A taxonomic monograph of *Ipomoea* integrated across phylogenetic scales

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ABSTRACT

Taxonomic monographs have the potential to make a unique contribution to understanding global biodiversity. However, such studies, now rare, are often considered too daunting to undertake within a realistic timeframe, especially as the world's collections have doubled in size in recent times. Here, we report a global-scale monographic study of morning glories (*Ipomoea*) that integrated DNA barcodes and high-throughput sequencing with the morphological study of herbarium specimens. Our approach overhauled the taxonomy of this megadiverse group, described 63 new species and uncovered significant increases in net diversification rates comparable to the most iconic evolutionary radiations in the plant kingdom. Finally, we show that more than 60 species of *Ipomoea*, including sweet potato, independently evolved storage roots in pre-human times, indicating that the storage root is not solely a product of human domestication but a trait that predisposed the species for cultivation. This study demonstrates how the world's natural history collections can contribute to global challenges in the Anthropocene.

INTRODUCTION

When Joseph Banks and Daniel Solander travelled with Captain Cook on the *Endeavour* in 1768, the plants they collected were new species to science[1]. Similarly, when Robert Brown sailed to Australia in 1801, he too discovered and described a completely new flora with many new species[2]. More than 200 years later, however, the task of deciding whether a specimen represents a new species has become much more difficult because taxonomists need to work through the large number of specimens held in natural history collections, a number which has doubled since 1960[3], and a massive accumulation of literature. The provisional nature of species curation adds to these difficulties, reflecting the fact that species-level taxonomy is incomplete and unsatisfactory for many taxa, especially insects and tropical plants[3]. These difficulties come at a time when improved taxonomic

knowledge is an urgent priority for policy makers[4], environmental scientists[5] and museum directors[6] throughout the world. The Global Strategy for Plant Conservation, for example, seeks to assess the conservation status of all plant species by 2020, but at present less than 25% of plant species have been assessed[7], largely because of incomplete taxonomic information[8]. Many suggestions have been made to enhance the accuracy, speed, accessibility and relevance of taxonomy[9,5,10–14]; but, nevertheless, the pace of flowering plant taxonomy has remained unchanged for the last 30 years[15]. Finding ways to address these substantial issues in a realistic timeframe is a recurring challenge[4].

Much existing taxonomy is inaccurate because it is essentially country- or region-based and inevitably depends on limited specimen sampling[16]. The choice of a particular geographical area to document species is a pragmatic decision and reflects national priorities and funding constraints as well as the interests of policy makers and taxonomists who are focussed on the plants and animals of their region. However, species are often widely distributed with the result that the same species may be described on multiple occasions from different countries under different names (synonymy). Over time, issues of synonymy, when combined with misidentification and poor species level sampling[3,10] result in many tropical plants being so poorly known that they are invisible to modern ecological and conservation tools[8]. Furthermore, when existing taxonomy is so provisional, determining whether potential new species are different from existing species is highly problematic with the consequence that half the world's natural history collections are incorrectly named[3]. An urgent priority is, therefore, to tackle the taxonomy of tropical plants from a global perspective.

DNA taxonomy was proposed 15 years ago as an alternative to morphology-based taxonomy[17,18], which was dismissed as slow and over-reliant on a dwindling number of experts[9]. Since then, DNA has played an increasingly important role in phylogeny reconstruction and higher-level classifications of major lineages[19,20], as well as in

identification of existing species[21,22], but it is only being used in an auxiliary capacity[18], if at all, for taxonomic revisions and monographs. Studies integrating DNA and morphology are few and tend to avoid species-rich tropical groups where the greatest taxonomic problems lie[7]. Furthermore, there is no consensus on how DNA sequence data can be best used to solve taxonomic problems at the species level.

This paper describes the integration of molecular phylogenetics with the morphological study of living plants and herbarium collections to produce a taxonomic study of the megadiverse genus *Ipomoea* L. (Convolvulaceae) —with an emphasis on the 423 species described from the American continent. In parallel to the morphological study of herbarium specimens from 72 European and American institutions, we sequenced DNA from 1,560 of those specimens for several DNA barcodes. We also sequenced a subset of 384 samples, representing 211 species, for the whole chloroplast genome and 605 putative single copy nuclear regions using Hyb-Seq[23] (Fig. 1). Integrating these two complementary sequencing strategies alongside a comprehensive morphological study enabled us to exploit the resources found in natural history collections and contribute to a diverse range of contemporary issues, including the origin of a major crop, the temporal and spatial dynamics of how the New World tropical flora was assembled, and the discovery of a substantial number of new species.

TACKLING MEGADIVERSE GROUPS ON A GLOBAL SCALE

Present in all tropical and subtropical regions of the world, *Ipomoea* is among the largest genera of plants[24]. The taxonomic knowledge of the genus at the beginning of our project, in 2012, was relatively poor. The extensive literature and the existing taxonomy contained as much error as valuable information, reflected in the fact that more than 50% of *Ipomoea* names in GBIF, assigned to over 40,000 plant specimen records, are not currently accepted (Supplementary Data File 1). Given this unsatisfactory situation, simple tasks such

as identifying specimens, enumerating species from a particular country or preparing conservation assessments were problematic.

We based our approach to this comprehensive study of *Ipomoea* on the experience we had gained from a previous Foundation Monograph of *Convolvulus*[25]. We began our work by preparing a working checklist of all recognised species of *Ipomoea* (Supplementary Methods, Section 1) together with their commoner synonyms and their approximate distribution. Based on the distribution of individual species and their authors, we were able to predict which herbaria were likely to hold important collections of *Ipomoea*, including type specimens (Supplementary Methods, Sections 2 and 3). With a minimum estimate of 200,000 specimens of *Ipomoea* in the world's herbaria (Supplementary Methods, Section 2), obtaining all specimens on loan was neither practical nor necessary. Fortunately, we had ready access to large collections of *Ipomoea* at Kew Gardens (K) and the Natural History Museum in London (BM). By combining the study of specimens at these institutions with images in virtual herbaria and the insights of previous taxonomists (Supplementary Methods, Sections 3 and 4), we were able to determine important and useful taxonomic characters and thus begin to delimit species (Supplementary Methods, Section 5).

From the outset of the project, we aimed to integrate molecular and morphological data at all stages of the taxonomic process, each kind of data providing reciprocal illumination for many taxonomic decisions (Fig. 2).

Our approach was based on the idea that higher confidence for each species hypothesis is achieved when morphology and DNA barcodes —and genomic data when available— correlate, corroborating a species hypothesis. With this aim, and in parallel to our morphological studies, we started sequencing three DNA barcodes (nuclear *ITS* and chloroplast *matK* and *rbcL* regions) from specimens available to us from our own collections, from K and BM, an additional 45 other herbaria and individual sources (Supplementary

Methods, Sections 6–8) (Extended Data Fig. 1) (Supplementary Data File 2). Our aim was to include, when possible, several specimens of every species in the phylogenies, as well as un-named specimens or specimens that we considered, from our morphological studies, to be interesting or puzzling. From this extensive sampling strategy, we gradually developed a provisional phylogenetic framework to inform species delimitation.

Given the time constraints and the large quantity of species we were trying to study, we were unable to optimize conditions for extracting and sequencing DNA from intractable specimens but, instead, opted to find alternative specimens or simply to move on. About one and a half years into the project we decided to focus our barcode sequencing solely on *ITS* as it had provided most resolution and the highest success in extracting and sequencing DNA (c. 60% specimens extracted were successfully amplified). We treated the *ITS* phylogeny (Supplementary Data File 3) as a single taxonomic character and thus equivalent to a single morphological character[26] that might sometimes provide information for species delimitation and sometimes not (Extended Data Fig. 2). In many cases, the *ITS* phylogeny corroborated a species hypothesis based on morphology by showing it to be monophyletic. In other cases, the *ITS* phylogeny also revealed that specimens *a priori* thought to be the same species were, in reality, different taxa, in which case we re-evaluated the morphology and sequenced additional specimens where these were available. For other species, the *ITS* phylogeny provided little or no resolution, for example in the group of species most closely related to the sweet potato (sometimes spelled sweetpotato), *Ipomoea batatas* (L.) Lam. In these cases, we tested species hypotheses using genomic data[27] (see below). If no genomic data were available, we based our species delimitation on morphology only (Supplementary Information, DNA barcodes as another taxonomic character).

We were nevertheless aware of the many limitations of single marker phylogenies[28–30] and of the inability of *ITS* to provide a robust and independent phylogenetic framework for

146 *Ipomoea*[31–33]. Our whole approach to the interpretation of the *ITS* phylogeny was, therefore,
147 one of extreme caution and, in addition, we had always planned to secure a greater amount of
148 sequence data using high-throughput sequencing. We used Hyb-Seq[23] to obtain 605 nuclear
149 regions and the whole chloroplast genome of 384 samples of *Ipomoea* representing 211
150 species (Supplementary Methods, Section 8). These data allowed us to obtain more robust
151 phylogenies for *Ipomoea* (Extended Data Fig. 3 and Extended Data Files 4-8), to test the
152 accuracy of the *ITS* phylogeny and to critically evaluate species delimitation in relation to the
153 sweet potato and its closest relatives[27]. In summary, incorporating molecular phylogenetics
154 into the taxonomic process provided a phylogenetic structure for *Ipomoea* as well as insights
155 into species relationships, ultimately contributing to the taxonomic process at a number of
156 levels (Table 1 and Fig. 2).

157 Species delimitation proceeds by looking for discrete and correlated characters that
158 separate entities that are hypothesised to be 'separately evolving metapopulation lineages'[34].
159 As the process of species delimitation is extended and complex, involving the integration of
160 morphology, DNA sequencing, previous literature, photographs and fieldwork, DNA
161 sequencing alone is not sufficient to underpin taxonomic decisions. In contrast, when
162 integrated with other sources of data it can be extremely powerful. We provide eight
163 examples to illustrate the process of species delimitation and taxonomic decision-making that
164 underpinned this work (Supplementary Information, Species Narratives).

165 **KEY TAXONOMIC RESULTS**

166 An accurate taxonomy of a plant group across its entire geographical distribution
167 enables the assembly of checklists and floras at different scales. Fig. 3a illustrates the power
168 and importance of continental-scale taxonomy conducted against the backdrop of a global
169 phylogenetic framework. This figure shows that the 109 species of *Ipomoea* known from
170 Bolivia[35–37] —20 of them described as new species during this project— are dispersed across

171 the entire phylogeny of the genus, underlining the limitations of geographically restricted
172 studies.

173 The power of the global approach is also illustrated by the number of specimens that
174 required a name change as a result of our studies —39% of specimens sequenced (Fig. 3b)
175 (see specific examples of species delimitations and synonymy in Supplementary Information,
176 Species Narratives). In addition to the large number of new identifications provided, we
177 described 63 new species, all of them dispersed throughout the phylogenetic breadth of
178 *Ipomoea*. Importantly, our contribution to the taxonomy of *Ipomoea* documented a 69%
179 synonymy rate: seven out of every ten published names are synonyms[38]. In addition, we
180 lectotypified 274 names and published 423 descriptions, 257 new illustrations, 43 distribution
181 maps and 27 identification keys[36–46].

182 Finally, our phylogenies confirm that many previously recognised segregated genera
183 are nested within *Ipomoea*[31,47] (Extended Data Fig. 3) and that an expanded *Ipomoea*
184 containing these species is necessary to make the genus monophyletic (Supplementary
185 Information, Phylogeny of *Ipomoea*). New combinations for all names in other genera that
186 need transferring into *Ipomoea* are provided in Supplementary Information, Nomenclatural
187 changes.

188 **RAPID RADIATIONS IN *IPOMOEA***

189 A by-product of our focus on species-level taxonomy and DNA sequencing was a
190 comprehensively sampled phylogenetic framework for *Ipomoea* that provided valuable
191 information at multiple levels. During our studies, we became aware of two very diverse
192 clades within *Ipomoea* in which species morphologies overlap considerably and phylogenetic
193 relationships are poorly resolved. One of these clades is concentrated in central South
194 America (Paraguay, southeast Bolivia, southwest Brazil, and northern Argentina), whilst the
195 other is more widespread in the Americas but with a particularly high concentration of

196 species in the Caribbean region. These two diverse clades are closely related in our nuclear
197 and chloroplast phylogenies, although the exact relationship differs between the two datasets
198 (Extended Data Fig. 3a and b). In view of the unique characteristics of these two clades, we
199 constructed a time-calibrated phylogeny for *Ipomoea* and estimated diversification rates
200 throughout the genus (Fig. 4 and Extended Data Figs. 4–6). This showed that diversification
201 rates were relatively constant in most of the genus, except for the part of the phylogeny that
202 contained these two diverse clades (and a small number of other species). In this part of the
203 phylogeny, there was initially a greater than 5.5-fold increase in net diversification rates
204 compared to the background rate across the rest of the tree (an increase from 0.127 to 0.719
205 species Myr^{-1}). Our analyses indicated that this was primarily a result of increased speciation
206 rates, with extinction rates remaining relatively constant. Although our analysis indicated a
207 diversification rate increase in the Lower Miocene, more recent phenomena might also
208 influence the distinctive diversification dynamics in this part of the phylogeny, for example,
209 many species in this part of the phylogeny occur exclusively in the Cerrado —a biome which
210 probably only became established within the last 10 Myr[48,49]— and there are likely to have
211 been numerous shifts into and out of this biome (Extended Data Fig. 7). Further, numerous
212 shifts between different growth habits are also likely to have occurred between comparatively
213 recently diverged lineages (Extended Data Fig. 7). A more densely sampled phylogeny is
214 required to determine the nature of the relationship between biome occupancy and growth
215 habit, and whether either of these two factors are likely to have promoted multiple nested
216 diversification rate shifts, rather than the single rate increase reported here. Regardless, our
217 results highlight an increase in net diversifications rates in *Ipomoea* that is likely to be of a
218 similar scale to some of the most iconic evolutionary radiations in the plant kingdom[50–53].
219 Further, unlike many plant radiations, which are strongly associated with a transition into a
220 particular biome, the radiation in *Ipomoea* occurs across a range of biomes, and in some

cases, in areas that have been greatly disturbed by human actions. Further study of diversification rate variation in *Ipomoea*, therefore, represents a promising avenue which could lead to fundamental insights into the effects of biome shifts and human disturbance on evolutionary diversification and the assembly of the Neotropical flora.

EVOLUTION OF THE SWEET POTATO

Most recent studies on the origin of the sweet potato (*Ipomoea batatas* (L.) Lam.) focus on the genetic variation contained within the crop[54,55] or on the sequencing of whole genomes of the crop and one or two related species[56,57]. Meanwhile, the origin and evolution of the sweet potato and its relationship with its wild relatives (CWR) has only recently been clarified[27]. The global study of the genus allowed us to identify all sweet potato CWR —two of them new species, *I. lactifera* J.R.I.Wood & Scotland[36] and *I. australis* (O'Donell) J.R.I.Wood & P.Muñoz[38]— and revealed the dual role of *I. trifida* (Kunth) G.Don, the closest wild relative, in the origin of the crop species[27].

Previous studies have shown that sweet potato CWR do not produce storage roots[58], so it has been assumed that the transition from non-storage root to storage root was mediated by human domestication[33], although direct evidence for this claim remains elusive. However, our broad comparative study of the genus offers a novel perspective on the evolution of storage roots in *Ipomoea* and a very different narrative for the evolution of the sweet potato. At least 63 species of *Ipomoea* have been recorded in previous literature and our own observations as having storage roots, several of them edible and some bigger than the roots in *I. batatas* (Fig. 5a and Extended Data Table 1). Mapping species with storage roots onto a phylogeny shows that storage roots evolved multiple times independently from species that do not have storage roots (or these have never been recorded) (Fig. 5b).

We wanted to explore this question further and used our time-calibrated phylogenies to investigate the temporal dynamics of sweet potato. We set out to determine whether our data

were consistent with sweet potato originating within the timeframe of human agriculture (roughly the last 10,000 years) or if it was older. Our results indicated that the sweet potato was likely to have diverged from its closest wild relative, *Ipomoea trifida*, over 1 million years ago[27] (Fig. 5b) and that part of the diversity existing within the crop largely pre-dated the origin of agriculture (Fig. 6). This timeframe is consistent with the idea that the sweet potato evolved long before the onset of human agriculture, and that the storage root was an existing trait that favoured the species being taken into cultivation by humans. Further, all other species with storage roots also evolved over 1 million years ago (Fig. 5b), many within the timeframe associated with the expansion of C4 grasses and the evolution of fire-adapted vegetation types[48,49] in which underground storage organs would be advantageous. In summary, the evidence presented here suggests that the storage root in cultivated sweet potato is not a product of human domestication but rather an existing trait that predisposed the plant for cultivation. To the best of our knowledge, this possibility has not been previously considered.

THE IMPORTANCE AND POTENTIAL OF TAXONOMIC MONOGRAPHY

Taxonomic studies based on the massive number of natural history collections held worldwide highlight the awesome complexity and wonder of the natural world. They merit a more important role in the task of addressing a range of environmental issues from food security, conservation and biodiversity inventories to ecology in general. The taxonomic community itself needs to embrace and rediscover the value of taxonomic monographs[25,59] within the context of what constitutes world-class science[60]. The full integration of two distinct skill sets, DNA sequencing and morphological studies, is necessary to achieve this. Although other scientific subjects bring a unique perspective to environmental science, including evolution, ecology and population genetics, monographic taxonomy undertaken

with modern methods at the global scale has the potential to play a vital role in the contemporary research agenda.

Taxonomy is often seen as a redundant science because of the mistaken idea that biodiversity is as well-known overall as it is in a few well-studied, high profile groups or countries. It is also undervalued by the inaccurate view that taxonomic knowledge steadily accumulates until all species of a particular group are discovered, whereas in reality names, synonyms, mistaken identifications and errors accumulate alongside accepted names and reliable information. This accretion needs to be sifted and new species identified to provide an accurate taxonomy, something that is lacking for the vast majority of tropical flowering plant genera of any reasonable size. With the rapid increase in the number of unstudied collections in the last fifty years, there is now a unique opportunity to embrace the challenges and opportunities that these specimens provide to produce taxonomically sound monographs of the plant diversity these natural history collections represent.

To fully exploit the opportunity and potential of global natural history collections, as undertaken in this study, demands the integration of different scientific expertise including specimen-based taxonomy, genomics and phylogenetics. This has implications for the type of training that the next generation of biodiversity scientists receive. It seems unrealistic to expect an individual scientist to be expert in all three disciplines but assembling small teams of people with such expertise to tackle the world's major taxonomic problems at a global scale is surely possible given existing resources and expertise. The skills and resources currently exist for many taxonomically diverse groups (and as long as taxonomic training continues or is increased) and we hope that this study acts as a catalyst in demonstrating the scale of progress that can be achieved in a realistic time-frame.

METHODS

In this section, we provide a summary of the methodology underlying our studies of *Ipomoea*. We provide a detailed description of every step in the Supplementary Methods. Although we report the morphology and molecular methods separately, they were, in fact, conducted in parallel and integrated throughout the process.

Herbarium and field work. We assembled a preliminary checklist from existing literature of all species of *Ipomoea* (Supplementary Methods, section 1) and identified herbaria that house significant collections that we would visit or from which we could obtain online images (Supplementary Methods, sections 2 and 3). Simultaneously, we surveyed morphological variation across the genus —with reference to existing literature as well as specimens— to identify taxonomically useful characters for species delimitation (Supplementary Methods, sections 4 and 5). We subsequently visited, received loans of material from or studied photographs from the following herbaria (acronyms according to[61]) in Europe (AAU, B, BM, C, CGE, E, G, GOET, K, L, LE, M, MA, OXF, P, PC, RBGE, S, TO and W), the United States (A, ARIZ, BISH, F, FTG, GA, GH, MICH, MO, NY, RSA, SELU, TEX, US and USDA), Latin America (Argentina: CTES, LIL; Bolivia: BOLV, HSB, LPB, USZ; Brazil: CEN, CPAP, CRIA, HEPH, HUEFS, IPA, JPB, MBM, PEUFR, R, RB, SP and UB; Colombia: COL; Cuba: HACB, HAJB; Mexico: IEB, MEXU; Panama: PAM; Paraguay: FCQ, PY, SCP; Peru: CIP, CUZ, USM), China (ISBC, KUN), South East Asia (Malaysia: KEP, SAN; Singapore: SING) and Australia (FRI). We studied the variation in all herbarium material seen and photographed and databased specimens (Supplementary Methods, Sections 2–5). We carried out fieldwork in Bolivia, Paraguay, Argentina and Brazil (Supplementary Methods, Section 6). We also developed a network of contacts with people interested in *Ipomoea* with whom we corresponded over a range of related issues (Supplementary Methods, Section 7).

Analysis of DNA barcodes. The analyses using barcodes were based on 3,035 *ITS, matK* and *trnH* sequences from 1,560 specimens (Passport Data in Extended Data File 1) (Extended Data Fig. 1). We aligned all sequences using MAFFT v.7.2.1[62,63] and ran Maximum Likelihood phylogenetic analyses in RAxML v.8[64], Approximate Maximum Likelihood in FastTree 2[65] and Bayesian inference in MrBayes[66] (Supplementary Methods, Section 8).

Analysis of genomic data. We obtained the whole chloroplast genome and 605 putative single-copy nuclear coding regions from 385 specimens representing 211 species using Hyb-Seq[23] (Supplementary Methods, Section 8). These specimens were selected based on quality and quantity of the available DNA with the aim of covering as much phylogenetic breadth as possible. We ran phylogenetic analyses on both sets of genomic data. For the nuclear data, we ran additional analyses using only the subset of 434 regions that passed the PHI recombination test[67]. In addition, mapping our data to the recently published *Ipomoea triloba* genome[57] warned some of our regions may not be single copy; hence, we ran further analyses using only the subset of 421 regions that we were confident are single copy (Supplementary Methods, Section 8). We used Maximum Likelihood, Approximate Maximum Likelihood and Bayesian Inference to analyse the chloroplast data. Regarding the nuclear coding regions, we used Maximum Likelihood and Approximate Maximum Likelihood for the analysis of concatenated alignments as well as inferred species trees from gene trees using coalescence methods. All methods and datasets recovered the same major clades within *Ipomoea* and the relationship between taxa within those clades was mostly congruent across phylogenies (Supplementary Discussion, Phylogeny of *Ipomoea*).

Divergence time estimates. We estimated divergence times within *Ipomoea* in treePL[68,69]. We used the nuclear NGS phylogeny inferred in FastTree 2[65] as input tree. We used a smoothing value of 0.01 following extensive cross-validation analyses (Supplementary Methods, Section 9), but also experimented with different smoothing values (0.01, 1, 100,

10000) to determine the sensitivity of divergence time estimates to different assumptions about among-branch-rate-variation. We also inferred time-calibrated phylogenies with the chloroplast phylogeny as the input tree. In this case, we also experimented with different smoothing values (0.01, 1, 100, 10000). For these phylogenies, we used a point calibration for the root node of 34.0 Myr. We consider this the most realistic age estimate for *Ipomoea*, following a series of analyses in which we experimented with different methods for calibrating a phylogeny for Convolvulaceae and Solanaceae. The analyses for Convolvulaceae and Solanaceae were performed in RevBayes[70] (Supplementary Methods, Section 9).

We used BAMM[71] to infer diversification rates. The time-calibrated phylogeny inferred from nuclear genomic data in treePL[69] was used as the input phylogeny. When performing this analysis, we specified clade specific sampling fractions. These were taken into account when estimating diversification rates. We performed several supplementary diversification rate analyses. These used the different time-calibrated phylogenies outlined above as input phylogenies (Supplementary Methods, Section 9).

Data availability

Passport data of all specimens included in the molecular studies presented in this paper is available in Extended Data File 2. Additional records and information of the collections included in this study and of specimens added subsequently are available through the project website (*https://herbaria.plants.ox.ac.uk/bol/ipomoea*). DNA barcode sequences are available through GenBank and genome assemblies are available through the Oxford Repository Archive (*https://doi.org/10.5287/bodleian:kepgnxzeK*). Illumina raw reads are available through the Sequence Read Archive (BioProject PRJNA453382). Alignment files and other materials are available from the corresponding author upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, supervision and project administration, R.W.S.; Funding acquisition, R.W.S., J.R.I.W., P.M.R. and T.C.; Methodology, R.W.S., J.R.I.W., A.L., S.K., K.W., B.K., D.H, D.F., P.M.R. and T.C.; Resources, J.R.I.W., B.R.M.W., P.M.R., A.S., Z.G., N.L.A. and M.D.R.; Formal analysis and investigation, P.M.R., T.C. and J.R.I.W.; Writing – original draft, P.M.R., R.W.S., T.C. and J.R.I.W.; Writing – reviewing and editing, all authors; Visualization, P.M.R.

AUTHOR INFORMATION

The authors declare no competing interests.

549 **Fig. 1 | Natural history collections facilitate biodiversity studies at a global scale.** This
550 map shows where the 1,560 herbarium specimens sequenced during our study of *Ipomoea*
551 were collected. Dots indicate the collection locality of specimens sequenced for DNA
552 barcoding; green dots indicate the subset of specimens that were also sequenced using Hyb-
553 Seq to obtain genomic-scale data.
554

555 **Fig. 2 | Integrating morphology and DNA in global taxonomic studies is key to utilizing**
556 **the resources of natural history collections**. The study of plant groups across their entire
557 geographical distribution results in an accurate taxonomy that enables the assembly of
558 national and regional checklists and floras, and also provides an essential framework for
559 subsequent evolutionary studies, conservation assessments and research on crop wild
560 relatives and food security.
561

562 **Fig. 3 | Megadiverse plant groups demand a global approach.** a) Nuclear genomic
563 phylogeny showing that the species recorded from Bolivia (green boxes) are scattered across
564 the phylogeny of the genus, which has a global distribution. b) *ITS* phylogeny of *Ipomoea*.
565 Red branches indicate specimens also sequenced using high-throughput sequencing. Black
566 boxes indicate specimens that we sequenced that changed their identification during our
567 studies, approximately 39% of them. Many more specimens not included in our molecular
568 analyses also required a change of name.
569

570 **Fig. 4 | Rapid radiations in *Ipomoea*.** A time-calibrated phylogeny of *Ipomoea*, with
571 branches coloured according to the inferred speciation rate. The map indicates the geographic
572 distribution of two species rich clades, the species within which exhibit highly overlapping

morphologies. Both of these two diverse clades (and a small number of other species) are part of a larger clade in which speciation rates are significantly higher than the rest of *Ipomoea*.

Fig. 5 | Storage roots evolved multiple times independently in *Ipomoea*. a) Storage roots in *Ipomoea lilloana* (top picture) are as big as those in the sweet potato (below); b) Time-calibrated nuclear ML phylogeny highlighting the position of 30 species with storage roots, indicated by red branches and dots. All these species originated at least 1Mya. We have recorded an additional 33 species with storage roots for which we do not have genomic data.

Fig. 6 | Diversity within sweet potato predates agriculture. Time-calibrated phylogenies for sampled specimens of *Ipomoea batatas* and its closest relative *Ipomoea trifida*. The divergence times indicate when lineages represented by different specimens are likely to have diverged. Divergence times inferred using **a)** nuclear (NGS) data and **b)** whole chloroplast genome data. The two *Ipomoea batatas* clades in **b)** correspond to the two chloroplast lineages hypothesized in reference 27.

Table 1 | Contribution of the DNA to the taxonomic decision process

At the species level taxonomy, DNA has…

1) Confirmed the monophyly of many species.

2) Drawn attention to the existence of unrecognised new species

3) Shown some species thought to be distinct are conspecific with others from different geographical areas, e.g. *Ipomoea acanthocarpa* from Africa with *I. piurensis* from America or *I. lindenii* from mainland America with the Jamaican endemic *I. cyanantha*.

4) Shown that some species sometimes thought to be the same are distinct, e.g. *I. paludicola* and *I. asarifolia*, *I. huayllae* and *I. aristolochiifolia*, *I. jalapa* and *I. pterocaulis*, etc.

5) Revealed wrongly identified specimens as they appear in parts of the phylogeny away from the clade with which they had been identified.

6) Provided a phylogenetic context to interpret morphology when specimens were poorly preserved.

Regarding evolutionary relationships between species, DNA has…

1) Revealed the existence of several clades and radiations.

2) Confirmed the monophyly of some groups previously recognised on morphological grounds such us *Pharbitis*, *Quamoclit*, *Astripomoea* and *Batatas*.

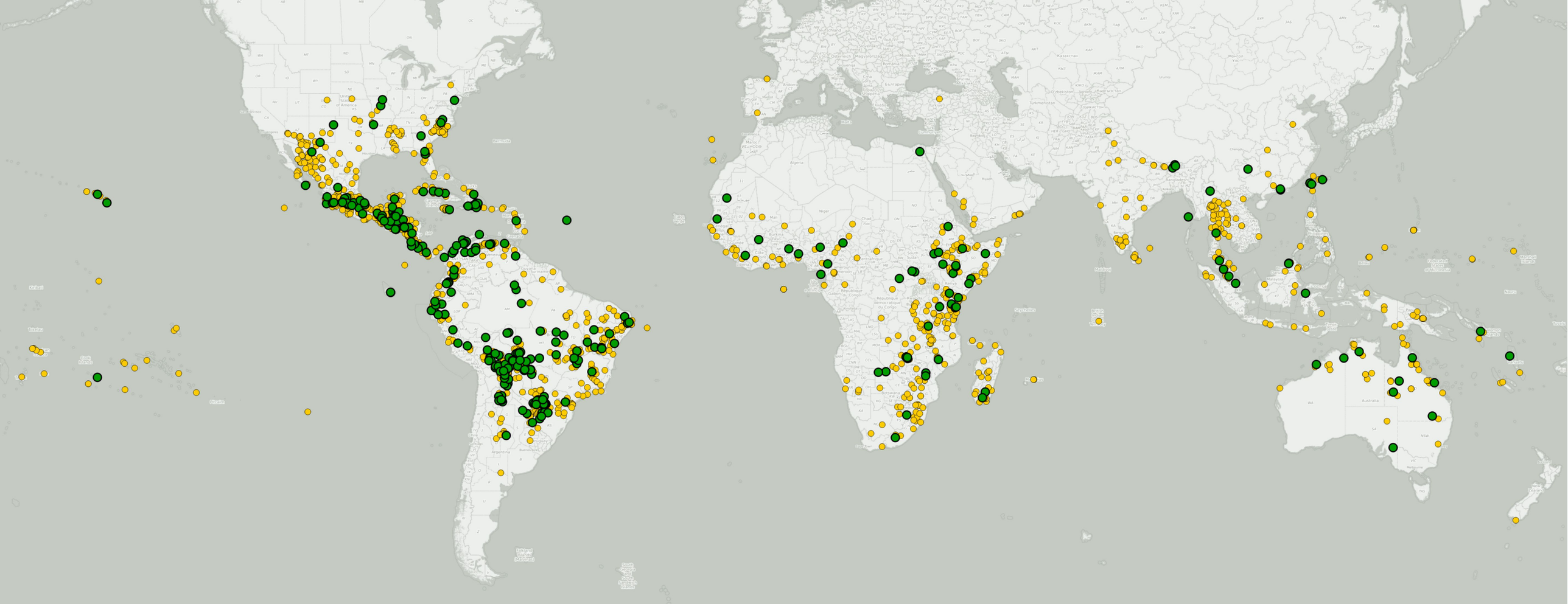
3) Shown that all previously recognised genera of the tribe *Ipomoeeae* (*Argyreia*, *Stictocardia*, etc.) are nested within *Ipomoea* and all but *Astripomoea* are not monophyletic.

4) Demonstrated that *Rivea* is nested within the clade dominated by *Argyreia* species.

5) Shown that some groups previously recognised are only monophyletic if certain species are excluded (e.g. Arborescens group).

6) Clarified the relationship between the sweet potato and its wild relatives and discovered two new species within this group.

588

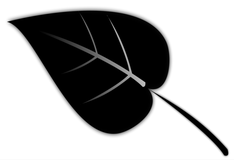


EXISTING DATA

LITERATURE REVIEW

PRELIMINARY CHECKLIST

HERBARIUM & FIELD WORK



ASSEMBLE REPRESENTATIVE SET OF SPECIMENS

MORPHOLOGICAL STUDY

GENERATION OF SPECIES HYPOTHESES

DATA INTEGRATION

LAB WORK

Subset of specimens

DNA EXTRACTION

SANGER SEQUENCING

HIGH-THROUGHPUT SEQUENCING

Independent test of accuracy

BARCODE PHYLOGENIES

GENOMIC PHYLOGENIES

UPDATE NOMENCLATURE, TYPIFICATION, IDENTIFICATION KEYS, DESCRIPTIONS, ETC.

MONOGRAPHIC STUDIES

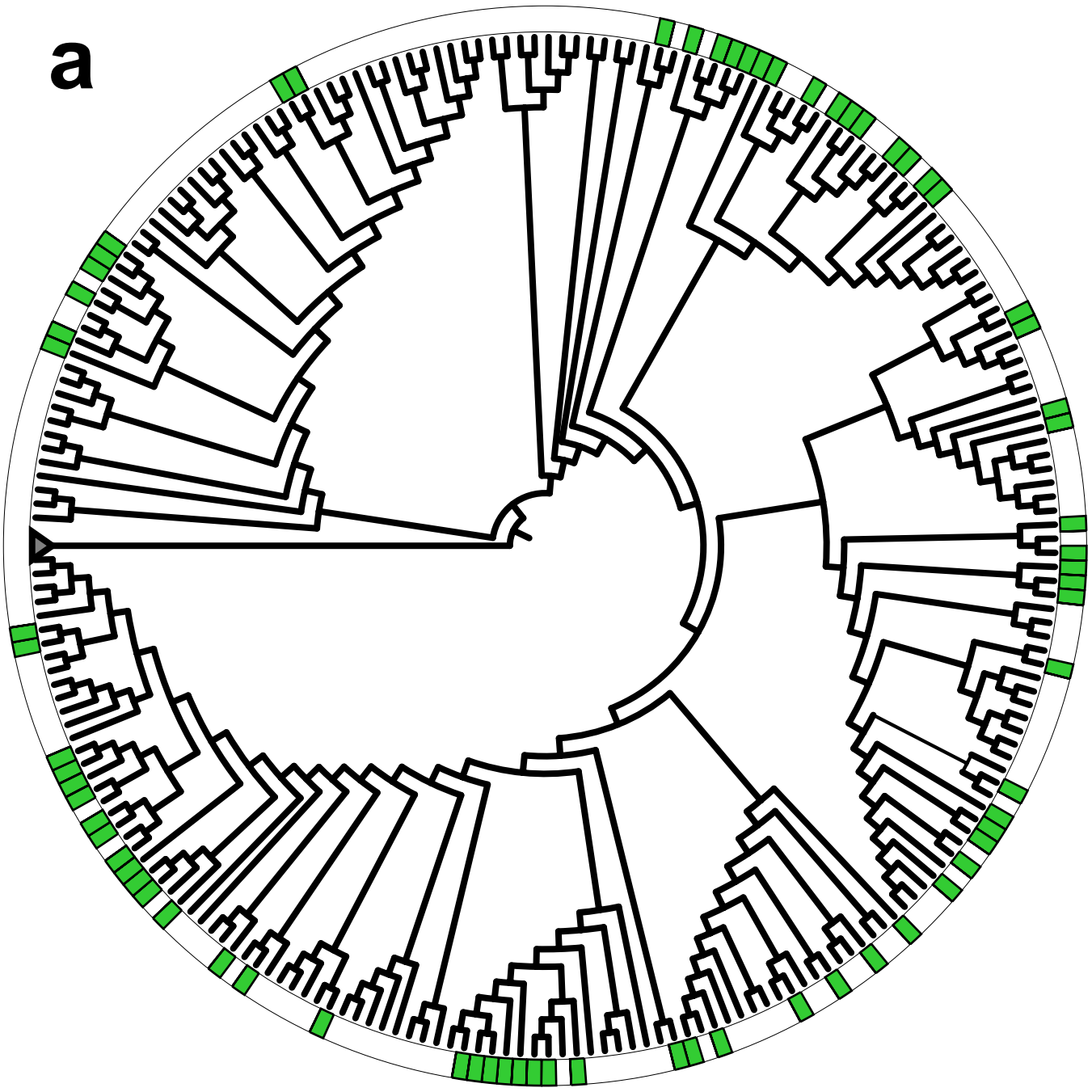
EVOLUTIONARY STUDIES

NATIONAL & REGIONAL FLORAS & CHECKLISTS

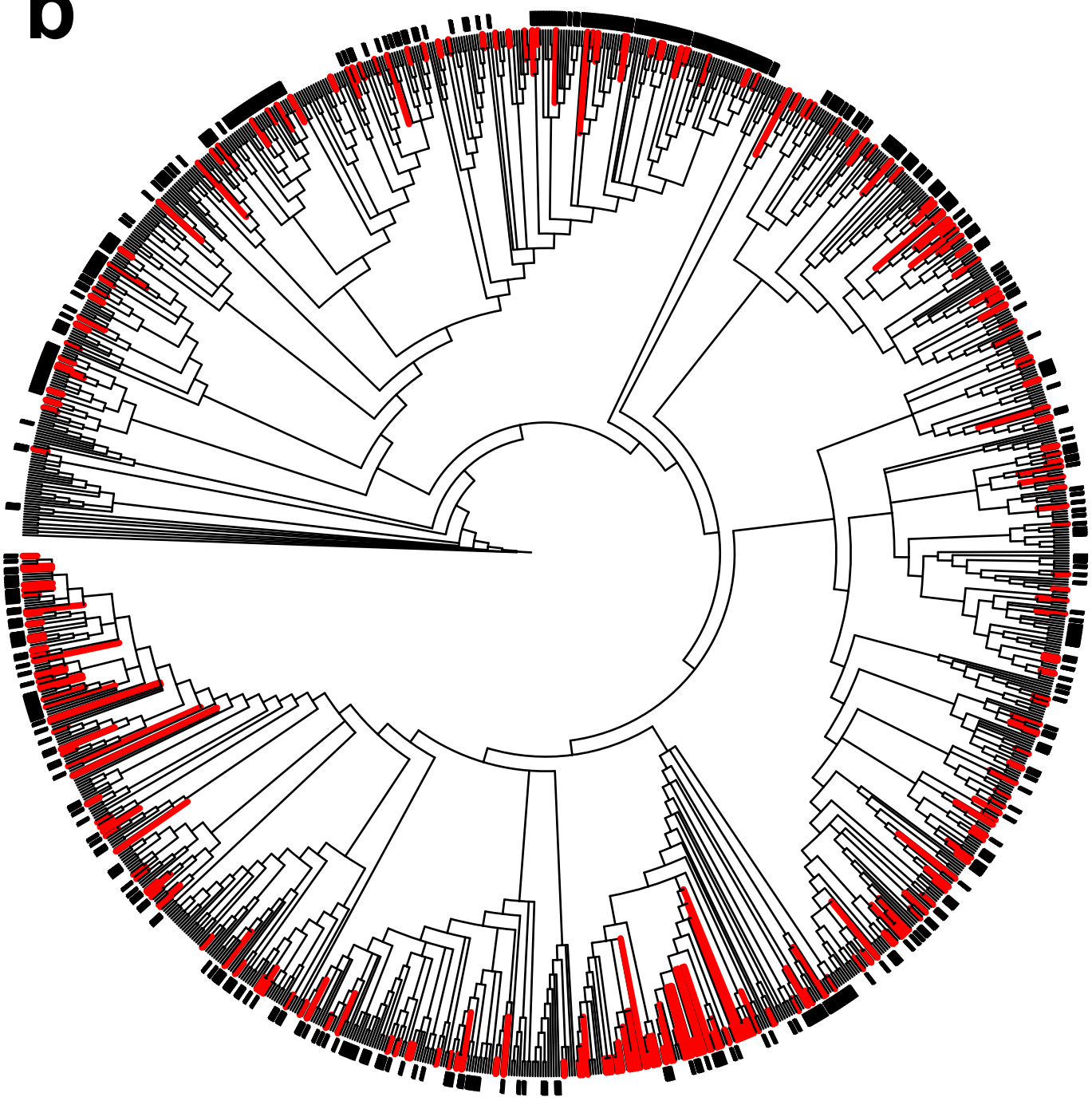
CONSERVATION ASSESSMENTS

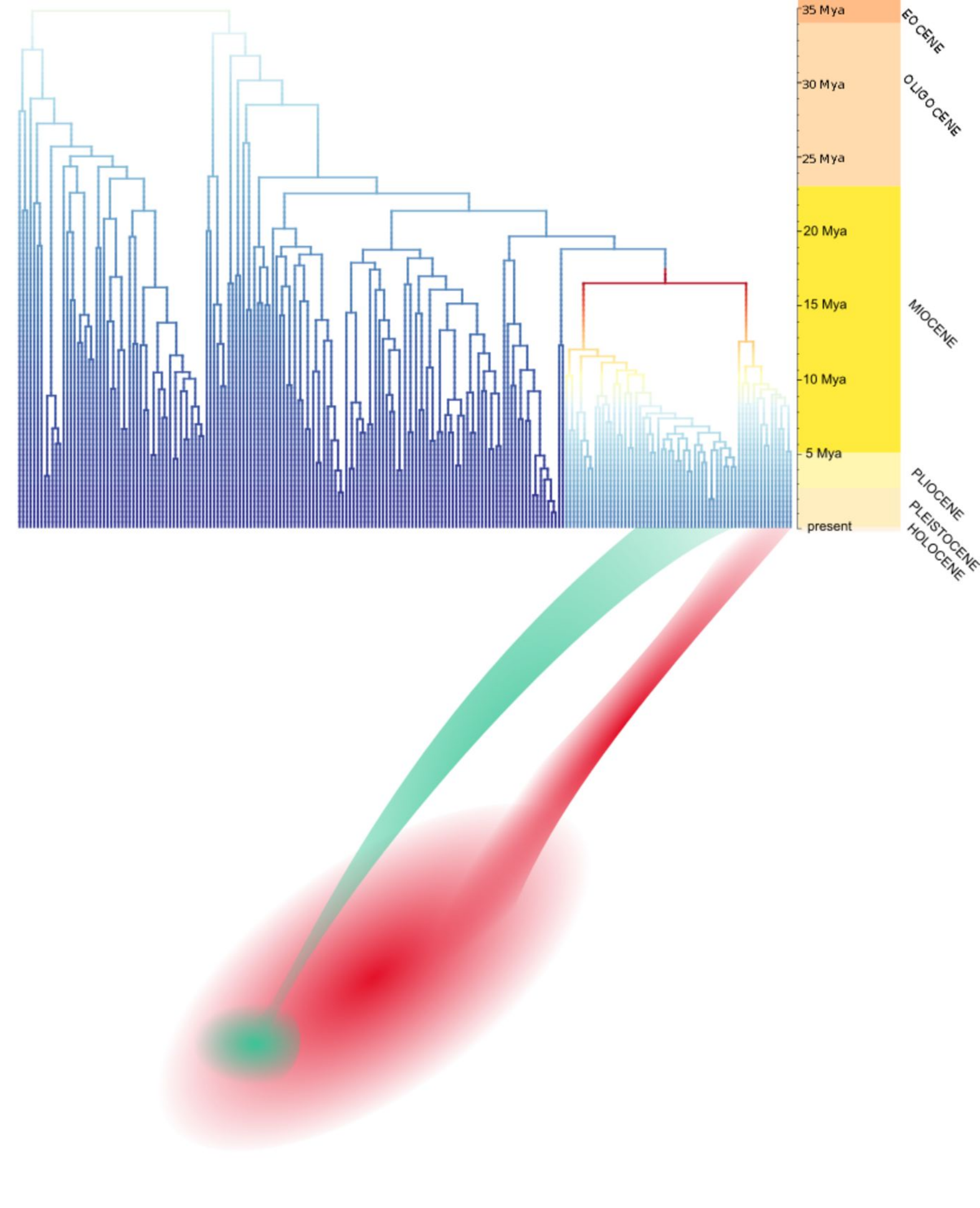
CROP WILD RELATIVES & BREEDING

a



b

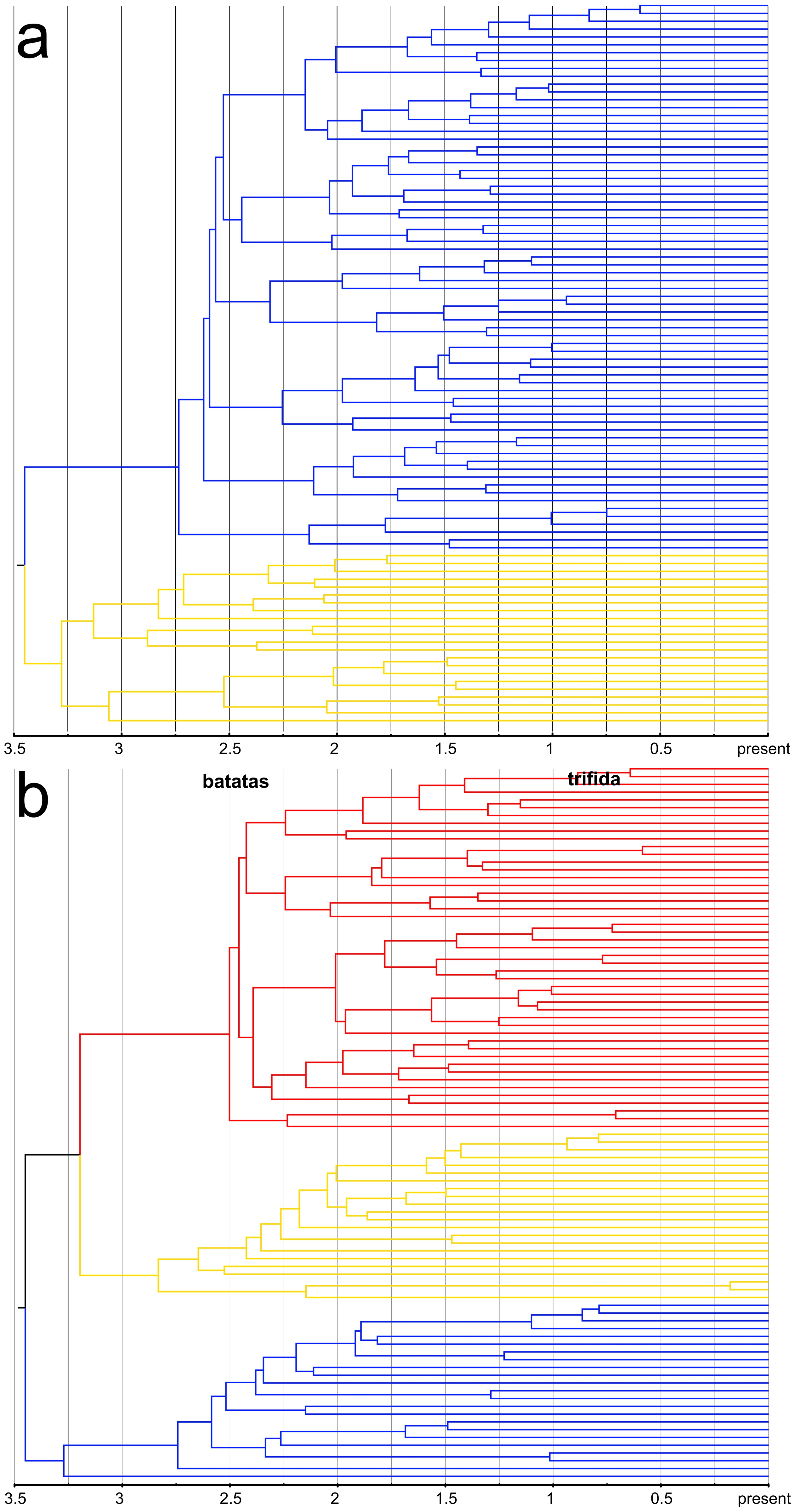



35 Mya
30 Mya
25 Mya
20 Mya
15 Mya
10 Mya
5 Mya
present
EOCENE
OLIGOCENE
MIOCENE
PLIOCENE
PLEISTOCENE
HOLOCENE

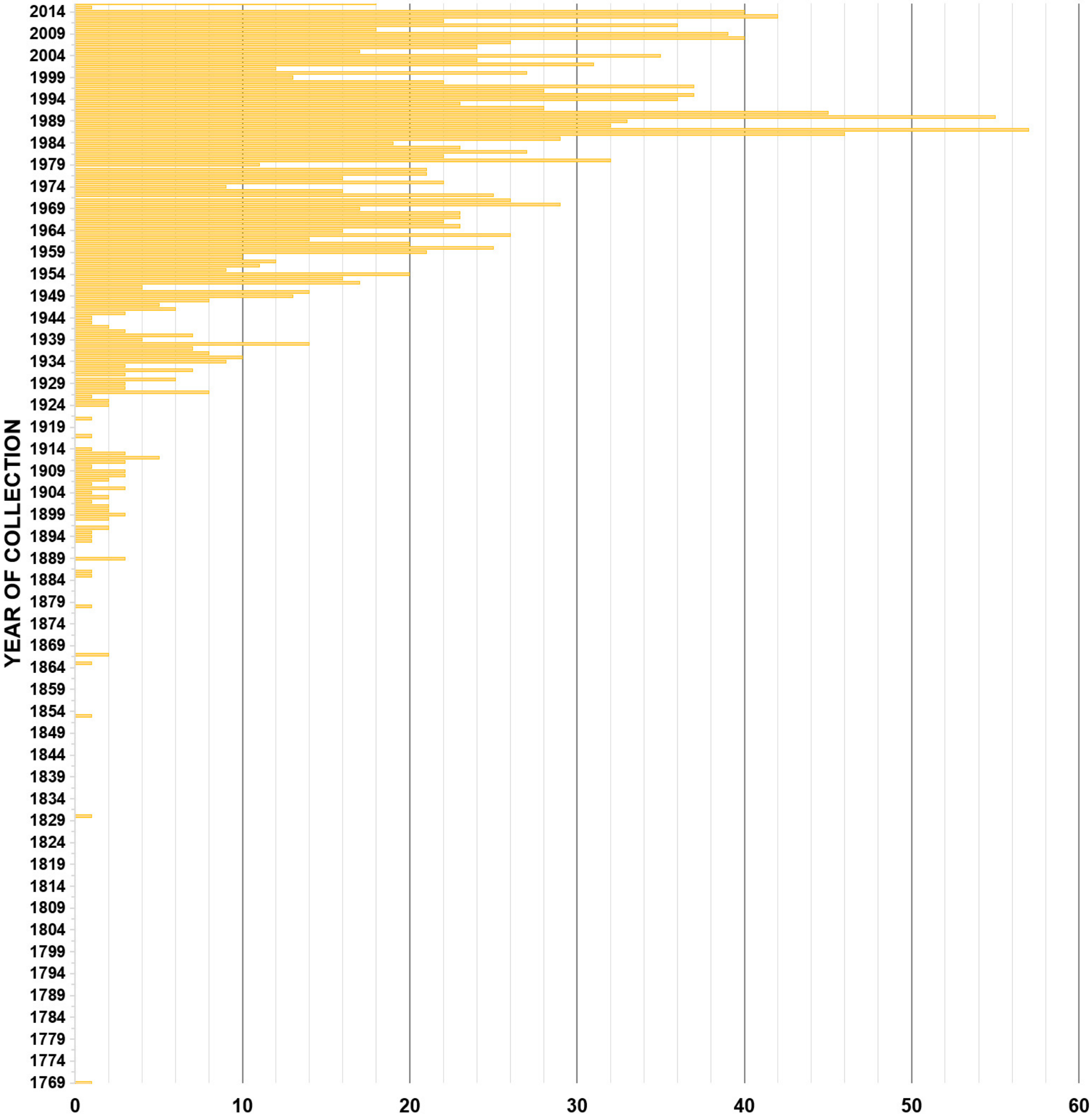
a

1. *Ipomoea malvaeoides* (2.2 Mya)
2. *I. hieronymi* (1.01)
3. *I. lilloana* (2.6)
4. *I. jalapa* (3.3)
5. *I. descolei* (4.2)
6. *I. polpha* (3.5)
7. *I. mauritiana* (2.9)
8. *I. bonariensis* (3.7)
9. *I. pintoi* (5.3)
10. *I. batatas* (2.6)
11. *I. pubescens* (5.3)
12. *I. ampullacea* (5.0)
13. *I. orizabensis* (2.2)
14. *I. ancisa* (3.0)
15. *I. sescossiana* (3.0)
16. *I. stans* (5.7)
17. *I. muricata* (4.5)
18. *I. capillacea* (3.6)
19. *I. plummerae* (3.6)
20. *I. bracteata* (3.99)
21. *I. argillicola* (2.9)
22. *I. leptophylla* (4.9)
23. *I. pandurata* (4.9)
24. *I. cairica* (8.1)
25. *I. weltischii* (9.1)
26. *I. oenotherae* (9.4)
27. *Turbina bracteata* (6.6)
28. *I. holubii* (=*T. holubii*) (5.2)
29. *I. alpina* (11.8)
30. *Argyreia bracteata* (11.7)

b


a
3.5
3
2.5
2
1.5
1
0.5
present
b
batatas
trifida
3.5
3
2.5
2
1.5
1
0.5
present

a


YEAR OF COLLECTION
2014
2009
2004
1999
1994
1989
1984
1979
1974
1969
1964
1959
1954
1949
1944
1939
1934
1929
1924
1919
1914
1909
1904
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1894
1889
1884
1879
1874
1869
1864
1859
1854
1849
1844
1839
1834
1829
1824
1819
1814
1809
1804
1799
1794
1789
1784
1779
1774
1769
0
10
20
30
40
50
60

b

NUMBER OF SPECIMENS SEQUENCED
NUMBER OF ACCESSIONS AND SAMPLES
0
200
400
600
800
1000
1200
1400
1402
853
780
621
28
26
131
60
104
590
Nuclear ribosomal ITS
Chloroplast matK
Chloroplast trnH
ITS only
matK only
trnH only
ITS + matK
ITS + trnH
matK + trnH
ITS + matK + trnH

a

SPECIES HYPOTHESIS

MULTIPLE ACCESSIONS

MONOPHYLY

[b]

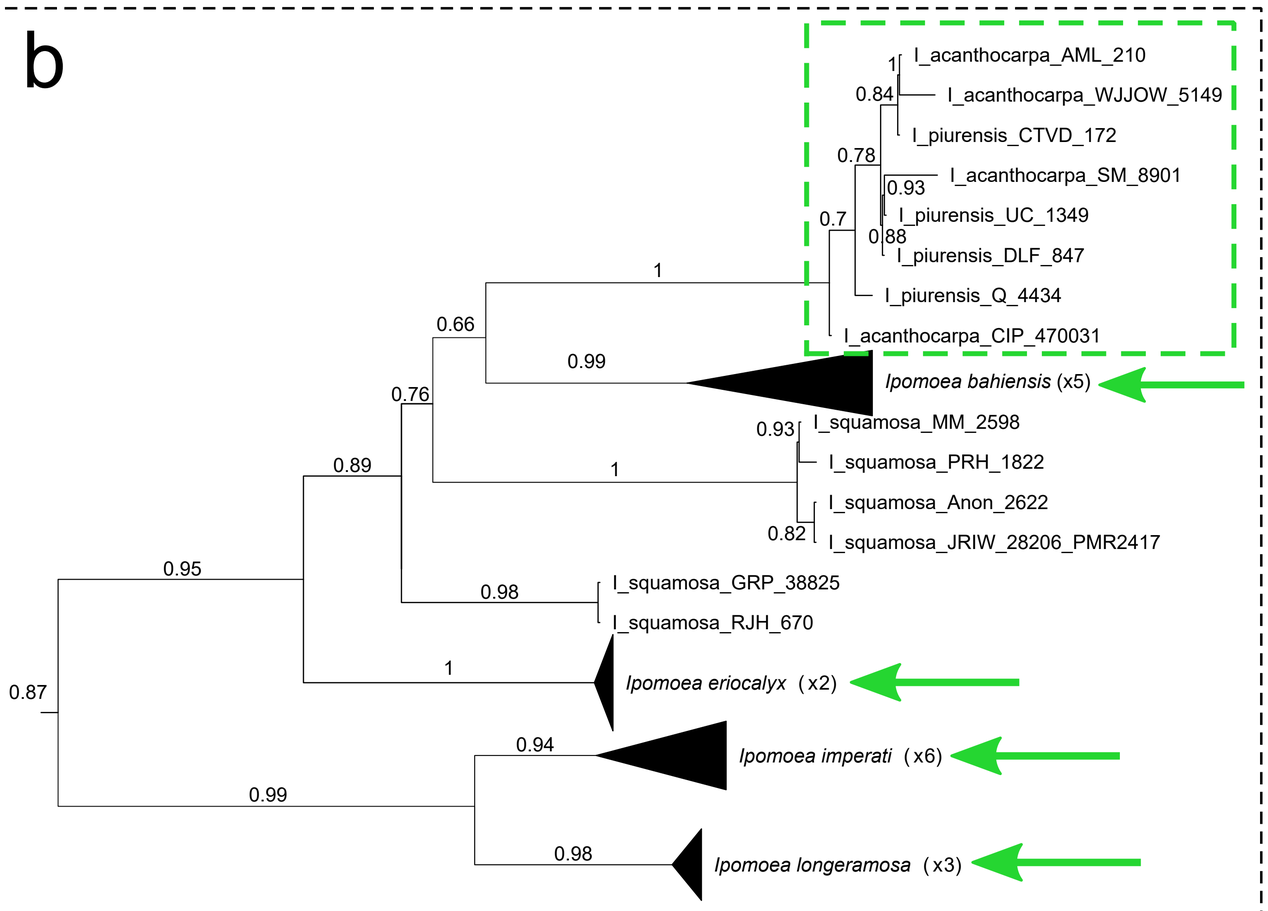
NON-MONOPHYLY
DIFFERENT CLADES (A, B, C, etc.)

[c]

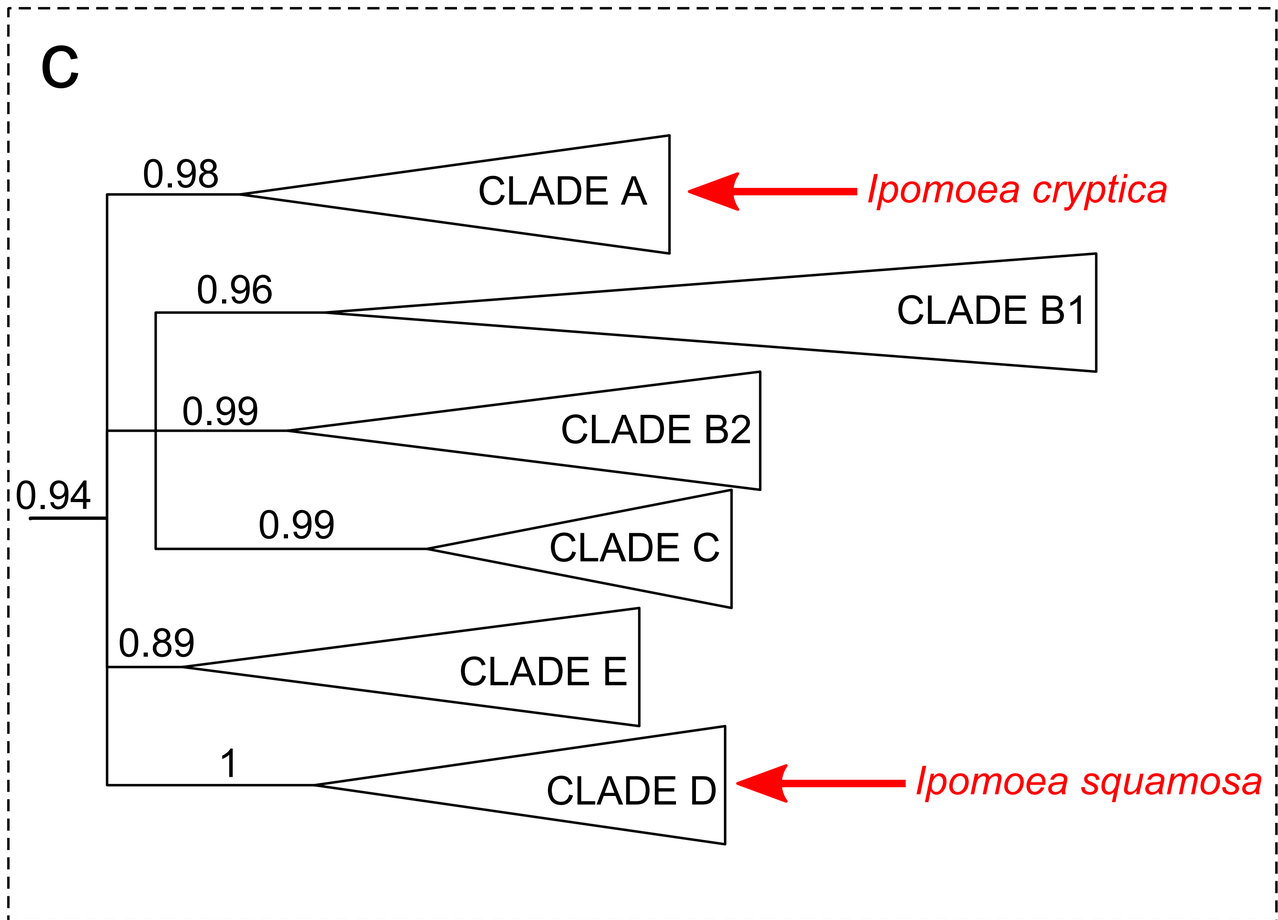
NON-MONOPHYLY
SAME CLADE

[d, e, f]

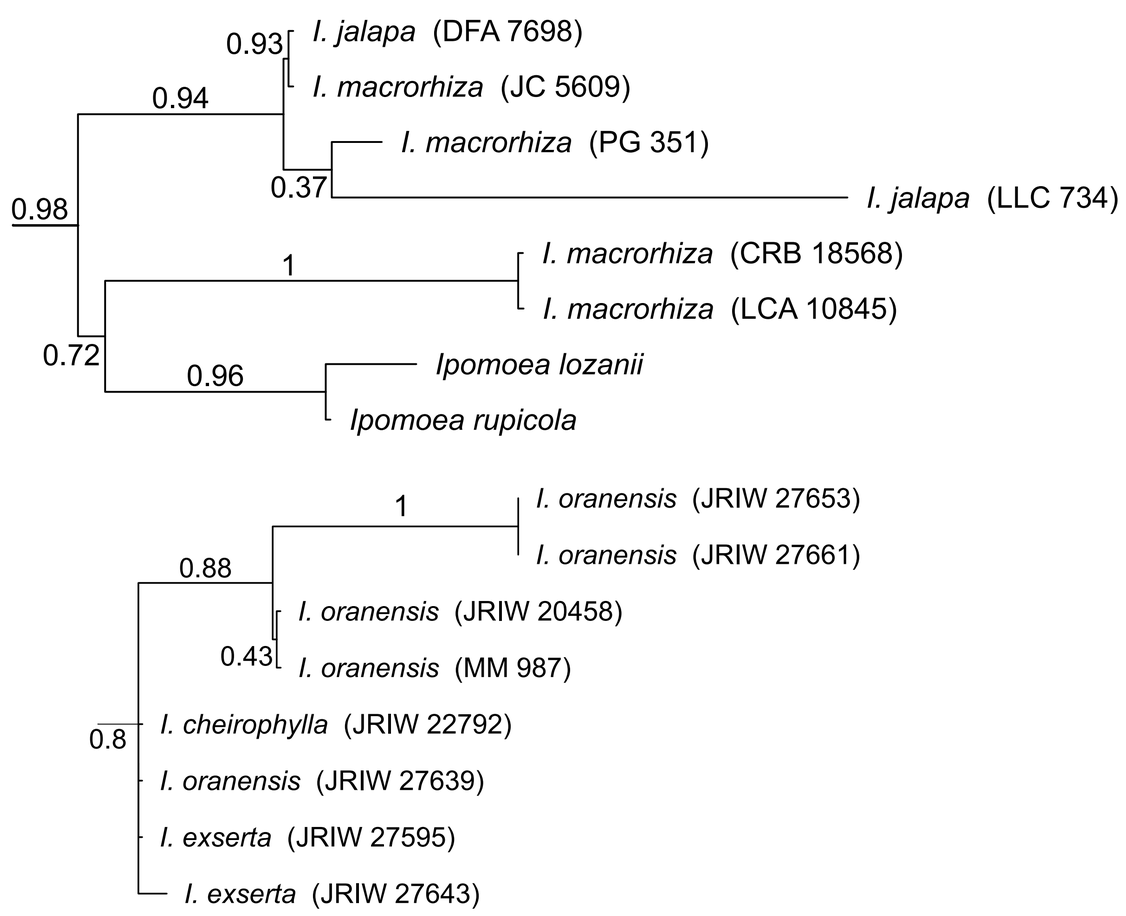
b



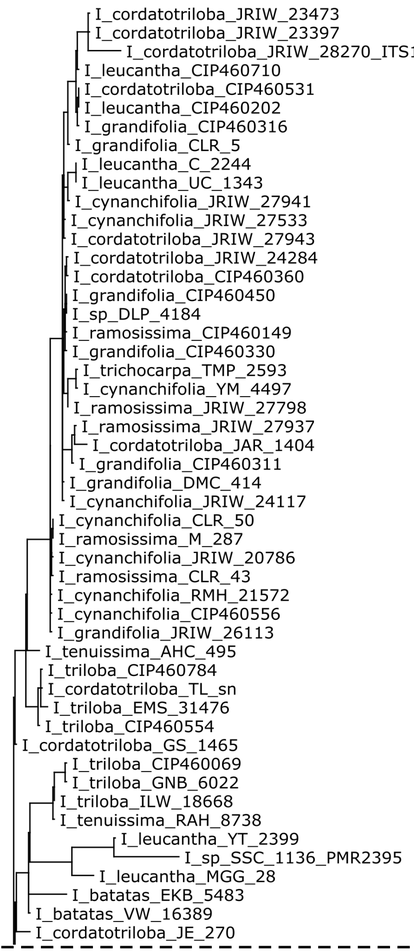
c



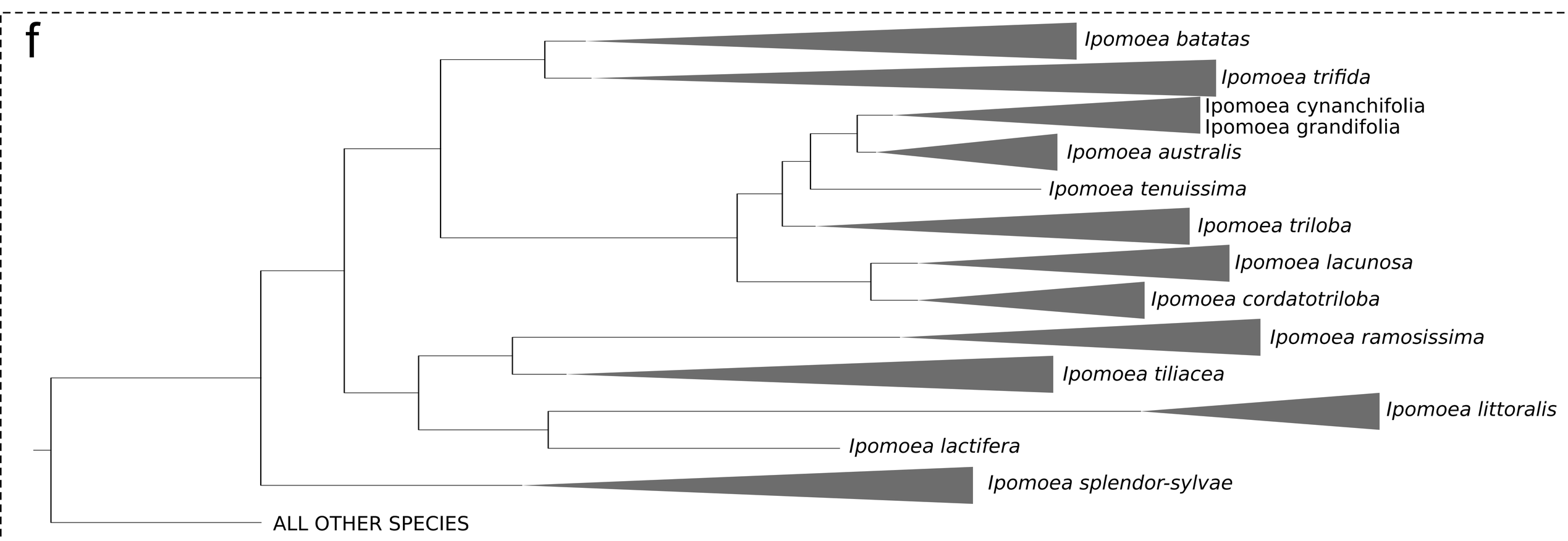
d



e



f



a

A1
A2
Ipomoea setosa
A3
Ipomoea cryptica
CLADE A
B1
B2
CLADE B
CLADE C
CLADE D
CLADE E
(incl. *Astripomoea*)
(incl. *Argyreia*, *Lepistemon*, *Lepistemonopsis*, *Rivea*, *Stictocardia* & *Turbina*)
ALL OTHER CONVOLVULACEAE

NEW WORLD CLADE
AFRICAN GRADE
OLD WORLD CLADE

b

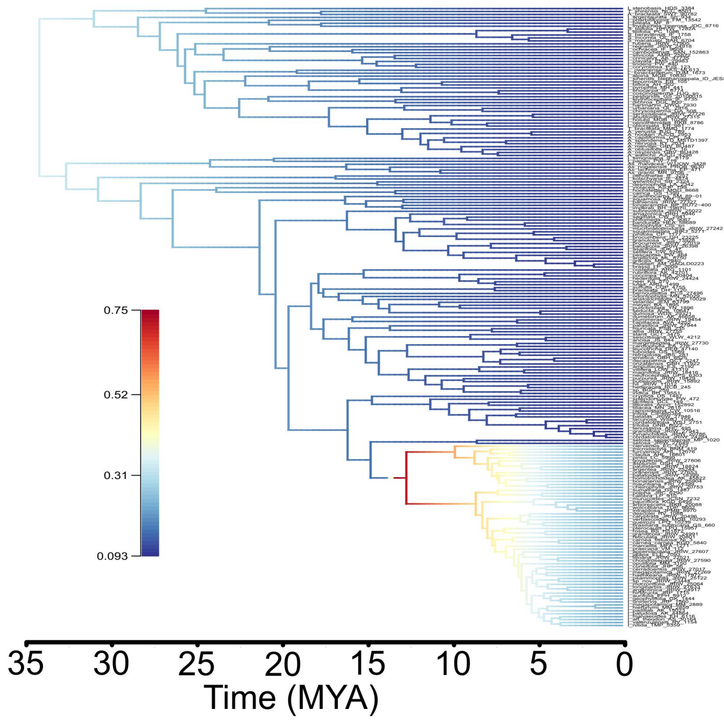
1/92
1/99
1/94
1/96
0.98/70
1
1/96
1/99
0.56/90
1/90
1/99
1/90

A1
A3
Ipomoea setosa
Ipomoea cryptica
A2
CLADE A
CLADE C
B2
B1*
CLADE B
CLADE D
CLADE E
(incl. *Astripomoea*)
(incl. *Argyreia* , *Lepistemon* , *Lepistemonopsis* , *Rivea* , *Stictocardia* & *Turbina*)
ALL OTHER CONVOLVULACEAE

NEW WORLD CLADE
AFRICAN GRADE
OLD WORLD CLADE

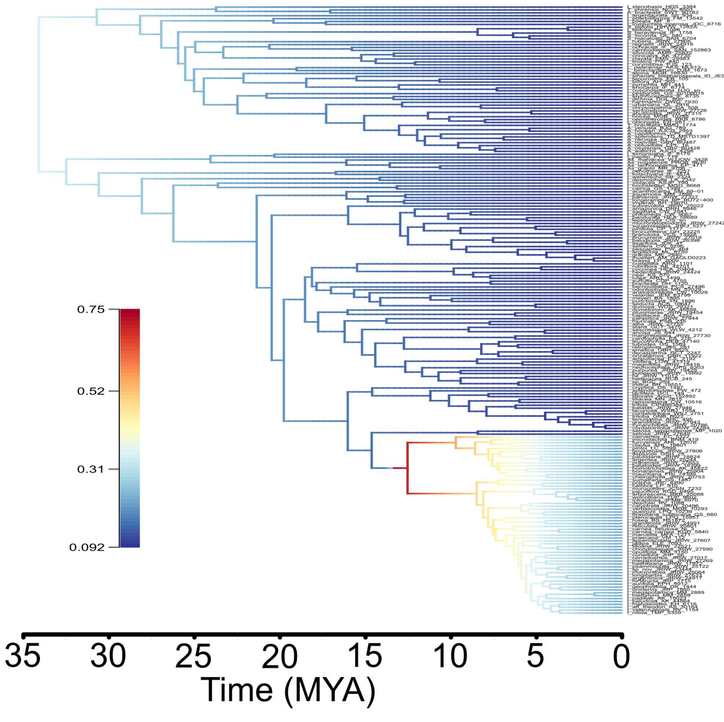
a. Smoothing = 1

p = 0.98



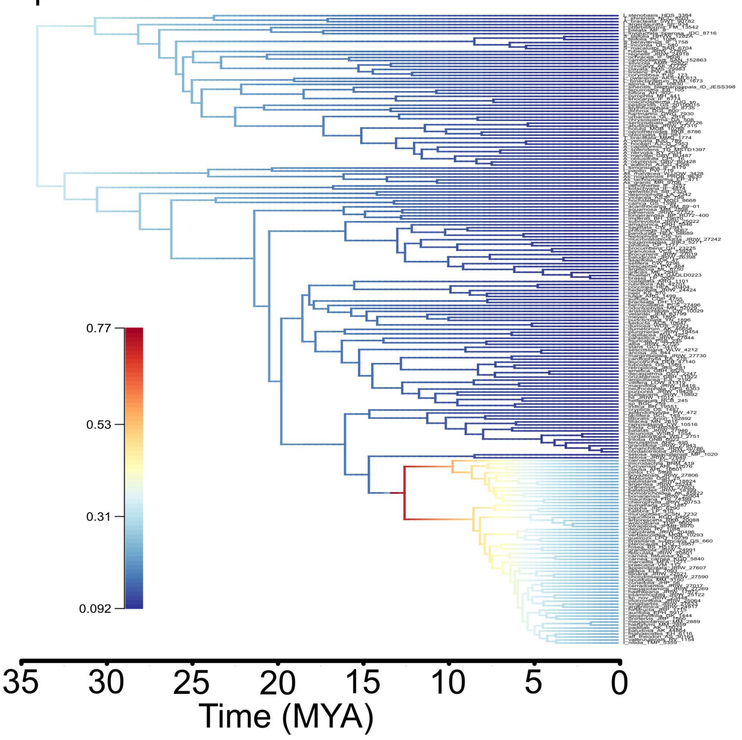
b. Smoothing = 100

p = 0.98



c. Smoothing = 10000

p = 0.98



p = 0.8

0.75

0.57

0.39

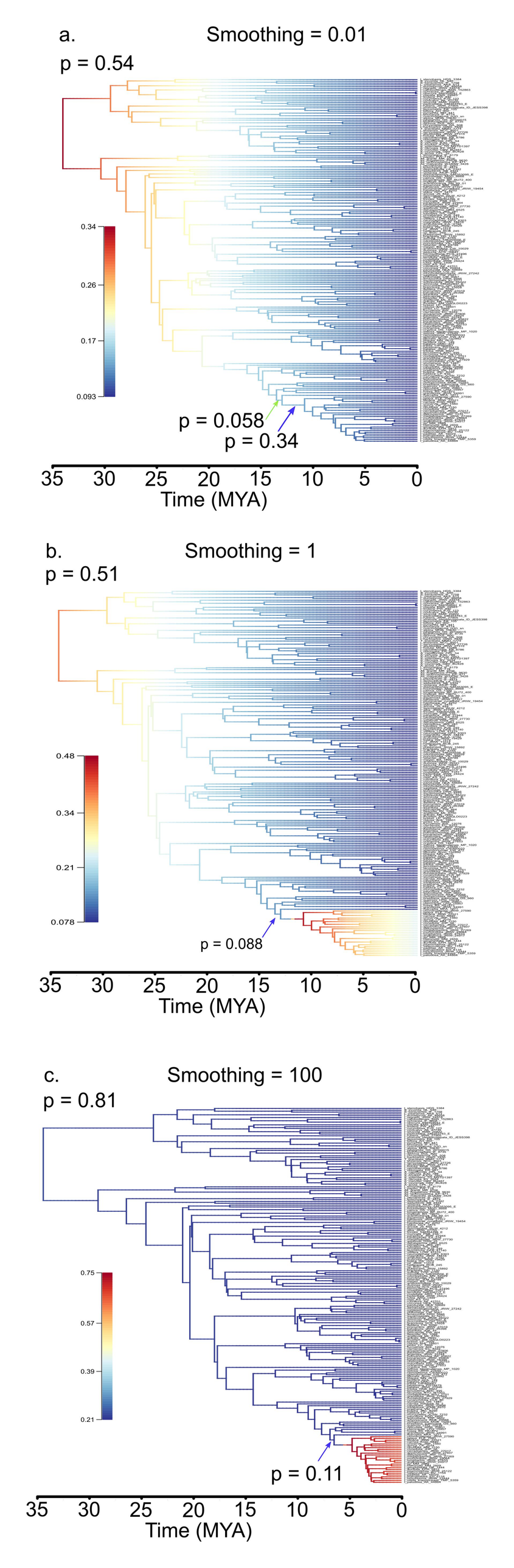
0.21

p = 0.058

p = 0.11

35 30 25 20 15 10 5 0

Time (MYA)


a.
Smoothing = 0.01
p = 0.54
0.34
0.26
0.17
0.093
p = 0.058
p = 0.34
35
30
25
20
15
10
5
0
Time (MYA)
b.
Smoothing = 1
p = 0.51
0.48
0.34
0.21
0.078
p = 0.088
35
30
25
20
15
10
5
0
Time (MYA)
c.
Smoothing = 100
p = 0.81
0.75
0.57
0.39
0.21
p = 0.11
35
30
25
20
15
10
5
0
Time (MYA)

BIOME HABIT

Ipomoea nitida
Ipomoea valenzulensis
Ipomoea aff. *theodori*
Ipomoea malvaeoides
Ipomoea paludosa
Ipomoea padillae
Ipomoea hieronymi
Ipomoea megapotamica
Ipomoea uninervis
Ipomoea geophylifolia
Ipomoea aurifolia
Ipomoea hirtifructa
Ipomoea argentinica
Ipomoea longibarbis
Ipomoea mucronifolia
Ipomoea aff. *psammophila*
Ipomoea psammophila
Ipomoea haenkeana
Ipomoea aff. megapotamica
Ipomoea cerradoensis
Ipomoea cuneifolia
Ipomoea opulifolia
Ipomoea chondrosepala
Ipomoea lilloana
Ipomoea jalapa
Ipomoea appendiculata
Ipomoea praecana
Ipomoea marcellia
Ipomoea carnea subsp. *carnea*
Ipomoea carnea subsp. *fistulosa*
Ipomoea reticulata
Ipomoea graniticola
Ipomoea rosea
Ipomoea pterocaulis
Ipomoea brasiliana
Ipomoea queirozii
Ipomoea verbascoidea
Ipomoea calyptrata
Ipomoea descolei
Ipomoea intrapilosa
Ipomoea wolcottiana
Ipomoea arborescens
Ipomoea pauciflora
Ipomoea murucoides
Ipomoea calobra
Ipomoea polpha
Ipomoea sumatrana
Ipomoea cheirophylla
Ipomoea mauritiana
Ipomoea bonariensis
Ipomoea homotrichoidea
Ipomoea batatoides
Ipomoea oranensis
Ipomoea argentea
Ipomoea paulistana
Ipomoea asplundii
Ipomoea goyazensis
Ipomoea pintoi
Ipomoea clausa
Ipomoea furcyensis
Ipomoea microdactyla
Ipomoea ciervensis
ALL OTHER SPECIES

-20 -15 -10 -5 PRESENT

BIOME

CERRADO-TYPE BIOME
NON-CERRADO-TYPE BIOME

HABIT

TRAILING
LIANA/CLIMBER
UNCERTAIN
ERECT
TREE/SHRUB
TRAILING/LIANA