

## Supporting Information for

### Bursts of rapid diversification, dispersals out of southern Africa, and two origins of dioecy punctuate the evolution of *Asparagus*

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**Author Contributions:** P.C.B. conducted experiments, analyzed data, and wrote the manuscript. P.C.B., J.B., S.B., E.M., Z.M., and J.L.-M. conceived the study. P.C.B., J.B., S.B., Z.M., and J.L.-M. developed experimental designs. Z.L., J-B.Y., M.P., O.S., and G.P. contributed to early design and analysis. All authors contributed to data collection/generation and manuscript edits.

**Appendix S1:** Accession and species sampling information

**Appendix S2:** Target capture results reported by HybPiper

**Appendix S3:** Ancestral range probabilities for all branches/nodes reported by BioGeoBEARS

Appendices S1–S3 are available at <https://zenodo.org/doi/10.5281/zenodo.12812248>.

#### This PDF file includes:

Results S1  
Figures S1 to S8  
Tables S1 to S3  
SI References

## Results S1

### Sequencing and target capture

After minimal filtering, the total number of Hyb-Seq reads per sample were variable, ranging from 162,802 to 174,960,651 (mean=33,736,507; median=27,672,928). The fraction of reads that mapped to reference target sequences (percent on-target reads) were also variable among Hyb-Seq experiments, ranging from 3.1% to 77.4% (mean=39%; median=40%). All samples (Hyb-Seq and whole genome shotgun sequencing [WGS]) yielded >1300 target orthologs, aside from three: *A. secalemontanus* (Burrows & Burrows 15560) yielded 483, *A. denudatus* (Burrows & Burrows 8392) yielded 711, and *A. angusticladus* (Burrows & Burrows 12678) yielded 973 (Appendix S2). Only 14 Hyb-Seq accessions yielded all 1726 targets, however 165 accessions yielded 1720–1726 targets, 210 yielded 1700–1726 targets, and 258 yielded 1650–1726 targets (Appendix S2). Eight of the ten WGS samples yielded >1700 targets (Appendix S2).

### Putative paralogs captured by Asparagaceae1726

Potential paralogs were scored for each locus using default HybPiper (Johnson et al., 2016) run parameters, which report paralogs based on the coverage and number of SPAdes (Bankevich et al., 2012) contig assemblies mapping to a target sequence with inferred paralog scoring based on “depth” (>75% of target length covered by >2 shorter contigs in addition to the putative ortholog assembly) and contiguous “length” (>1 SPAdes contig mapping to >75% of the reference target sequence) of non-primary assemblies for each target (Johnson et al., 2016). Target paralogs detected by HybPiper’s “length” criteria were generally low in this dataset, ranging between 5–33 (mean/median=15) in WGS samples and 0–231 (mean=16; median=15) in Hyb-Seq samples (Appendix S2). The *Hemiphylacus* sample yielded the largest number of possible long paralog assemblies—231 in total—whereas the next two highest totals were 97 (in *A. gobicus* [P.C. Bentz 75]) and 50 (in *A. niassanus*) (Appendix S2). Compared to the long paralog warnings, HybPiper flagged an average of approximately three times as many paralogs with its “depth” detection scheme per sample (Appendix S2).

### Rampant paraphyly and polyphyly across the *Asparagus* phylogeny

Across the *Asparagus* tree, there are many examples of polyphyletic species including strongly supported branches (local posterior probability [LPP]=1). In the Racemose clade, *A. decipiens* was paraphyletic with the budded species *A. aethiopicus* (Fig. S1); *A. tugelicus* evolved in a paraphyletic clade of *A. kwazuluanus*; *A. filicladus* evolved from an ancestral form of *A. acocksii*, which was paraphyletic with the former; and *A. densiflorus* was polyphyletic with two cultivated lineages forming a clade separate from wild forms of the species (Fig. S1). *Asparagus densiflorus* (Kunth) Jessop has long been plagued by taxonomic issues (Wong et al., 2022). Both *A. densiflorus* clades may represent distinct species, or perhaps the *A. densiflorus* cultivars sampled here were derived from separate ancestral species not sampled in this study. Resolving either of those hypotheses is out of the scope of this study, but the polyphyly of *A. densiflorus* in the current analysis illustrates a need for continued taxonomic work on species circumscription within the genus. For instance, recent taxonomic work (Burrows & Burrows, in prep.) shows that *A. densiflorus* of Obermeyer et al. (1992) can be divided into nine clearly separable species. In the Setaceus clade, *A. setaceus* is polyphyletic, arising once in a clade with *A. sylvicola* and again in a clade with *A. brevipedicellatus* (Fig. S1). *Asparagus setaceus* (Kunth) Jessop is another taxonomically problematic

species and was polyphyletic in our species tree analysis (Fig. S1). However, one of the two clades of *A. setaceus*, including an accession from Li et al. (2020) and *Burrows & Burrows 16255*, may represent *Asparagus plumosus* Baker—a species commonly accepted to be synonymous with *A. setaceus* (POWO, 2024). In the Myrsiphyllum clade, accessions of *A. asparagoides* and *A. ovatus* were highly polyphyletic and paraphyletic with various species (Fig. S1). In the Suaveolens clade, *A. spinescens* was paraphyletic with the budded species *A. suaveolens* and *A. burchellii*; *A. flavicaulis* was paraphyletic with *A. candelus*; and *A. capensis* was either paraphyletic with *A. stipulaceus*, *A. litoralis*, and *A. praetermissus*, or polyphyletic (Fig. S1). In the Africani clade, *A. lugardii* was polyphyletic due to one accession (i.e., *Burrows & Burrows 15214*) residing outside a clade with the remaining seven accessions of the species (Fig. S1). In the Exuvialis clade, *A. exuvialis* was paraphyletic with two budded species: *A. ecklonii* and *A. namaquensis* (Fig. S1). In the Asparagus clade, a grade of *Asparagus gobicus* N.A.Ivanova ex Grubov accessions caused this species to be paraphyletic with the nested/budded species *Asparagus dauricus* Fisch. ex Link and *Asparagus kiusianus* Makino. All three of these species occur in similar environments – arid, sandy wastelands sometimes by the sea – but exhibit different geographic ranges: *A. kiusianus* is endemic to the Japanese islands (Ōi, 1965); *A. dauricus* is widespread across Mongolia, China, and Korea, and the extant ancestral species *A. gobicus* is more restricted to Mongolia and parts of China (Xinqi and Tamanian, 2000). Also in the Asparagus clade, *A. longiflorus* resulted in a polytomy with *A. breslerianus*; and *A. persicus* and *A. pseudoscaber* were paraphyletic and in a polytomy with *A. officinalis* (Fig. S1).

### **Range expansions out of Africa**

We found support for eight independent shifts out of Africa that led to colonization of Eurasia, six of which involved the most recent common ancestor (MRCA) of extant bisexual lineages, including: the MRCA of *A. cooperi* and *A. devenishii* (Africani clade); *A. africanus* (Africani clade); *A. virgatus* (setaceus clade); *A. falcatus* (Racemose clade); *A. racemosus* (Racemose clade); and *A. abyssinicus* (Asparagus clade). We also found support for three separate expansions into Macaronesia involving two bisexual lineages that dispersed from southern Africa (i.e., the MRCA of *A. umbellatus* and *A. arborescence* [Setaceus clade] and the MRCA of *A. scoparius* and *A. plocamoides* [Africani clade]) and the dioecious species *A. horridus* (Asparagus clade) which likely dispersed from the Arabian Peninsula (Fig. S6a) or northern Africa (Figs. S6b, S7). Following the establishment of the Eurasian dioecy clade in eastern Asia, a secondary expansion led to colonization of Europe (main text, Fig. 3), which disagrees with previous findings that suggest dispersal into Eurasia began westward from southern Africa to northern Africa and Europe, then eastward into Asia (Norup et al., 2015). However, the sparse sampling of dioecious species by Norup et al. (2015), and application of misreported range data for *A. officinalis* (further discussed in main text), likely explains our incongruent results.

### **Delineation of four additional major clades of *Asparagus***

**Scandens clade** – *Asparagus scandens* (Thunb.) Oberm. of the Scandens clade has long troubled taxonomists and, due to the sharing of several traits typical of Myrsiphyllum species—including flattened (leaflike) cladodes—*A. scandens* is often lumped into Myrsiphyllum (formerly genus *Myrsiphyllum* Willd.) (Malcomber and Demissew, 1993). The key traits commonly used to identify Myrsiphyllum species are the presence of basally connivent perianth segments and connivent filaments (Malcomber and Demissew, 1993), but this would exclude the Scandens clade (as

delimited here) as well as *Asparagus ramosissimus* Baker (Malcomber and Demissew, 1993) for which there was strong support for its placement in the Myrsiphyllum clade (Fig. S1). Not only does the Scandens clade exhibit morphological affinity to the Myrsiphyllum clade, but phylogenomic analysis supports a Myrsiphyllum-Scandens clade (LPP=0.83) over alternative resolutions (Fig. S5). Due to shared morphology and weak support in phylogenomic analyses it is possible that the Scandens clade is more related to Myrsiphyllum than any other clade, but our analyses failed to show consistent support for that hypothesis. According to our analyses, the most probable relationship between the Myrsiphyllum and Scandens clades was a polytomy including two additional major clades (Fig. S1). Considering the absence of a connivent perianth and filaments in *A. ramosissimus*, it is possible that ancestral polymorphisms—both phenotypic and genotypic—were lingering in ancestral populations of *Asparagus* and were carried over into the two contemporary clades Myrsiphyllum and Scandens. For example, perhaps over time, as new species formed and continued to diverge from ancestral populations, various polymorphisms (i.e., connivent or spreading perianth segments and filaments) may have become fixed in different populations/species (i.e., *Asparagus mollis* (Oberm.) Fellingham & N.L.Mey., in the Scandens clade and *A. ramosissimus* in the Myrsiphyllum clade) leading to different ancestral traits sorting between closely related species. Of course, it remains possible that *A. mollis* and *A. ramosissimus* independently evolved floral traits that differ from their ancestors. In any event, the placement of *A. scandens* in our analyses (Fig. S1) is incongruent with previous work that placed it sister to the Retrofracti clade with significantly less sequence data (Norup et al., 2015).

**Nutlet clade** – Species tree analysis also revealed strong support for a monophyletic Nutlet clade (Fig. S1), suggesting a single origin of a nutlet fruit type in *Asparagus*. A nutlet fruit represents the main synapomorphy of the Nutlet clade and was likely derived from an ancestral black or red berry fruit type, which are ubiquitous in the Suaveolens and Africani-Sympodioidi clades, respectively. Norup et al. (2015) sampled two nutlet bearing species and showed moderate support for a bifurcation between those and the Suaveolens clade but referred to the nutlet bearing clade as ‘Recurvispinus’ and lumped it in with the greater Suaveolens clade.

**Sympodioidi clade** – As described here, the Sympodioidi clade is equivalent to the Sympodioidi series previously described (Obermeyer et al., 1992) and is identifiable by their dichotomously branching stems with hard/woody scales and umbellate inflorescences. The Sympodioidi clade was strongly supported as monophyletic and sister to the greater Africani clade (Fig. S1), whereas a previous analysis of the same Sympodioidi species showed weak support for the nesting of Sympodioidi within the Africani clade (Norup et al., 2015).

**Macowanii clade** – Resolution of a Macowanii clade sister to the Racemose clade was strongly supported in analyses performed here (Fig. S1) and in previous work (Norup et al., 2015). The early branching of Macowanii taxa from the larger Racemose clade, coupled with distinct inflorescence morphologies found in Macowanii taxa (i.e., solitary flowers) compared to most Racemose taxa (i.e., compound inflorescences) supports delineation of the two clades.

### **New combinations of *Asparagus* species associated with this study**

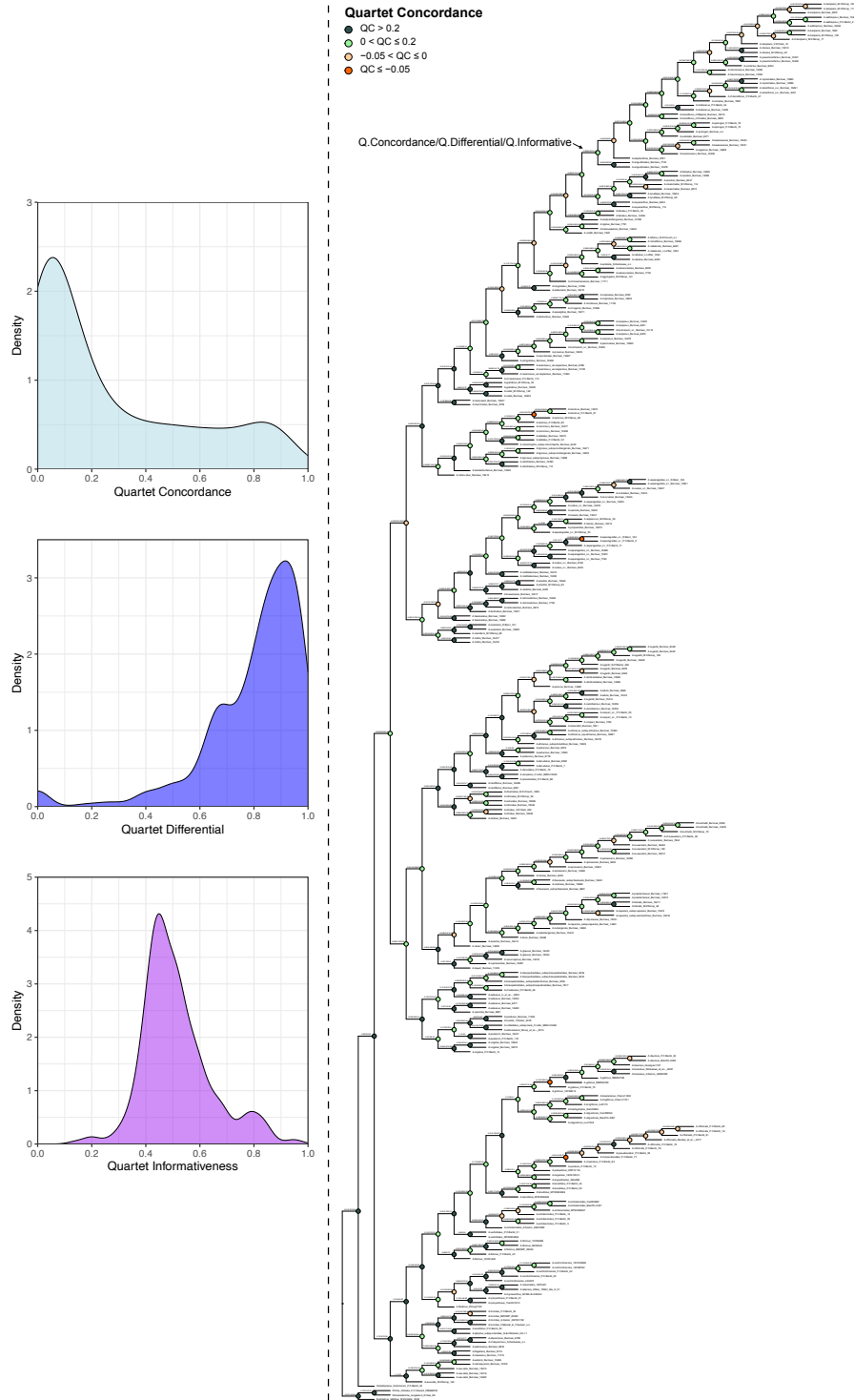
Alongside this study, a taxonomic revision of *Asparagus* species in Africa was completed by John E. Burrows and Sandra M. Burrows for a separate publication. (Appendix S1). The following species and subspecies (marked with ‘MS’) were described for the first time in the aforementioned revision of *Asparagus*: *Asparagus atrobracteatus* MS, *Asparagus brevipedicellatus* MS subsp. *barbertonicus* MS, *Asparagus brevipedicellatus* MS subsp. *brevipedicellatus* MS, *Asparagus candelus* MS, *Asparagus cederbergensis*

MS, *Asparagus cupressoides* MS, *Asparagus dolomiticus* MS, *Asparagus ferox* MS, *Asparagus helmei* MS, *Asparagus humifusus* MS, *Asparagus inopinatus* MS, *Asparagus kwazuluanus* MS, *Asparagus linearis* MS, *Asparagus macrocarpus* MS, *Asparagus namaquensis* MS, *Asparagus niassanus* MS, *Asparagus oubergensis* MS, *Asparagus paniculatus* MS, *Asparagus petiolatus* MS, *Asparagus pongolanus* MS, *Asparagus praetermissus* MS, *Asparagus procerus* MS, *Asparagus pseudoconfertus* MS, *Asparagus recurvatus* MS, *Asparagus saxicola* MS, *Asparagus secalemontanus* MS, *Asparagus soutpansbergensis* MS, *Asparagus tugelicus* MS, *Asparagus zanjianus* MS, *Asparagus lignosus* Burm.f. subsp. *rooibergensis* MS, *Asparagus capensis* L. subsp. *saximaritimus* MS, *Asparagus lignosus* Burm.f. subsp. *rooibergensis* MS.

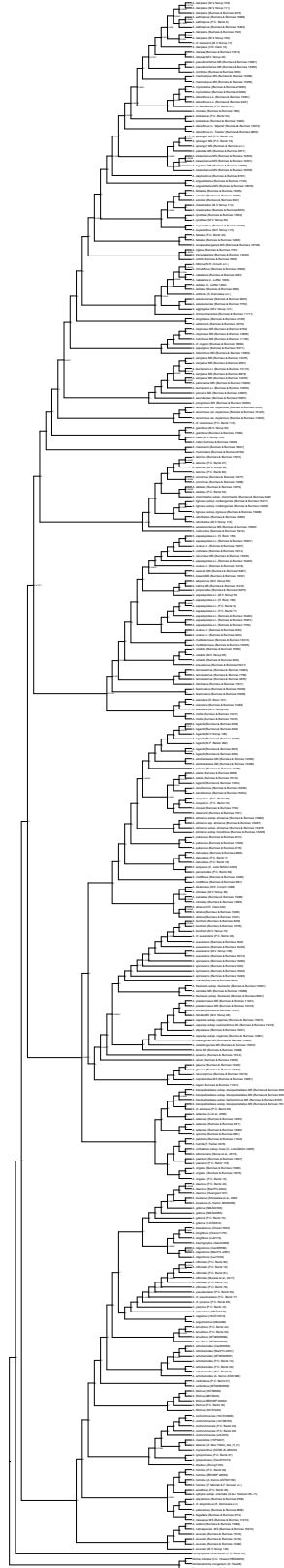
Additionally, three taxa were raised to the species level and nine were reinstated, since their taxonomic reorganization in Flora of Southern Africa (Obermeyer et al., 1992), Flora of Tropical East Africa (Demissew, 2006), Flora Zambesiaca (Demissew 2008), and Plant of the World Online (2024): *Asparagus litoralis* (Suess. & Karling) MS was raised to species from *Asparagus capensis* L. var. *litoralis* Suess. & Karling; *Asparagus decipiens* (Baker) MS was raised to species from *Asparagus racemosus* Willd. var. *decipiens* Baker; *Asparagus comatus* (Baker) MS was raised to species from *Asparagus sarmentosus* L. var. *comatus* Baker. The following taxa were reinstated, relative to previous taxonomic combinations: *Asparagus multiflorus* Baker, *Asparagus puberulus* Baker, *Asparagus abyssinicus* Hochst. ex A.Rich, *Asparagus lugardii* Baker, *Asparagus myriocladus* Baker, *Asparagus sprengeri* Regel, *Asparagus ecklonii* Baker, *Asparagus wildemanii* Weim., *Asparagus zanzibaricus* Baker, *Asparagus racemosus* Willd. var. *zeylanicus* Baker. See Appendix S1 for more information about specific samples and taxonomic authorities used in this study.



**Figure S1.** Final species tree phylogram of all accessions from this study showing local posterior probability branch support when  $<0.99$ . Bifurcations for which a polytomy could not be rejected ( $p$ -value  $>0.05$ ) when tested with ASTRAL (Zhang et al., 2018) were collapsed into polytomies.

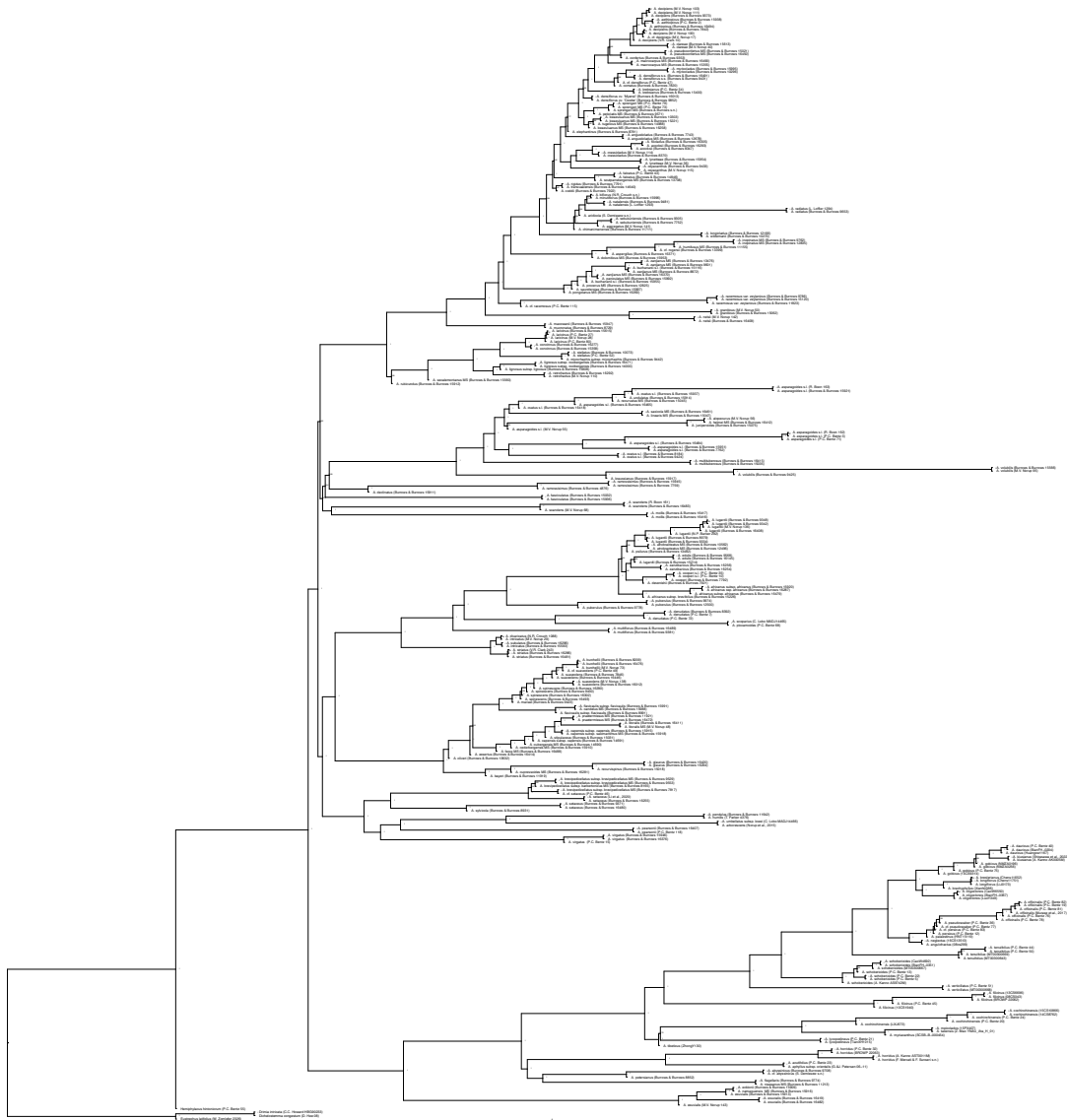


**Figure S2.** Right panel shows bifurcating species tree cladogram with results from Quartet Sampling (Pease et al., 2018) (plot: [https://github.com/ShuiyinLIU/QS\\_visualization](https://github.com/ShuiyinLIU/QS_visualization)). Left panel shows histograms of the following metrics from Quartet Sampling. Quartet Concordance overall had a left skewed density distribution (mean=0.23; median=0.09), which is suggestive of considerable gene tree discordance at many nodes. Quartet Differential overall (mean=0.87; median=0.91) suggested limited skew in alternative quartet support. Quartet Informativeness (QI) was moderate across all nodes (mean=0.52; median=0.48) indicating a high degree of information in the gene trees.

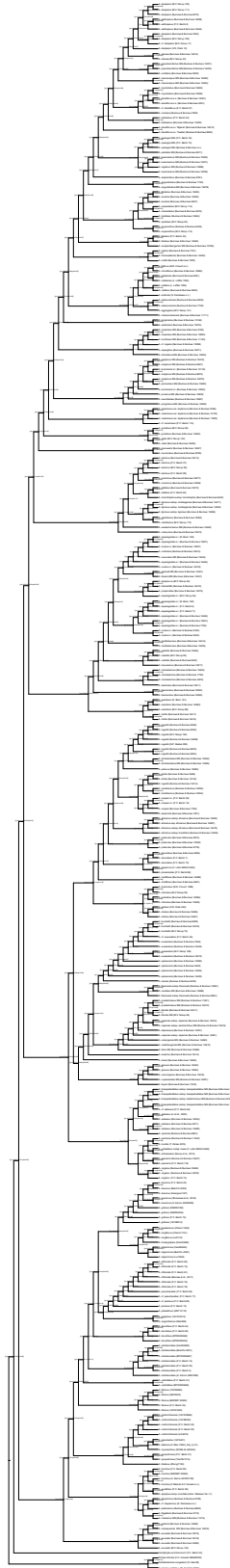


**Figure S3.** Preliminary species tree cladogram of all accessions showing  $p$ -values from a polytomy test performed with ASTRAL (Zhang et al., 2018). A polytomy could not be rejected for branches with a  $p$ -value  $>0.05$  and were subsequently collapsed.

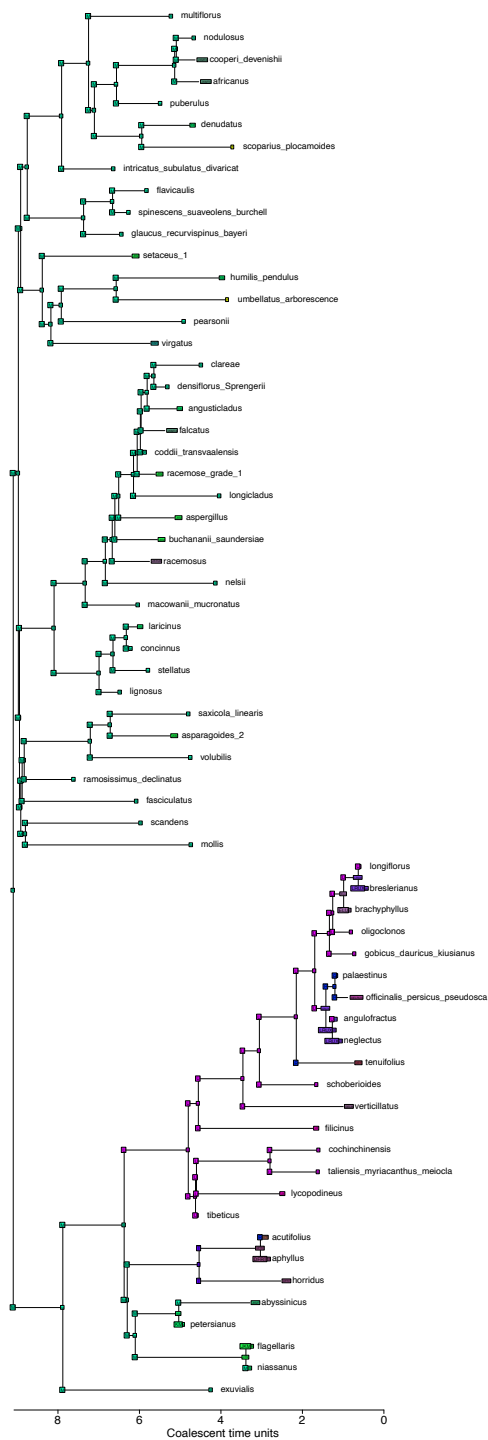




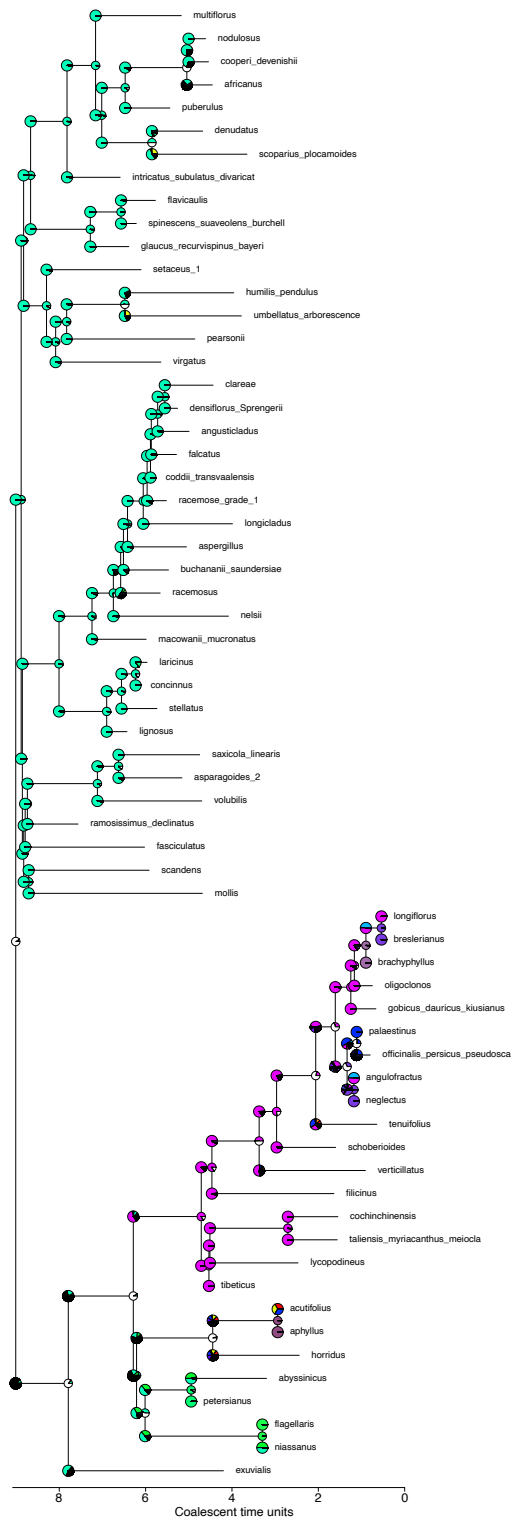
**Figure S4.** Preliminary species tree phylogram of all accessions showing local posterior probability branch support from ASTRAL (Zhang et al., 2018) for forced bifurcations.



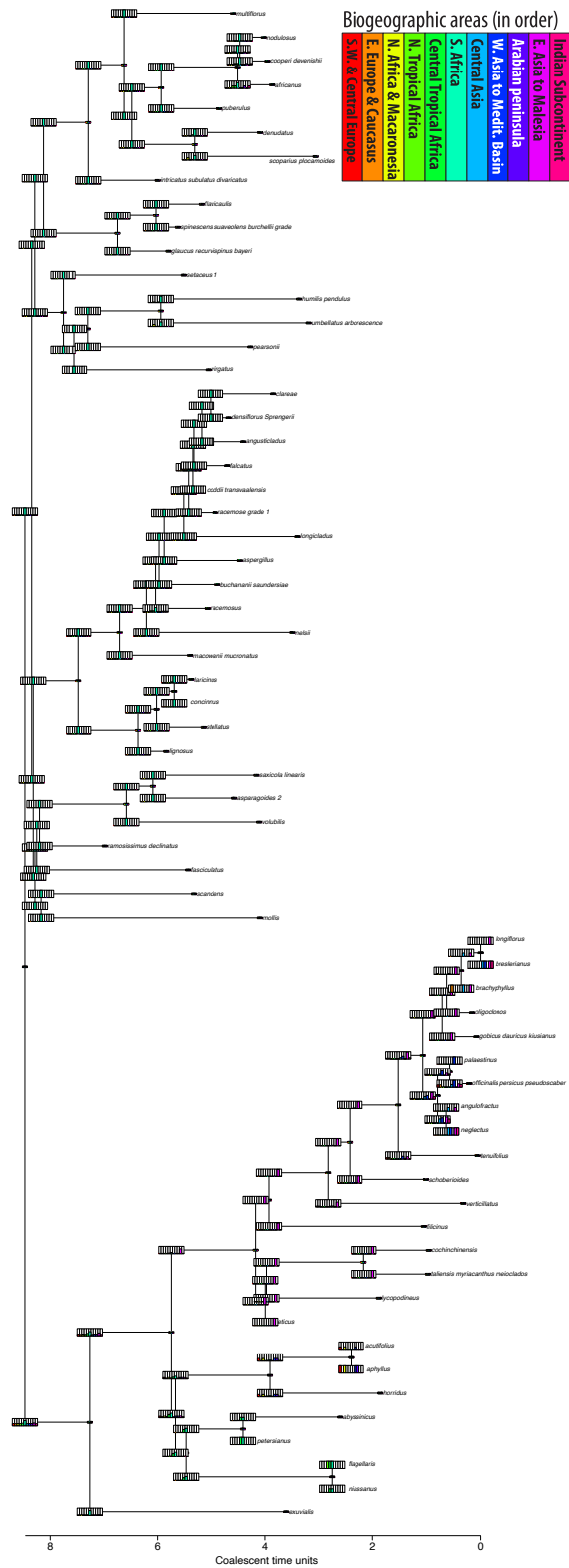
**Figure S5** Preliminary species tree cladogram showing quartet frequency support from ASTRAL (Zhang et al., 2018) for the top three topologies. Frequencies represent proportion of gene tree quartets supporting the main topology ( $q1$ : shown) and two alternatives ( $q2$  and  $q3$ ).



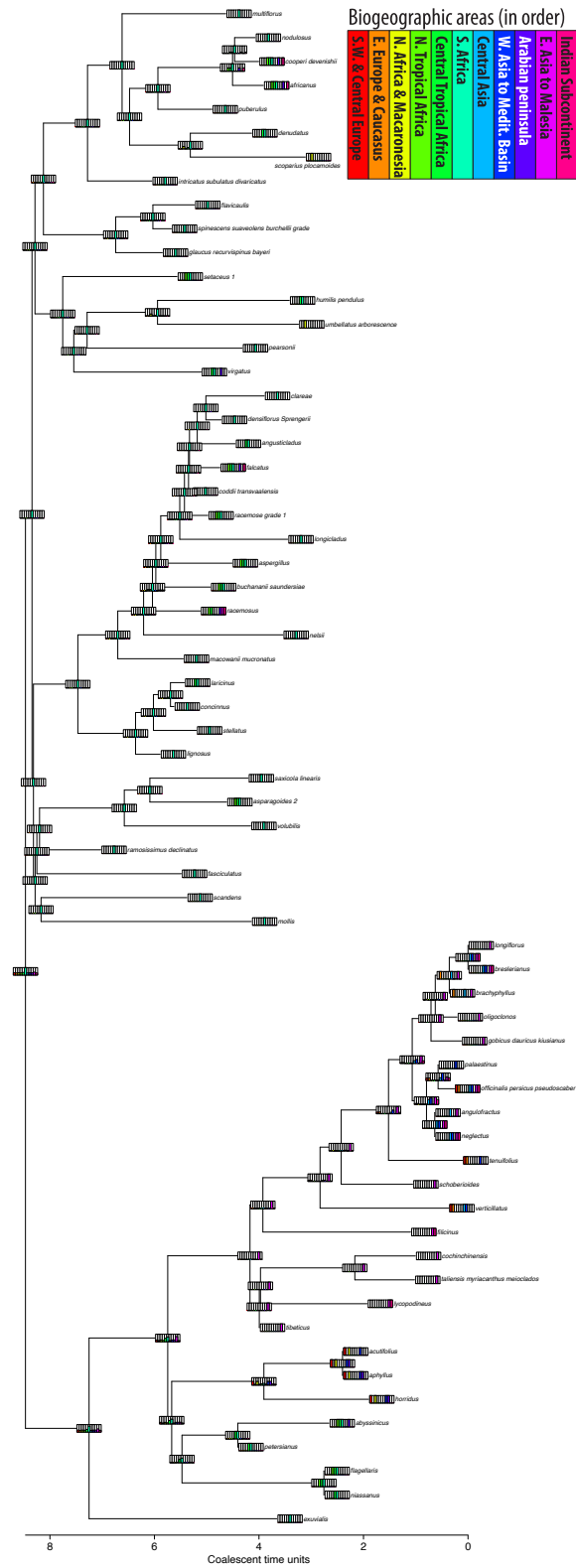
**Figure S6a.** Ancestral range estimation results showing letter codes representing the most probable ancestral *range* for each internal node and split according to BioGeoBEARS model DEC+J (Matzke, 2016). Splits are defined as the *ranges* immediately following cladogenesis and are plotted on branch corners. Geographic *areas* include: (D) Southwestern + Central Europe, (E) Eastern Europe + Caucasus, (F) Northern Africa + Macaronesia, (J) Northern Tropical Africa, (K) Central Tropical Africa, (L) Central Asia, (M) Southern Africa + Madagascar, (R) Western Asia to Mediterranean Basin, (T) Arabian Peninsula, (U) Eastern Asia to Malesia, and the (X) Indian Subcontinent. *Area* = discrete geographic region. *Range* = species distribution encompassing any combination of *areas*. See Dataset 3 for a list of collapsed lineages.



**Figure S6b.** Ancestral range estimation probabilities (pies) for the ancestral *range* distribution of each internal node and split estimated using the BioGeoBEARS model DEC+J (Matzke, 2016). Pie colors correspond to geographic *ranges* plotted on the tree in Fig. S6a. Splits are defined as the *ranges* immediately following cladogenesis and are plotted at corners. *Area* = discrete geographic region. *Range* = species distribution encompassing any combination of *areas*.



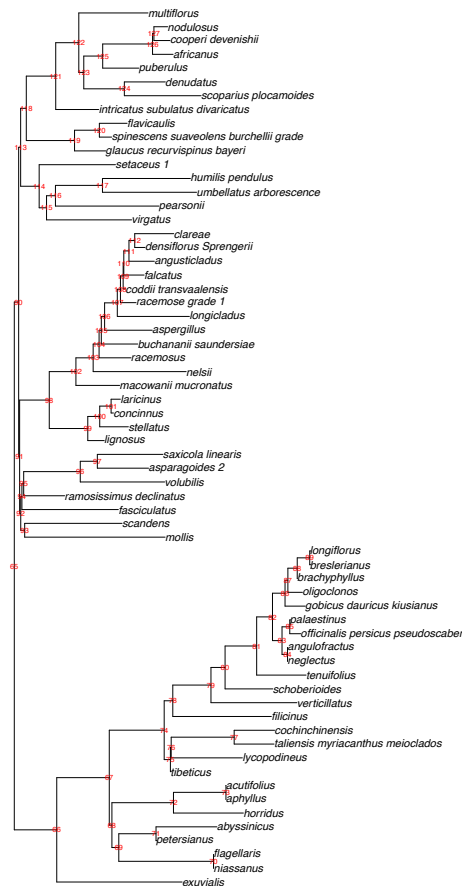
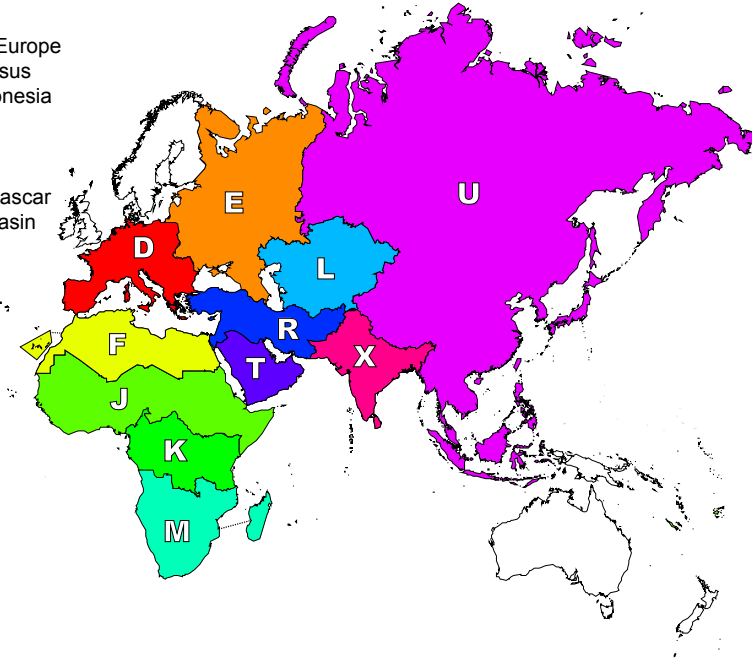
**Figure S7a.** BioGeoBEARS (Matzke, 2016) plot showing bar charts of relative probabilities of geographical *area* occupancy (i.e., probability that a *range* included any of the 11 predefined *areas*) for each internal split. Splits are defined as the *ranges* immediately following cladogenesis and are plotted on branch corners. *Area* = discrete geographic region. *Range* = species distribution encompassing any combination of areas.



**Figure S7b.** BioGeoBEARS (Matzke, 2016) plot showing bar charts of relative probabilities of geographical area occupancy (i.e., probability that a *range* included any of the 11 predefined areas) for each node. *Area* = discrete geographic region. *Range* = species distribution encompassing any combination of areas.

**Code Geographic area**

- D Southwestern + Central Europe
- E Eastern Europe + Caucasus
- F Northern Africa + Macaronesia
- J Northern Tropical Africa
- K Central Tropical Africa
- L Central Asia
- M Southern Africa + Madagascar
- R Western Asia to Medit. Basin
- T Arabian Peninsula
- U Eastern Asia to Malaysia
- X Indian Subcontinent



**Figure S8.** Top plot shows the 11 geographic areas defined for ancestral range estimation with BioGeoBEARS (Matzke, 2016). Bottom plot shows the phylogeny used for ancestral range estimation with node numbers corresponding to BioGeoBEARS results in Dataset S2. Australia was not included in ancestral range tests since *Asparagus racemosus* Willd. is the only species native there.

**Table S1.** Model test results among biogeographic models estimated with BioGeoBEARS (Matzke, 2016).

Model	LnL	Parameters	Parameter estimates			AICc	AICc_wt
			<i>d</i>	<i>e</i>	<i>j</i>		
DEC	-305.6	2	0.053	0.085	0	615.4	0.2
<b>DEC+J</b>	<b>-303.1</b>	<b>3</b>	<b>0.069</b>	<b>0.36</b>	<b>1.00E-05</b>	<b>612.7</b>	<b>0.8</b>
DIVALIKE	-361.5	2	0.06	1.00E-12	0	727.3	1.00E-25
DIVALIKE+J	-361.5	3	0.06	1.20E-08	1.00E-05	729.5	3.40E-26
BAYAREALIKE	-321.8	2	0.04	0.2	0	647.7	1.90E-08
<b>BAYAREALIKE+J</b>	<b>-308.6</b>	<b>3</b>	<b>0.038</b>	<b>0.16</b>	<b>0.0048</b>	<b>623.7</b>	<b>0.0033</b>

**Note:** AICc = Akaike information criterion (AIC) corrected for sample size. AICc\_wt = AIC weighted based on relative likelihood of the model divided by the sum of the relative likelihood of all models (higher AICc\_wt values are favored) (Burnham and Anderson, 2002). Parameter definitions: *d* = base rate of range expansion; *e* = rate of range contraction; *j* = per-event weight of founder-event speciation at cladogenesis (Matzke, 2014).



**Table S2.** Nested model test results comparing log-likelihoods (LnL) between nested models from BioGeoBEARS (Matzke, 2016). Table shows results from testing for significant model improvement when applying the *j* parameter to each of the biogeographic models.

<b>Alt. model</b>	<b>Null</b>	<b>LnL alt.</b>	<b>LnL null</b>	<b>DF</b>	<b>D stat.</b>	<b><i>p</i>-value</b>
<b>DEC+J</b>	<b>DEC</b>	<b>-303.1</b>	<b>-305.6</b>	<b>1</b>	<b>4.96</b>	<b>0.026</b>
<b>DIVALIKE+J</b>	<b>DIVALIKE</b>	-361.5	-361.5	1	-0.0076	1
<b>BAYAREALIKE+J</b>	<b>BARYAREALIKE</b>	-308.6	-321.8	1	26.28	3.00E-07

**Note:** Significant model improvement was inferred based on a *p*-value significance cutoff of >0.05. The *j* parameter allows for founder events within clades (Matzke, 2014).

**Table S3.** Comparing morphology-based taxonomic treatments of subgeneric groups of *Asparagus* in southern Africa with species tree clade assignments from this study.

Current study	Baker (1896)	Jessop (1966)	Obermeyer et al. (1992)
Clade	Section	Section	Series
<b>Africani</b>	Declinati (1) Umbellati (2) Thunbergiani (1) Africani (1)	Africani (2) Racemosi (1)	Africani (3) Retrofracti (4)
<b>Asparagus</b>	-	-	-
<b>Exuviali</b>	Declinati (2)	Exuviali (1)	Exuviali (1)
<b>Macowanii</b>	Declinati (1)	Africani (2)	Retrofracti (1) Globosi (1)
<b>Myrsiphyllum</b>	Declinati (1) Striati (1) Myrsiphylli (5)	Africani (1) Racemosi (1) Scandentes (1) Crispi (1) Myrsiphyllum (2)	Myrsiphyllum <sup>a</sup> (11)
<b>Nutlet</b>	-	Capenses (1)	Suaveolens (3)
<b>Racemose</b>	Thunbergiani (1) Racemosi (2) Falcati (5)	Racemosi (13)	Africani (1) Exuviali (1) Racemosi (6) Protasparagus (14) Globosi (4)
<b>Retrofracti</b>	Thunbergiani (3) Africani (2)	Africani (5)	Africani (1) Retrofracti (3) Globosi (3)
<b>Scandens</b>	Striati (1)	Scandentes (1)	Penduli (1) Myrsiphyllum <sup>a</sup> (1)
<b>Setaceus</b>	Declinati (2)	Africani (2)	Penduli (2) Retrofracti (1) Globosi (2)
<b>Suaveolens</b>	Capenses (5)	Capenses (3)	Suaveolens (9)
<b>Sympodioidi</b>	Umbellati (1) Striati (2)	Striati (2)	Sympodioidi (4)

**Note:** Parenthesized numbers represent the number of species from each respective, previously described, subgeneric group that were placed in corresponding clades from this study. Baker (1896) proposed that all diversity of southern African lineages of *Asparagus* could fit into 9 total sections, whereas Jessop (1966) proposed 8 sections and Obermeyer et al. (1992) proposed 9 series for such.

<sup>a</sup> Represents genus *Myrsiphyllum* Willd.

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