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# A taxonomic monograph of *Ipomoea* integrated across phylogenetic scales

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## **SUPPLEMENTARY REFERENCES**

# SUPPLEMENTARY METHODS

## SECTION 1 | PRELIMINARY CHECKLIST

As a starting point in the preparation of the monograph of *Ipomoea*, we created a working list of all accepted names in the tribe *Ipomoeae* (species with spiny pollen) in the Convolvulaceae (*Argyreia* Lour., *Astripomoea* A.Meeuse, *Blinkworthia* Choisy, *Lepistemon* Blume, *Lepistemonopsis* Dammer, *Rivea* Choisy, *Stictocardia* Hallier f. and *Turbina* Raf. as well as *Ipomoea*) as these had been shown to be nested within *Ipomoea*<sup>1</sup> by previous authors. We complemented the checklist with the approximate geographical distribution of each species by major area (country or continental region). We rejected the strategy we had used earlier in our study of *Convolvulus* L.<sup>2</sup> of downloading all *Ipomoea* names from IPNI as this allowed us to filter out the large number of long discarded names. Today, this preparatory task could be much simplified by downloading data from the continuously curated World Checklist of Selected Plant Families compiled by Kew (<http://wcsp.science.kew.org>) but this solution was not available when we began our studies. Our list was constructed area by area:

- For *Ipomoea* in the Americas, the starting point was Austin & Huaman's checklist for the continent<sup>3</sup>. This was supplemented, updated and modified following Austin & Bianchini's supplement<sup>4</sup>, Flora Mesamericana<sup>5</sup> and checklists of the Caribbean<sup>6</sup>, Brazil (<http://floradobrasil.jbrj.gov.br/>) and the Southern Cone<sup>7</sup>.
- No standard checklist existed for the species in the Old World. We relied on Flora Europaea<sup>8</sup> and Johnson's checklist for Australia<sup>9</sup> for these two continents. We checked all recent floras and modern works for Africa and Asia, as well as some older works<sup>10–21</sup>.
- Names from other genera in tribe *Ipomoeae* (few in the Americas) were traced under *Turbina*, *Stictocardia* and *Argyreia* in various checklists and older accounts.

After the construction of the first draft of the list, we checked IPNI, Tropicos and other databases for names published more recently and the list was regularly updated on subsequent occasions. Places of publication were traced through IPNI and Tropicos when necessary.

During our work on species descriptions, we searched for synonyms and infraspecific taxa in different works. Choisy's account in the Prodrômus<sup>22</sup> provided a comprehensive list of pre-1845 synonyms which we could use to trace back names published in the works of Don, Rafinesque, Vahl, Willdenow, Desrousseaux, Roemer and Schultes, Sprengel and others. We also scanned *Flora Brasiliensis*, magazines such as the Botanical Register and Curtis's Botanical Magazine, the papers by Hallier, Urban, O'Donnell, House, Matuda, Austin and many others. The online availability of a wide range of older journals through JSTOR, as well as the help of library staff at Oxford and Kew, was invaluable. Further, the study of various herbarium specimens (see below) revealed putative types that we had not found in the literature search.

## SECTION 2 | SELECTION OF SPECIMENS FOR STUDY

The number of herbarium specimens for any large plant genus is enormous. In the case of *Ipomoea*, it probably exceeds 200,000 specimens worldwide. In January 2019, the GBIF database, which includes data only from a subset of the world's herbaria, listed 84,770 records of *Ipomoea* associated with preserved specimens (132,570 including duplicates in multiple herbaria). As it was clearly impossible to examine such a large number of specimens, we prioritised and made efforts to see:

- Type specimens of all species described in *Ipomoea*, transferred to *Ipomoea* from other genera or considered as likely to belong to *Ipomoea*.
- All or as many specimens as possible of rare species represented by <10 collections, a significant proportion of all accepted species (49% in GBIF).
- Specimens representing anomalous records either geographically or ecologically were traced wherever possible.
- Representative specimens from all countries in the Americas and of all states in the larger countries such as Brazil.

Less effort was made to trace specimens of common, easily recognised species from countries or states where they might be expected to occur. In addition, we noted that:

- Many specimens were of poor quality and careful examination of these added little or nothing to our understanding of the morphology and variation of the species —although specimens might represent an important extension to the range of rare species.
- Some thirty species of *Ipomoea* accounted for 53% of the 132,570 specimens of *Ipomoea* in GBIF. As examination of more than 20 specimens of a given species is unlikely to add significantly to our understanding of morphological variation, little is gained by the study of a large number of specimens of one species once material has been examined from its entire geographical range.

In total, we have studied specimens from 47 European and American herbaria (see list in main methods section). In addition, the extensive range of images available online has allowed us to locate and confirm the identity of almost all types. We have only rarely needed to request images of types, but those provided by G, LE, MA, TO and W have been especially useful. We requested the loan of type specimens in very few cases.

### A. HERBARIUM STUDIES AND TAXONOMIC DECISIONS

Herbarium specimens are invaluable as a permanent record of a specimen's occurrence and characteristics, and facilitated taxonomic decision-making in different ways. During our study of herbarium material, the wrong identification on a label was often a clue to the right identification. In some cases, an earlier valid name simply needed to replace a well-known later synonym: *Ipomoea alba* L. (published in 1753) replaced *I. bona-nox* L. (published in 1762) and *I. indica* (Burm.) Merr. (published in 1755 as *Convolvulus indicus*) replaced *I. congesta* R.Br. and *I. acuminata* (Vahl) Roem. & Schult. (published in 1810 and 1819 respectively). In other cases, a wrong identification was corrected because the name had been misapplied: *I. hederifolia* L. and *I. mauritiana* Jacq. thus replaced *I. coccinea* L. and *I. digitata* L., which

had been demonstrated to be localised endemics to the eastern United States and Hispaniola respectively.

Unidentified or incorrectly identified herbarium specimens can be sorted into putative species, which can then be examined for distinguishing characters. In this process, specimens were sorted into separate piles based on the presence of salient characteristics. Each pile could then be studied more intensively to identify additional diagnostic characters that confirmed or rejected the unity of the specimens grouped in individual piles. In practice, this process was mainly used to sort unnamed material (i.e. specimens from the “indet” folders found in most herbaria) but was also useful in other situations, for example in distinguishing *I. eremnibrocha* D.F.Austin from *I. isthmica* J.R.I.Wood & Buril.

All descriptions and diagnoses in our study were based essentially on the examination of herbarium specimens but over 25% of species found in the Americas were also seen in the field. We compared specimens to identify and select salient characters in the same species and distinguishing characters between species. We also made reference to protologues, species descriptions and notes in academic and popular floristic works which might highlight diagnostic characters that could have been overlooked, particularly as colour and habit are often lost in herbarium specimens. In this context, it was particularly useful to have the universal approach of a monograph rather than the country-based approach of a flora. This enabled us to see, for example, the greater variation in Old World specimens of *I. mauritiana* Jacq. compared to specimens in the New World, to recognize the unity of *I. acanthocarpa* (Choisy) Asch. & Schweinf. with *I. piurensis* O'Donell, or to see the obvious morphological links between New World *I. sericosepala* J.R.I.Wood & Scotland and its allies with Old World *Turbina shirensis* A.Meeuse. Even within the New World, the monographic approach allowed us to pick out morphological discontinuities such as between Venezuelan, Colombian and Mexican specimens of *I. chenopodiifolia* (M.Martens & Galeotti) Hemsl. or, conversely, where previously accepted species were seen to overlap in their morphological characters and were treated as subspecies of a single species as in the case of *Ipomoea setosa* Ker Gawl. *s.l.*

Many species were only known from the type or a small number of collections. These may be problematic taxonomically as it is difficult to assess the reliability and consistency of characters. Herbarium visits, loans and specimen images made more specimens available, sometimes showing the existence of specimens with intermediate characters. Many examples could be cited, including *I. amnicola* Morong and *I. chiliantha* Hallier f.; *I. tubulata* Sessé & Moc. and *I. dumosa* (Benth.) L.O.Williams; *I. reticulata* O'Donell and *I. saopaulista* O'Donell; *I. campestris* Meisn. and *I. stenophylla* Meisn.; *I. grandifolia* (Dammer) O'Donell, *I. cynanchifolia* Meisn. and *I. ramosissima* (Poir.) Choisy; *I. alterniflora* Griseb., *I. obtusata* Griseb. and *I. excisa* Urb.; *I. lenis* House and *I. durangensis* House. In each case, a decision had to be made as to the taxonomic status of each species based on the information available, molecular and or morphological evidence, backed sometimes by geography or ecology. Decisions were made on the merits of each case but we tended to maintain species where information was limited.

Study of herbarium specimens has also resulted in the discovery of new species, these being added to the working checklist in the form of provisional names as they were discovered<sup>23–33</sup>.

### SECTION 3 | PHOTOGRAPHIC RECORDS

These were essentially of two kinds: photographs of living plants in the field and photographs of herbarium specimens. The former have the advantage over field observations of being permanently accessible and of being sourced from a variety of field workers, not just the taxonomist. The disadvantage, of course, is that the taxonomist can only see what the photograph shows. However, some photos supplied by contacts (e.g. of *Ipomoea platensis* Ker Gawl. or *I. retropilosa* subsp. *cundinamarcana* J.R.I.Wood & Scotland) were of considerable importance, emphasising the value of collaborative contacts in the *taxonomic* process.

Photographs of herbarium specimens are essentially a substitute for loans and provide a record of specimens that have been seen in different herbaria. In the case of *Ipomoea*, high-resolution images through JSTOR or the various virtual herbaria sites are almost as good as the herbarium specimens themselves and important diagnostic information is usually visible (except for seeds, filament indumentum and stigma shape). Clearly, the image can only be as good as the original specimen. Images have been crucial in resolving issues around *I. peruviana* O'Donell and *I. cuscoensis* J.R.I.Wood & P.Muñoz; *I. longeramosa* Choisy and *I. dajabonensis* Alain or *I. carmesina* Proctor and *I. lineolata* Urb., as well as issues involving species treated as synonyms. Both field photographs and images of specimens also play an important role in the public dissemination of our own results and publications both in print and online.

Finally, we obtained photographs of almost all specimens from which we extracted DNA and these images are available online through the different virtual herbaria or our project website.

### SECTION 4 | PREVIOUS LITERATURE AND TAXONOMIC RESEARCH

Any taxonomic study inevitably builds on the work of earlier scientists going back at least to Linnaeus. Knowledge has been cumulative as well as corrective. It is obviously pointless to reinvent the wheel as some species have been correctly delimited, some relationships postulated with reasonable support and some distinguishing characters have been highlighted for almost two hundred years. While it is obvious that important works from the 19<sup>th</sup> century, such as those of Choisy and Meissner, contain many errors and serious questions are rightly asked about their species concepts, many of the species they recognized still stand today and at least some of their genera and infrageneric groupings coincide with clades that have emerged from our molecular studies. The 20<sup>th</sup> century has seen numerous publications related to *Ipomoea*, some of which such as those by Urban or Standley, clearly show failings because of poor species concepts. On the other hand, publications by O'Donell are outstandingly reliable. Interestingly, all the species that O'Donell described from Argentina are still accepted today. His delimitation of species occurring beyond Argentina is slightly less reliable, suggesting that insights from field knowledge are important.

From the above discussion, it is clear that the insights of previous botanists are important for informing taxonomic decisions. Consequently, we generally treated diagnostic taxonomic characters used by O'Donell, Austin, McDonald and others in the keys that they constructed as correct unless demonstrably mistaken.

## SECTION 5 | MORPHOLOGICAL CHARACTER SELECTION AND TAXONOMIC DECISIONS

Although there was a degree of informed subjectivity in our studies of morphological variation, some important, objective processes are described below. It is important to note that once a specimen(s) can be placed within a morphologically recognizable clade, it is easier to delimit species because the specimen(s) only needs to be compared with a small number of other specimens and species from the same clade. Most clades in *Ipomoea* are quite small in terms of species numbers, which facilitates species delimitation considerably.

Some species are delimited by what are essentially weak quantitative characters, based on differences in the dimension of the corolla, leaves or other morphological features. These weak quantitative characters may be acceptable to delimit species if they are maintained over a large number of specimens. Conversely, they have been rejected where an entity is represented by very few specimens or a single one. This underlines the importance of seeing a range of specimens to confirm the consistency of “quantitative” characters.

Many characters correlate closely, thus indicating that one or more can be inferred when another is present (and essentially constitute a single character, not separate characters). Thus, a comose ovary correlates with a pubescent or comose capsule. A bilocular ovary correlates with a 4-seeded capsule while a triglobose stigma and a trilocular ovary correlate with a six-seeded capsule, although it should be noted that many stigmas appear merely globose and capsules may have fewer than four seeds by abortion. An erect habit generally correlates with linear or oblong leaves and a terminal subracemose inflorescence. Habit can usually, therefore, be inferred from leaf shape, the principal exception being the erect *Ipomoea carnea* subsp. *fistulosa* which has the axillary inflorescences and ovate, cordate leaves characteristic of a twining species. Another correlation (though less strict) is between the woody habit of the tree and liana species with the development of the inflorescence on short leafy side shoots. Species with a subcylindrical corolla tube have exerted, subequal stamens.

The annual/perennial distinction is (apparently) diagnostic for individual species in *Ipomoea* but in most herbarium specimens there is no rootstock and this distinction can only be inferred by the slender habit. However, there is a good proxy character. Specimens that present both corollas and capsules (especially when both are frequent) are annual. In contrast, perennials are marked by having corollas but no capsules or conversely capsules but no corollas. This is a partial explanation for why the fruit of many species is unknown.

Some characters are clearly the result of adaptation and are taxonomically significant although also homoplastic across the genus: notably corolla shape and colour, which are clearly linked to pollinators and flowering time (night/day); habit, twining species with ovate, cordate leaves and axillary inflorescences clearly visible to pollinators v. erect species with a terminal inflorescence—which must be advantageous in grassland habitats. Less obvious adaptations relate to seeds. Seeds with long marginal hairs may benefit from wind dispersal. In contrast, annual species usually (always?) lack marginal hairs and long-range dispersal may be irrelevant as they favour ruderal habitats where seeds readily germinate in disturbed soil. Clearly fibrous roots relate to annual species whereas tuberous storage roots and xylopodia are associated with perennials that need to survive prolonged dry seasons. Many of these adaptive characters are often of value in species delimitation.

Other characters that apparently provide no obvious evolutionary or environmental value are perhaps of even more taxonomic importance. One such character is the absence of hairs on the exterior of the corolla, which appears nearly always to be constant in any given species. Even more significant is the range of variation seen in the sepals. These vary in size, relative size between inner and outer sepals, in indumentum, in ornamentation and texture and in the shape of the base and the apex, none of this variation with any apparent adaptive use. Characters in Supplementary Table 2 are useful in distinguishing *Ipomoea* species. However, they are not always practical when studying herbarium specimens: capsules, seeds and roots are usually missing, whereas flower colour and texture may be lost in the drying process.

## SECTION 6 | FIELDWORK

We carried out fieldwork in Argentina, Bolivia, Brazil and Paraguay, resulting in new country records and the discovery of new species, these being added to the working checklist in the form of provisional names as they were discovered. Fieldwork is an important source of reliable ecological and phenological information —labels and literature often provide very sparse information although a few collectors are exemplary in the information they provide.

Field work pre-dating and throughout the *Ipomoea* project (pre- and post-2012, respectively) has done much to enhance recognition of species and their ecology. It has drawn attention to characters that are diagnostic in distinguishing species. It has shown that non-morphological characters such as flowering season or habitat may help to characterize species, when accurately known. Fieldwork has shown how some characters (habit, indumentum, leaf shape and size, corolla colour and size) can be very variable within a species or, in the case of sepals, at different stages of development. Fieldwork has resulted in more samples of poorly known species or of poorly known parts of otherwise well-known species, such as their seeds and rootstock. It has provided information not available from herbarium specimens such as subtleties of flower colour (the dark centre in *I. australis*, for example) and plant size and habit (the growth form of *I. juliaguttiereae* J.R.I.Wood & Scotland). In addition, sight of *I. pterocaulis* J.R.I.Wood & L.V.Vasconc. in the field drew immediate attention to its winged stems, a character barely visible on the flowering shoots represented in herbaria. Field observation immediately distinguished the inflorescence of *I. regnellii* Meisn. from *I. chapadensis* J.R.I.Wood & L.V.Vasconc.. It has helped understanding infraspecific variation (the frequent immediate sympatry of the different forms of *I. plummerae* A.Gray testifies to their recognition as formas, not varieties or subspecies). Seeing a range of specimens in different localities in the field (as in the herbaria) has made it possible to confirm whether a particular character (indumentum, for example) was constant in a population and over different populations, so confirming or rejecting taxonomic decisions.

## SECTION 7 | CONTACTS AND CORRESPONDENCE

Another useful aspect of our working practice has been the contact with other botanists and travellers interested in one or other aspect of *Ipomoea*. We have corresponded or consulted directly with researchers whose insights have been useful, such as (inter alia) Dan Austin (USA), Andy McDonald (USA), Bob Jarret (USA) Antonio Krapovickas (Argentina), Teresa Buril (Brazil) and Rosangela Bianchini (Brasil). Contacts such as Hector Keller (Argentina), Ledis Regalado (Cuba), Brenda Bedolla (Mexico), Moises Mendoza (Bolivia and Brazil) and Modesto Zarate, Maira Tatiana Martinez, Daniel Soto and Julia Gutierrez (Bolivia) provided



specimens, photographs and other information that added new information. Other researchers such as Rosa Degen (Paraguay), Hector Keller (Argentina) and Luciano de Queiroz (Brazil) facilitated fieldwork in Argentina, Brazil and Paraguay. We were also able to collaborate in publications with various different botanists, including Catia Urbanetz (Brazil) and Liziane Vasconcelos (Brazil), as well as with others named above. A full list of collaborators is provided in the accompanying monograph<sup>25</sup>.

## SECTION 8 | DNA STUDIES

We negotiated and arranged to sample leaf material for DNA extraction from collections of *Ipomoea* held at five major European herbaria: BM, E, K, L and P. We complemented these with material from other herbaria from across Europe and the Americas (see passport data in Extended Data File 1). Our sampling strategy followed the protocol outlined in reference 34 but attempted to achieve universal coverage of all species for which green material was available. We targeted post-1960 specimens based on our ability to obtain DNA from the closely related genus *Convolvulus*<sup>35</sup>, although we also attempted, and in several cases successfully sequenced, older collections when suitable material was available. Where possible, we sampled two to four specimens per species and avoided oversampling well-represented widespread species.

We extracted DNA from about 2,100 specimens and successfully sequenced 1,560 of them for three standard DNA barcodes (3,035 sequences in total): the nuclear ribosomal *Internal Transcribed Spacer* (*ITS*, 1,402 specimens successfully sequenced) and chloroplast markers *matK* (853 specimens) and *trnH-psbA* (780 specimens) (Extended Data Figure 1 and Extended Data File 1). In addition, we sequenced a subset of 384 specimens (c. 211 taxa) using Hyb-Seq<sup>36</sup> to obtain 605 putative single copy nuclear regions and the whole chloroplast genome (Extended Data File 1).

### A. DNA EXTRACTION

We extracted DNA from herbarium material using QIAGEN DNeasy Plant Mini Kit and from germplasm collections using the CTAB method<sup>37</sup>. We quantified DNA concentrations using a Qubit fluorometer and only used samples with DNA concentration higher or slightly lower than 5 ng/μl for high-throughput sequencing.

### B. PHYLOGENETIC ANALYSIS USING DNA BARCODE SEQUENCES

We used Sanger sequencing to obtain DNA barcode regions. We assembled forward and reverse reads into consensus sequences using either Mega v.5.0 or 6.0<sup>38</sup> or Geneious v.9.1.2<sup>39</sup>.

We aligned all DNA barcode sequences using MAFFT v.7.2.1 (L-INS-I strategy)<sup>40,41</sup> and only retained those positions with < 30% gaps for subsequent phylogenetic analysis. We then ran phylogenetic analyses using Maximum Likelihood in RAxML v.8<sup>42</sup>, Approximate Maximum Likelihood in FastTree 2<sup>43,44</sup> and Bayesian inference in MrBayes v.3.2<sup>45–47</sup>.

### C. HIGH-THROUGHPUT SEQUENCING

a) **Character sampling and target capture probes.** We developed probes targeting 605 putative single copy nuclear regions of our samples through comparison of genomic data from *Ipomoea lacunosa* L. (unpublished, assembled into scaffolds, N50=46047) and of coding sequences (CDS) of *Solanum tuberosum* ITAG2.4<sup>48</sup>. Regions between *Ipomoea* and *Solanum* with a one-to-one match at 70% identity along at least half the length of a *Solanum* CDS were

filtered to retain *Ipomoea* loci that were at least 1000 bp. Along these loci, 100 bp RNA probes were developed by MycroArray (Ann Arbor, MI) excluding probes with GC content < 25 %.

**b) Design of target regions.** We performed a BLAT comparison between the *Ipomoea* genome and the *Solanum* CDS regions (minIdentity=0.85). From the resulting file, we removed entries where the hit was 50 bp or less. We subsequently filtered this trimmed file to find *Solanum* loci that appeared only once. From those single hits, entries were retained where the CDS hit was > 50% the total length of the CDS, and the length of the *Ipomoea* genome was between 959 and 10,000 bp. In addition, entries where different *Solanum* CDS hit identical spots in *Ipomoea* were removed. This procedure resulted in 605 *Solanum* CDS matching 506 *Ipomoea* scaffolds.

**c) Design of baits.** We designed \*100mer baits with 1x tiling density, 20,020 baits in total. Each bait candidate was blasted against the *I. lacunosa* genome and filtered by melting temperature (T<sub>m</sub>) as follows. For each blast hit, a hybridization T<sub>m</sub> was predicted using salt and temperature conditions matching the hybridization conditions. Then, for each bait candidate, the number of blast hits with T<sub>m</sub> falling into the following six temperature bins were counted: 40–60 °C, 60–62.5 °C, 62.5–65 °C, 65–67.5 °C, 67.5–70 °C and above 70 °C. During capture, the optimal hybridization temperature was 65 °C. Bait candidates were accepted if they satisfied one of these conditions: 1) no blast hit with T<sub>m</sub> > 60 °C; 2) no more than two hits at 65–67.5 °C and ten hits at 62.5–65 °C, and two neighbour candidates on at least one side being rejected; 3) No more than a single hit at or above 70 °C, no more than one hit at 65–67.5 °C and two hits at 62.5–65 °C and two neighbour candidates on at least one side being rejected.

**d) Hybridization and DNA sequencing of the main set of samples.** We prepared DNA libraries using the NEB's Ultra DNA Library Prep Kit for Illumina v.3.0 (New England BioLabs). We implemented target enrichment using MYBaits<sup>49</sup> to capture the nuclear regions of interest following the protocol for Hyb-Seq<sup>36</sup> and using Beckman Coulter Agentcourt AMPure XP for product purification. We sequenced a 1:1 mixture of target enriched and unenriched libraries, in order to obtain the chloroplast genome and the nuclear ribosomal *ITS* region with genome skimming<sup>50</sup>. Sequencing was conducted using Illumina HiSeq-3000. We trimmed the sequences for Illumina adapters and for quality, Q15 on the left and Q10 on the right of the reads. We obtained 100 bp paired reads. Exact read duplications were reduced to the expected target coverage level based on sequence coverage.

**e) Assembly of nuclear regions.** We conducted a three-stage assembly process to create sequence contigs that corresponded to the target sequences: first, we used YASRA<sup>51</sup> to create gene assemblies that corresponded to the target sequences. YASRA cannot utilise paired end information, but if good overlap is found in the sequence reads, it can extend the assembly beyond the target sequence boundary. We then used PRICE<sup>52</sup> to utilise paired end sequence information to extend the sequence assemblies further, using the output from YASRA as target regions. We then implemented SSPACE<sup>53</sup> to extend the gene assemblies further. Final assembled contigs were aligned back to the reference sequences using BLASTN<sup>54</sup> to target assembled contig assignments.

Target gene duplication can have several causes and occurs in multiple forms. Among others, multiple assembled contigs can align back to a single target sequence. This can be a similar sequence in the genome such as a paralog or can be multiple alleles that have enough sequence difference to create multiple contigs. In addition, alleles can be collapsed in the

assembly and we attempted to break these out into the correct number based on the ploidy using the phasing of the shared SNPs (see below). In the duplication processes, we used the target-based trimmed assembled contigs so we have complete sequence alignment and target to assembled contig contiguity between the samples. For each of the 384 samples, we identified the targets that align to multiple assembled contigs. Each case was combined with the multiple genes and the genes assigned to that target sequence from all the other 383 samples. The target sequence was aligned to outgroup genomes of tomato and *Mimulus*<sup>55</sup>, matching sequences, when found, were trimmed and combined into this sequence set. The sequences were then multiply aligned with MUSCLE<sup>56,57</sup> and a distance-based neighbour-joining tree was made using PHYLIP<sup>58</sup>. Finally, we “walked” through the tree structure and identified the multiple target matching contigs and the tomato outgroup. If one assembled contig was found within tomato (below in the tree structure) and one was outside, then the inside assembled contig was retained and the other considered a paralogous gene. If both were within or outside the tomato outgroup then both were retained. At a later stage in our project, a sweet potato genome assembled into chromosomes and an *Ipomoea trifida* genome became available<sup>59,60</sup>. We then mapped our nuclear regions to these and confirmed that a majority of them map to only one position in each of those genomes.

**f) Phylogenetic analysis using nuclear coding regions.** We aligned every region individually using L-INS-I strategy in MAFFT (gap penalty = 1.53)<sup>40,41</sup> and subsequently used default parameters in Gblocks<sup>61,62</sup> to remove poorly aligned positions from the alignment. Retaining either all gaps, half gaps or no gaps in Gblocks did not change the result of the analysis.

We took several steps to reduce the possible effect of recombination and incomplete lineage sorting. First, we conducted the PHI statistical test<sup>63</sup> to identify regions in our set of nuclear regions that could be affected by recombination (Extended Data File 2) and ran all subsequent analyses using two different datasets, one including all nuclear regions and another one including only the regions that did not show evidence of recombination.

We estimated evolutionary models for each region using jModelTest 2<sup>64</sup> and obtained independent gene trees using default parameters in FastTree 2.1.9<sup>43,44</sup> and the species tree using Astral-II<sup>65</sup>. We obtained additional phylogenies from concatenated alignments using FastTree 2.1.9<sup>43,44</sup> in CIPRES<sup>66</sup>.

During the course of our study, the genomes of other species in *Ipomoea* were released, namely those of *Ipomoea batatas*<sup>59</sup>, *I. triloba*<sup>67</sup> and *I. trifida*<sup>67</sup>, all of them assembled into chromosomes, as well as a new version of the *I. lacunosa* genome sequenced using PacBio and assembled into much longer scaffolds<sup>68</sup>. Mapping our putative single-copy nuclear regions to these reference genomes indicated that some of our regions might not be truly single copy regions. Subsequently, we ran additional analyses with various filter thresholds removing all regions for which there was any uncertainty in their status as single-copy. The most stringent filter meant we retained 421 regions that we were confident are single copy. Our results and phylogenetic hypotheses for all filtered datasets we analysed were the same in terms of topology and support values.

**g) Assembly of chloroplast genomes.** We assembled the chloroplast genomes using SPAdes<sup>69</sup> and the chloroplast genome of *Ipomoea batatas* cultivar Xushu18<sup>70</sup> as reference. The chloroplast genomes show the same general structure as in most other angiosperms, with one

long single copy, one short single copy and two inverted repeats. Genome size in our *Ipomoea* samples ranged from 160,382 to 174,715 base pairs, except for *Ipomoea lactifera* J.R.I.Wood & Scotland, in which there were several large deletions (150,628 base pairs). We annotated all chloroplast genomes with Geneious v.9.1.8<sup>39</sup> from the sweet potato cultivar Xushu18<sup>70</sup>.

**h) Phylogenetic analysis using chloroplast genomes.** We identified 81 coding regions and 28 highly variable non-coding regions in our chloroplast genomes (Extended Data File 2). We aligned every region individually using PRANK<sup>71</sup>, edited the alignments using Gblocks<sup>61,62</sup> and then concatenated coding and non-coding regions in two independent mega-alignments.

We defined two partitions for coding and non-coding regions and a GTR+I+G model of sequence evolution was assigned by jModelTest 2<sup>64</sup>. We then inferred phylogenetic trees using Neighbor-Joining and Parsimony analysis as implemented in PAUP 4.0<sup>72</sup>, Maximum Likelihood using RAxML v.8.0<sup>42</sup>, Approximate Maximum Likelihood using FastTree 2<sup>43,44</sup> and Bayesian analysis using MrBayes 3.2<sup>45–47</sup>.

## SECTION 9 | TIME-CALIBRATED PHYLOGENIES

### A. DIVERGENCE TIMES

No known fossil calibrations can reliably be assigned to specific nodes within *Ipomoea*, or the family within which it is nested, Convolvulaceae<sup>34,73–75</sup>. This includes the recently discovered Palaeocene fossil *Ipomoea meghalayensis* Srivastava, Mehrotra, and Dilcher<sup>76</sup>, which we consider to be of uncertain identity (William Hawthorne, *pers. comm.* as its leaf characters could place it more reliably in several other taxa). We therefore constructed a time-calibrated phylogeny for Convolvulaceae and its sister family Solanaceae to incorporate fossil calibrations within Solanaceae. Although there are potential fossil calibrations within Solanaceae, its fossil record is also poor, and the extent to which it provides a reliable basis for calibrating a phylogeny is uncertain. For example, the Palaeocene fossil *Physalis infinemundi* Wilf<sup>77</sup> is around 28 million-years older than a previous divergence time estimate for its clade (Solanoideae), which was based on previously known fossil calibrations<sup>77,78</sup>. In this study, we used different calibration strategies to account for this uncertainty.

In one analysis, we used two calibrations. We used the *Physalis infinemundi* fossil as a minimum age (52 million-years) for the Solanoideae stem node, whilst we used a maximum of 130 million-years for the divergence between Convolvulaceae and Solanaceae. This maximum corresponds to the time of the sudden emergence of tricolpate pollen in the fossil record, which is associated with the origin of Eudicotyledoneae<sup>79</sup>. This is likely to be considerably older than the actual divergence between the two families considered here. However, it is impossible to justify specific alternative (and younger) maximum constraints. We therefore used this maximum to prevent our analyses from being misleadingly precise.

In a second analysis, we used a single calibration at the divergence between Convolvulaceae and Solanaceae. This is a secondary calibration from Magallon and colleagues<sup>80</sup>, a study that used 132 fossil calibrations throughout Spermatophyta. We implemented this calibration as a normal distribution (mean = 67.34, SD = 9.980). This calibration is likely to place the entire phylogeny on a considerably younger time-scale than our alternative calibration strategy, and we consider that it will lead to considerable underestimation of divergence times. However, this provides a useful basis for testing

hypotheses relating to the origin of sweet potato. By biasing the analysis to younger ages, we can carry out the most robust test of whether sweet potato evolved in pre-human times.

We inferred time-calibrated phylogenies with these two calibration strategies from 4 chloroplast genes (*atpB*, *matK*, *ndhF*, *rbcL*), the chloroplast intergenic spacer *trnL-trnF*, and the nuclear *ITS* marker. A total of 56 species were sampled representing the major lineages within each family. We intentionally sampled a relatively low number of species within each family to reduce the effect of violating the birth-death branching process assumption. This assumes constant rates of speciation and extinction and is invariably used when constructing time-calibrated phylogenies in a Bayesian framework.

We aligned sequences in MAFFT v7.271<sup>40,41</sup> using the L-INS-I setting and a gap opening penalty of 1.53. Ambiguously aligned regions were removed using default settings in Gblocks<sup>61,62</sup>, and Sequence Matrix v1.8<sup>81</sup> was used to concatenate aligned sequences. We used MrBayes v3.2.6<sup>47</sup> (GTR+G+I model) to infer the tree topology for subsequent divergence time analyses. This analysis was run for 2,000,000 generations and the final split frequency between runs was < 0.01.

We used RevBayes v1.0.4<sup>82,83</sup> to infer time-calibrated phylogenies (GTR+G+I model with an uncorrelated lognormal (UCLN) relaxed clock). We used a birth-death branching process as the tree prior. We fixed the topology to that inferred in MrBayes and generated start trees consistent with the two calibration strategies in TreePL<sup>84</sup>. For the calibration strategy that used *Physalis infinemundi*, we ran the analysis for 80,000 generations. For the strategy that used the secondary calibration from Magallon and colleagues, we ran the analysis for 427,000 generations. Two independent runs were performed. Sufficient mixing and convergence were assessed in Tracer v1.6.0<sup>85</sup>. All ESS values exceeded 200.

These time-calibrated phylogenies provide age estimates for the *Ipomoea* crown node. Two alternative estimates are inferred, depending on the calibration strategy. We use these age estimates to calibrate the root node of our NGS *Ipomoea* phylogenies.

An important problem when estimating divergence times within *Ipomoea* is that there are likely to be significant differences in diversification rates among clades. This violates a key assumption of Bayesian analyses, where the birth-death branching process assumes a constant rate of speciation and extinction. Because of this, we estimated divergence times within *Ipomoea* using treePL<sup>84</sup> —a method that does not use a birth-death branching process. Although uncertainty in estimated ages is more difficult to express within this framework, it is more valid than using a method for which a fundamental assumption is likely to be violated.

With treePL we used the nuclear topology inferred in FastTree as the input tree. A smoothing parameter (describing the magnitude of among-branch-rate-variation) of 0.01 was used following extensive cross validation. The root node was calibrated to either one of the two mean posterior age estimates (MPes) inferred with each calibration strategy (outlined above). We also inferred time-calibrated phylogenies with other smoothing parameters (0.1, 1, 10, 100, 1000) to evaluate the robustness of our inferences to differing assumptions about the magnitude of among-branch-rate-variation.

We also inferred time-calibrated phylogenies with the chloroplast topology as input. We could therefore explore whether the different topology affected divergence time estimates and subsequently inferred diversification rates. A smoothing parameter of 1000 was used following extensive cross-validation analyses, and the root node was calibrated to one of the two MPes

inferred with each calibration strategy. We also inferred time-calibrated phylogenies with different smoothing parameters (0.01, 0.1, 10, 100, 1000).

## **B. DIVERSIFICATION RATES**

We inferred diversification rates in BAMM<sup>86</sup>. We used time-calibrated phylogenies, based on either the nuclear or chloroplast topologies, as well as each of the two calibration strategies, as input trees. We used the *set\_priors.R* script (downloaded with BAMM) to select the appropriate priors. Four independent runs were performed for 1,000,000 generations. We assessed convergence using a custom R script that required the package BAMMtools. A 10% burn-in was used. We compared Bayes factors between different models to identify the number of rate-shifts that occurred within our time-calibrated phylogenies. We then extracted the credible shift set—which represents the set of trees with different rate shift patterns that account for 95% of the posterior probability.

## SUPPLEMENTARY DISCUSSION

### SECTION 1 | DNA BARCODES AS ANOTHER TAXONOMIC CHARACTER

For many species, delimitations based on morphology were corroborated by multiple accessions of the species forming a highly supported clade in the *ITS* tree (see examples in Extended Data Fig. 2). In such cases, we accept that the delimitation of the species is consistent in both morphology and molecular data. In contrast, if specimens *a priori* assigned to the same species are distantly related in the barcode phylogeny —strong disagreement between morphology-based hypothesis and molecular data— we acknowledge that it is necessary to re-examine all data to check whether the conflict is real (i.e., different specimens represent different evolutionary entities that have not been identified in morphological studies) or simply, as in many cases, they were wrongly identified.

Equally, in those cases for which morphological observations recognised two distinct species, we accepted the two species if either of them was more closely related to any other species in the phylogenetic tree. Similarly, if our morphology-based observations led to a hypothesis that two previously recognised species could in fact be conspecific, we interpreted this as partly corroborated by *ITS* if the specimens from both species formed a clade albeit unresolved or with accessions from both species intermingled.

It is important to note that we were extremely cautious when species hypotheses based on morphology were not corroborated by *ITS*. This caution reflects the well-known limitations associated with *ITS* phylogenies (small DNA sequences, lack of resolution, low support values). Therefore, when we had a species hypothesis not corroborated by *ITS*, either due to a lack of resolution or poorly supported resolution, we accepted our morphology-based hypotheses (Fig. 2), as we could not be sure whether the phylogeny reflected an accurate pattern or the pattern observed was simply due to the limitations associated with *ITS*. We adopted this approach based on our experience with the group of species closely related to the sweet potato<sup>87</sup>. In the *ITS* phylogeny, most species in this group are not monophyletic but result in a polytomy. However, the genomic phylogenies, with more data, supported the monophyly of most accepted species.

### SECTION 2 | PHYLOGENY OF *IPOMOEA*

Our phylogenies confirm that the genus *Ipomoea*, as previously defined, is not monophyletic: all other genera traditionally recognised in the tribe *Ipomoeae* are nested within *Ipomoea*, as suggested by previous studies using smaller data sets<sup>1,88</sup>. Furthermore, elements belonging to those other genera —except *Astripomoea*— do not form monophyletic groups but intermingle with various species of *Ipomoea* (Extended Data Fig. 3 and Supplementary Data Files 2–7). This lack of monophyly provides further support for the most logical taxonomic decision: to expand the genus *Ipomoea* to include the smaller genera and make it monophyletic. In its new circumscription, *Ipomoea* includes all members of Convolvulaceae with spiny pollen and is the only genus in the tribe *Ipomoeae*.

In addition, the three subgenera traditionally recognised in *Ipomoea*, as well as most sections and series, are also polyphyletic. In contrast, we identified several major clades, some of them lacking diagnostic morphological characters<sup>25</sup> (Extended Data Fig. 3 and Supplementary Data Files 2–7). This reflects the impossibility of obtaining monophyletic,

diagnostic and mutually exclusive groups within *Ipomoea* following the principles of diagnosability in the traditional Linnean System<sup>89</sup>. In conclusion, we did not attempt any formal recognition of infrageneric ranks as in Linnaean taxonomy, although this has been attempted in other megadiverse genera such as *Begonia*<sup>90</sup>. The problem with infrageneric ranks is that it is necessary to place all species in a taxon at each rank; given the complex tree model of *Ipomoea* and low level of diagnosability this is virtually impossible if the wish is to maintain monophyletic and diagnostic taxa.

All datasets and methods of phylogenetic inference used in our studies recover the same major clades within *Ipomoea*. The relationship between taxa within clades is mostly congruent across phylogenies. *Ipomoea* is divided into two major clades. The first one is dominated by taxa from the Old World but the second clade includes a mainly African paraphyletic grade (*sensu* Huxley<sup>91,92</sup>) and a New World clade (green colour in Extended Data Fig. 3).

- The Old World clade includes around a third of the species in *Ipomoea*. Although our study of the Old World species is less advanced than the study of the New World species, some patterns in the Old World clade are worth highlighting, for example the fact that all genera previously recognised in *Ipomoeae* except *Astripomoea* belong to this clade —except *Turbina amazonica* D.F.Austin & Staples, which is in the New World clade— and none of them is monophyletic.

Although the Old World clade is dominated by species restricted to the Palaeotropics, at least one clade consists entirely of American species and at least two other species have a distribution restricted to the New World, most likely indicating the distribution of these taxa is the result of long-distance dispersal by natural means.

- We identified three small clades that form a grade between the Old World clade and the New World clade. These three clades are found in both nuclear and chloroplast phylogenies and the more extensive taxon sampling in the *ITS* phylogeny adds several species to each of them. The largest group in this grade is formed by all taxa previously included in *Astripomoea* and some species of *Ipomoea*, whereas the two smaller clades include only *Ipomoea* species. All species in this grade are restricted to the African continent and Madagascar.
- The New World clade includes about two thirds of the total number of species of *Ipomoea*. In addition, several subclades can be identified and diagnosed morphologically:
  - **Clade A**, with around 250 species, is by far the largest clade in New World *Ipomoea*. It is further divided into three sub-clades, two large (A1 and A2) and a smaller one comprising the sweet potato and its wild relatives (A3), and three species that are not included in any of these sub-clades (*Ipomoea cryptica*, *I. setosa* and *I. peruviana*).
  - **Clade B** is another large clade which includes some well-known species for their use in gardening and as invasive species, for example *I. alba*, *I. indica*, *I. nil*, *I. purpurea* or *I. tricolor*. Species in this clade have been traditionally classified in subgenus *Quamoclit*, section *Pharbitis* and various other sections and series, although these ranks are not monophyletic and their use must be discontinued.



- **Clade C** contains fewer species than A and B. Of interest is the position of *Turbina amazonica*, distributed across Amazonia, which is the only species of *Turbina* in the NW clade. Also, an outstanding element is the sub-clade of several species restricted to Australia and *Ipomoea pes-caprae*, a coastal species from sandy areas present in most tropical regions of the world.
- **Clade D** is a small clade formed of seven American species.
- **Clade E** is a small clade that includes *I. aquatica*, the second most significant crop species in the genus. All species in this clade except *I. habeliana* Oliv. are Palaeotropical. Another member of this clade is *I. cairica*, a species with a widespread distribution introduced in some regions and now reported to be invasive<sup>93</sup>.

As part of our studies, we have identified several instances of closely related species with highly disjunct distribution patterns, that is, a taxon or group of taxa nested in a clade where all other taxa inhabit a different geographical region —often a different continent. As well as *I. habeliana* mentioned above these cases often include specific species, such as:

- *Ipomoea littoralis*, the only sweet potato close wild relative restricted to the Old World and absent from the Americas.
- *Ipomoea tuboides*, a Hawaiian endemic nested in a clade of Mexican species in Clade B.
- *Ipomoea aculeata*, the only Old World species in Clade B.
- *Ipomoea asterophora*, a Western New Guinea endemic and the only non-American species in clade A2.

In some cases, taxa with a distribution most likely explained as the result of long-distance dispersal have subsequently speciated. Our phylogenies indicate that:

- All Australian endemics that we have sequenced come in one of two clades nested in American clades: *I. abrupta*, *I. calobra*, *I. costata* and *I. polpha* are nested in Clade A, whereas *I. argillicola*, *I. brassii*, *I. gracilis* and *I. muelleri* are nested in Clade C. This suggests the Australian species originated following long-distance dispersal of their ancestors from the American continent.
- *Ipomoea sumatrana* and *I. campanulata*, two species restricted to SE Asia, as well as *I. albivenia* and *I. verbascoidea*, two African species, are nested in different parts of Clade A1, dominated by American species.
- A clade of American species (*I. clavata*, *I. corymbosa*, *I. crinicalyx*, *I. cuscoensis*, *I. daturiflora*, *I. echinocalyx*, *I. lindenii*, *I. pedicellaris*, *I. sidifolia* and *I. silvicola*) is nested in the Old World clade.

All these cases, confirmed using genomic data, are most easily explained as the result of long-distance dispersal by natural means. In some cases, taxa with a distribution explained by long-distance dispersal have subsequently speciated. Our results show that long-distance dispersal by natural means is commonplace in *Ipomoea* and thus its potential relevance in the current distribution of species must be considered.

## SECTION 3 | SPECIES NARRATIVES

**Taxonomic decisions** are a process involving in varying degrees:

- Study of specimens and representative sampling
- Study of names and type specimens
- Reference to a range of publications
- Phylogenetic study using DNA sequences
- Fieldwork
- Visits to herbaria
- Collaboration and contacts
- Photos and images
- Geographical and ecological occurrences

The literature on ‘integrative taxonomy’ and ‘DNA taxonomy’ often lacks specific examples and enough narrative detail to determine how taxonomic decisions are made. In the account that follows, we provide eight case studies to describe the often complex and dynamic nature of taxonomic decision-making. These examples highlight the process of species delimitation showing how new collections often have to be compared with only partially known existing material and species. They also demonstrate the accumulative element in species delimitation as new material, photographs and observations become available over time. They also show how a carefully constructed phylogeny, albeit based on a single DNA marker, can provide clarity and subsequently play an important role in making or at least facilitating taxonomic decisions. Importantly, all these examples demonstrate the importance of examining material from the entire range of variation across several countries to obtain accurate species delimitation and determine synonymy. Although there were other contributors, much of the specimen-based work was carried out by John R.I. Wood, one of the authors of this paper, and therefore the following narratives are written in the first person.

### **EXAMPLE 1: DNA PROVIDES EVIDENCE THAT NEW COLLECTIONS SIMILAR TO AN EXISTING SPECIES ARE ONLY DISTANTLY RELATED AND, WHEN COMBINED WITH MORPHOLOGICAL DATA, ARE RECOGNISED AS A NEW SPECIES (*Ipomoea longibarbis* J.R.I.Wood & Scotland)**

*Ipomoea longibarbis* is a species of the Bolivian Chaco<sup>23</sup>. It was first collected in 1952 by Martín Cárdenas but languished unrecognised in the Lillo herbarium (LIL, Argentina) until 2014. The same species was collected a couple of times in the 1990s and then quite frequently after 2000, always along the fringes of the western Chaco in Bolivia.

I became aware of this plant around 2010, when examining material in the Santa Cruz herbarium (USZ, Bolivia) at the start of my focus on *Ipomoea*. My first impression was of a species closely related to *Ipomoea argentinica* Peter, which is common around Santa Cruz but which was immediately distinguished by the conspicuous spreading hairs on the calyx as well as the deciduous bracteoles. Although I had never collected this species myself, I was able to borrow specimens from USZ to study in the UK.

In 2012, I was able to show this material to Rosangela Simao-Bianchini from the Instituto de Botânica de Sao Paulo (Brazil) during her visit to Kew. She suggested the plant was *Ipomoea rubens* Choisy. On comparing the specimens, it was easy to see why she had suggested this, as the sepals are almost indistinguishable. I was, however, unconvinced, as I

knew *I. rubens* to be a plant of river and lake margins, whereas the Chaco plant was a plant of dry forest. There were also some superficial morphological differences, *I. rubens* often having shallowly 3-lobed leaves while those of the Chaco species were always entire. Closer study showed that the hairs on the seeds of the Chaco species were long, fine and caducous while those of *I. rubens* were shortly but densely pilose and persistent.

In this situation, re-finding and collecting material of the Chaco plant was a priority of our field trip to Bolivia in early 2013. We duly found the plant and brought specimens back to Oxford for study. These were sequenced along with specimens of *Ipomoea rubens* from Bolivia and elsewhere. The molecular analysis showed that the species were completely unrelated, *I. rubens* belonging to the essentially Palaeotropical Grade of *Ipomoea* while the Chaco species was part of the Jalapa radiation (Clade A) in the essentially Neotropical Grade (Extended Data Fig. 3). During 2013–14, additional material of the Chaco plant was found in various herbaria in Argentina and the United States as well as in Bolivia, totalling 14 collections. We described it as a new species with the name *Ipomoea longibarbis*<sup>23</sup>.

At least six specimens of *I. rubens* were sequenced for *ITS*, three from the New World and three from the Old World. These showed the species to be monophyletic and strongly suggest an African origin, as it belongs to a well-supported clade of wholly African species. It is not clear how *I. rubens* arrived in the New World, but it is locally abundant and has every appearance of being a native species in Bolivia, Argentina, Paraguay and Brazil.

*I. rubens* and *I. longibarbis* are good examples of convergence of traits and of the importance of different ecologies in suggesting taxonomic distinction.

**EXAMPLE 2: DNA PROVIDES EVIDENCE THAT NEW COLLECTIONS SIMILAR TO AN EXISTING SPECIES ARE ONLY DISTANTLY RELATED AND WHEN COMBINED WITH MORPHOLOGICAL DATA ARE RECOGNISED AS A NEW SPECIES (*Ipomoea graniticola* J.R.I.Wood & Scotland)**

I first found *Ipomoea graniticola* on a granite inselberg at El Cerrito, Bolivia, in May 2008. The distinctive leaves which were divided into five narrow leaflets immediately caught my attention as unusual, even though the flowers had almost all fallen. I first thought this species might be *I. subrevoluta* Choisy because of the similar leaflets but was doubtful that they were conspecific from the beginning because of the very different habitats. The new plant was growing on dry granite, whereas *I. subrevoluta* is a plant of streamsides in cerrado-like vegetation.

I returned to the site in April 2009 and collected flowers. Based on these two collections, I noted that the plant could not be *I. subrevoluta* because of the much longer sepals and rather distinct capsule (see figure in <sup>23</sup>). Based on the material in the Kew Herbarium, I noted the close similarity with *I. rosea* Choisy from Bahia (Brazil) because of the similar sized sepals. I therefore reached the conclusion that the plant I collected was *Ipomoea rosea* and included it under this name in the Red book of plants from Bolivian Eastern Cerrados<sup>94</sup>. The situation did not change until 2012, when I showed the specimens to Rosangela Bianchini. She said that it was not *I. rosea*, because the sepals lacked appendages on their abaxial surface, and suggested it was *I. subrevoluta*. I had not noticed the sepal appendages in *I. rosea* before but I was still unconvinced. Hence, I was keen to obtain sequence data for these three species. The analysis of *ITS* sequences showed that *I. subrevoluta* is in a completely different clade to *I. rosea* and the Cerrito plant, which were distinct and closely related. I therefore went ahead and described

the Cerrito species as *I. graniticola*, based on “the absence of the tooth-like appendage on the abaxial surface of the sepal”<sup>23</sup>. I included one additional record from Brazil (Mato Grosso), which I had found during visits to MO in 2013 and RB in 2014.

The story does not end here. In 2013, on a visit to Paraguay, I had noted a collection from an isolated inselberg in northern Paraguay, which I had concluded —doubtfully— was *I. rosea* because of the distinctive leaves and appendages on the abaxial surface of the leaves. I had been doubtful principally because of the great distances separating the populations. On our next visit to Paraguay in April 2016, I examined this specimen more carefully and then re-examined the more extensive material of *I. graniticola*, which I had collected in February 2016 as well as material of *I. rosea* at Kew. I found that the sepal appendage character was not constant, being usually (but not always) present in *I. rosea* and usually (but not always) absent in *I. graniticola*. However, careful examination revealed another character – the leaves of *I. rosea* always have three oblong-elliptic leaflets, even though the basal leaflets may be partially bifurcate, whereas those of *I. graniticola* are always five in number and narrowly oblong in shape. Based on this redefinition of the species, the Paraguay material fell into *I. graniticola* whose range was thus extended to Paraguay. Additional confirmation came from Liziane Vasconcelos, from Universidade Estadual de Feira de Santana (Brazil), who reported that *I. rosea* was a plant of the Caatinga in Bahia, not of granite outcrops.

One final development came with reports of *I. graniticola* from similar inselbergs in NE Brazil, which was reported in our paper in 2017<sup>32</sup>.

**EXAMPLE 3: DNA PROVIDES EVIDENCE THAT NEW COLLECTIONS SIMILAR TO AN EXISTING SPECIES ARE ONLY DISTANTLY RELATED AND WHEN COMBINED WITH MORPHOLOGICAL DATA ARE RECOGNISED AS A NEW SPECIES (*Ipomoea cryptica* J.R.I.Wood & Scotland)**

*Ipomoea squamosa* Choisy is a relatively well-known and widely distributed species of seasonally dry forest throughout tropical America from Bolivia and Brazil north to Mexico. It is characterised by its ovate leaves, which are often hastate to subsagittate at the base although sometimes cordate, its pink funnel-shaped corolla, which is glabrous on the exterior and, in particular, by its unequal, scarious-margined sepals, the outer sepals 4–6 mm long and the inner 7–10 mm. Its delimitation became complicated after the description of *I. anisomeres* B.L.Rob. & Bartlett. This was distinguished from *I. squamosa* by the very short outer sepals (< 3 mm long), the white corolla (often with a dark throat) and the pubescent seeds. The pubescent seeds are perhaps the most satisfactory character separating the two species, as the seeds of *I. squamosa* are long-pilose and slightly woolly. In succeeding years, *I. anisomeres* was recorded sporadically throughout Mesoamerica and northern South America over much the same range as *I. squamosa*.

These two species are never easy to distinguish in the herbarium, as capsules and seeds are commonly absent and flower colour is often lost in the drying process. Taxonomists have depended principally on the very short outer sepal of *I. anisomeres* to distinguish this species. It was not surprising, therefore, that plants with a very small outer sepal collected in Bolivia were also identified as *I. anisomeres*, despite field notes recording the flower colour as pink. As late as January 2015, I was following this approach and these records were listed in the *Catálogo de las Plantas Vasculares de Bolivia* as *I. anisomeres*<sup>95</sup>.

In July 2014, I travelled to Bolivia and made several collections of a plant resembling *I. anisomeres* but with pink flowers. These were identified in the field as *I. squamosa* but when four different samples were sequenced for *ITS* in late 2014, they proved to be a quite different species, sister to the Batatas clade (Clade A3 in Extended Data Fig. 3) and phylogenetically distant from *I. squamosa* and *I. anisomeres*, which are in Clade D. As this entity was so difficult to characterise, we described it as the new species *I. cryptica*<sup>23</sup>.

At present, *I. cryptica* is only confirmed by molecular evidence and the presence of pink flowers from Bolivia but specimens from Brazil and Peru appear to be this species. In 2017, Maira Martinez collected fruiting material of *I. cryptica* in Bolivia, showing that it had a strongly rostrate capsule and seeds with distinct white marginal hairs unlike the pubescent hairs of *I. anisomeres*. However, additional collections and sequencing are still required to clarify the distribution of this species and establish if and where *I. anisomeres* occurs south of Colombia.

#### **EXAMPLE 4: A VALIDLY PUBLISHED BUT OVERLOOKED SPECIES FROM OBSCURE LITERATURE (*Ipomoea montecristina* Hadač)**

*Ipomoea montecristina* was collected by Hadač on Monte Cristi in Guantanamo province (Eastern Cuba) in 1968. It was published two years later<sup>96</sup> but the types were not deposited in a Cuban herbarium, and it remained unnoticed by Cuban botanists and by the international botanical community for many years. The species was not recognised by Austin and Huáman<sup>3</sup> and was unknown to me when I visited Cuba in November 2015.

I began my visit to Cuba at the Instituto de Ecología y Sistemática (HAC) where I examined all collections of *Ipomoea*. Amongst these were two collections from Eastern Cuba, which appeared to represent a new species. They lacked corollas but the sericeous leaves and coriaceous sepals were distinctive. Later during my trip, I visited the herbarium of the National Botanical Garden (HAJB) and found around ten collections of the same species. All of these originated from Eastern Cuba, principally from limestone “pinars” at Monte Cristi and Abra de Mariana near San Antonio del Sur. These comprised better material with corollas, capsules and seeds. None had been identified by Dr Manitz from Berlin (a specialist in the *Ipomoea* of Cuba) and I was confident they represented an undescribed species and annotated them as such.

Soon after my return to Britain I was revising the *Catalogue of Seed Plants of the West Indies*<sup>6</sup> and checking whether my list of Caribbean *Ipomoea* species was complete, when I saw *I. montecristina* Hadač listed. The epithet immediately suggested the plant I had seen in the Cuban herbaria, and reference to the protologue confirmed this suspicion. The description and type locality indicated clearly that the Cuban plant was indeed *I. montecristina*.

#### **EXAMPLE 5: DNA EVIDENCE SHOWS THAT PUTATIVE NEW SPECIES WITH A DISTINCTIVE MORPHOLOGICAL CHARACTER THAT IS SHARED WITH AN EXISTING SPECIES, IS PHYLOGENETICALLY DISTINCT AS BOTH SPECIES HAVE DIFFERENT CLOSE RELATIVES (*Ipomoea huayllae* J.R.I.Wood & Scotland)**

*Ipomoea aristolochiifolia* G.Don is one of the more widespread species in the American continent, extending from Argentina to northern Mexico. It is a slender species with a relatively small blue corolla with a pale tube, subequal often warted, narrowly ovate sepals with a white margin and a relatively large, often rostrate capsule. Although it is very variable in some

characters such as indumentum and leaf dentation, it is usually easily distinguished by an unusual character in *Ipomoea*, the peduncle passes through the leaf sinus.

In 2014, I visited the La Paz herbarium (LPB) and was shown specimens of what appeared to be a rather large-flowered hairy form of *Ipomoea aristolochiifolia*. It transpired that there were two separate collections made on successive days from the same area. I requested duplicates of these specimens to take back to Oxford together with images of the collection showing the distinctive peduncle passing through the sinus of the leaf base. I examined these carefully and suspected they represented a distinct species because of the larger dimensions of all flower parts and leaves as well as the denser indumentum of all vegetative parts. In Oxford, samples of this species were sequenced and came up with a slightly surprising result. It showed that it was indeed in the same clade as *Ipomoea aristolochiifolia*, but was more closely related to another putative new species from further south in Bolivia, which did not have the distinctive peduncle character. We described both these species as new as *I. huayllae* J.R.I.Wood & Scotland and *I. odontophylla* J.R.I.Wood & Scotland in Kew Bulletin<sup>23</sup>. Both are essentially pin-point endemics but fortunately grow in protected areas.

**EXAMPLE 6: DNA EVIDENCE AND PHYLOGENETIC ANALYSIS SUPPORT THAT TWO MORPHOLOGICALLY INDISTINGUISHABLE BUT GEOGRAPHICALLY SEPARATE SPECIES FROM DIFFERENT CONTINENTS ARE TREATED AS A SINGLE SPECIES (*Ipomoea acanthocarpa* (Choisy) Aschers. & Schweinf.)**

*Ipomoea acanthocarpa* was first discovered by the Austrian collector Teodor Kotschy in the Sudan in 1839. It was distributed by Hochstetter under this name to various herbaria but was only formally published as a new species by Choisy in 1845 under the name *Calonyction acanthocarpum* Choisy<sup>22</sup>. Why Choisy placed it in the genus *Calonyction* is unclear, as he had based that genus on having a conspicuous corolla similar to *Datura* and with exerted stamens. This does not fit *Ipomoea acanthocarpa* at all, but Choisy could not have known this as he did not describe the corolla. Just over 20 years later, Ascherson and Schweinfurth transferred the species into *Ipomoea*.

*Ipomoea acanthocarpa* is widespread across the Sahel region of Africa, extending from Senegal in the west to Sudan and Ethiopia in the east. Collections are not very numerous, especially in the east of its range, but it is present in most countries in this extensive region.

Over a hundred years later, during the course of his revisionary work on American Convolvulaceae, O'Donnell came across specimens of an unnamed *Ipomoea* from Peru (Haught 142) and from the other side of the continent in eastern Brazil (Froes & Black 24742). He correctly identified these as the same species describing them under the name *Ipomoea piurensis* O'Donnell in 1953 after the Peruvian department of Piura. Over the years, *Ipomoea piurensis* has been reported from a number of American countries including Colombia, Ecuador, Guyana and Venezuela<sup>3</sup> but never in great frequency.

No one had considered *Ipomoea acanthocarpa* and *I. piurensis* could be conspecific before we sequenced examples of the two species during the course of our studies. The eight representative samples from Africa and the Americas formed a monophyletic clade with the African specimens nested inside the American, strongly suggesting that a single species was involved. Examination of a large number of African and American specimens in different herbaria indicated that there were no morphological differences and thus the two species should

be treated as the same under the oldest name, *I. acanthocarpa*. In passing, it is worth noticing that this species is widespread but very dispersed in its distribution in both continents. Recent collections have added Costa Rica, Colombia and Bolivia to its American distribution, the last two as a result of this study.

The molecular sequences did indicate something else interesting (Extended Data File 2). Although *Ipomoea acanthocarpa* was first found in Africa in 1839, it clearly belongs to a larger clade of entirely American species including *I. bahiensis*, *I. squamosa* and *I. eriocalyx*. This suggests that it is a plant of American origin, which has colonised Africa, going in the reverse direction to *I. rubens*. Whether the introduction to Africa was by ancient long-distance dispersal or by relatively recent human activity is unclear but its wide distribution in Africa might suggest the former.

#### **EXAMPLE 7: IMPROBABLE HIGHLY DISJUNCT DISTRIBUTION PATTERNS CONCEAL THAT SPECIES ARE CONSPECIFIC (*Ipomoea longeramosa* Choisy)**

*Ipomoea longeramosa* Choisy was described based on a collection by Martius from Brazil<sup>22</sup>. It was re-described unnecessarily by Meisner based on another Brazilian collection as *I. geranioides* Meisn.<sup>97</sup> and, although both names co-existed for a long time, *I. longeramosa* was accepted as the correct name from the mid-20<sup>th</sup> century onwards. It was essentially a rather poorly known plant with a core distribution in the caatinga region of north eastern Brazil. Austin and Huaman<sup>3</sup> cited a record from Venezuela and, during the course of our monographic studies, we found additional records in Guyana and in Mato Grosso (western Brazil). This was the situation until the end of 2015.

*Ipomoea longeramosa* is an annual species with palmately divided leaves and small cream or yellowish flowers with a darkish centre. Many specimens are rather depauperate as a result of a short growing period in a dry year but in a year of good rainfall some specimens are very vigorous and look somewhat like *Distimake quinquefolia* (L.) A.R. Simões & Staples. *I. longeramosa*, however, has distinct apiculate sepals, which are a good character delimiting the species.

Late in 2015, I made a major effort to understand the many endemic species from Cuba. One of these was a small annual species described by Wright as *I. punctata* C.Wright because of its gland-dotted leaves but subsequently renamed *I. flavopurpurea* Urban because of its yellowish flowers with a purplish centre. This was a rare species but I was happy to find three additional collections in the Cuban herbaria during my visit in November 2015. It never crossed my mind that this could be the Brazilian *I. longeramosa* until I visited the Stockholm herbarium in January 2016 to see Ekman's collections from Cuba. Amongst these was a collection of *I. flavopurpurea* which O'Donnell had annotated with the name *I. longeramosa*. This was a *eureka* moment for me as it was immediately obvious that the Cuban plant was indistinguishable from *I. longeramosa*<sup>28</sup>.

At about the same time, I turned my attention to the endemic species of Hispaniola. Only one new endemic species had been described in recent times, *I. dajabonensis* Alain<sup>98</sup>. Austin and Huáman<sup>3</sup> had treated this as a synonym of *I. plummerae*, but this had always seemed unlikely to me as *I. plummerae* is otherwise unknown from the Caribbean, and is a mountain plant rarely if ever found below 1500m. However, I had been unable to find a type specimen until I happened upon a duplicate of the type specimen in the virtual herbarium of the Berlin

Botanical Garden. This allowed immediate identification of *I. dajabonensis* with *I. longeramosa*, whose range was thus extended to the Dominican Republic.

Yet another development came as a result of my visit to Argentina with Tom Carruthers in April 2016. Our host was Hector Keller from Universidad del Nor Este, Argentina, who made a point of showing us unusual Convolvulaceae. One of these was a species of *Distimake* allied to *D. cissoides* (Lam.) A.R. Simões & Staples, which he thought might be a new species or hybrid involving *D. cissoides*. Promising to look into this possibility, I took a specimen back with me to the UK and searched through the South American collections of *Distimake* at Kew to try and find a match for Keller's specimen. Although I decided in the end that his specimen was a variant of *D. cissoides*, I did make an interesting discovery. Amongst unidentified specimens of *Distimake* was a plant I had collected in 2008. Having become very familiar with *Ipomoea longeramosa*, I was immediately able to recognise this specimen as belonging to this species, thus extending its range to Bolivia.

A few final observations. The distribution of *I. longeramosa* is clearly centred on NE Brazil but it occurs in scattered populations over much of tropical South America and the Caribbean. It has probably been overlooked elsewhere and it would be reasonable to predict its occurrence in other countries, particularly Colombia and perhaps Mexico. At present, we have only sequenced material from Brazil and Bolivia. It would be ideal to sequence Caribbean material but no suitable material has yet become available.

#### **EXAMPLE 8: DIFFERENT INTERPRETATIONS OF SPECIES IN THE LITERATURE RESULT IN LONG-LASTING CONFUSION (*Ipomoea tubulata* Sessé and Mociño)**

This species grows around Uruapan in Michoacán state in Mexico. It was first described as *Quamoclit tubulosa* Martens & Galeotti based on a collection by Galeotti. Hemsley transferred the name to *Ipomoea* as *I. tubulosa* in 1882 but this was an illegitimate later homonym of *I. tubulosa* Willd. ex Roem. & Schult. In 1893, Hallier suggested this was conspecific with a plant collected by Fenzl, which was labelled *Exogonium uhdeanum* but never described, thus rendering the subsequent combination by Austin (*Ipomoea uhdeana*) in 1978 illegitimate.

Without reference to *Quamoclit tubulosa* in 1907, House described the same species from the Vulcan de Colima based on a collection by Bárcena at MEXU under the name *Ipomoea urbinei* House. This specimen has been lost, so the species was essentially ignored by other authors throughout most of the 20<sup>th</sup> century. Consequently, when another specimen emerged from Uruapan, it was described as new by Standley as *Exogonium woronowii*, without reference either to *Quamoclit tubulosa* or to *Ipomoea urbinei*.

Also in 1907, but in the Bulletin of the Torrey Botanical Club, House had described a second species from Oaxaca as *Exogonium luteum*. House did not apparently notice how similar the two species were as he made no comparison between them in the protologue<sup>99</sup>. In fact, *Exogonium luteum* House differs principally in its yellow flowers (hence *luteum*), and the more deeply divided corolla limb with spreading, elongate, oblong rather than triangular lobes. This name could not be transferred to *Ipomoea* as there is already an *Ipomoea lutea* Hemsl. so in 1978, Austin renamed it *Ipomoea shinersii* D.F.Austin, for the first time drawing attention to the similarities between the two species (*Quamoclit tubulosa* and *Exogonium luteum*) and treating them as two species of the same genus. However, in uniting the two species he rendered



the name *I. shinniersii* illegitimate as he should have taken up the older name *Ipomoea woronovii*. (It was in this same paper that he made the illegitimate combination *Ipomoea uhdeana* as well, failing to note it was conspecific with *I. woronovii*). Realizing his mistake in 1983, he corrected the names treating *Quamoclit tubulosa* as *I. woronovii* (Standl.) D.F.Austin var. *woronovii* and *Exogonium luteum* as *I. woronovii* var. *lutea* (House) D.F.Austin.

This was not the end of the matter as Austin had ignored *Ipomoea urbinei* House, published in 1907. In 1987 Andy McDonald investigated this species and in the absence of a type specimen, lectotypified it with the illustration in House's *Muhlenbergia* publication, which is clearly conspecific with *Quamoclit tubulosa* but failed to make the link with *I. woronovii*. At some stage over the next 15 years, McDonald and Austin clearly discussed and reviewed the status of *Quamoclit tubulosa* and *Exogonium luteum* and in 2002 published a joint paper in *Novon* in which they treated the two taxa as separate species, the former under the name *Ipomoea urbinei*, the latter as a newly described *Ipomoea electrina* **D.F.Austin & J.A.McDonald**.

This should have settled everything. However, in the 2012 account of *Ipomoea* in *Flora Mesoamericana* Austin, MacDonald and Murguía-Sánchez treated *Exogonium luteum* as a synonym of *Ipomoea urbinei* with no mention of *I. electrina*<sup>5</sup>. When I queried Andy McDonald about this in November 2016, he answered indicating that he stood by the 2002 paper and suggested there had been confusion.

Austin and McDonald had ignored yet another publication, the earlier *Flora Mexicana* by Sessé and Mociño<sup>100</sup> where *Ipomoea tubulata* was described from Uruapan. This species has been tentatively identified by McVaugh in 2000 in the *Botanical results of the Sessé and Mociño Expedition*<sup>101</sup> but again the publication was ignored. A check in JSTOR revealed there were two perfectly good specimens in the Madrid (MA) herbarium, one of which labelled Uruapan was selected as lectotype in our monograph<sup>25</sup>.

A final note. Although I have no doubt *Ipomoea tubulata* is distinct from *I. electrina*, its distinction from *I. dumosa* is not always satisfactory. *I. tubulata* occurs in Colima and Michoacán, basically in an area extending from the Vulkan Colima to the region around Uruapan. In eastern Michoacán and the Estado Mexico, plants intermediate between *I. dumosa* and *I. tubulata* occur. In the monograph, these are treated in a footnote but may turn out to be hybrids or may result in yet another name change with *I. tubulata* being treated as a subspecies of *I. dumosa*.

## SECTION 4 | NOMENCLATURAL CHANGES

We have made combinations for all names in current floras and checklists, especially 'A nomenclatural review of *Argyreia* (Convolvulaceae)'<sup>102</sup> which has a comprehensive list of names in *Argyreia*. Accepted names **in bold**. Question marks indicate uncertain identification.

*Argyreia adpressa* (Choisy) Boerl.; basionym: *Moorcroftia adpressa* Choisy in Mém. Soc. Phys. Genève 6: 431 [Convolv. Orient.: 49] (1834) = ***Ipomoea adpressa*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia akoensis* S.Z.Yang, P.H.Chen & Staples, *Taiwania* 60: 117 (2015) = ***Ipomoea akoensis*** (S.Z.Yang, P.H.Chen & Staples) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia albiflora* Traiperm & Staples, Phytotaxa 204: 226 (2015), non *Ipomoea albiflora* Moric. = ***Ipomoea candida*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia androyensis* Derooin, Candollea 48: 449 (1993), non *Ipomoea androyensis* Derooin = ***Ipomoea derooinii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia ankylophlebia* Traiperm & Staples, Syst. Bot. 41: 1020 (2016) = ***Ipomoea ankylophlebeia*** (Traiperm & Staples) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia apoensis* (Elmer) Ooststr.; basionym: *Rivea apoensis* Elmer in Leaflet. Philipp. Bot. 7: 2604 (1915) = ***Ipomoea apoensis*** (Elmer) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia arakuensis* N.P.Balakr., Bull. Bot. Surv. India 3: 163 (1962) = uncertain species = ? ***Ipomoea concanica*** J.R.I.Wood & Scotland

*Argyreia argentea* (Roxb.) Sweet; basionym: *Lettsomia argentea* Roxb., Fl. Ind. 2: 79 (1824), non *Ipomoea argentea* Meisn. = ***Ipomoea argenteosericea*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia atropurpurea* (Wall.) Raizada = ***Ipomoea atropurpurea*** (Wall.) Sweet, Hort. Brit., ed. 2: 372 (1830)

*Argyreia baoshanensis* S.H.Huang, Acta Phytotax. Sin. 24: 19 (1986) = uncertain species = ? ***Ipomoea barlerioides*** (Choisy) Benth. ex C.B.Clarke

*Argyreia barbata* (Wall.) Raizada = ***Ipomoea barbata*** (Wall.) Choisy, Mém. Soc. Phys. Genève 6: 458 (1834)

*Argyreia barbigera* Choisy in Mém. Soc. Phys. Genève 6: 424 [Convolv. Orient.: 42] (1834), non *Ipomoea barbigera* Sweet = ***Ipomoea prainii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia barnesii* (Merr.) Ooststr.; basionym: *Rivea barnesii* Merr., Publ. Bur. Sci. Gov. Lab. 17: 40 (1904) = ***Ipomoea barnesii*** (Merr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia barnesii* var. *urdanetensis* (Elmer) Ooststr.; basionym: *Rivea urdanetensis* Elmer, Leaflet. Philipp. Bot. 7: 2605 (1915) = ***Ipomoea barnesii*** var. *urdanetensis* (Elmer) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia baronii* Derooin, Candollea 4 8: 451 (1993) = ***Ipomoea baronii*** (Derooin) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia bella* (C.B.Clarke) Raizada; basionym: *Lettsomia bella* C.B.Clarke in Hooker, Fl. Brit. India 4: 192 (1883), non *Ipomoea bella* A. Chev. = ***Ipomoea euantha*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia bifrons* Ooststr., Blumea 5: 362 (1943) = ***Ipomoea bifrons*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia boholensis* (Merr.) Ooststr.; basionym: *Lettsomia boholensis* Merr. Philipp. J. Sci. 29: 485 (1926) = ***Ipomoea boholensis*** (Merr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia boseana* Santapau & V.Patel, Trans. Bose Res. Inst. Calcutta 22: 35 (1958) = uncertain species = ? ***I. himalayana*** J.R.I.Wood & Scotland

*Argyreia bracteata* Choisy, Mém. Soc. Phys. Genève 6: 412 [Convolv. Orient.: 30] (1834), non *Ipomoea bracteata* Cav. = ***Ipomoea austroindica*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia breviscapa* (Kerr) Ooststr.; basionym: *Lettsomia breviscapa* Kerr in Bull. Misc. Inform. Kew 1941: 13 (1941) = ***Ipomoea breviscapa*** (Kerr) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia capitiformis* (Poir.) Ooststr.; basionym *Convolvulus capitiformis* Poir. in Lamarck, Encycl., Suppl. 3: 469 (1814) = ***Ipomoea capitiformis*** (Poir.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia caudata* Ooststr., Blumea 5: 379 (1943), non *Ipomoea caudata* Fernald = ***Ipomoea borneoensis*** J.R.I.Wood & Scotland *comb. nov.*

*Argyreia celebica* Ooststr. Blumea 5: 377 (1943) = ***Ipomoea celebica*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia cheliensis* C.Y.Wu, Yunnan Trop. Subtrop. Fl. Res. Rep. 1: 126 (1965) = ***Ipomoea cheliensis*** (C.Y.Wu) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia cinerea* Ooststr., Blumea 5: 374 (1943) = ***Ipomoea cinerea*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia coacta* (C.B.Clarke) Alston; basionym: *Argyreia hirsuta* var. *coacta* C.B.Clarke in Hooker, Fl. Brit. India 4: 189 (1883) = ***Ipomoea coacta*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia collinsae* (Craib) Na Songkhla & Traiperm; basionym: *Rivea collinsae* Craib in Bull. Misc. Inform. Kew 1916: 266 (1916) = ***Ipomoea collinsae*** (Craib) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia confusa* (Prain) Raizada; basionym: *Lettsomia confusa* Prain in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 96 (1894) = ***Ipomoea confusa*** (Prain) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia congesta* Ooststr., Blumea 7: 176 (1952), non *Ipomoea congesta* R.Br. = ***Ipomoea congestiflora*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia coonoorensis* W.W.Sm. & Ramaswami, Rec. Bot. Surv. India 6: 30 (1914) = ***Ipomoea coonoorensis*** (W.W.Sm. & Ramaswami) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia corneri* Hoogland, Blumea 7: 192 (1952) = ***Ipomoea corneri*** (Hoogland) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia crispa* Ooststr., Blumea 7: 172 (1952), non *Ipomoea crispa* Hallier f. = ***Ipomoea acehensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia cucullata* Ooststr., Blumea 5: 366 (1943) = ***Ipomoea cucullata*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia cuneata* (Willd.) Ker Gawl.; basionym: *Convolvulus cuneatus* Willd., Sp. Pl. 1: 873 (1798) = ***Ipomoea cuneata*** (Willd.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia cymosa* (Roxb.) Sweet; basionym: *Lettsomia cymosa* Roxb., Fl. Ind. 2: 82 (1824), non *Ipomoea cymosa* G. Mey. = ***Ipomoea cymulosa*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia daltonii* C.B.Clarke in Hook., Fl. Brit. India 4: 190 (1883) = ***Ipomoea daltonii*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia discolor* Ooststr., Blumea 7: 175 (1952), non *Ipomoea discolor* Kunth = ***Ipomoea carrii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia dokmaihom* Traiperm & Staples, Syst. Bot. 41: 1021 (2016) = ***Ipomoea dokmaihom*** (Traiperm & Staples) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia elliptica* (Roth ex Roem. & Schult.) Choisy = ***Ipomoea elliptica*** Roth ex Roem. & Schult., Syst. Veg., 4: 248 (1819)

*Argyreia elongata* Forman in Coode & al., Checkl. Fl. Pl. Gymnosperms Brunei Darussalam: 435 (1997), non *Ipomoea elongata* Choisy = ***Ipomoea dransfieldii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia erinacea* Ooststr., Blumea 5: 374 (1943) = ***Ipomoea erinacea*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia eriocephala* C.Y.Wu, Yunnan Trop. Subtrop. Fl. Res. Rep. 1: 125 (1965), non *Ipomoea eriocephala* Moric. = ***Ipomoea chengyiwuensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia formosana* Ishigami ex T.Yamaz., J. Jap. Bot. 44: 160 (1969) = ***Ipomoea formosana*** (Ishigami ex T.Yamaz.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia fulgens* Choisy, Mém. Soc. Phys. Genève 6: 415 [Convolv. Orient.: 33] (1834) = ***Ipomoea fulgens*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia fulvocymosa* C.Y.Wu, Yunnan Trop. Subtrop. Fl. Res. Rep. 1: 135 (1965) = ***Ipomoea fulvocymosa*** (C.Y.Wu) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia fulvovillosa* C.Y.Wu & S.H.Huang in Wu, Fl. Reipubl. Popul. Sin. 64(1): 164 (1979) = ***Ipomoea fulvovillosa*** (C.Y.Wu & S.H.Huang) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia glabra* Choisy in Zoll., Syst. Verz. 2:128, 130 (1854), non *Ipomoea glabra* Choisy = ***Ipomoea zollingeri*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia hancorniiifolia* Gardner ex Thwaites, Enum. Pl. Zeyl.: 210 (1860) = ***Ipomoea hancorniiifolia*** (Gardner ex Thwaites) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia henryi* (Craib) Craib = ***Ipomoea henryi*** Craib, Bull. Misc. Inform. Kew 1911: 423 (1911)

*Argyreia hirsuta* Wight & Arn., Madras J. Lit. Sci. 5: 18 (1837), non *Ipomoea hirsuta* R.Br. = ***Ipomoea villifolia*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia hirsutissima* (C.B.Clarke) Raizada; basionym: *Lettsomia hirsutissima* C.B.Clarke in Hook.f., Fl. Brit. India 4: 193 (1883), non *Ipomoea hirsutissima* Gardner = ***Ipomoea oreogena*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia hookeri* C.B.Clarke in Hook.f., Fl. Brit. India 4: 185 (1883), non *Ipomoea hookeri* G.Don = ***Ipomoea himalayana*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia hylophila* (Kerr) Staples & Traiperm = ***Ipomoea hylophila*** Kerr, Bull. Misc. Inform. Kew, 1941: 17 (1941)

*Argyreia inaequisepala* Traiperm & Staples, Syst. Bot. 41: 1025 (2016) = ***Ipomoea inaequisepala*** (Traiperm & Staples) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia involucrata* C.B.Clarke in Hook.f., Fl. Brit. India 4: 187 (1883), non *Ipomoea involucrata* P.Beauv. = ***Ipomoea dalzellii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia involucrata* var. *inaequalis* C.B.Clarke in Hook.f., Fl. Brit. India 4: 187 (1883) = ***Ipomoea dalzellii*** var. *inaequalis* (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia ionantha* (Kerr) Khunwasi & Traiperm; basionym: *Lettsomia ionantha* Kerr, Bull. Misc. Inform. Kew 1941: 15 (1941) = ***Ipomoea ionantha*** (Kerr) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia kerrii* Craib, Bull. Misc. Inform. Kew 1911: 422 (1911) = ***Ipomoea kerrii*** (Craib) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia kleiniana* (Roem. & Schult.) Raizada = ***Ipomoea kleiniana*** Roem. & Schult., Syst. Veg. 4: 789 (1819)

*Argyreia kondaparthiensis* P.Daniel & Vajr., J. Econ. Taxon. Bot. 3: 675 (1982) = ***Ipomoea kondaparthiensis*** (P.Daniel & Vajr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia kunstleri* (Prain) Prain ex Ooststr.; basionym: *Lettsomia kunstleri* Prain in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 100 (1894) = ***Ipomoea kunstleri*** (Prain) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia kurzii* (C.B.Clarke) Boerl.; basionym: *Lettsomia kurzii* C.B.Clarke in Hook.f., Fl. Brit. India 4: 196 (1883) = ***Ipomoea kurzii*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia lamii* Ooststr., Blumea, Suppl. 4: 239 (1958) = ***Ipomoea lamii*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia lanceolata* Choisy, Mém. Soc. Phys. Genève 6: 421 [Convolv. Orient.: 39] (1834), non *Ipomoea lanceolata* G.Don = ***Ipomoea lancifolia*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia laotica* Gagnep. Notul. Syst. (Paris) 3: 134 (1915) = ***Ipomoea laotica*** (Gagnep.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia lawii* C.B.Clarke in Hook.f., Fl. Brit. India 4: 190 (1883) = ***Ipomoea lawii*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia leschenaultii* Choisy, Mém. Soc. Phys. Genève 6: 413 [Convolv. Orient.: 31] (1834) = ***Ipomoea leschenaultii*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia leucantha* Traiperm & Staples, Thai Forest Bull., Bot. 36: 100 (2008), non *Ipomoea leucantha* Jacq. = ***Ipomoea thailandica*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia linggaensis* Ooststr., Blumea 7: 171 (1952) = ***Ipomoea linggaensis*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia longifolia* (Collett & Hemsl.) Raizada; basionym: *Lettsomia longifolia* Collett & Hemsl., J. Linn. Soc., Bot. 28: 95 (1890), non *Ipomoea longifolia* Willd. = ***Ipomoea shanensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia longipes* (Gagnep.) Traiperm & Staples; basionym: *Erycibe longipes* Gagnep. in Notul. Syst. (Paris) 3: 140 (1915), non *Ipomoea longipes* Garcke = ***Ipomoea gagnepainii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia luzonensis* (Hallier f.) Ooststr., Blumea 5: 379 (1943) = ***Ipomoea luzonensis*** (Hallier f.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia maingayi* (C.B.Clarke) Hoogland; basionym: *Lettsomia maingayi* C.B.Clarke in Hook.f., Fl. Brit. India 4: 195 (1883) = ***Ipomoea maingayi*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia marlipoensis* C.Y.Wu & S.H.Huang in Wu, Fl. Yunnanica 2: 676 (1979) = ***Ipomoea marlipoensis*** (C.Y.Wu & S.H.Huang) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia mastersii* (Prain) Raizada; basionym: *Lettsomia mastersii* Prain in J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 63(2): 98 (1894) = ***Ipomoea mastersii*** (Prain) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia maymyensis* (Lace) Raizada = ***Ipomoea maymyensis*** Lace, Bull. Misc. Inform. Kew 1914: 380 (1914)

*Argyreia mekongensis* Gagnep. & Curchet, Notul. Syst. (Paris) 3: 134 (1915) = ***Ipomoea mekongensis*** (Gagnep. & Curchet) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia melvillei* (S.Moore) Staples; basionym: *Lettsomia melvillei* S.Moore in J. Bot. 43: 144 (1905) = ***Ipomoea melvillei*** (S.Moore) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia micrantha* Ooststr., Blumea 5: 375 (1943), non *Ipomoea micrantha* Hallier f. = ***Ipomoea kinabaluensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia mollis* (Burm.f.) Choisy, non *Ipomoea mollis* G.Don = ***Ipomoea sericea*** (L.) Blume, Bijdr.: 720 (1825-26)

*Argyreia monglaensis* C.Y.Wu & S.H.Huang Huang in Wu, Reipubl. Popul. Sin. 64(1): 164 (1979) = ***Ipomoea monglaensis*** (C.Y.Wu & H.S.Huang) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia monosperma* C.Y.Wu, Yunnan Trop. Subtrop. Fl. Res. Rep. 1: 127 (1965), non *Ipomoea monosperma* Spreng. ex Choisy = ***Ipomoea uniseminalis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia nana* (Collett & Hemsl.) S.Shalini, Lakshmin. & D.Maity = ***Ipomoea nana*** Collett & Hemsl., J. Linn. Soc., Bot. 28: 87 (1890)

*Argyreia nellygherya* Choisy, Mém. Soc. Phys. Genève 6: 414 [Convolv. Orient.: 32] (1834) = ***Ipomoea nellygherya*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia nervosa* (Burm.f.) Bojer; basionym: *Convolvulus nervosus* Burm.f., Fl. Indica: 48, t. 20, fig. 1 (1768) = ***Ipomoea nervosa*** (Burm.f.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia nitida* (Desr.) Choisy, non *Ipomoea nitida* Griseb. [= *Argyreia purpuricarpa* Elmer, Leaflet. Philipp. Bot. 5: 1766 (1913)] = ***Ipomoea purpuricarpa*** (Elmer) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia nuda* Ooststr., Blumea 5: 686 (1945), non *Ipomoea nuda* Peter = ***Ipomoea bunnemeyeri*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia oblongifolia* Ooststr., Blumea 5: 376 (1943), non *Ipomoea oblongifolia* (Hassl.) O'Donnell = ***Ipomoea kalimantanensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia obtusifolia* Lour., Fl. Cochinch. 1: 134 (1790) = ***Ipomoea obtusifolia*** (Lour.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia onilahiensis* Derooin, Candollea 48: 453 (1993) = ***Ipomoea onilahiensis*** (Derooin) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia ooststroomii* Hoogland, Blumea 7: 189 (1952) = ***Ipomoea ooststroomii*** (Hoogland) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia osyrensis* (Roth ex Roem. & Schult.) Choisy = ***Ipomoea osyrensis*** Roth ex Roem. & Schult., Syst. Veg. 4: 239 (1819)

*Argyreia paivae* A.R.Simões & P.Silveira, Blumea 56: 50 (2011) = ***Ipomoea paivae*** (A.R.Simões & P.Silveira) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia pallida* Choisy, Mém. Soc. Phys. Genève 6: 416 [Convolv. Orient.: 34] (1834), non *Ipomoea pallida* Santapau & V.Patel = ***Ipomoea burmannica*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia parviflora* (Ridl.) Ooststr.; basionym: *Lettsomia parviflora* Ridl. in Bull. Misc. Inform. Kew 1925: 86 (1925), non *Ipomoea parviflora* Vahl = ***Ipomoea subpeltata*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia paucinervia* Ooststr., Blumea 6: 347 (1950) = ***Ipomoea paucinervia*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia pedicellata* Ooststr. Blumea 5: 379 (1943) = ***Ipomoea pedicellata*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia penangiana* (Choisy) Boerl.; basionym: *Moorcroftia penangiana* Choisy in Mém. Soc. Phys. Genève 6: 432 [Convolv. Orient.: 50] (1834) = ***Ipomoea penangiana*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia philippinensis* (Merr.) Ooststr.; basionym: *Lettsomia philippinensis* Merr. in Philipp. J. Sci. 26: 488 (1925) = ***Ipomoea phiippinensis*** (Merr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia pierreana* Bois, Rev. Hort. (Paris) 78: 560 (1906) = ***Ipomoea pierreana*** (Bois) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia pilosa* Wight & Arn., Madras J. Lit. Sci. 5: 18 (1837), non *Ipomoea pilosa* Cav. = ***Ipomoea pilosula*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia popahensis* (Collett & Hemsl.) Staples = ***Ipomoea popahensis*** Collett & Hemsl., J. Linn. Soc., Bot. 28: 95 (1890)

*Argyreia pseudorubicunda* Ooststr., Blumea 7: 173 (1952) = ***Ipomoea pseudorubicunda*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia reinwardtiana* (Blume) Miq. = ***Ipomoea reinwardtiana*** Blume, Bijdr.: 720 (1826)

*Argyreia reticulata* (Prain) Hoogland; basionym: *Lettsomia penangiana* var. *reticulata* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 100 (1894), non *Ipomoea reticulata* O'Donell = ***Ipomoea hooglandii*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia reticulata* var. *microcalyx* Hoogland, Blumea 7: 191 (1952) = ***Ipomoea hooglandii*** J.R.I.Wood & Scotland var. ***microcalyx*** (Hoogland) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia ridleii* (Prain) Prain ex Ooststr.; basionym: *Lettsomia ridleii* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 98 (1894) = ***Ipomoea ridleii*** (Prain) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia robinsonii* (Ridl.) Ooststr.; basionym: *Lettsomia robinsonii* Ridl. in J. Fed. Malay States Mus. 8(4): 65 (1917), non *Ipomoea robinsonii* House = ***Ipomoea kerinciensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia roseopurpurea* (Kerr) Ooststr.; basionym: *Lettsomia roseopurpurea* Kerr in Bull. Misc. Inform. Kew 1941: 15 (1941) = ***Ipomoea roseopurpurea*** (Kerr) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia roxburghii* (Sweet) Choisy = ***Ipomoea roxburghii*** Sweet, Hort. Brit.: 289 (1826)

*Argyreia rubicunda* Choisy, Mém. Soc. Phys. Genève 6: 426 [Convolv. Orient.: 44] (1834) = ***Ipomoea rubicunda*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia samarensis* Ooststr., Blumea 6: 347 (1950) = ***Ipomoea samarensis*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia scortechinii* (Prain) Prain ex Hoogland; basionym: *Lettsomia scortechinii* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 98 (1894) = ***Ipomoea scortechinii*** (Prain) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia sericea* Dalzell in Dalzell & Gibson, Bombay Fl.: 169 (1861), non *Ipomoea sericea* (L.) Blume = ***Ipomoea concanica*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia setosa* (Roxb.) Sweet; basionym: *Lettsomia setosa* Roxb., Fl. Ind. 2: 80 (1824), non *Ipomoea setosa* Ker-Gawl. [incl. var. *minor*] = ***Ipomoea baccata*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia setosa* var. *minor* C.B.Clarke in Hook.f., Fl. Brit. India 4: 194 (1883) = ***Ipomoea baccata*** J.R.I.Wood & Scotland var. ***minor*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia siamensis* (Craib) Staples = ***Ipomoea siamensis*** Craib, Bull. Misc. Inform. Kew 1911: 424 (1911)

*Argyreia sikkimensis* (C.B.Clarke) Ooststr.; basionym: *Lettsomia sikkimensis* C.B.Clarke in Hook.f., Fl. Brit. India 4: 194 (1883) = ***Ipomoea sikkimensis*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia sorsogonensis* Ooststr. ex Staples & Traiperm, Taxon 66: 466 (2017) = ***Ipomoea sorsogonensis*** (Ooststr. ex Staples & Traiperm) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia sphaerocephala* (Prain) Prain ex Hoogland; basionym: *Lettsomia sphaerocephala* Prain, J. Asiat. Soc. Bengal., Pt. 2, Nat. Hist. 73(2): 19 (1904), non *Ipomoea sphaerocephala* D.Don = ***Ipomoea erythocephala*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia splendens* (Hornem.) Sweet [= *Lettsomia splendens* Roxb.] = ***Ipomoea splendens*** (Roxb.) Sims, Bot. Mag., 53: t. 2628 (1826) — authority uncertain

*Argyreia srinivasanii* Subba Rao & Kumari, Fl. Visakhapatnam Distr. (Andhra Pradesh) 1: 556 (2003) = ? ***Ipomoea pilosula*** J.R.I.Wood & Scotland

*Argyreia stenophylla* (Kerr) Staples & Traiperm; basionym: *Lettsomia stenophylla* Kerr in Bull. Misc. Inform. Kew 1941: 16 (1941), non *Ipomoea stenophylla* Meisn. = ***Ipomoea Chiangmaiensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia strigillosa* C.Y.Wu, Yunnan Trop. Subtrop. Fl. Res. Rep. 1: 133 (1965) = ***Ipomoea strigillosa*** (C.Y.Wu) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia suddeana* Traiperm & Staples, Phytotaxa 164: 281 (2014) = ***Ipomoea suddeana*** (Traiperm & Staples) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia sumbawana* Ooststr., Blumea 5: 362 (1943) = ***Ipomoea sumbawana*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia thomsonii* (C.B.Clarke) Craib ex C.R.Babu; basionym: *Lettsomia thomsonii* C.B.Clarke in Hook.f., Fl. Brit. India 4: 193 (1883) = ***Ipomoea thomsonii*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia thorelii* Gagnep., non *Ipomoea thorelii* Gagnep. = *Argyreia poilanei* Ooststr., Blumea 12: 39 (1963) = ***Ipomoea poilanei*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia thwaitesii* (C.B.Clarke) D.F.Austin in Dassanayake et al.; basionym: *Argyreia populifolia* var. *thwaitesii* C.B.Clarke in Hook.f., Fl. Brit. India 4: 187 (1883) = ***Ipomoea thwaitesii*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia tomentosa* Choisy, Mém. Soc. Phys. Genève 6: 426 [Convolv. Orient.: 44] (1834), non *Ipomoea tomentosa* Choisy = ***Ipomoea myanmarensis*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia vahibora* Derooin, Bull. Mus. Natl. Hist. Nat., B, Adansonia 13: 179 (1991) = ***Ipomoea vahibora*** (Derooin) J.R.I.Wood & Scotland *comb. nov.*

*Argyreia variabilis* Traiperm & Staples, Thai Forest Bull., Bot. 36: 98 (2008), non *Ipomoea variabilis* Choisy = ***Ipomoea traipermiae*** J.R.I.Wood & Scotland *nom. nov.*

*Argyreia velutina* C.Y.Wu, Trop. Subtrop. Fl. Res. Rep. 1: 129 (1965), non *Ipomoea velutina* R.Br. = ? ***Ipomoea fulvocymosa*** J.R.I.Wood & Scotland

*Argyreia venusta* Choisy, Mém. Soc. Phys. Genève 6: 419 [Convolv. Orient.: 37] (1834), non *Ipomoea venusta* (M.Martens & Galeotti) Godm. & Salvin = ***Ipomoea formosa*** J.R.I.Wood & Scotland *nom. nov.*



- Argyreia versicolor* (Kerr) Staples & Traiperm; basionym: *Lettsomia versicolor* Kerr, Bull. Misc. Inform. Kew 1941: 17 (1941), non *Ipomoea versicolor* Meisn. = ***Ipomoea enigmatica*** J.R.I.Wood & Scotland *nom. nov.*
- Argyreia wallichii* Choisy, Mém. Soc. Phys. Genève 6: 421 [Convolv. Orient.: 39] (1834), non *Ipomoea wallichii* Steud. = ***Ipomoea staplesii*** J.R.I.Wood & Scotland *nom. nov.*
- Argyreia wallichii* var. *coriacea* C.B.Clarke in Hook.f., Fl. Brit. India 4: 187 (1883) = ***Ipomoea staplesii*** J.R.I.Wood & Scotland var. ***coriacea*** (C.B.Clarke) J.R.I.Wood & Scotland *comb. nov.*
- Argyreia walshae* Ooststr., Blumea 5: 361 (1943) = ***Ipomoea walshiae*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*
- Argyreia zeylanica* (Gaertn.) Voigt. = ***Ipomoea zeylanica*** Gaertn., Fruct. Sem. Pl. 2: t. 178 [fig. 1] (1791)
- Astripomoea cephalantha* (Hallier f.) Verdc.; basionym: *Astrochlaena cephalantha* Hallier f., Bot. Jahrb. Syst. 18: 122 (1893), non *I. cephalantha* Baker = ***Ipomoea mwanzae*** J.R.I.Wood & Scotland *nom. nov.*
- Astripomoea delamereana* (Rendle) Verdc.; basionym: *Astrochlaena delamereana* Rendle, J. Bot. 39: 60 (1901) = ***Ipomoea delamereana*** (Rendle) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea grantii* (Rendle) Verdc., non *I. grantii* Oliv. [= *Astrochlaena ugandensis* Rendle, Fl. Trop. Africa 4(2): 124 (1905)] = ***Ipomoea ugandensis*** (Rendle) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea hyoscyamoides* (Vatke) Verdc.; basionym: *Convolvulus hyoscyamoides* Vatke, Linnaea 43: 520 (1882) = ***Ipomoea hyoscyamoides*** (Vatke) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea hyoscyamoides* var. *melandrioides* (Haller f.) Verdc.; basionym: *Astrochlaena melandrioides* Hallier f., Bot. Jahrb. Syst. 18: 122 (1893) = ***Ipomoea hyoscyamoides*** (Vatke) Verdc. var. ***melandrioides*** (Haller f.) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea lachnosperma* (Choisy) A.Meeuse = ***Ipomoea lachnosperma*** Choisy, Prodr., 9: 356 (1845)
- Astripomoea longituba* Verdc., Kew Bull. 14: 337 (1960), non *I. longituba* Hallier f. = ***Ipomoea kenyensis*** J.R.I.Wood & Scotland *nom. nov.*
- Astripomoea malvacea* (Klotzsch) A.Meeuse; basionym: *Breweria malvacea* Klotzsch in Peters, Reise Mossamb. Bot.: 245 (1861) = ***Ipomoea malvacea*** (Klotzsch) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea malvacea* var. *ependunculata* (Rendle) Verdc.; basionym: *Astrochlaena malvacea* var. *ependunculata* Rendle, J. Bot. 39: 59 (1901) = ***Ipomoea malvacea*** var. ***ependunculata*** (Rendle) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea malvacea* var. *floccosa* (Vatke) Verdc.; basionym: *Ipomoea floccosa* Vatke, Linnaea 43: 512 (1882) = ***Ipomoea malvacea*** var. ***floccosa*** (Vatke) J.R.I.Wood & Scotland *comb. nov.*
- Astripomoea malvacea* var. *involuta* (Rendle) Verdc.; basionym: *Astrochlaena involuta* Rendle, J. Bot. 39: 59 (1901) = ***Ipomoea malvacea*** var. ***involuta*** (Rendle) J.R.I.Wood & Scotland *comb. nov.*

*Astripomoea malvacea* var. *parviflora* (Rendle) Staples; basionym *Astrochlaena stuhlmannii* var. *parviflora* Rendle, Fl. Trop. Afr. 4(2): 122 (1905) = ***Ipomoea malvacea*** var. ***parviflora*** (Rendle) J.R.I.Wood & Scotland *comb. nov.*

*Astripomoea malvacea* var. *volkensis* (Dammer) Verdc.; basionym: *Astrochlaena volkensis* Dammer, Pflanzenw. Ost-Afrikas C: 331 (1895) = ***Ipomoea malvacea*** var. ***volkensis*** (Dammer) J.R.I.Wood & Scotland *comb. nov.*

*Astripomoea nogalensis* (Chiov.) Verdc.; basionym: *Astrochlaena nogalensis* Chiov., Fl. Somala 1: 236 (1929) = ***Ipomoea nogalensis*** (Chiov.) J.R.I.Wood & Scotland *comb. nov.*

*Astripomoea polycephala* (Hallier f.) Verdc.; basionym: *Astrochlaena polycephala* Hallier f., Bot. Jahrb. Syst. 18: 122 (1893) = ***Ipomoea polycephala*** (Hallier f.) J.R.I.Wood & Scotland *comb. nov.*

*Astripomoea procera* Thulin, Nordic J. Bot. 23(5): 631 (2005) = ***Ipomoea procera*** (Thulin) J.R.I.Wood & Scotland *comb. nov.*

*Astripomoea rotundata* (Pilg.) A.Meeuse; basionym: *Astrochlaena rotundata* Pilg., Bot. Jahrb. Syst. 45: 222 (1910), non *I. rotundata* Verdc. = ***Ipomoea meeusei*** J.R.I.Wood & Scotland *nom. nov.*

*Astripomoea tubiflora* (Hallier f.) Verdc.; basionym: *Astrochlaena tubiflora* Hallier f., Ann. Ist. Bot. Roma 7: 228 (1898), non *I. tubiflora* Hook.f. = ***Ipomoea rivae*** J.R.I.Wood & Scotland *nom. nov.*

*Blinkworthia convolvuloides* Prain, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 63(2): 91 (1894), non *I. convolvuloides* Hallier f. = ***Ipomoea blinkworthii*** J.R.I.Wood & Scotland *nom. nov.*

*Blinkworthia discostigma* Hand.-Mazz., Sinesia 2: 6 (1931) = ***Ipomoea discostigma*** (Hand.-Mazz.) J.R.I.Wood & Scotland *comb. nov.*

*Blinkworthia lycioides* Choisy, Mém. Soc. Phys. Genève 6: 430 [Convolv. Orient.: 48] (1834), = ***Ipomoea lycioides*** (Choisy) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon binectarifer* (Wall.) Kuntze; basionym: *Convolvulus binectariferus* Wall, Fl. Ind. [Carey & Wallich] ed. 2: 47 (1824) = ***Ipomoea binectarifera*** (Wall.) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon binectarifer* var. *borneensis* Ooststr., Blumea 5: 343 (1943) = ***Ipomoea binectarifera*** var. ***borneensis*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon binectarifer* var. *eymae* Ooststr., Fl. Males., Ser. 1, Spermat. 4: 490 (1953) = ***Ipomoea binectarifera*** var. ***eymae*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon binectarifer* var. *glaber* T.N.Nguyen, J. Biol. (Vietnam) 7: 41 (1985) = ***Ipomoea binectarifera*** var. ***glabra*** (T.N.Nguyen) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon binectarifer* var. *taynguyenensis* T.N.Nguyen, J. Biol. (Vietnam) 7: 41 (1985) = ***Ipomoea binectarifera*** var. ***taynguyenensis*** (T.N.Nguyen) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon binectarifer* var. *trichocarpus* (Gagnep.) Ooststr.; basionym: *Lepistemon trichocarpus* Gagnep., Notul. Syst. (Paris) 3: 152 (1915) = ***Ipomoea binectarifera*** var. ***trichocarpa*** (Gagnep.) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon intermedius* Hallier f., Bot. Jahrb. Syst. 28: 31 (1899), non *Ipomoea intermedia* Schult. = ***Ipomoea sinica*** J.R.I.Wood & Scotland *nom. nov.*

*Lepistemon leiocalyx* Stapf, Bull. Misc. Inf. Kew 1895: 100 (1895) = ***Ipomoea leiocalyx*** (Stapf) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemon owariensis* (P.Beauv.) Hallier f. = ***Ipomoea owariensis*** P.Beauv., Flore d'Oware, 2: 41, t. 82 (1816)

*Lepistemon parviflorum* Pilg., Bot. Jahrb. Syst. 45: 219 (1910), non *I. parviflora* Vahl = ***Ipomoea pilgeri*** J.R.I.Wood & Scotland *nom. nov.*

*Lepistemon urceolatum* (R.Br.) F.Muell. = ***Ipomoea urceolata*** R.Br. Prodr. Fl. Nov. Holland. 485 (1810)

*Lepistemon verdcourtii* P.Mathew & Biju, Kew Bull. 46: 560 (1991) = ***Ipomoea verdcourtii*** (P.Mathew & Biju) J.R.I.Wood & Scotland *comb. nov.*

*Lepistemonopsis volkensis* Dammer, Pflanzenw. Ost-Afrikas C: 331 (1895) = ***Ipomoea volkensis*** (Dammer) J.R.I.Wood & Scotland *comb. nov.*

*Paralepistemon curtoi* (Rendle) Lejoly & Lisowski = ***Ipomoea curtoi*** Rendle, J. Bot. 46: 183 (1908)

*Rivea hypocrateriformis* (Desr.) Choisy; basionym: *Convolvulus crateriformis* Desr., Encycl. [J. Lamarck et al.] 3(2): 561 (1792) = ***Ipomoea hypocrateriformis*** (Desr.) J.R.I.Wood & Scotland *comb. nov.*

*Rivea ornata* (Roxb.) Choisy; basionym: *Lettsomia ornata* Roxb. Fl. Ind. 2: 86 (1824) = ***Ipomoea ornata*** (Roxb.) J.R.I.Wood & Scotland *comb. nov.*

*Rivea wightiana* R.R.Mill, Edinburgh J. Bot. 53: 241 (1996) = ***Ipomoea wightiana*** (R.R.Mill) J.R.I.Wood & Scotland *comb. nov.*

*Stictocardia beraviensis* (Vatke) Hallier f. = ***Ipomoea beraviensis*** Vatke, Linnaea, 43: 514 (1882)

*Stictocardia cordatosepala* Ooststr., Blumea 5: 351 (1943), non *I. cordatosepala* Britten = ***Ipomoea lombokii*** J.R.I.Wood & Scotland *nom. nov.*

*Stictocardia discolor* Ooststr., Blumea 5: 350 (1943), non *I. discolor* Kunth = ***Ipomoea orientalis*** J.R.I.Wood & Scotland *nom. nov.*

*Stictocardia incompta* [incompta] (Hallier f.) Hallier f. = ***Ipomoea incompta*** Hallier f., Bot. Jahrb. Syst. 18: 151 (1893)

*Stictocardia jucunda* (Thwaites) C.R.Gunn = ***Ipomoea jucunda*** Thwaites, Enum. Pl. Zey.: 211 (1864)

*Stictocardia laxiflora* (Baker) Hallier f., non *Ipomoea laxiflora* H.J.Chowdhery & Debta = ***Ipomoea buchananii*** Baker, Bull. Misc. Inf. Kew 1894: 73 (1894)

*Stictocardia laxiflora* var. *woodii* (N.E.Br.) Verdc.; basionym: *Ipomoea woodii* N.E. Br., Bull. Misc. Inf. Kew 1894: 101 (1894) = ***Ipomoea buchananii*** var. *woodii* (N.E.Br.) J.R.I.Wood & Scotland *comb. nov.*

*Stictocardia lutambensis* (Schulze-Menz) Verdc. = ***Ipomoea lutambensis*** Schulze-Menz, Notizbl. Bot. Gart. Berlin-Dahlem 14: 111 (1938)

*Stictocardia macalusoi* (Mattei) Verdc. = ***Ipomoea macalusoi*** Mattei, Boll. Reale Orto Bot. Giardino Colon. Palermo 7: 106 (1908)

*Stictocardia mojangensis* (Vatke) D.F.Austin & E.Eich = ***Ipomoea mojangensis*** Vatke, Linnaea 43: 515 (1882)

*Stictocardia neglecta* Ooststr., Blumea 5: 348 (1943) = ***Ipomoea neglecta*** (Ooststr.) J.R.I.Wood & Scotland *comb. nov.*

*Stictocardia queenslandica* (Domin) R.W.Johnson; basionym: *Argyreia queenslandica* Domin, Biblioth. Bot. 89: 533 (1928) = ***Ipomoea queenslandica*** (Domin) J.R.I.Wood & Scotland *comb. nov.*

*Stictocardia sivarajanii* Biju, Pushp. & P.Mathew, Novon 9: 147 (1999) = ***Ipomoea sivarajanii*** (Biju, Pushp. & P.Mathew) J.R.I.Wood & Scotland *comb. nov.*

*Stictocardia tiliifolia* (Desr.) Hallier f. = ***Ipomoea tiliifolia*** (Desr.) Roem. & Schult., Syst. Veg., ed. 15 bis, 4: 229 (1819).

*Stictocardia tiliifolia* subsp. *marquesensis* Staples & Butaud, Phytologia 98(3): 204 (2016) = ***Ipomoea tiliifolia*** subsp. *marquesensis* (Staples & Butaud) J.R.I.Wood & Scotland *comb. nov.*

*Turbina abutiloides* (Kunth) O'Donell = ***Ipomoea abutiloides*** (Kunth) G.Don, Gen. Hist. 4: 273 (1838)

*Turbina amazonica* D.F.Austin & Staples = ***Ipomoea amazonica*** (D.F.Austin & Staples) J.R.I.Wood & Scotland, Kew. Bull. 70(31): 27 (2015)

*Turbina bracteata* Deroin, Bull. Mus. Natl. Hist. Nat. B, Adanonia Sér. 4, 14: 342 (1993), non *I. bracteata* Cav. = ***Ipomoea porphyrea*** J.R.I.Wood & Scotland *nom. nov.*

*Turbina cordata* (Choisy) D.F.Austin & Staples, non *Ipomoea cordata* L.B.Sm. & B.G.Schub. = ***Ipomoea sericosepala*** J.R.I.Wood & Scotland, Kew. Bull. 70(31): 21 (2015)

*Turbina corymbosa* (L.) Raf. = ***Ipomoea corymbosa*** (L.) Roth ex Roem. & Schult., Syst. Veg., ed. 15 bis, 4: 232 (1819)

*Turbina holubii* (Baker) A.Meeuse = ***Ipomoea holubii*** Baker, Bull. Misc. Inf., Kew 1894: 72 (1894)

*Turbina inopinata* Heine, Fl. Nouv.-Calédonie & Dépend. 13: 86 (1984) = ***Ipomoea inopinata*** (Heine) J.R.I.Wood & Scotland *comb. nov.*

*Turbina longiflora* Verdc., Kirkia 6: 121 (1967), non *I. longiflora* Willd. = ***Ipomoea mozambicensis*** J.R.I.Wood & Scotland *nom. nov.*

*Turbina oblongata* (E.Mey. ex Choisy) A.Meeuse = ***Ipomoea oblongata*** E.Mey. ex Choisy, Prodr. [A.P. de Candolle] 9: 368 (1845)

*Turbina oenotheroides* (L.f.) A.Meeuse; basionym: *Convolvulus oenotheroides* L.f., Suppl. Pl. 157 (1782) = ***Ipomoea oenotheroides*** (L.f.) A.Meeuse & Welman

*Turbina perbella* Verdc., Webbia 13: 328 (1958) = ***Ipomoea perbella*** (Verdc.) J.R.I.Wood & Scotland *comb. nov.*

*Turbina racemosa* (Poir.) D.F.Austin = ***Ipomoea racemosa*** Poir., Encycl., Suppl. 4: 633 (1816)

*Turbina robertsiana* (Rendle) A.Meeuse = ***Ipomoea robertsiana*** Rendle, J. Bot. 39: 18 (1901)

*Turbina shirensis* (Oliv.) A.Meeuse = *Paralepistemon shirensis* (Oliv.) Lejoly & Lisowski = ***Ipomoea shirensis*** Oliv., Icon. Pl.: t. 1474 (1884)

*Turbina stenosphon* (Hallier f.) A.Meeuse = ***Ipomoea stenosphon*** Hallier f., Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 107(1): 50 (1898)

*Turbina stenosphon* var. *pubescens* Verdc., Kew Bull. 13: 217 (1958) = ***Ipomoea stenosphon*** var. ***pubescens*** (Verdc.) J.R.I.Wood & Scotland *comb. nov.*

*T. suffruticosa* (Burch.) A.Meeuse = ***Ipomoea suffruticosa*** Burch., Trav. S. Africa 2: 226 (1824)

## SECTION 5 | TIME-CALIBRATED PHYLOGENIES

### A. DIVERGENCE TIME ESTIMATES

With the calibration strategy that uses *Physalis infinemundi*<sup>77</sup>, the mean posterior estimate (MPE) for the *Ipomoea* crown node is 19.4 MYRs. With the calibration strategy that uses the secondary calibration from Magallon and colleagues<sup>80</sup>, the MPE is 8.4 MYRs. We use these age estimates for the entirety of *Ipomoea* to calibrate the root node of our nuclear and chloroplast *Ipomoea* phylogenies and infer age estimates for clades within *Ipomoea*.

For our discussion (see below) of the effects of among-branch-rate-variation on divergence time estimates within *Ipomoea*, and its implications for inferring patterns of diversification-rate-variation, we refer only to the case where the root node is calibrated to 19.4 MYRs. We do not compare the effects of the two calibration strategies because neither is applied to nodes within *Ipomoea*. The two strategies will therefore only affect divergence time estimates for the entire genus, and not the relative ages of clades within the genus (unlike among-branch-rate-variation, which affects the inferred duration of individual branches and thus the relative ages of different clades). By extension, this means that the alternative calibration strategies will not affect inferred patterns of diversification-rate-variation within the genus. By contrast, in our discussion of the origin of the sweet potato (see main text), we refer to the case where the root node is calibrated to 8.4 MYRs. This calibration strategy leads to younger divergence time estimates within *Ipomoea*, providing the most robust test of whether the sweet potato evolved in pre-human times.

When inferring divergence times within *Ipomoea* in our nuclear and chloroplast phylogenies, we used a range of smoothing values (spanning six orders of magnitude) that differed from the optimum values inferred in cross-validation analyses (0.01 for the nuclear data and 10000 for the chloroplast data). In treePL<sup>84</sup>, a higher smoothing value means that rate differences between branches are penalised to a greater extent. By using different smoothing values, we can therefore evaluate how assumptions about among-branch-rate-variation affect divergence time estimates (high smoothing values assume less among-branch-rate-variation than low smoothing values). This is important because among-branch-rate-variation cannot be directly inferred from molecular sequence data. Analyses may therefore be highly sensitive to underlying assumptions.

For the nuclear data, divergence time estimates are fairly insensitive to the smoothing value, although inferred ages are slightly older with 0.01 —the optimum smoothing value (Supplementary Table 3). For the chloroplast data, divergence time estimates are considerably younger with the two higher smoothing values (100 and 10000) than the two lower smoothing values (0.01 and 1) (Supplementary Table 4).

There are several differences between age estimates inferred with chloroplast data compared to nuclear data. One of the most consistent differences is that the old world clade is younger with the chloroplast data than with the nuclear data, regardless of the smoothing value (Supplementary Tables 3 and 4). These differences are likely to result from the different patterns of among-branch-rate-variation in the chloroplast and nuclear datasets and topological differences between the chloroplast and nuclear phylogenies.

The approach taken here – comparing different smoothing values and different datasets – is designed to evaluate the extent to which uncertainty or error in divergence time estimates

is sensitive to assumptions about among-branch-rate-variation. Bayesian analyses – and the 95% HPD intervals they generate – are often advocated as a useful framework for accounting for this uncertainty. However, in order to implement relaxed clock methods in a Bayesian framework, a tree prior is used that assumes branching events occur at a constant rate over time. In our *Ipomoea* phylogeny, this assumption is likely to be violated. Given the size of our *Ipomoea* phylogeny, and the fact that there is no other information about the timescale of *Ipomoea* evolution with which to constrain our analysis, violation of this assumption may significantly bias divergence time estimates, including 95% HPD intervals. Further, Bayesian analyses are highly computationally intensive. It would be challenging to compare divergence times in our two large datasets using the variety of different assumptions that we compare here.

TreePL explicitly assumes that rates are inherited between ancestral and descendent branches. Therefore, our analyses are performed within the same methodological framework and will not explore all potential patterns of among-branch-rate-variation. Among-branch-rate-variation may therefore lead to error or uncertainty in divergence time estimates that is not accounted for here. However, all analyses that incorporate among-branch-rate-variation are necessarily limited in scope or rely on arbitrary assumptions (as outlined above in Bayesian analyses). This is because the extent of among-branch-rate-variation cannot be inferred directly from molecular sequence data. Our analyses therefore represent the most thorough evaluation possible of how among-branch-rate-variation affects divergence time estimates.

## B. DIVERSIFICATION RATE ESTIMATION

Estimates of relative clade ages directly affect inferences of diversification rate variation. We therefore inferred diversification rates in BAMM, with the time-calibrated phylogenies outlined above that use different smoothing values. We could therefore evaluate how inferences about diversification rate variation are sensitive to uncertainty and error in estimates of relative clade ages.

Extended Data Fig. 4 summarises diversification rates for nuclear time-calibrated phylogenies inferred with smoothing parameters that differ from the optimum smoothing value. This figure shows that regardless of the smoothing value, a single diversification rate increase at the origin of the diverse South American and Central American clades has by far the highest posterior probability (alternative positions for rate shifts with posterior probabilities greater than 0.05 are indicated with blue arrows).

Extended Data Fig. 5 summarises diversification rates for a chloroplast time-calibrated phylogeny inferred with the optimum smoothing value (10000). A single rate increase at the origin of the diverse South American clade has a posterior probability of 0.79. Two alternative patterns of diversification-rate-variation, with rate increases on more ancestral branches (blue and green arrows in Extended Data Fig. 5) have posterior probabilities of 0.11 and 0.0058 respectively. The Central American clade is not associated with a diversification rate increase in this analysis. This likely stems from the different topology between the nuclear and chloroplast phylogeny. Unlike in the nuclear phylogeny, the diverse Central American and South American clades are not sister taxa in the chloroplast phylogeny.

We also estimated diversification rates in chloroplast phylogenies inferred with alternative smoothing values (Extended Data Fig. 6). These show that a single rate shift at or

near the origin of the diverse South American clade has the highest posterior probability – apart from when a smoothing value of 0.01 is used.

## SUPPLEMENTARY TABLES

**Supplementary Table 1** | Species of *Ipomoea* with storage roots\*. Bold indicates species with edible roots. Numbers indicate references in the Supplementary Reference list.

<i>Ipomoea acutisepala</i> <sup>103</sup>	<i>I. macrorrhiza</i> <sup>104</sup>
<b><i>I. albivenia</i></b> <sup>105,106</sup>	<i>I. madrensis</i> <sup>107,108</sup>
<i>I. alpina</i> <sup>13,109</sup>	<i>I. malpighipila</i> <sup>103</sup>
<i>I. ampullacea</i> <sup>107</sup>	<i>I. maurandioides</i> <sup>110</sup>
<i>I. ana-mariae</i> <sup>111</sup>	<b><i>I. mauritiana</i></b> <sup>112,113,#</sup>
<i>I. ancisa</i> <sup>114</sup>	<i>I. muricata</i> <sup>115</sup>
<i>I. argillicola</i> <sup>116</sup>	<i>I. oenotherae</i> <sup>117</sup>
<b><i>I. batatas</i></b> <sup>107,#</sup>	<i>I. orizabensis</i> <sup>114</sup>
<b><i>I. bolusiana</i></b> <sup>106,117,118</sup>	<i>I. pandurata</i> <sup>119</sup>
<i>I. bonariensis</i> <sup>110</sup>	<i>I. pedicellaris</i> <sup>107</sup>
<b><i>I. bracteata</i></b> <sup>107,115</sup>	<i>I. pinto</i> <sup>111</sup>
<b><i>I. cairica</i></b> <sup>120,121</sup>	<i>I. platensis</i> <sup>110</sup>
<i>I. capillacea</i> <sup>107,108,115</sup>	<b><i>I. plummerae</i></b> <sup>107,108,122</sup>
<b><i>I. conzatii</i></b> <sup>123</sup>	<b><i>I. polpha</i></b> <sup>116</sup>
<i>I. descolei</i> <sup>110</sup>	<i>I. pubescens</i> <sup>107,110,124</sup>
<i>I. elongata</i> <sup>125</sup>	<i>I. purga</i> <sup>125–127</sup>
<i>I. funicularis</i> <sup>128</sup>	<i>I. repanda</i> <sup>113</sup>
<b><i>I. graniticola</i></b> <sup>#</sup>	<i>I. rupestris</i> <sup>111</sup>
<i>I. hieronymi</i> <sup>110</sup>	<i>I. schulziana</i> <sup>110</sup>
<i>I. hirsutissima</i> <sup>23,#</sup>	<b><i>I. serrana</i></b> <sup>111</sup>
<i>I. holubii</i> <sup>118</sup>	<i>I. sescossiana</i> <sup>107,114</sup>
<i>I. inaccessa</i> <sup>24</sup>	<i>I. simulans</i> <sup>125,127</sup>
<i>I. jalapa</i> <sup>126</sup>	<b><i>I. stans</i></b> <sup>114,129</sup>
<b><i>I. jicama</i></b> <sup>125,130</sup>	<i>I. stuckertii</i> <sup>110</sup>
<i>I. jujuyensis</i> <sup>110</sup>	<i>I. subspicata</i> <sup>103</sup>
<i>I. lanuginosa</i> <sup>110</sup>	<i>I. tastensis</i> <sup>125</sup>
<b><i>I. leptophylla</i></b> <sup>129</sup>	<i>I. tenuiloba</i> <sup>107,108,122</sup>
<i>I. lilloana</i> <sup>110,#</sup>	<i>I. thurberi</i> <sup>107,122</sup>
<i>I. lindheimeri</i> <sup>124</sup>	<i>I. tolmerana</i> <sup>128</sup>
<i>I. longiflora</i> <sup>107</sup>	<i>I. volcanensis</i> <sup>110</sup>
<i>I. longifolia</i> <sup>107</sup>	<i>I. welwitschii</i> <sup>17</sup>
<i>I. longistaminea</i> <sup>111</sup>	

\*In addition to these species, *I. jacalana*, *I. laeta*, *I. parasitica*, *I. scopulorum* and *I. violacea* are cited by some authors as having enlarged roots, but this information is not clear and needs confirmation.

# Personal observation.



**Supplementary Table 2** | Morphological traits that are useful to distinguish species in *Ipomoea*.

TRAIT	DESCRIPTION
<b>Habit</b>	Annual v perennial; herb v. liana; liana v. tree; Erect v. climbing or trailing (trailing is intermediate and not very useful diagnostically)
<b>Leaf form</b>	Although many species have variable leaf shapes, many do not and the variation that takes place is only within a certain range. The shape of the base, apex and margin may all be useful and are more or less constant within a species (Note cuneate-rounded-truncate-shallowly cordate-cordate-sagittate intergrade so the important distinctions are not from adjacent states but more distant ones, thus cuneate v. cordate is probably diagnostic whereas truncate-shallowly cordate is probably not)
<b>Indumentum</b>	Again, to be treated with caution as many species have a glabrous or hirsute form but the hair type is often diagnostic as is the density. Many species are characteristically glabrous, sericeous or tomentose and this is readily recognizable. See <i>descolei</i> , <i>syringiifolia</i> , <i>argentinica</i> , <i>sericosepala</i> etc.
<b>Peduncle</b>	Absence, short or long
<b>Bracteoles</b>	Caducous or persistent; linear or expanded. Expanded and persistent usually correlate.
<b>Pedicels</b>	Absence, short or long
<b>Inflorescence</b>	Flowers solitary, in cymes, compounded cymes or raceme- or corymb-like structures. Difficult to define, somewhat variable and may be reduced but a distinctive inflorescence is highly characteristic of many species
<b>Sepals</b>	The most distinctive and variable of all characters. Note size, shape and texture external and internal indumentum, presence of appendages, glands, murication, ribs etc, difference in size and form between inner and outer, apex, margin. Accrescence in fruit and persistence
<b>Corolla</b>	Shape, colour (beware albino forms and colour change during the drying process), external indumentum (best seen in bud). Size is useful but to be treated with caution and needs to be based on a range of specimens. The lobing of the corolla limb (or its absence) is also diagnostic in a number of species
<b>Capsule shape and size</b>	Rounded to conical, sometimes rostrate, recurved capsules in fruit.
<b>Seeds</b>	Varied in shape. Usually smooth, glabrous, minutely tomentellous or pubescent, most commonly with long marginal hairs; sometimes dimorphic hairs, sometimes woolly. BEWARE: long marginal hairs can be caducous, leaving a glabrous capsule.

**Supplementary Table 3** | Inferred ages (millions of years) for major clades within *Ipomoea* using TreePL and the nuclear dataset.

Clade	Smoothing			
	<b>0.01*</b>	<b>1</b>	<b>100</b>	<b>10000</b>
<b>A</b>	10.6	9.1	9.1	9.1
<b>B</b>	10.5	10.5	10.5	10.5
<b>C</b>	11.0	9.1	9.1	9.1
<b>D</b>	10.3	9.2	9.2	9.2
<b>E</b>	14.4	13.5	13.4	13.4
<b>Incl. Astripomoea</b>	13.3	13.7	13.7	14.0
<b>Old World</b>	18.0	17.5	17.5	17.5

**Supplementary Table 4** | Inferred ages (millions of years) for major clades within *Ipomoea* using TreePL and the chloroplast dataset.

Clade	Smoothing			
	0.01	1	100	10000*
<b>A</b>	13.6	13.6	9.5	9.5
<b>B</b>	14.5	14.5	11.3	11.3
<b>C</b>	12.7	12.2	5.8	5.7
<b>D</b>	12.2	11.8	8.7	8.7
<b>E</b>	14.8	14.7	11.5	11.5
<b>Incl. Astripomoea</b>	13.0	12.5	12.3	12.3
<b>Old World</b>	16.8	15.8	13.5	13.4

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