As of May 2023, 1750 collections in our database correspond to the sweet potato group, i.e., species closely related to sweet potato (see below). At the time of writing, we have also sequenced over 2500 herbarium specimens representing c. 460 *Ipomoea* species, ~60 % of species in the genus, using either Sanger or high-throughput sequencing. Although it was not our original goal, this comprehensive taxon and data sampling allowed us to study sweet potato and its relatives in depth.

First, we aimed at species delimitation. Our methodology (Scotland and Wood 2012, Muñoz-Rodríguez et al. 2019) combined herbarium-based (i.e., morphological) analyses with phylogenetic analysis of DNA sequence data, with constant cross referencing between the two. The integration of DNA sequence data in the taxonomic process allowed us to detect misidentified specimens and, secondly, to generate more robust species delimitation hypotheses with both morphological and DNA support.

Ipomoea batatas has been traditionally classified in *Ipomoea* section or series *Batatas* alongside a variable number of wild species (Choisy 1845, Grisebach 1864, House 1908, van Ooststroom 1953, Austin 1978, 1988). Hereinafter we refer to this group of species as the *Batatas* group (or Clade A3 sensu Muñoz-Rodríguez et al. 2019). The wild species in the group are of interest for sweet potato improvement and food security. However, species differentiation in the *Batatas* group based on morphology is difficult and often relies on subtle differences in sepal size and shape (Fig. 1, A–D, Austin 1978, Wood et al. 2020). Other morphological characters are not reliable given the variability within species and frequent character overlap. For that reason, species identification in the *Batatas* group is challenging and specimen misidentification is frequent. A consequence of this is that phyloge-

netic analyses that do not include an *Ipomoea* taxonomist or do not challenge prior identifications of the specimens sequenced almost always include misidentified specimens. It is therefore essential for such works to include voucher specimens, the identification of which can subsequently be verified.

As explained above, we generated comprehensive DNA sequence data for *Ipomoea*. Our aim was to incorporate as many species as possible, and several specimens per species when possible. Specifically, for the Batatas group, we first sequenced multiple specimens of every species using Sanger sequencing to obtain DNA barcodes (*nrITS*, *matK*, *rpl32-trnL*). In other clades of the *Ipomoea* phylogeny, DNA barcodes enable a quick, reliable differentiation between species. In the Batatas group, however, DNA barcodes do not provide enough resolution to differentiate species; except for a small number of species, most species within Batatas form a largely unresolved polytomy in DNA barcode phylogenies (Muñoz-Rodríguez et al. 2018). We thus incorporated high-throughput sequence data in our sweet potato studies. We specifically used HybSeq to obtain whole chloroplast genomes and 386 putative single copy nuclear coding regions from multiple specimens of every species. This allowed us to obtain phylogenetic trees with strongly supported nodes and, for the first time, to define clear boundaries between species and to better understand their evolutionary relationships (Muñoz-Rodríguez et al. 2018).

Thus, as currently recognised and supported by our results, the Batatas group includes *Ipomoea batatas* and 15 wild relatives: *I. aequatoriensis* T. Wells and P. Muñoz, *I. australis* (O'Donell) J.R.I. Wood and P. Muñoz, *I. cordatotriloba* Dennst., *I. cynanchifolia* Meisn., *I. grandifolia* (Dammer) O'Donell, *I. lactifera* J.R.I. Wood & Scotland, *I. lacunosa* L., *I. leucantha* Jacq., *I. littoralis* Blume, *I. ramosissima* (Poir.) Choisy, *I. splendor-sylvae* House, *I. tenuissima* Choisy, *I. tiliacea* (Willd.) Choisy, *I. trifida* (Kunth) G. Don and *I. triloba* L.. We confirmed that most species are monophyletic, with only the two putative hybrid species, *I. leucantha* and *I. grandifolia* needing further study, and clarified the relationship between them and with sweet potato itself. Importantly, three of these species were described as new to science by us: *Ipomoea australis*, *I. lactifera*, and *I. aequatoriensis*. The discovery of *Ipomoea aequatoriensis* turned out to be especially important, since we were able to show that this species is the sweet potato's closest relative and, most likely, a direct descendant of sweet potato's progenitor species (Muñoz-Rodríguez et al. 2022).

Subsequently, having comprehensive *Ipomoea* phylogenies also allowed us to show that storage roots are commonplace in *Ipomoea*, and that the storage root of *Ipomoea batatas* is not the result of domestication but a trait that predisposed the species for cultivation. We were also able to show that the origin of sweet potato predates humans, and that at least part of the diversity existing within the crop also predates human involvement (Muñoz-Rodríguez et al. 2019).

In summary, in the context of a taxonomic monograph, we produced extensive data that allowed us to study sweet potato's origin in detail. We identified all sweet potato wild relatives, including its closest relatives. Our work is just one example of how the results of a taxonomic monograph have implications that go beyond taxonomy to dramatically improve our understanding of the natural world.

The future of botanical monographs

Good taxonomy provides a solid foundation for the conservation of the world's biodiversity. In the current context of climate change and biodiversity crisis, we need to accelerate the speed at which biodiversity is studied and new species are described, and to provide a robust taxonomic backbone to integrate existing knowledge. A monograph may simply assemble all existing knowledge of a group of organisms in the same publication, but more often monographs comprise new research that comprehensively revises the existing taxonomy and systematics of a group with new data building on previous research efforts. Although underutilised, they stand at the forefront of taxonomic research and thus have the potential to be key resources for biodiversity studies.

Modern-day taxonomists willing to start a monograph must deal with three main challenges. First, they face centuries of accumulated, sometimes obscure literature, which frequently contains as much error as useful information. Second, the number of specimens in the world's herbaria has increased exponentially in recent decades (Bebber et al. 2010), making it logistically complicated to study a representative number of specimens of any one group. Third, the current publishing environment and rewards system in science do not encourage researchers to produce taxonomic monographs. Instead, researchers prioritise smaller, often DNA-focused approaches that can be published faster in higher-impact journals, although the results may be relatively trivial. These problems are further exacerbated in the case of the very big genera (Frodin 2004), where the sheer amount of information available inhibits attempts to monograph them (Scotland and Wood 2012).

Although the number of botanical monographs decreased in the second half of the 20th century, they have received renewed support in recent years and there seems to be revived interest in them (Gorneau et al. 2022). Furthermore, we argue that the integration of herbarium-based research, readily-available techniques of molecular data analysis and big data places present-day botanists in an unparalleled position to study the world's plants. First, the number of herbaria worldwide has doubled in recent decades and the number of collections they preserve has grown exponentially (Bebber et al. 2010, Goodwin et al. 2015). This presents a challenge but also an opportunity to monographers, who now have more information than ever before to refine and

enhance their morphological studies and avoid potential errors (Bakker et al. 2020). Secondly, as the price of molecular sequence data generation steadily decreases, molecular data, even if only DNA barcodes, are now accessible to most researchers. Thirdly, high-resolution specimen images, especially images of type specimens, are increasingly available via virtual herbaria, JSTOR or other online repositories. Fourthly, we now have almost unrestricted access to historical publications via the Biodiversity Heritage Library, JSTOR, or herbaria Digital Libraries (e.g., Royal Botanic Garden in Madrid). In the case of more recent publications, those not published in open access journals can be easily accessed through platforms such as ResearchGate, or simply by e-mailing the authors.

In summary, the number and diversity of specimens in herbaria worldwide, the increasing affordability of sequence data generation, and the immediate online access to voucher specimens, species information and researchers worldwide, make taxonomic monographs more feasible and faster to produce than ever before, and should lead to a renaissance of botanical monographs. Whether the taxonomic community has the motivation, the funding and the workforce required remains an open question, but, as we have shown with the sweet potato, the results of these much-needed studies have implications far beyond taxonomy.

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Jahr/Year: 2023

Band/Volume: [29](#)

Autor(en)/Author(s): Munoz-Rodriguez Pablo, Wood John R. I., Scotland Robert W.

Artikel/Article: [An integrated approach to studying tropical plant diversity – Taxonomic monographs, herbarium specimens and the sweet potato \(*Ipomoea batatas*\) 85-93](#)