

Long-distance dispersal events rather than growth habit and life-history traits affect diversification rate in tribe Apieae (Apiaceae)

KAMIL E. FRANKIEWICZ^{1,*}, ŁUKASZ BANASIAK¹, ALEXEI OSKOLSKI^{2,3},
JEAN-PIERRE REDURON⁴, JORGE ALFREDO REYES-BETANCORT⁵,
MOHAMMED ALSARRAF¹, PAULINA TRZECIAK⁶ and KRZYSZTOF SPALIK¹

¹*Institute of Evolutionary Biology, Faculty of Biology, University of Warsaw, Biological and Chemical Research Centre, Żwirki i Wigury 101, 02-089 Warsaw, Poland*

²*Department of Botany and Plant Biotechnology, University of Johannesburg, PO Box 524, Auckland Park 2006, Johannesburg, South Africa*

³*Komarov Botanical Institute, Prof. Popov str. 2, 197376 St. Petersburg, Russia*

⁴*Via Apia, 10 rue de l'Arsenal, 68100 Mulhouse, France*

⁵*Jardín de Aclimatación de la Orotava, Instituto Canario de Investigaciones Agrarias (ICIA), C/Retama no. 2, 38400 Puerto de la Cruz, S/C de Tenerife, Spain*

⁶*Faculty of Biology and Veterinary Sciences, Nicolaus Copernicus University, Lwowska 1, 87-100, Toruń, Poland*

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Factors influencing diversification rates may be of intrinsic (e.g. morphological novelties) or extrinsic (e.g. long-distance dispersal, availability of ecological niches) nature. Growth habit may influence diversification rates because herbaceous plants often have shorter generation times and a more pronounced *r* reproductive strategy than their woody relatives. We examined life history and habit evolution, wood anatomy and biogeographical history of Apiaceae tribe Apieae in conjunction with diversification rate analysis to explore which factors may have affected clade species richness and to elucidate the constraints on the evolution of secondary woodiness in this group. We demonstrate that diversification rates are similar in morphologically homogeneous and diverse clades and in herbaceous and woody lineages. The only clade with a significantly elevated diversification rate is Southern Hemisphere *Apium*, in which diversity probably resulted from several long-distance dispersal events. We also show that wood anatomy in herbaceous and woody species does not differ considerably regardless of their continental or insular origin, but it is affected by stem architecture and plant reproductive strategy. As the taxonomy of Apieae suffers from inflation with numerous monotypic genera, we propose to include *Canaria* in *Rutheopsis*, and *Foeniculum*, *Schoenoselinum*, *Ridolfia* and *Pseudoridolfia* in *Anethum*.

ADDITIONAL KEYWORDS: *Apium* – *Billburttia* – biogeography – derived woodiness – *Deverra* – insular woodiness – net speciation – pervasive parenchyma – secondary woodiness – taxonomy.

INTRODUCTION

The species richness of a clade results from an interplay between speciation and extinction, i.e. from diversification rate (DR), which is heavily affected by a multitude of factors (Ricklefs, 2007). Net speciation rate varies between clades, and gaining an understanding of the factors that influence this is one of the main

goals of modern ecology. It is tempting to assume that clades with more species have higher DR than those with fewer species, but in fact such an observation may be purely an artefact of a poorly chosen evolutionary model and insufficient or non-random sampling (Revell, Harmon & Glor, 2005; Ricklefs, 2007; Cusimano & Renner, 2010). Indeed, several taxa have been falsely identified as having inflated DR, only because of the great number of species they include. One such case is *Astragalus* L. (Fabaceae), commonly perceived as

*Corresponding author. E-mail: frankiewicz@biol.uw.edu.pl

having extremely high DR, whereas it was shown to diversify at a rate similar to its closest relatives in the astragalean clade (Sanderson & Wojciechowski, 1996). Moreover, Fabaceae as a whole were shown to have a low DR, and the extremely high species richness should rather be attributed to the great age of the family, allowing for multiple speciation events (Magallón & Sanderson, 2001; Lavin, Herendeen & Wojciechowski, 2005). Including clade age in the estimation of its DR is therefore crucial, because (1) old clades might be wrongfully identified as having a high DR and (2) a young clade might be misconstrued as having a low DR as all young clades will include fewer species, regardless of their DR. Estimation of DR in relatively young clades is also prone to ‘push of the past’ and ‘pull of the present’ artefacts (e.g. types of survivorship biases that can lead to the retrieval of an apparent slowdown or acceleration in DR towards the present resulting from the fact that older clades that survived to the present are likely to have experienced an early burst of diversification, whereas younger clades may have over-estimated DR because they do not yet have enough time to die off; Nee, May & Harvey, 1994; Budd & Mann, 2018).

Only after avoiding the aforementioned problems and having identified a clade with higher DR might one start to seek explanations of a high net speciation. Most DR studies to date have tried to identify a unique trait or set of traits explaining higher speciation and/or lower extinction. Putative explanations invoked for plants have included: biotic vs. abiotic pollination; biotic fruit dispersal; presence of floral nectar spurs; self-sterility; dioecy; and herbaceous vs. woody growth habit (Baldwin & Sanderson, 1998; Dodd, Silvertown & Chase, 1999; Sims & McConway, 2003; Ferrer & Good, 2012; Käfer *et al.*, 2014). Growth habit has a particular potential to influence DR as herbaceous plants tend to have shorter generation times and a more pronounced *r* reproductive strategy than their woody relatives, thus promoting more rapid diversification. On the other hand, Nürk, Atchison & Hughes (2019) demonstrated that at least some derived woody clades, i.e. lineages with shrubby or arborescent habits derived from herbaceous ancestors, have inflated DR.

The evolution of derived woodiness has been explained (among other hypotheses) based on cavitation resistance it provides (Lens *et al.*, 2013a). Drier environments cause higher embolism formation rates, promoting the evolution of counter-adaptations: experimental studies showed that derived woody species are less embolism-susceptible than their herbaceous relatives (Dória *et al.*, 2018, 2019). Thus, the habit shift from herbaceous ancestor to woody descendants may turn out to be beneficial (a ‘key innovation’; Donoghue, 2005; Simões *et al.*, 2016)

and lead to higher net speciation. However, derived woodiness is best known from oceanic islands (where it is often termed ‘insular woodiness’, e.g. Dulin & Kirchoff, 2010; Kidner *et al.*, 2015; Merckx *et al.*, 2015), and therefore it is also possible that higher DR results not from the habit shift itself, but from long-distance dispersal (LDD) leading to an arrival in previously unoccupied habitats. The latter explanation is particularly likely because derived woodiness has also been postulated to evolve merely as a by-product of postponed generative reproduction and prolonged lifespan in moderate climates with low seasonality (Carlquist, 1974; Dulin & Kirchoff, 2010).

The significance of dispersal followed by diversification (‘dispersification’ *sensu* Moore & Donoghue, 2007) to previously unoccupied areas has gained empirical support in certain clades; for example, comparison of multiple mammalian sister clades showed that the clade which stayed in the area unequivocally resolved as ancestral presented lower species richness than the one which settled in a new zone (Verdú, 2002; Kisel *et al.*, 2011), and the availability of novel niches after recurring, successful dispersal events was evoked to explain megadiversity of *Carex* L. (Martín-Bravo *et al.*, 2019). Additionally, it was shown that rapid diversification may parallel little morphological change (Adams *et al.*, 2009) and vice versa (‘disparification’ *sensu* Simões *et al.*, 2016). Indeed, multiple recent studies failed to pinpoint morphological traits putatively responsible for the high clade diversification: this is best seen in Andean *Lupinus* L. and European *Dianthus* L., two genera of almost unparalleled DR (Hughes & Eastwood, 2006; Valente, Savolainen & Vargas, 2010; see also: Adams *et al.*, 2009; Magallón & Sanderson, 2001; Scholl & Wiens, 2016). Such cases reinforce the presence of external factors in driving up DR, e.g. physical isolation (leading to geographical radiation *sensu* Simões *et al.*, 2016) or climatic shifts (leading to climatic radiation *sensu* Simões *et al.*, 2016). In the case of Andean *Lupinus*, the answer might indeed be the multitude of empty ecological niches and the geographical isolation, which followed orogenesis, whereas for *Dianthus* an adaptation to climatic factors (e.g. high seasonality) probably played this role. In fact, the ability of rapid ecological niche shifts has been shown to underpin species diversification (Kozak & Wiens, 2010), because such taxa will more easily expand to new adaptive zones (leading to the onset of geographical barriers and higher speciation) and will be less likely to die off as a result of local niche changes (leading to a lower extinction rate).

Apiaceae tribe Apieae is particularly suited for a study of factors affecting DR because, while retaining the basic morphological uniformity so characteristic

of the subfamily Apioideae (Plunkett *et al.*, 2018), it represents a considerable diversity of life histories (annuals, biennials, perennials), life/growth forms (therophytes, hemicryptophytes, chamaephytes) and reproductive strategies (monocarpic and polycarpic; Downie *et al.*, 2010; Jiménez-Mejías & Vargas, 2015; Plunkett *et al.*, 2018). Apieae comprise *c.* 46 species that are distributed in the Palaearctic and Mediterranean regions of the Northern Hemisphere and in Madagascar, southern Africa, South America and Australasia in the Southern Hemisphere. Its generitype, *Apium* L., is one of only few apioid genera with an amphitropic and amphiantarctic distribution (Spalik *et al.*, 2010). Although intergeneric relationships in the tribe are reasonably well established (Jiménez-Mejías & Vargas, 2015), previous biogeographical analyses were based on a limited taxonomic sampling (Spalik *et al.*, 2010), and the previous node calibration employed only two molecular markers (Fernández-Mazuecos *et al.*, 2014). Moreover, studies on its wood anatomy, a possible proxy for ecological niche shifts, are almost non-existent (Rodríguez, 1957; Rakotondrandrasana *et al.*, 2017).

Since the shrubby genera of Apieae (*Billburttia* Magee & B.-E. van Wyk from Madagascar, *Deverra* DC. from continental Africa) are nested among the herbaceous taxa, it is most likely that woodiness in this tribe is phylogenetically derived. This condition has been documented in many families, especially on oceanic islands, including Apiaceae (Jorgensen & Olesen, 2001; Lens *et al.*, 2013b; Carlquist, 2017; Whittaker *et al.*, 2017; Dória *et al.*, 2018; Frankiewicz *et al.*, 2020). However, among the insular endemic Apieae, only the two species of Malagasy *Billburttia* are shrubby, whereas the remaining ones [three species of *Ammi* L. from the Azores, *Canaria tortuosa* (Webb & Berthel.) Jim. Mejías & P. Vargas and *Rutheopsis herbanica* (Bolle) A. Hansen & G. Kunkel from the Canary Islands, *Naufraga balearica* Constance & Cannon from the Balearic Islands, *Apium filiforme* Hook. from New Zealand and *Apium fernandezianum* Johow from the Juan Fernández Islands] never evolved shrubby or treelet habit and are morphologically similar to their continental relatives (Jiménez-Mejías & Vargas, 2015). In other clades of Apiaceae, secondary woodiness has evolved on the Azores (*Angelica lignescens* Reduron & Danton), the Canary Islands [species of *Pimpinella* L., *Daucus elegans* (Webb ex Bolle) Spalik, Banasiak & Reduron], the Juan Fernández Islands (species of *Eryngium* L.), Madeira [*Daucus decipiens* (Schrad. & J.C. Wendl.) Spalik, Wojew., Banasiak & Reduron, *Daucus edulis* (Lowe) Wojew., Reduron, Banasiak & Spalik] and New Zealand (species of *Scandia* J.W. Dawson). It needs to be kept in mind that the lack of shrubby or tree(let) habit among some insular endemics may be

due to chance, but there are also tentative, functional explanations for the morphological and ecological stasis of insular Apieae.

First, it may have resulted from their young age coupled with a relatively recent arrival on the islands. Unlike islands of volcanic origin, those that originated by separation from larger landmasses never experienced the 'barren land' stage, and their floras resulted from a mixture of vicariance, extinction and stochastic dispersal events. This is the case for Madagascar which separated from India *c.* 90 Mya (Raval & Veeraswamy, 2003) and New Zealand which detached from the Gondwana landmass *c.* 85 Mya (Laird & Bradshaw, 2004). In both cases, newly arrived species had to compete for already occupied niches. Species found on volcanic islands (e.g. the Azores, Canary Islands and Juan Fernández Islands) probably experienced similar problems, unless their arrival occurred soon after the islands emerged. It turns out, however, that in many cases studied so far (e.g. *Daucus* L., *Echium* L., *Sideritis* L., *Sonchus* L.) derived woody clades are relatively young in comparison with the age of the islands they inhabit (e.g. Lee *et al.*, 2005; Kim *et al.*, 2008; Nürk *et al.*, 2019; Frankiewicz *et al.*, 2020; Huysduynen *et al.*, 2020). Additionally, one may speculate that the evolution of derived woodiness may be prohibited by young age of the clade itself, as it takes time to evolve a woody habit from an ancestral, herbaceous life form. However, although data on the age of derived woody species are scarce (Kim *et al.*, 2008; Nürk *et al.*, 2019) and data on how quickly woody habit can evolve from a herbaceous ancestor are almost non-existent, it was shown that in *Daucus biscoffii* (J.A. Schmidt) Spalik & Banasiak (Daucinae, Apioideae, Apiaceae) the evolution of a treelet life form took only 130 000 years (Frankiewicz *et al.*, 2020). Simultaneously, experiments with the double *soc1*ful mutant of *Arabidopsis thaliana* (L.) Heynh. demonstrated that increased deposition of xylem may result from a knock-out of only two flowering-time genes (Melzer *et al.*, 2008; Lens, Smets & Melzer, 2012b). Based on this, admittedly scarce, evidence, it does not seem likely that the evolutionary age alone is a preclusion for the evolution of derived woodiness. Second, intrinsic stem and wood anatomical traits might have prohibited the deposition of secondary xylem cylinder (e.g. reduction in cambial activity up to its complete loss) or precluded the development of greater stature (e.g. due to the presence of non-lignified fibres that do not provide sufficient mechanical support).

Taking advantage of the diversity of Apieae and the relatively small number of species allowing for thorough sampling, we tried to identify the factors that have influenced DR and habit shifts in the tribe with particular attention on secondary woodiness. First,

we conducted diversification rate analysis to identify clade(s) with elevated DR. We then reconstructed the biogeographical history of the tribe and the evolution of habit. Comparing these results with the DR analysis allowed us to speculate whether intrinsic (life form and history) or extrinsic (biogeographical) factors most probably shaped DR in Apieae. Second, we studied wood anatomy of derived woody *Deverra* and selected continental and insular herbaceous species and estimated their ages. In this way, we were able to assess if the scarcity of derived woody life forms in insular Apieae is likely to be the result of anatomical constraints or whether it may be an effect of external factors (e.g. late arrival to their current location leading to ecological limitations). Additionally, we addressed the problem of a high number of monotypic genera in Apieae, and we propose a simplified classification.

MATERIAL AND METHODS

MOLECULAR DATA

The present study included 41 of 46 currently recognized species of Apieae (Apioideae, Apiaceae) and two outgroups (Jiménez-Mejías & Vargas, 2015; Plunkett *et al.*, 2018). Due to a lack of material for molecular studies, we omitted the following species: *Ammi procerum* Lowe, *Anethum theurkauffii* Maire, *Apium larranagum* M.Hiroe, *Deverra reboudii* Coss & Durieu and *Stoibrax hanotei* (Braun.-Blanq. & Maire) B.L.Burtt. The studied species were represented by 122 molecular sequences of four markers: nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS; 47 accessions), and plastid *rpoC1* (16 accessions), *rpl16* (20 accessions) and *rps16* (39 accessions) introns. Eighty sequences were retrieved from GenBank, and 42 were newly obtained (Supporting Information, Table S1). The two Canarian endemic species, *Canaria tortuosa* and *Rutheopsis herbanica*, were represented by three specimens each to assess their monophyly and a putative sister relationship. To obtain the new sequences, c. 20 mg of dried leaves from herbaria was used to isolate DNA with the DNeasy Plant Mini Kit (Qiagen, Venlo, the Netherlands). The chosen loci were amplified by PCR using previously developed protocols and primers (Banasiak *et al.*, 2016; Khederzadeh *et al.*, 2017), Sanger sequencing was performed by Genomed S.A. (Warsaw, Poland), and the obtained reads were assembled using SeqMan Pro 13.0.2 (DNAStar, Madison, WI, USA). All newly generated sequences were deposited in GenBank (Table S1).

The sequences were aligned using the E-INS-i algorithm implemented in MAFFT 7.271 (Katoh & Standley, 2013). Primer and partial exon sequences flanking the non-coding regions were manually

trimmed in Mesquite 3.51 (Maddison & Maddison, 2019). Subsequently, the ‘automated1’ algorithm implemented in trimAl 1.2 (Capella-Gutiérrez, Silla-Martínez & Gabaldón, 2009) was used to remove the ambiguously aligned positions. The congruence of nrDNA ITS and plastid DNA (pDNA) phylogenetic signals was checked using Concaterpillar 1.7.2 (Leigh *et al.*, 2008). Although the incongruence between nuclear and plastid signals was significant with $P = 0.03$, the comparison of respective phylogenetic trees indicated that this incongruence was caused by the relative position of three taxa, *Modesciadium* P.Vargas & Jim.Mejías, *Schoenoselinum* Jim.Mejías & P.Vargas and *Stoibrax* Raf., and it concerned the tips of the tree rather than its backbone. Therefore, subsequent analyses were performed using the combined matrix. In the preliminary phylogenetic analyses, *C. tortuosa* and *R. herbanica* were each monophyletic and sister taxa. Therefore, in the final analyses each of these species was represented by a single accession (#0599 and #0575, respectively).

PHYLOGENETIC INFERENCE

The BIC metric implemented in PartitionFinder2 (Lanfear *et al.*, 2012) was used to choose the optimal partitioning scheme and nucleotide substitution model for this and subsequent analysis. The phylogenetic estimation was performed using the maximum likelihood (ML) method as implemented in RAxML 8.2.4 (Stamatakis, 2014), and the Bayesian inference (BI) implemented in MrBayes 3.2.6 (Ronquist *et al.*, 2012). The Bayesian analysis was carried out for 100 million generations with four Monte Carlo Markov chains sampled every 10 000 generations. Two independent runs were carried out for each analysis, the initial 25% of saved trees were discarded as burn-in and the remaining 15 000 trees were summarized in a 50% majority rule consensus tree. The convergence of the independent runs and the effective sample size (ESS) were checked using Tracer 1.7.1 (Rambaut *et al.*, 2018). For ML analyses, bootstrap support (BS) was estimated based on 1000 rapid bootstrap replicates.

NODE CALIBRATION, ANCESTRAL STATE RECONSTRUCTION AND DIVERSIFICATION RATE ESTIMATION

The node calibration strategy followed Frankiewicz *et al.* (2020). In brief, we used BEAST 1.10.4 (Drummond & Rambaut, 2007) and chose a random local clock allowing for accommodation of the molecular evolution rate differences between short- (annual, biennial) and long-lived (perennial) lineages, a birth–death speciation model, and we employed the results

of the analysis conducted with PartitionFinder2 described earlier to select the optimal partitioning scheme and substitution model. We used three secondary calibration points representing nodes with posterior probability of 1.0 from the chronogram of subfamily Apioideae obtained by [Banasiak et al. \(2013\)](#). The chosen nodes represented the most recent common ancestors of Apieae, of *Anethum graveolens* L. and *Deverra denudata* (Viv.) Pfisterer & Podlech and of *Ammi majus* L. and *D. denudata*. We ran two independent Markov chains for 100 million generations each, sampling every 10 000 generations and discarded the initial 25% of trees from each run as a burn-in. The remaining trees were summarized in a maximum clade credibility (MCC) tree. To check for eventual systematic bias in the secondary divergence estimation, we compared the median ages for all pairs of corresponding nodes between the trees of [Banasiak et al. \(2013\)](#) and this study, fitting the major axis with fixed zero intercept, i.e. optimizing only for the slope parameter, using the R package *smatr* ([Warton et al., 2012](#)). *Naufraga balearica* was located on a long branch in ML and Bayesian phylogenetic inferences. Therefore, we decided to perform the dating analysis twice. In the first run, we included all species (i.e. including *N. balearica*), and in the second run, *N. balearica* was excluded from the analysis. As such an omission could affect the tree topology, we decided to enforce the monophyly of the clade including *Naufraga* Constance & Cannon: *Apium* and a clade containing *Anethum* L., *Foeniculum* Mill., *Pseudoridolfia* Reduron, Mathez & S.R.Downie, *Ridolfia* Moris and *Schoenoselinum* (hereafter referred to as the *Anethum* alliance following [Jiménez-Mejías & Vargas, 2015](#)). The results of both runs were similar, but the analysis with *N. balearica* had a problem with reaching convergence, and the resulting stationary distribution was ‘chunky’, i.e. the analysis repeatedly stuck in numerous, distinct local optima. Moreover, all parameter estimates of the model with *N. balearica* had higher variance than their counterparts from the model without this species. It is best evidenced by the comparison of model likelihood variance (35.9 vs. 54.4, without and with *N. balearica*, respectively) and its standard error (0.08 vs. 0.80, respectively). These results clearly show that *N. balearica* is an outlier in terms of molecular evolution rate that does not fit the model well, leading to the disturbance of model parameter estimation. Therefore, all subsequent analyses were carried out without this species.

The data on lifespan (0: annual; 1: biennial; 2: perennial), reproductive strategy (0: monocarpic; 1: polycarpic) and life form (0: therophyte; 1: hemicryptophyte; 2: chamaephyte) were assessed based on herbarium specimens and the literature.

Because there is no convincing evidence that the rate of morphological evolution is correlated with the rate of nucleotide substitution ([Goloboff et al., 2019](#)), we performed phylogenetic mapping of these characters with maximum parsimony (MP), which ignores branch lengths, and with ML using a chronogram. For MP, we employed the ‘pace’ function from the R package *phangorn* ([Schliep, 2011](#)) with ordered (Wagner) parsimony for lifespan and with unordered (Fitch) parsimony for reproductive strategy and life form. To perform ML ancestral state estimation, we used the ‘ace’ function from the R package *ape* ([Paradis & Schliep, 2019](#)) with the Akaike information criterion to select the best model of evolution for each trait from among three available ones (equal rates, symmetrical, all rates different). In the case of lifespan, a constraint of ordered evolution was applied before selection of the best fitting model.

We inferred diversification rates using the ‘medusa’ function from the R package *geiger* ([Alfaro et al., 2009](#); [Pennell et al., 2014](#)), which uses the Akaike information criterion to select for the best evolutionary model and, unlike other methods, detects abrupt rather than gradual changes in diversification rates. ‘Medusa’ allows us to account for incomplete sampling, but only when the precise locations of missing taxa on a phylogram are known. Based on their generic assignment, the five species missing in our chronogram are disposed evenly among the clades, but their precise location is not known. Therefore, we decided to exclude this information from the analyses. This probably lowered the DR for the whole tree, affecting all clades to a similar degree. Because we are interested in identifying branches with an elevated DR rather than estimating the value itself, such an approach is suitable.

ESTIMATION OF THE BIOGEOGRAPHICAL SCENARIO

To infer the biogeographical scenario, we compiled the information about species distributions from the literature, herbarium specimens and online databases ([Tutin, 1968](#); [Davis, 1972](#); [Townsend, 1989](#); [Felinier, Jury & Herrero, 2003](#); [Euro+Med, 2006](#); [Dimopoulos et al., 2016](#)). We used 13 areas that corresponded to Takhtajan’s floristic regions or well-demarcated geographical areas (e.g. islands) with borders adjusted to the distribution of Apieae. This particularly concerned the division of the Mediterranean into five areas, because the distribution of Apieae in this region does not conform to the well-established split along the Italian Peninsula ([Médail & Diadema, 2009](#); [Fig. 1](#)). The present-day ranges of four species (*Ammi majus*, *Apium graveolens* L., *Foeniculum vulgare* Mill. and



Figure 1. Schematic division of the Mediterranean and adjacent islands into seven areas used in the estimation of the biogeographical scenario: (A) Iberian Peninsula, (B) Mediterranean (north-western) Africa, (C) Saharo-Arabian region, (D) eastern Mediterranean, (E) northern Mediterranean, (F) the Canary Islands, and (G) the Azores. The remaining areas correspond to well-demarcated geographical areas (Australia, Juan Fernández, Madagascar, New Zealand, South Africa, South America) and are not shown.

Ridolfia segetum Moris) are exceptionally wide and to some extent were affected by human introduction. Therefore, biogeographical analyses were carried out twice. In the first run, all present-day ranges of these species were used. In the second run, we confined their distributions to these reconstructed as ancestral in the first analysis.

The biogeographical analyses followed a dispersal-extinction-cladogenesis (DEC) model and were performed using Lagrange v.20130526 (Ree & Smith, 2008) with a configuration file created using an online tool (Ree, 2013). We employed the dated MCC tree with the outgroup pruned. Preliminary analyses showed that employing an adjacency matrix reflecting biologically feasible connections between the areas does not influence resolved areas to a considerable degree; therefore, in the final analysis we allowed for connections between all areas (Lagrange configuration file is available online, see Data Availability). LDD is stochastic in nature, and the factors playing a role in its occurrences are not well understood (Higgins, Nathan & Cain, 2003; Nathan, 2006). Therefore, estimating how much more likely short-distance dispersal (SDD) over LDD is poses a problem. Nevertheless, previous studies on apioids showed that dispersal in one hemisphere is much more common than between hemispheres (Banasiak *et al.*, 2013). Additionally, Spalik *et al.* (2014) provided evidence that models constraining the probability of LDD over SDD better explain species distributions in Apiaceae

tribe Oenantheae. To accommodate this uncertainty, we ran two analyses. One assumed that both types of dispersal are equally likely. In the other, dispersals between hemispheres were treated as ten times less likely than within the same hemisphere. The results of the analyses were almost identical. Because the model with constraints has more support in previous studies, the results from that model are presented here, and the configurational file and the results of the unconstrained model are available online.

WOOD ANATOMICAL ANALYSES

Fourteen species represented by 21 samples were considered for the wood anatomical study. Sampled taxa included seven species of shrubby *Deverra*, three herbaceous insular endemics (*C. tortuosa* and *R. herbanica* from the Canary Islands and *Apium fernandezianum* from the Juan Fernández Islands) and four herbaceous continental species [*Ammi majus*, *Apium graveolens*, *Foeniculum vulgare* and *Petroselinum crispum* (Mill.) Fuss.]. Details on wood anatomy of six species (*Ammi majus*, *Apium graveolens*, *Deverra denudata*, *D. scoparia* Coss. & Durieu, *Foeniculum vulgare*, *Petroselinum crispum*) were extracted from the Xylem Database (Schweingruber & Landolt, 2010), and 15 samples representing ten species were obtained from herbaria (B, E, WU), cultivated material (Conservatoire botanique de Mulhouse, France) and

wild populations. Voucher specimens are listed in [Supporting Information Table S1](#).

Thick basal stem samples were soaked in boiling water until they sank. They were then sectioned on a sledge microtome (SM2010R, Leica Biosystems, Wetzlar, Germany) to obtain 20–60- μ m-thick transverse and longitudinal sections and stained with a 0.5% aqueous solution of safranin and 0.5% aqueous solution of alcian blue. Sections were dehydrated in ethanol solutions of increasing concentration, and then mounted in Euparal (Carl Roth, Karlsruhe, Germany). Samples too thin to be sectioned on a sledge microtome were fixed in 70% formalin-acetic acid-ethanol solution, embedded in Technovit 7100 resin (Kulzer, Hanau, Germany) and sectioned on a rotary microtome to obtain 7–10- μ m-thick transverse and longitudinal sections, which were stained with PAS reaction without dinitrophenylhydrazine (DNPH). Wood anatomical characters were examined using light microscopy following the IAWA list of microscopic features for hardwood identification (IAWA Committee, 1989). Pieces of wood were macerated following Franklin (1945) and vessel elements and fibres were then measured.

RESULTS

PHYLOGENETIC RELATIONSHIPS

Pursuant to the results of PartitionFinder2 the dataset was partitioned into ITS and plastid markers partitions and assigned the GTR+G substitution model for ML analysis, while for the Bayesian inference the dataset was not partitioned and assigned the GTR+I+G model (topological analysis) and GTR+I+G+X (node calibration).

The trees obtained in ML and Bayesian analyses were topologically congruent with previous studies (Spalik *et al.*, 2010; Jiménez-Mejías & Vargas, 2015) and comprised five major clades: *Stoibrax*; the *Anethum* alliance; the *Apium* clade; *Deverra*; and the crown clade (Fig. 2). *Stoibrax* was resolved as a sister to the remaining clades. The *Anethum* alliance comprised five monospecific or oligospecific genera and included the cultivated species *Foeniculum vulgare* and *Anethum graveolens*. *Apium* was sister to monospecific *Naufraga* that was located on an exceptionally long branch. In *Apium*, two clades were resolved: the first consisted of European *Apium graveolens* and southern African *Apium decumbens* Eckl. & Zeyh., and the second clade comprised the remaining congeners from the Southern Hemisphere (hereafter referred to as the Southern Hemisphere *Apium* clade). The support for the monophyly of *Deverra* was moderate with BS

value of 76% and posterior probability (PP) of 0.8. The crown clade encompassed three subclades: *Billburttia*; *Ammi*; and the *Petroselinum* alliance. The last of these comprised five monospecific genera (*Petroselinum* Hill, *Modesciadium*, *Sclerosciadium* W.D.J.Koch ex DC., *Rutheopsis* A.Hansen & G.Kunkel and *Canaria* Jim. Mejías & P.Vargas). The last two, both endemic to the Canary Islands, were resolved as sisters with short branches. Support for most backbone branches was high, except for the common ancestor of the *Apium* clade and the *Anethum* alliance (BS = 56%, PP < 0.5), and for the crown clade (BS = 71%, PP = 0.79).

DIVERGENCE TIME ESTIMATION AND DIVERSIFICATION RATES

Prior and posterior age distributions of the three nodes selected as calibration points differed to varying degrees, although in all cases there was considerable overlap between the previous analysis and the present study (Fig. 3). The 95% confidence interval for the slope parameter of the major axis was 0.92–1.07; therefore, there is no evidence for the systematic bias in secondary divergence time estimates as compared to the primary calibration.

Our results are generally congruent with previous phylogenetic dating of Apieae by Fernández-Mazuecos *et al.* (2014), but their node age estimations had much broader 95% highest posterior density intervals (HPDs). The crown age of Apieae was estimated at 13.79 Mya, with 95% HPD of 16.41–11.24 Mya. The last common ancestor of the *Apium* clade and the *Anethum* alliance lived 10.72 Mya, with 95% HPD of 12.68–8.65 Mya. The stem age of *Deverra* was resolved at 9.86 Mya (95% HPD 11.66–8.08), and its two major clades diverged 9.17 Mya (95% HPD 11.07–7.41) and subsequently diversified *c.* 4.5 Mya. The other woody clade, *Billburttia*, originated at roughly the same time (9.00 Mya, 95% HPD 10.87–7.14). Assuming that vicariance immediately followed dispersal, the ages of the insular endemics are 1.82 Mya (95% HPD 2.65–0.97) for *Apium filiforme*, 0.38 Mya (95% HPD 0.80–0.05) for *Apium fernandezianum*, 1.33 Mya (95% HPD 2.20–0.52) for Azorean *Ammi* and 3.39 Mya (95% HPD 4.63–2.21) for Canarian *Canaria* and *Rutheopsis*, with a subsequent split into these two species *c.* 0.63 Mya (95% HPD 1.16–0.20).

The Akaike information criterion chose the Yule speciation model and retrieved a DR (net speciation) for Apieae as a whole equal to 0.22, with 0.15–0.31 95% confidence intervals. The only shift in DR was detected for the Southern Hemisphere *Apium* clade (i.e. excluding *Apium decumbens* and *Apium graveolens*) with DR equal to 0.66 and 95% confidence interval of 0.32–1.19.

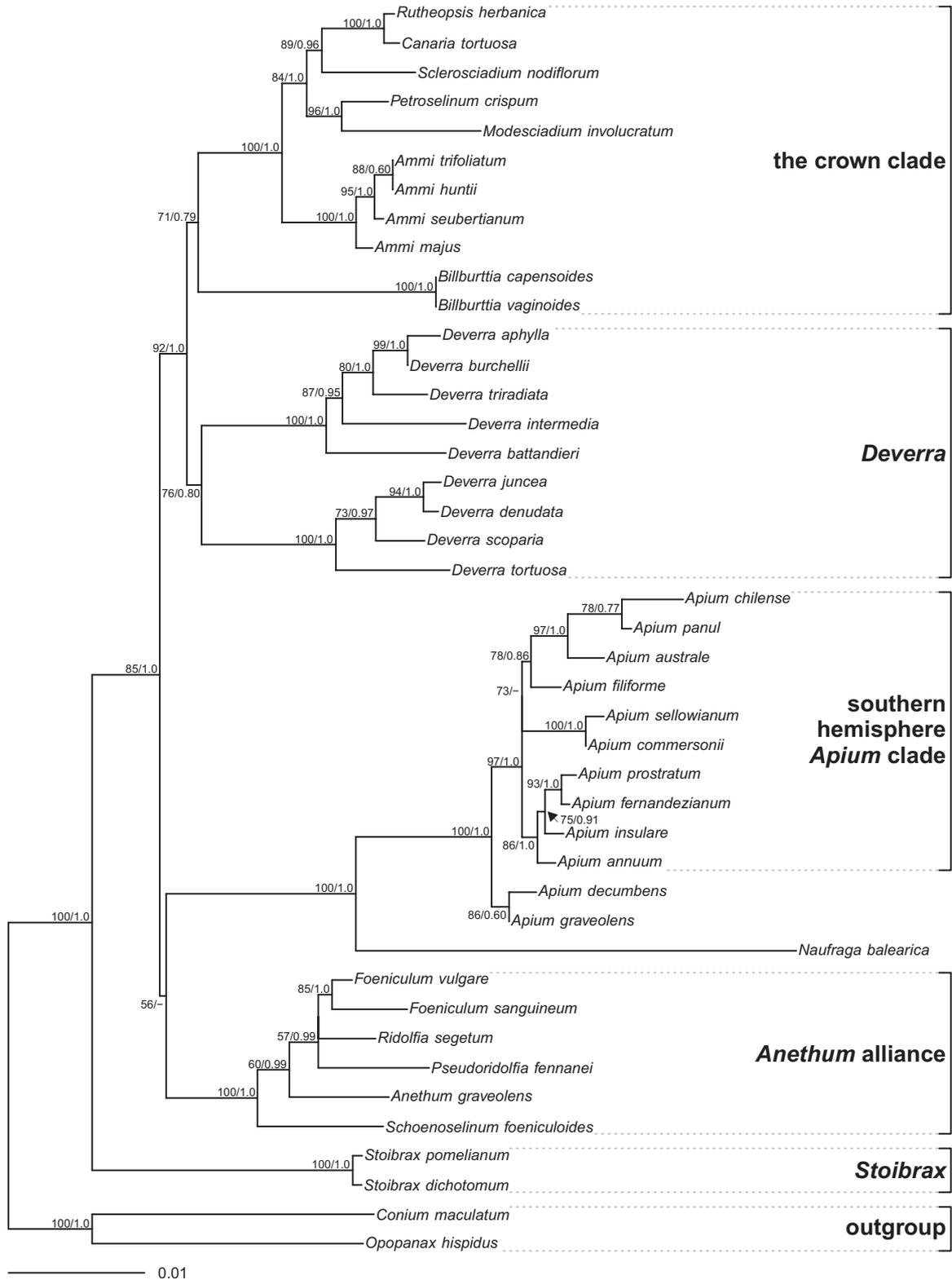


Figure 2. Maximum likelihood tree inferred from combined sequences of nrDNA ITS and plastid DNA *rpoC1*, *rpl16* and *rps16* introns. Bootstrap support and posterior probability for nodes also found in the Bayesian majority-rule consensus tree are given along the branches. Major clades are bracketed. The scale bar represents the mean number of nucleotide substitution per site.

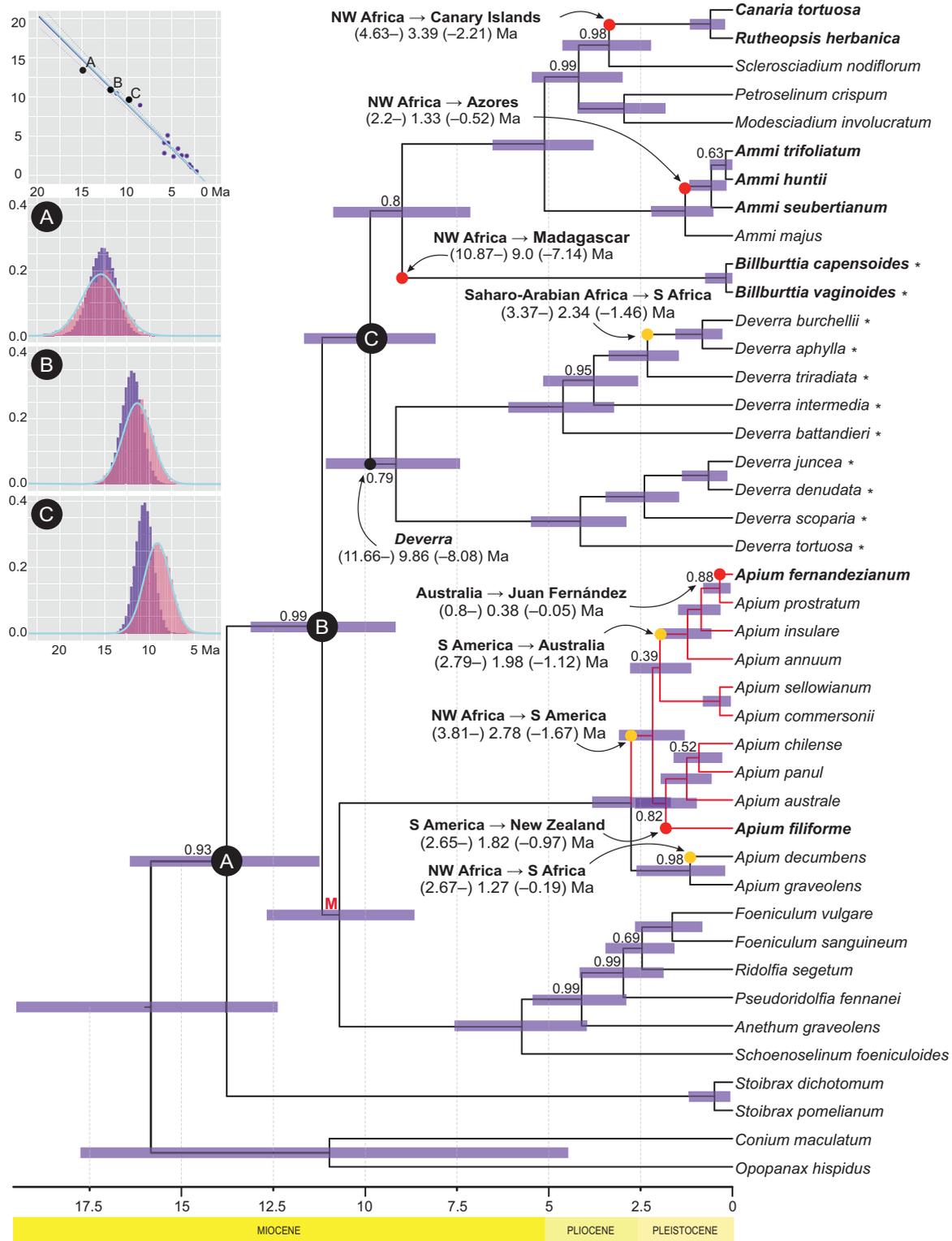


Figure 3. Maximum clade credibility tree summarizing Bayesian MCMC analyses of Apiaceae and outgroups using BEAST. Scatter plot represents the correlation between median ages of corresponding nodes in the primary (abscissa) and secondary (ordinate) calibrated trees. Violet lines (solid and dashed) represent the major axis with 95% confidence interval compared to blue line which represents that expected under an assumption of no systematic bias in age estimations. A, B and C denote the calibration points with the respective plots of prior (blue curves) and posterior (violet histograms) age distributions,

RECONSTRUCTION OF THE ANCESTRAL HABIT

When interpreting the reconstructions of lifespan, reproductive strategy and life form, it should be remembered that although changes in these traits were estimated separately, they are highly inter-related. Annuals and biennials are always monocarpic, whereas perennials may be monocarpic or polycarpic. Biennials and perennials cannot be therophytes, because the latter are always annual. However, annuals may survive winter as seeds (therophytes) or seedlings (hemicryptophytes). Chamaephytes (shrubs or subshrubs) are by definition perennial. Nevertheless, the evolution of lifespan, reproductive strategy and life form was highly homoplastic (Fig. 4).

The results of the ancestral state reconstruction varied depending on the chosen method (ML or MP). The most recent common ancestor of *Apieae* was resolved as a monocarpic biennial hemicryptophyte with MP, whereas in ML reconstruction the annual lifespan was most likely. In the *Anethum* alliance, ML and MP reconstructions were similar. In this clade, a shift from biennial hemicryptophyte to annual therophyte was inferred for a grade comprising *Anethum*, *Pseudoridolfia* and *Ridolfia* with subsequent lifespan prolongation in *Foeniculum*. The most recent common ancestor of *Apium* was inferred as a biennial monocarpic hemicryptophyte (both methods), and two independent shifts to annual therophytes in *Apium annuum* P.S.Short and *Apium decumbens* were reconstructed. In contrast, longer lifespan evolved twice: in the South American *Apium* clade (*Apium filiforme*, *Apium australe* Thouars, *Apium panul* Reiche, *Apium chilense* Hook. & Arn.) and in the Juan Fernández endemic *Apium fernandezianum*.

The evolution of habit in the crown clade and *Deverra* was homoplastic and the retrieved reconstructions were ambiguous for many internal nodes, particularly for the common ancestor of these two clades. *Deverra* and *Billburttia* form a grade of polycarpic chamaephytes, whereas the remaining species are monocarpic therophytes or hemicryptophytes. *Ammi majus*, the only continental representative of the genus and its first-diverging species, is annual, whereas the

remaining species, which are endemic to the Azores, are biennial. *Canaria* and *Rutheopsis*, both endemic to the Canary Islands, are perennials in contrast to their continental relative, annual *Sclerosciadium*.

BIOGEOGRAPHICAL SCENARIOS

The evolutionary history of *Apieae* mostly took place in the Mediterranean region with the exception of *Apium*, *Billburttia* and *Deverra* that also colonized the Southern Hemisphere. A full DEC reconstruction of the biogeographical history of *Apieae* is presented in Supporting Information Figure S1, and major dispersal events are indicated in Figure 3.

The western Mediterranean region (north-western Africa and the Iberian Peninsula) was resolved as the place of origin of *Apieae*. An exclusively Mediterranean African distribution was retained in the *Anethum* alliance until the ancestor of *Ridolfia* and *Foeniculum* broadened its range to include the Iberian Peninsula, where *Foeniculum* subsequently diversified (cf. Taxonomy of *Apieae*).

The ancestor of the Southern Hemisphere *Apium* clade dispersed from Mediterranean Africa to South America; an independent dispersal to southern Africa gave rise to *Apium decumbens*. The South American lineage diversified into five continental species and subsequently colonized Australia and, independently, New Zealand. *Apium fernandezianum* from the Juan Fernández Islands is probably of Australian rather than South American origin.

Deverra originated and diversified in the Mediterranean (north-western) Africa, where most of its species still occur. One branch broadened its range to include southern Africa and subsequently diversified. A dispersal from the Mediterranean Africa to Madagascar gave rise to the common ancestor of *Billburttia*.

The common ancestor of *Ammi* occurred in the western Mediterranean, from where it dispersed to the Azores. Nowadays, *Ammi majus* is the only continental species, and in the Azores its three congeners speciated sympatrically. A dispersal from north-western Africa to the Canary Islands was retrieved for the common ancestor of *Rutheopsis* and *Canaria*.

whereas pink histograms represent posterior age distributions for the calibration points from the previous study (Banasiak *et al.*, 2013), which were used to calculate parameters for priors. Violet bars represent 95% highest posterior density intervals for age distributions. Red dots denote dispersal to the islands, yellow dots denote long-distance dispersal events, and the black dot represents the age of *Deverra*. Red branches were reconstructed as having a diversification rate significantly higher than the background value for the whole tree, and the red letter M denotes the node with enforced monophyly. For clarity, only posterior probability values < 1.0 are shown. Insular endemics are in bold type, and derived woody taxa are marked with asterisks. The time scale is in millions of years.

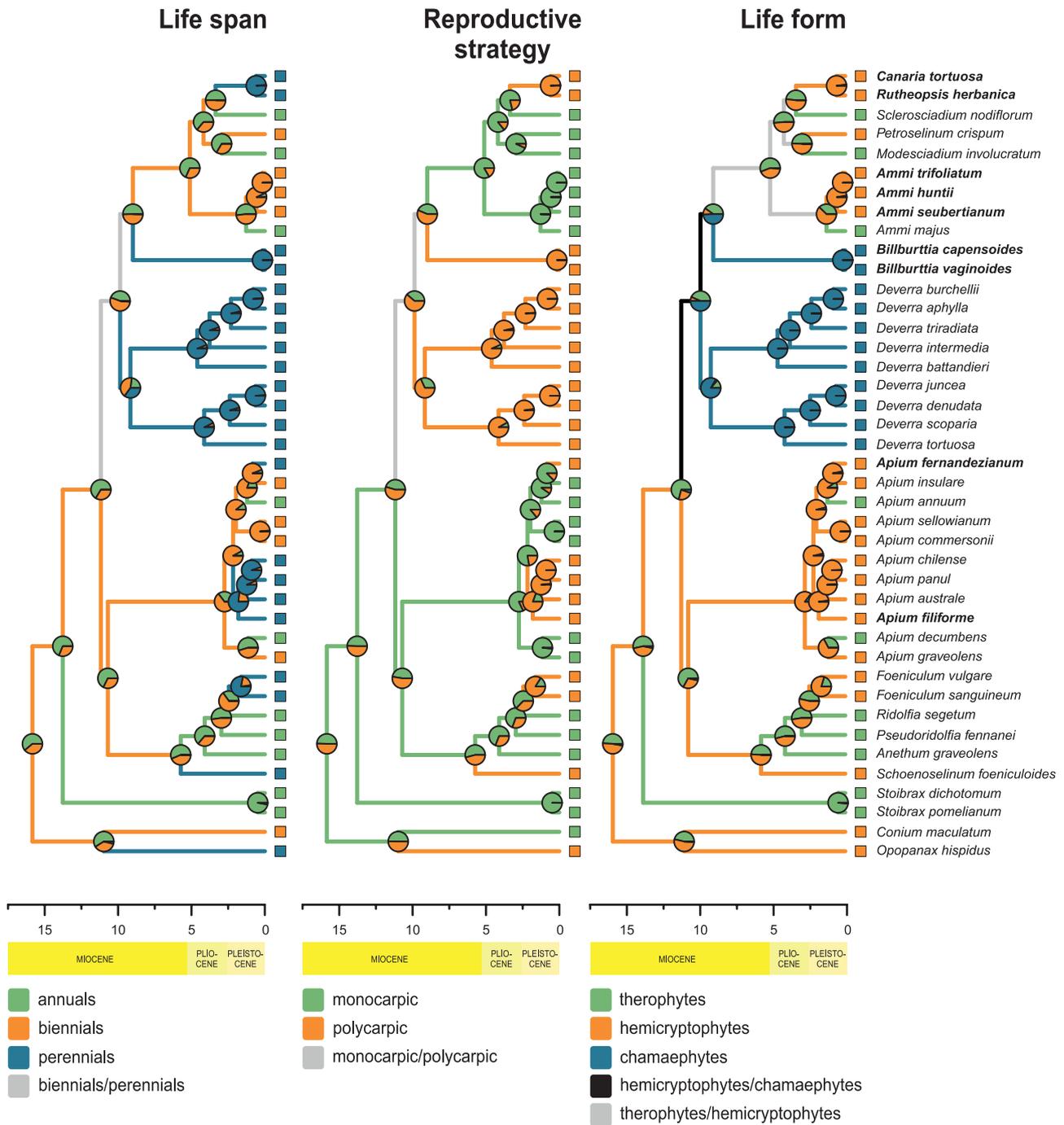


Figure 4. Evolution of lifespan, reproductive strategy and life form reconstructed using maximum parsimony (branch colours) and maximum likelihood estimates (pie charts show relative likelihoods). The all rates different (ARD) model was chosen as the best fit for evolution of lifespan, the equal rates/symmetrical (ER/SYM) model was chosen for reproductive strategy, and the symmetrical (SYM) model was chosen for life form.

GENERAL OBSERVATIONS ON WOOD ANATOMY OF
APIEAE

These observations were based on our original data for *Apium fernandezianum*, *C. tortuosa*, *R. herbanica* and *Deverra* spp. compared with four species (*Ammi*

majus, *Apium graveolens*, *Foeniculum vulgare* and *Petroselinum crispum*) from the Xylem Database. The two species of *Deverra*, *D. denudata* and *D. scoparia*, were included in our data and in the literature: regardless of the source, their wood tissues were much

alike and detailed descriptions based on the original material are given in the next section.

Species included in the anatomical study are commonly divided into herbaceous (*Ammi majus*, *Apium fernandezianum*, *Apium graveolens*, *C. tortuosa*, *P. crispum*), woody (*Deverra* spp.) and intermediate forms (*F. vulgare*). However, anatomical traits do not allow for a clear distinction among these groups: all studied species deposit a continuous cylinder of secondary xylem. In *Apium graveolens*, *P. crispum* and *R. herbanica*, the wood cylinder comprises two zones (inner, devoid of fibres and instead with pervasive parenchyma; and outer, in which the ground tissue is composed of libriform fibres); in the remaining species, the wood cylinder cannot be subdivided into such zones and the ground tissue is made of fibres. In *Apium fernandezianum*, the shape of the vascular bundle is retained through its secondary growth (similarly to *Apium graveolens* from the Xylem Database), and narrow portions of xylem between them (i.e. prolongations of medullary rays) are sometimes lignified. In *C. tortuosa*, the proportions are inverted: the zones of secondary xylem that developed as prolongations of medullary rays are broad and lignified, and parenchymatous sheaths are present along borders of these areas. A similar condition was reported in *Billburttia* (Rakotondrandrasana *et al.*, 2017), and prominent lignification of the medullary rays was also present in three *Deverra* spp. Although most samples were obtained from the same height (i.e. base of the main stem), the radius of the xylem cylinder was distinctly narrower in the herbaceous species (from 0.17 mm in *Apium fernandezianum* and 0.60 mm in the closely related *Apium graveolens* to 2.00 mm in *P. crispum* and 2.20 mm in *Ammi majus* from the same clade) than in *F. vulgare* (6.00 mm) and in woody *Deverra* (commonly > 5.00 mm, up to 12.00 mm in *D. scoparia* from the Xylem Database). Growth ring boundaries were observed in *Deverra* and *F. vulgare*. Wood is diffuse-porous, with a tendency to semi-ring-porosity in some *Deverra* spp. (including *D. denudata* and *D. scoparia* from the Xylem Database). No distinct pattern of vessel disposition was observed in any of the studied species. In *Deverra*, a weak tendency towards a dendritic pattern is present. In the remaining species, vessels are often solitary or in small, radial multiples. Perforation plates are exclusively simple. Intervessel pitting is mostly alternate, opposite or transitional between these two types. In *Apium fernandezianum*, *Ammi majus*, *F. vulgare* and *P. crispum*, scalariform pitting is additionally present. Vessels are mostly narrow and numerous to very numerous, whereas vessel elements are universally short (based on original material as such data are missing for the species from the Xylem Database).

The libriform fibres in herbaceous species and *F. vulgare* are thin- or thin- to thick-walled, whereas in *Deverra* they are thin- to thick- or very thick-walled. Fibre length is similar in both groups (in our material).

Axial parenchyma is scanty paratracheal, and also vasicentric in *Deverra*, *Ammi majus* and *Apium fernandezianum*. *Canaria tortuosa* and *R. herbanica* lack axial parenchyma completely. In *Apium fernandezianum* and *C. tortuosa* the only structures corresponding to rays are areas formed as prolongations of medullary rays, whereas narrow, newly formed rays are absent. In the remaining species, ray width varies from uni- to decaseriate. Rays are composed of upright and square cells in *Ammi majus*, *Apium graveolens* and *R. herbanica*. In *F. vulgare*, all ray cells are procumbent, whereas in *P. crispum* and *Deverra* spp. rays are heterogeneous.

Generally, observed differences in wood structure between woody and herbaceous Apieae come down to the 'degree of woodiness' (i.e. how thick a secondary xylem cylinder is) and particular traits of libriform fibres (mostly thicker in *Deverra* spp. and thinner in herbaceous taxa). Other observed dissimilarities most probably resulted from the young age of sampled specimens and the short lifespan of some species (e.g. lack of growth ring boundaries, radial disposition of vessels, rays composed of upright cells in selected herbaceous species). We did not observe any qualitative wood traits that could differentiate between 'herbaceous' and 'woody' groups.

WOOD ANATOMY OF *DEVERRA*

Wood descriptions of *Deverra* are based on samples of *D. aphylla* DC., *D. burchellii* Eckl. & Zeyh., *D. denudata*, *D. juncea* Ball, *D. scoparia*, *D. tortuosa* DC. and *D. triradiata* Hochst. ex Boiss. (Fig. 5A–F). Growth ring boundaries are indistinct (*D. aphylla* #1710, *D. burchellii* #2156, *D. triradiata* #1707) to distinct (remaining samples, including a second sample of *D. burchellii* #2336) and marked with either bands of weakly lignified fibres stained with alcian blue instead of safranin (three to six cells thick in *D. burchellii*), bands of marginal parenchyma [roughly tetraseriate in *D. denudata*; uni- or biseriate (or triseriate) in *D. scoparia* and *D. tortuosa*], broader bands of pervasive axial parenchyma (*D. tortuosa*, *D. aphylla* #1710; Fig. 5A), difference in the radial size of fibres (*D. aphylla*) or transition from thicker- in latewood to thinner-walled fibres in earlywood (*D. juncea*; *D. triradiata*; *D. scoparia*; wood measurement matrix is available online, see Data Availability below). Wood is diffuse-porous with vessels disposed in radial multiples, clusters and partly solitary; in certain species with vague dendritic pattern (*D. burchellii*, disappearing

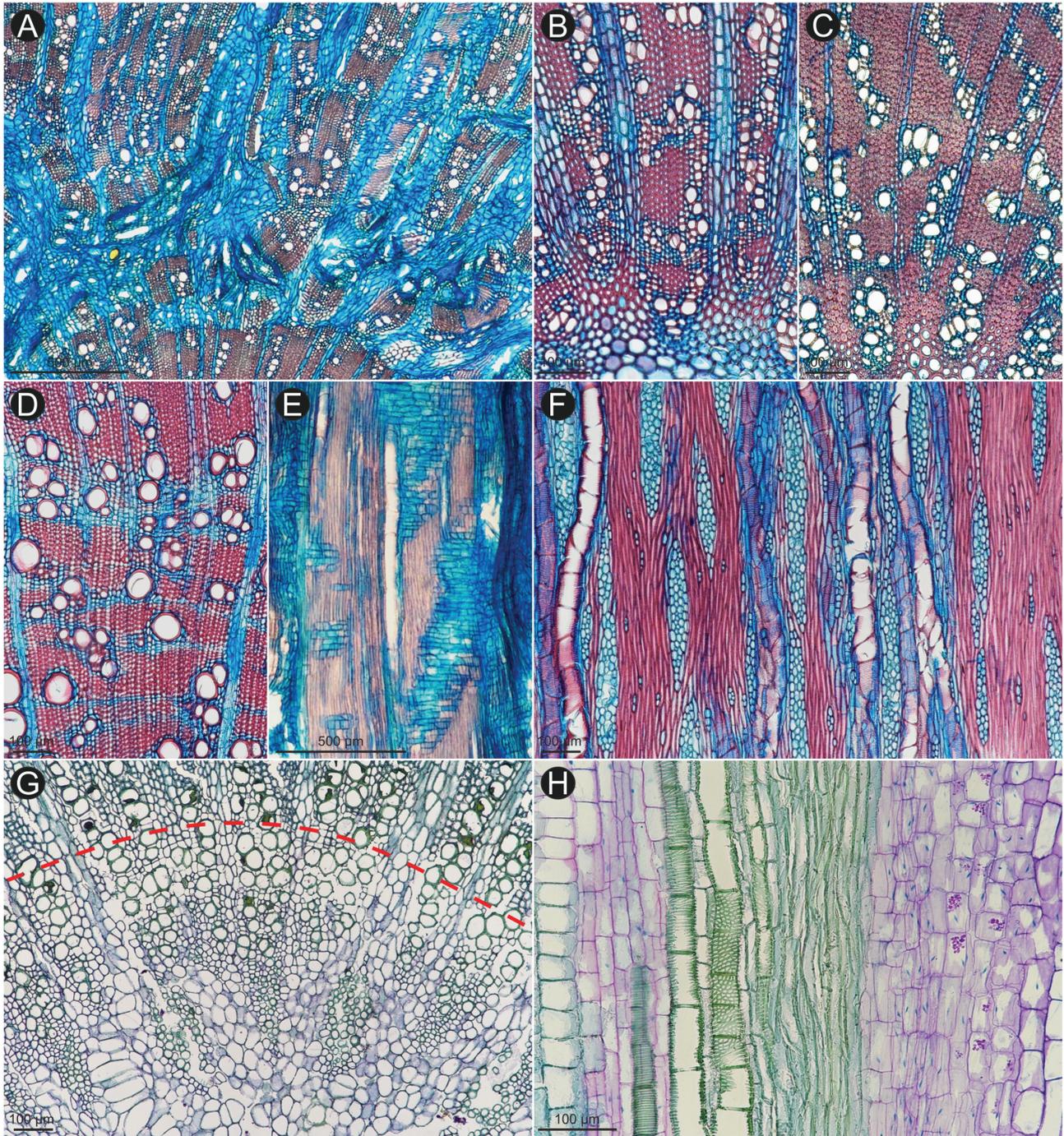


Figure 5. Transverse (A–D, G), radial (E, H) and tangential (F) wood sections of representative species of Apieae. A, *Deverra tortuosa*: locally abundant axial parenchyma. B, *Deverra aphylla*: early secondary xylem without or with only very weak lignification of medullary rays. C, *Deverra triradiata*: early secondary xylem with prominent lignification of medullary rays. D, *Deverra scoparia*: diffuse-porous wood with bands of axial parenchyma. E, *Deverra tortuosa*: multiple rays composed mostly of procumbent cells. F, *Deverra scoparia*: short vessel elements with exclusively simple perforation plates, multiple multiserial rays and a few uniseriate rays. G, *Rutheopsis herbanica*: early secondary xylem; the dashed line demarcates inner, parenchymatous wood from outer, fibrous wood. H, *Canaria tortuosa* (from left to right): pith, primary and secondary xylem stained in green, and bark.

towards outside; *D. aphylla*; *D. scoparia*; *D. tortuosa*; *D. triradiata*; Fig. 5B–D). In *D. juncea*, a tendency to semi-ring-porosity was observed. Vessels are angular (to rounded in *D. aphylla* and *D. juncea*), very narrow (mean tangential diameter $\leq 20 \mu\text{m}$), very numerous (in all cases mean number of vessels mm^{-2} exceeded 250) and their mean length is $\leq 200 \mu\text{m}$ (except for *D. aphylla* where mean length is $245 \mu\text{m}$). Mean vessel wall thickness spans 2–3 μm . Perforation plates are always simple (Fig. 5E). Intervessel pitting is mostly alternate, but opposite and transitional pitting is also present. In *D. juncea*, *D. scoparia*, *D. tortuosa* and *D. triradiata*, rare scalariform pits were also observed. Intervessel pit borders are circular to oval and also polygonal in *D. burchellii* (sometimes), *D. denudata* (often), *D. juncea* (rarely) and *D. tortuosa* (very rarely); in *D. juncea*, they are clearly bordered. Mean vertical pit diameter is 2.9–4.3 μm , and maximal pit diameter is $> 4.0 \mu\text{m}$ in all species (up to 6.1 μm), except *D. juncea* where pit diameter is $\leq 3.7 \mu\text{m}$. Pit apertures are slit-like. Vessel-axial parenchyma and vessel-ray pitting is similar to intervessel pitting with clearly reduced borders or is simple, except for *D. scoparia*, *D. triradiata* and *D. tortuosa*, in which it is distinctly bordered; in the last species, it is sometimes palisade, but mostly opposite to scalariform.

Libriform fibres are non-septate and thin- to thick-walled (*D. burchellii*, *D. juncea*, *D. scoparia*, in which fibre wall thickness marks the growth ring boundary, *D. tortuosa*), thick- to very thick-walled (*D. aphylla*) or solely very thick-walled (*D. denudata*). In *D. triradiata*, fibres are very thick-walled in the first growth ring (especially towards latewood) and thin- to thick-walled in the second and third. Mean fibre length spans 241–346 μm and their mean wall thickness is 1.6 μm in *D. juncea*, c. 2.5 μm in *D. scoparia* and *D. tortuosa*, and 3.2–3.7 μm in the remaining species.

Axial parenchyma is scanty paratracheal in strands of: one to three cells (*D. burchellii*), three or four cells (*D. denudata*), (two to) five or six cells (*D. aphylla*), two or three cells (*D. juncea*), and two or four cells (*D. triradiata*). Vasicentric axial parenchyma in uni- or biseriate sheaths near the vessels and vessel groups is present in *D. triradiata*, *D. scoparia*, *D. aphylla* and *D. denudata*. Interrupted uni- to triseriate bands of axial parenchyma occur in *D. scoparia*; uni- to triseriate (or tetraseriate) marginal bands are found also in *D. denudata* and *D. tortuosa*. In *D. aphylla* and *D. tortuosa*, wide bands (about five to 25 cells) of axial parenchyma devoid of vessels occur (Fig. 5A, D).

Prominent lignification of medullary rays at the beginning of secondary xylem formation was observed in *D. denudata*, *D. scoparia* and *D. triradiata* (Fig. 5B, C). Rays are uni- and multiseriate 3.9(–6.0) cells wide, up to 7.6 mm^{-1} , in *D. burchellii*, in which they are lignified in the inner portion of the stem, and

become simultaneously unligified towards the outer part. Ray cells are mostly square with some upright ones also present. In *D. denudata*, rays do not start at the pith, so the first formed rays are separated from it by a thick layer of thick-walled fibres. In this species, rays are mostly or exclusively multiseriate, composed of upright and square cells with some procumbent ones intermixed. They could not be measured as the rays in tangential longitudinal sections were distorted to a large degree. In *D. aphylla*, rays are uni- and multiseriate 4.8(–8.0) cells wide; multiseriate rays are of two distinct sizes and 7.2 mm^{-1} . The tallest rays exceeded the length of the section ($> 1 \text{mm}$). They are composed mostly of upright and square cells with some procumbent ones intermixed throughout the ray body. Multiseriate ray cells are lignified in the inner portion of the stem, and towards the outer part of the stem ray cell walls are non-lignified. In some cases, lignification occurs also in outermost regions meaning that the ray is composed of lignified–non-lignified–lignified regions. In *D. juncea* rays are uni-, bi- and triseriate and composed mostly of upright and square cells with very rare procumbent ones. In *D. scoparia* (11.1 rays mm^{-1} ; multiseriate rays are 3.6 (–6.0) cells wide; Fig. 5F), *D. tortuosa* (5.3 mm^{-1} ; multiseriate rays are 3.4 (–11.0) cells wide) and *D. triradiata* (5.8–8.3 mm^{-1} ; multiseriate rays are 3.9(–7.0) cells wide), multiseriate rays consist of procumbent cells occasionally mixed with square ones, whereas uniseriate rays are mostly composed of square cells (*D. scoparia*), exclusively upright (*D. tortuosa*) or square to upright (*D. triradiata*). Rare secretory canals are present in *D. burchellii* and *D. tortuosa*.

WOOD ANATOMY OF HERBACEOUS INSULAR ENDEMICIS (*APIUM FERNANDEZIANUM*, *CANARIA TORTUOSA*, *RUTHEOPSIS HERBANICA*)

In all samples, a continuous, a very narrow ring of secondary xylem (c. 0.17 mm wide in *Apium fernandezianum*, c. 0.24 mm in *C. tortuosa* and 1.15 mm in *R. herbanica*) is present. In *R. herbanica*, the ring of wood consists of two regions: an inner region with pervasive parenchyma as ground tissue and an outer fibrous region (Fig. 5G). In the other two species, the secondary xylem ring consists of the portions of radially extended vascular bundles and medullary rays found at the beginning of activity of the vascular cambium. In *C. tortuosa*, the extensions of medullary rays are broad (about ten- to 40-seriate), almost vesselless, and they consist mostly of fibres with lignified walls. These extensions are lined with inconspicuous (uni- to triseriate) parenchymatous sheaths along their borders. In contrast, the extensions of medullary rays in *Apium fernandezianum* are narrow (bi- to hexaseriate) and they consist mostly

of parenchymatous cells, occasionally with lignified walls. Growth rings are absent, but in *R. herbanica*, the outer region of the secondary xylem ring is distinctive from the middle and innermost regions in the presence of thicker walled libriform fibres. Wood is diffuse-porous. Vessels are partly solitary (13–24%), partly in small clusters; in all species, radial multiples (a result of the young age of plants) are well seen, especially in *Apium fernandezianum* and *C. tortuosa*; in the latter, radial multiples are often direct prolongations of primary bundles. Vessels are circular to oval (Fig. 5G), rounded in *Apium fernandezianum* or slightly angular in other species, very narrow (mean tangential diameter < 24 µm) and numerous (mean number of vessels is 75–118 mm⁻²; not measured in *Apium fernandezianum* due to narrowness of the xylem cylinder). Mean vessel wall thickness is 2.7–3.1 µm. Mean vessel element length spans 174–243 µm and perforation plates are exclusively simple. Intervessel pits are circular to oval, 3.2–4.3 µm wide in vertical diameter, alternate in *C. tortuosa* (Fig. 5H) and opposite to alternate with transitional forms in other species; scalariform pitting was rarely observed in *Apium fernandezianum* (in this species, all pits are clearly bordered), and in *R. herbanica* vessels embedded in the inner, parenchymatous region have scalariform pitting. Apertures are lens-like, sometimes wide. Vessel-axial parenchyma pitting in *Apium fernandezianum* is similar to intervessel pitting with slightly reduced borders, but in the remaining species this character could not be assessed. Vessel-ray pitting was evaluated only for *R. herbanica* and it is similar to intervessel pits with clear borders.

Libriform fibres are thin-walled in *R. herbanica* and thin- to thick-walled in other species; they are non-septate in *C. tortuosa* (Fig. 5H), often septate in *R. herbanica* and sometimes nucleated in *Apium fernandezianum*. Mean fibre length spans 238–445 µm and mean fibre wall thickness is 1.7–2.4 µm.

Axial parenchyma is scanty paratracheal in strands of two or three cells in *Apium fernandezianum*, and absent in the remaining species. In *R. herbanica*, rays are uni- and multiseriate, composed mostly of upright cells; in the remaining species the only structures corresponding to rays are areas developed as prolongations of medullary rays (as described above), while narrow, newly formed rays are absent.

DISCUSSION

BIOGEOGRAPHY AND DIVERSIFICATION OF APIEAE

Apium consists of two main clades: the first one is formed only by Mediterranean *Apium graveolens* and southern African *Apium decumbens*, whereas the

remaining species group in what we refer to as the Southern Hemisphere *Apium* clade (Fig. 2). For this genus, the biogeographical analyses reconstructed two independent dispersal events from the Mediterranean to the Southern Hemisphere: one to southern Africa (for the ancestor of *Apium decumbens*) and the other one to South America (for the common ancestor of the Southern Hemisphere *Apium* clade). These results are congruent with scenarios postulated in previous biogeographical analyses of *Apium* (Spalik *et al.*, 2010). The only clade resolved as having higher DR than the background value was the Southern Hemisphere *Apium* clade. It diversified in South America and subsequently dispersed westwards to New Zealand and Australia, from where it colonized the Juan Fernández Islands (Fig. 3). The fruits of *Apium* are smooth and do not have any obvious adaptations to LDD. However, most *Apium* spp. are plants of coastal habitats, and seabirds seem to be most efficient dispersal agents on oceanic islands (Magnússon *et al.*, 2014). This is further supported by the recent review of Juan Fernández flora by Bernardello *et al.* (2006), who concluded that bird zoochory is the major way that new species reach the archipelago, and that Australia is the third largest source of its indigenous species.

Explanations of an elevated DR in certain lineages may involve intrinsic clade traits (e.g. life form and life history or adaptive morphological novelties) and extrinsic factors (particularly colonization of new areas and niches following LDD; Kisel *et al.*, 2011; Fattorini *et al.*, 2017). A number of studies have shown that dispersal into new areas is the key factor leading to a higher DR (e.g. Moore & Donoghue, 2007; Uribe-Convers & Tank, 2015; Simões *et al.*, 2016), especially in groups with no obvious morphological innovations (e.g. the Southern Hemisphere *Apium* clade). Arrival to a new area could result in a higher diversification rate of the successful immigrant due to the isolation by distance of its populations at the extremes of its geographical range and due to the habitat diversity of the colonized area promoting adaptive radiation. A broader range may also mitigate, to some degree, extinction caused by local environmental changes, because dispersal might salvage a species from extirpation when it goes extinct in its ancestral area (Kisel *et al.*, 2011; Fattorini *et al.*, 2017). The evolutionary history of the Southern Hemisphere *Apium* clade indeed includes multiple LDD and speciation events with a limited morphological change.

Intrinsic factors, on the other hand, do not seem to influence DR in Apieae as evidenced by the fact that clades of high lifespan and reproductive strategy diversity (e.g. the *Anethum* alliance) and exceptionally homogeneous clades (e.g. *Deverra*) have DR values that do not significantly differ from the background DR. An often-evoked hypothesis

(Smith & Beaulieu, 2009; García-Verdugo *et al.*, 2014; Boucher *et al.*, 2017) assuming that herbaceous plants have shorter lifespans and a pronounced *r* strategy promoting a higher rate of molecular evolution does not seem to pertain to Apiaceae because, apart from *Apium*, herbaceous and woody clades diversify at similar rates. Therefore, we suppose that the extrinsic factors, namely dispersification *sensu* Moore & Donoghue (2007), rather than the intrinsic properties of *Apium* are responsible for the elevated net speciation rate in its Southern Hemisphere clade. The two derived woody genera (*Billburttia* and *Deverra*) have DR values similar to the rest of the tribe, suggesting that higher net speciation observed in selected insular woody clades (Nürk *et al.*, 2019) may be a result of arrival in new areas and not a habit shift itself.

EVOLUTION OF DERIVED WOODINESS

The distinction between herbaceous and woody species is not straightforward as virtually all non-monocot angiosperms deposit at least some secondary xylem: it is the *amount* of deposited wood, not its presence or absence, which differentiates them (e.g. Kidner *et al.*, 2015). With minor exceptions, larger life form is paralleled by the deposition of a greater amount of secondary wood. Therefore, we refer to the therophytes and hemicryptophytes as *herbaceous*, and treat chamaephytes as *woody* as we did in our previous study of secondarily woody Apiaceae belonging to subtribe Daucinae (Frankiewicz *et al.*, 2020). Nevertheless, a binary distinction between woody and herbaceous habits is problematic in Apiaceae because their xylem traits are similar. Also, the wood anatomy of the studied insular endemics (*Apium fernandezianum*, *C. tortuosa* and *R. herbanica*) was not qualitatively distinct from other studied taxa. Simultaneously, reconstruction of the ancestral habit (Fig. 4) showed that the woody life form evolved either once in the common ancestor of *Deverra* and *Billburttia* and was subsequently lost or it evolved independently in these two closely related clades. This suggests a considerable lability of life form in Apiaceae similarly to some other lineages of Apiaceae, including southern African protoapioids (Calviño *et al.*, 2006; Magee *et al.*, 2010), Bupleureae (Stepanova & Oskolski, 2010) and Daucinae (Frankiewicz *et al.*, 2020). Habit lability, as exemplified by numerous shifts from herbaceous to woody life forms (derived woodiness) in closely related taxa, has been documented in multiple plant families (e.g. Böhle, Hilger & Martin, 1996; Lens *et al.*, 2012a; Kidner *et al.*, 2015; Gehrke, Kandziora & Pirie, 2016; Neupane *et al.*, 2017). These studies also suggest that usually there are no intrinsic, anatomical constraints (e.g. lack of cambium) precluding the evolution of

derived woodiness and that the evolution of woodiness (or lack thereof) should rather be seen in terms of external spurs or constraints.

Of the two shrubby genera in Apiaceae, *Deverra* is found in northern Africa and the Saharo-Arabian region, often in deserts (Chrtek, Osbornova & Sourkova, 1984). The molecular estimate of its age (9.86 Mya, 95% HPD 11.66–8.08) corresponds with the aridification of northern Africa and the onset of the Sahara desert in the Tortonian stage (11–7 Mya) of the Late Miocene (Schuster *et al.*, 2006; Zhang *et al.*, 2014). Therefore, the evolution of woodiness as a mean counteracting cavitation is plausible (Huysduynen *et al.*, 2020). It is also possible that this woody life form was later retained in *Billburttia*, as evidenced by marginally higher support for a single origin of woodiness in Apiaceae (ML analysis in Fig. 4). Alternatively, if the shrubby habit in *Billburttia* formed only after its dispersal to Madagascar, its woodiness might have been a by-product of the moderate climate. *Billburttia* occurs in high-elevation tropical mountains, habitats known to promote the evolution of derived woodiness regardless of water availability (Magee *et al.*, 2009; Kidner *et al.*, 2015; Rakotondrandrasana *et al.*, 2017; Nürk *et al.*, 2019). These habitats in Madagascar are also home to four other genera of derived woody Apiaceae in tribe Heteromorphae (*Andriana* B.-E. van Wyk, *Cannaboides* B.-E. van Wyk, *Pseudocannaboides* B.-E. van Wyk and *Tana* B.-E. van Wyk) (Van Wyk, Tilney & Winter, 1999).

The remaining insular endemic species in Apiaceae are herbaceous and much younger than *Billburttia* and also younger than the islands they populate. *Apium filiforme* from New Zealand is 1.82 Myr old (95% HPD 2.61–0.19), the last common ancestor of Canarian *C. tortuosa* and *R. herbanica* lived 3.39 (4.62–2.21) Mya (the Canary islands are 20–1 Myr old), the last common ancestor of the Azorean *Ammi* lived 1.33 Mya (2.20–0.52; the Azores formed 8.0–0.3 Mya), and *Apium fernandezianum* from Robinson Crusoe Island (part of the Juan Fernández Islands) was resolved as 0.38 Myr old (0.80–0.05; the archipelago is 4.2–3.8 Myr old; Fernández-Palacios *et al.*, 2011; Rodrigues *et al.*, 2013; Lara *et al.*, 2018).

As argued earlier, the young age of the clade alone is unlikely to preclude evolution of derived woodiness. Since the newcomers arrived at their current locations relatively recently, they probably faced complex local floras with few open ecological opportunities, and this could have impacted their ability to shift habits. All these species have a longer lifespan than their continental sister clades (Fig. 4). MP ancestral state reconstruction in *Ammi* implies that the biennial lifespan was ancestral and annual habit in *Ammi majus* is a derived condition, whereas ML provides only weak support for the ancestral annual habit and

its subsequent elongation. For the Canary Islands and the Juan Fernández Islands endemics, both methods point clearly to a lifespan elongation. However, lifespan prolongation occurred also in other lineages of Apieae (e.g. after dispersal to Australia in the common ancestor of *Apium filiforme*, *Apium chilense*, *Apium panul* and *Apium australe* or in *Foeniculum*) obscuring the possible relationship between longer lifespan and insular habitat.

VARIATION IN THE AMOUNT OF AXIAL PARENCHYMA

Carlquist (2001a: 172) defined pervasive parenchyma as a ‘replacement of imperforate tracheary elements, such as libriform fibres, with axial parenchyma’. Although this trait is often associated with succulent habit (Gibson, 1973; Carlquist, 2001b, 2015), a large amount of parenchyma is not necessarily related to water retention. Daniel (1916) and Radkevich (1928) suggested that the presence of pervasive parenchyma may result from the development of leaf rosettes. These structures emerge through shortening of internodes, which in turn are in need of less mechanical support than their long counterparts, therefore allowing for the replacement of supportive fibres with less reinforcing parenchyma. This idea was further supported by Ko *et al.* (2004), who showed that the deposition of fibrous secondary xylem may be induced by mechanical stress. Ragni *et al.* (2011) showed that in plants with leaf rosettes (i.e. with shortened internodes) the fibres in wood appear only after flowering, whereas in related species without rosettes such a relationship was not observed. In our study of Daucinae (Frankiewicz *et al.*, 2020), a clade of Apiaceae often characterized by the production of leaf rosettes, we noted a relationship between the stem anatomy and the reproductive strategy: in monocarpic annuals, secondary xylem consisted exclusively of fibrous wood, whereas in monocarpic biennials and polycarpic perennials, the xylem cylinder comprised an inner zone with pervasive parenchyma instead of fibres whereas the outer zone was fibrous. We speculated that this pattern may be explained by gibberellic acid affecting two processes: the shift from the vegetative to the generative phase and the deposition of fibres. In such a case, annuals which undergo the shift early in their lifetime deposit only fibrous wood, whereas in biennials and perennials the shift is postponed. Therefore, the deposition of fibres starts later, leading to the deposition of parenchymatous wood in earlier stages of plant development. Our hypothesis is supported by multiple studies showing that gibberellic acid plays role in both processes (e.g. Moritz *et al.*, 2000; Israelsson, Sundberg & Moritz, 2005; Mauriat & Moritz, 2009; Strabala & MacMillan, 2013;

Ye & Zhong, 2015; Conti, 2017; Ragni & Greb, 2018) and also by recent evidence of the role of florigen in xylem maturation (Shalit-Kaneh *et al.*, 2019).

Among the species considered for wood anatomy in the present study, pervasive parenchyma was observed in *Apium graveolens*, *P. crispum* and *R. herbanica*, whereas *Ammi majus*, *C. tortuosa* and *F. vulgare* were devoid of it (due to the low quality of sections, we could not describe this trait in *Apium fernandezianum*). Five species conform to the pattern previously observed in Daucinae: *Apium graveolens*, *P. crispum* and *R. herbanica* form leaf rosettes and are either polycarpic perennials or monocarpic biennials, *Ammi majus* is a monocarpic annual and *F. vulgare* is a polycarpic perennial, but does not produce leaf rosettes. We did not observe pervasive parenchyma in one polycarpic perennial with a leaf rosette, *C. tortuosa*, although this condition is present in its sister species (*R. herbanica*) with a similar habit. It is possible that although both species are polycarpic, first flowering occurs earlier in *Canaria* than *Rutheopsis*, thus allowing for the deposition of only fibrous wood. However, this requires further examination.

Deverra is a polycarpic, perennial shrub without leaf rosettes, and under our assumptions it is expected to be devoid of pervasive parenchyma. Nevertheless, two species in this genus (*D. aphylla* and *D. tortuosa*) were shown to develop abundant axial parenchyma in wide bands. However, these parenchyma bands are distinctly different from the type observed in leaf rosette-bearing species: the bands never develop as an inner zone of secondary xylem cylinder, but instead they are embedded in the fibrous ground tissue. These parenchymatous bands lack vessels, suggesting that they are not directly derived from cambium, but rather develop through divisions of axial parenchyma. This is further supported by the fact that their cells do not form clear radial files. Therefore, in Apieae, the abundant parenchyma of at least two main types can be distinguished: (1) pervasive parenchyma associated with shortening of internodes and biennial/perennial habit; and (2) that observed in *Deverra*. There are at least three possible explanations of the occurrence of an abundant axial parenchyma in this genus.

The typical habit of *Deverra* is a shrub with numerous erect elongated shoots that arise from the woody caudex made of densely branched short basal shoots (Chrtek *et al.*, 1984). Wide bands of axial parenchyma in the wood of their caudex may be formed in response to activation of epicormic buds responsible for production of lateral branches (Burrows, 2000; Meier, Saunders & Michler, 2012).

Abundant parenchyma may also be related to xylem wounding (e.g. Eyles, Davies & Mohammed, 2003). Typically, trauma stimulates cambial cell proliferation

leading to centripetal sealing of the wound, whereas xylem parenchyma remains inactive in this process. In *Deverra* locally banded parenchyma is most probably *not* derived directly from cambium, but rather forms through proliferation of wood parenchyma. Axial (mostly marginal) parenchyma divisions were observed in response to stem damage in *Adansonia* L. and *Cavanillesia* Ruiz & Pav. (Fisher, 1981) and to girdling in lianas (Dobbins & Fisher, 1986), and a similar mechanism fits the pattern observed in *Deverra*.

Finally, production of parenchyma bands in *Deverra* can be associated with ‘stem particulation’ (e.g. Barykina, 2000): the phenomenon of splitting of the stem in shrubs with a prominent taproot, usually from arid environments and attributed to the formation of a new plant. Although stem particulation has never been studied in *Deverra*, its habitat and conspicuous taproot make the presence of this process likely.

There is no obvious reason to favour one of these explanations above others, and it is possible that all three are involved in the formation of parenchymatous bands in *Deverra*. Nevertheless, the presence of epicormic traces seems least speculative in this highly branched shrub from the often stressful environments known to promote activity of epicormic buds (Chrték *et al.*, 1984; Meier *et al.*, 2012).

TAXONOMY OF APIEAE

Apiaceae were recently revised by Jiménez-Mejías & Vargas (2015), who revealed polyphyly of *Anethum*, *Stoibrax* and *Seseli* L. and introduced three generic names for the disparate members of these genera: *Anethum foeniculoides* Maire & Wilczek was placed in *Schoenoselinum*, *Stoibrax involucreatum* (Maire) B.L.Burt was placed in *Modesciadium*, and *Seseli webbii* Coss. was transferred to *Canaria* (as *C. tortuosa*). Although this treatment restored the monophyly of the genera of Apiaceae, it resulted in an unwieldy over-splitting: with no more than 50 species, the tribe has as many as 15 genera with nine of them monospecific (ten with *Rutheopsis*, which was not included in the aforementioned study) and four containing two or three species each. The taxonomy of Apiaceae has long been inflated with small genera, and in the most recent treatment of the family, 40% of genera are monospecific (Plunkett *et al.*, 2018). A monospecific genus is taxonomically uninformative and is better avoided unless it constitutes an isolated lineage with no close relatives or if its inclusion into the sister genus diffuses the definition of the latter (Spalik, Wojewódzka & Downie, 2001). Therefore, we propose a simplified treatment of the tribe.

Our analyses strongly support a close relationship between *C. tortuosa* and *R. herbanica*. Both species are endemic to the Canary Islands and are glabrous

perennials with yellow flowers and glabrous, ovoid to oblong fruits with thickened ribs. *Rutheopsis herbanica* occurs only in Lanzarote and Fuerteventura, whereas *C. tortuosa* inhabits El Hierro, La Palma, La Gomera, Tenerife and Gran Canaria (Kunkel, 1991). Although these species differ somewhat in leaf division and the shape of the leaf lobes, they are morphologically similar. Therefore, *Canaria* was included in *Rutheopsis* in the most recent treatment of the family (Plunkett *et al.*, 2018), although its only species has not been yet formally transferred. These two species form a sister clade to the Moroccan endemic *Sclerosciadium nodiflorum* Coss., and this closeness is corroborated by carpological characters (Jiménez-Mejías & Vargas, 2015). However, this species differs notably from its Canarian relatives in its annual lifespan, white flowers and compact umbellets superficially similar to those of *Oenanthe* L. Therefore, we agree with Jiménez-Mejías & Vargas (2015) that these two clades should be recognized as separate genera. Similarly, *P. crispum* and *M. involucreatum*, which are sister species in our phylogenetic analyses, differ considerably in the presence of bracts, flower colour and fruit morphology (Jiménez-Mejías & Vargas, 2015), characters that are commonly used in taxonomic keys. Therefore, although an eventual inclusion of *Modesciadium* in *Petroselinum* could simplify the taxonomy of Apiaceae, it would not aid species identification.

The species forming the *Anethum* alliance are closely related based on molecular data and morphologically similar due to their upright and branched stems, conspicuous umbels with bright yellow flowers lacking an involucre or involucre (a rare feature in the family) and finely dissected leaves with linear lobes. In traditional classification systems of Apiaceae based on fruit characters, they were often placed in separate subdivisions (Reduron *et al.*, 2009). However, two of its members that are now placed in separate genera were described in *Anethum*. These are *Schoenoselinum foeniculoides* (Maire & Wilczek) Jim. Mejías & P. Vargas (= *Anethum foeniculoides* Maire & Wilczek) and *Foeniculum vulgare* (= *Anethum foeniculum* L.) including subsp. *piperitum* (Ucria) Bég. (= *Anethum piperitum* Ucria). In fact, the latter sometimes includes plants with reddish flowers (Reduron, 2007), which are also diagnostic for the closely related *Foeniculum sanguineum* Triano & A. Pujadas; however, preliminary molecular analyses suggest that *F. sanguineum* should be retained as a separate species rather than included into *Foeniculum vulgare* subsp. *piperitum* (Pujadas Salvà *et al.*, 2015). The close proximity of *Anethum* and *Foeniculum* was also recognized by Maire (1936) when describing his *Anethum theurkauffii*. He noted that this species exhibited characters intermediate between these two genera and therefore suggested the reinstatement of the Linnaean *Anethum sensu lato*.

For *Ridolfia segetum*, a new name in *Anethum* is necessary because of the binomial *Anethum segetum* L. that is synonymous by neotypification with *Anethum graveolens* (Jarvis *et al.*, 2006). The name was commonly misapplied to *R. segetum* (e.g. de Candolle, 1830), although Gussone (1827) clearly indicated some differences, particularly in fruit characters, between *Meum segetum* (L.) Guss. and *Anethum segetum* L.

TAXONOMIC TREATMENT

Rutheopsis A.Hansen & G.Kunkel, Cuad. Bot. Canaria 26–27: 61 (1976); = *Canaria* Jim.Mejías & P.Vargas, Phytotaxa 212(1): 73 (2015).

1. ***Rutheopsis herbanica*** (Bolle) A.Hansen & G.Kunkel, Cuad. Bot. Canaria 26–27: 61 (1976).
2. ***Rutheopsis tortuosa*** (Webb & Berthel.) Frankiewicz, Reyes-Bet., Reduron & Spalik **comb. nov.**; basionym: *Ferula tortuosa* Webb & Berthel., Hist. Nat. Iles Canaries (Phytogr.) 3(2; 2): 161 (1843); = *Foeniculum tortuosum* (Webb & Berthel.) Benth. ex Christ, Bot. Jahrb. Syst. 6: 497 (1885); = *Canaria tortuosa* (Webb & Berthel.) Jim.Mejías & P.Vargas, Phytotaxa 212(1): 74 (2015); = *Seseli webbii* Coss., Bull. Soc. Bot. France 3: 57 (1856), non *Seseli tortuosum* L., Sp. Pl. 1: 260 (1753).
Anethum L., Sp. Pl. 1: 263 (1753); = *Foeniculum* Mill., Gard. Dict. Abr., ed. 4. [513] (1754); = *Schoenoselinum* Jim.Mejías & P.Vargas, Phytotaxa 212(1): 75 (2015); = *Ridolfia* Moris, Ind. Sem. Hort. Taur. (1841); Fl. Sard. ii. 212. t. 75 (1842); = *Pseudoridolfia* Reduron, Mathez & S.R.Downie, Acta Bot. Gallica 156(3): 496 (2009).
1. ***Anethum graveolens*** L., Sp. Pl. 1: 263 (1753); = *Anethum segetum* L., Mant. Pl. Altera 219 (1771).
2. ***Anethum foeniculum*** L., Sp. Pl. 1: 263 (1753); = *Foeniculum vulgare* Mill., Gard. Dict., ed. 8. n. 1 (1768).
a. ***Anethum foeniculum*** L. subsp. ***foeniculum***
b. ***Anethum foeniculum*** subsp. ***piperitum*** (Ucria) Reduron & Spalik, **comb. nov.**; basionym: *Anetum piperitum* Ucria, in Nuov. Racc. Opusc. Aut. Sicil. 6 (Pl. Linn. Op. Addend. & Secund. Linn.Syst.) 250 (1793).
3. ***Anethum sanguineum*** (Triano & A.Pujadas) Spalik, Banasiak & Frankiewicz, **comb. nov.**; basionym: *Foeniculum sanguineum* Triano & A.Pujadas, Acta Bot. Malac. 40: 75 (2015); = *Foeniculum vulgare* var. *sanguineum* (Triano & A.Pujadas) Reduron, Bull. Soc. Bot. Centre-Ouest 49: 124 (2018).
4. ***Anethum foeniculoides*** Maire & Wilczek, Bull. Soc. Hist. Nat. Afrique N. 27: 66, 225 (1936); =

- Schoenoselinum foeniculoides* (Maire & Wilczek) Jim.Mejías & P.Vargas, Phytotaxa 212(1): 76 (2015).
5. ***Anethum theurkauffii*** Maire, Bull. Soc. Hist. Nat. Afrique N., 27: 226 (1936).
 6. ***Anethum ridolfia*** Spalik & Reduron, **nom. nov.**, = *Ridolfia segetum* Moris, Ind. Sem. Hort. Taur. (1841); Fl. Sard. ii. 212. t. 75 (1842), non *Anethum segetum* L., Mant. Pl. Altera 219 (1771).
 7. ***Anethum fennanei*** (Reduron, Mathez & S.R.Downie) Reduron & Spalik, **comb. nov.**; basionym: *Pseudoridolfia fennanei* Reduron, Mathez & S.R.Downie, Acta Bot. Gallica 156(3): 496 (2009).

CONCLUSIONS

Apieae originated in the western Mediterranean, probably in north-western Africa, from where they dispersed to Macaronesia and the Southern Hemisphere. *Apium* experienced the most LDD events: twice from the Northern to the Southern Hemisphere, and subsequently from South America to Australia (and the Juan Fernández Islands), and, independently, to New Zealand. The Southern Hemisphere *Apium* clade has significantly higher diversification rates than the rest of the tribe. Simultaneously, clades that are morphologically diverse do not differ in net speciation rate from the morphologically homogeneous clades. Therefore, it is probable that LDD events, not morphological traits, have driven the increase in diversification rates in Apieae.

It is not clear whether derived woodiness evolved in Apieae once (in the common ancestor of *Deverra* and *Billburtia*) or twice (independently in these two genera). Nevertheless, its timing overlapped with the onset of desertification in northern Africa, and therefore it could have evolved as a response counteracting cavitation. There are no cases of typical insular woodiness in Apieae: most insular endemics are herbaceous, and Malagasy *Billburtia* might have evolved woodiness before arriving in Madagascar. At the same time, herbaceous representatives (continental and insular) do not differ in qualitative wood traits from woody representatives to any significant degree. Therefore, the evolution of secondary woodiness in these lineages may have been constrained by ecological opportunities (i.e. late arrival of these plants, when ‘woody’ ecological niches were already occupied) rather than innate anatomical characters. Simultaneously, wood anatomy is probably affected by stem architecture and plant reproductive strategy: leaf rosette-bearing species with biennial/perennial habit tend to deposit wood composed of parenchymatous and fibrous zones, whereas annuals and species without leaf rosettes

have an exclusively fibrous xylem. This may be caused by a common developmental mechanism responsible for deposition of fibres and the shift from vegetative to generative phase.

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AUTHOR CONTRIBUTIONS

K.F. prepared and analysed wood anatomical sections, gathered ecological and morphological data, performed analyses, and wrote the manuscript. Ł.B. supervised the phylogenetic study and reviewed the manuscript. A.O. supervised wood anatomical analysis and reviewed the manuscript. J.-P.R. provided plant material and taxonomic information, J.A.R.B. collected samples in the field and provided information on their ecology. M.A. obtained new DNA sequences. P.T. obtained wood anatomical sections. K.S. designed and supervised the study, contributed to the taxonomic treatment and edited the manuscript. The authors have no conflicts of interest to declare.

DATA AVAILABILITY

Materials are available online in FigShare: doi.org/10.6084/m9.figshare.14045510 and consist of (1) matrices of molecular sequences before and after trimming, plastid and ITS consensus trees, chronogram, and morphological data matrix; (2) Lagrange configurational files with unconstrained and constrained model; (3) the results of biogeographical analysis with unconstrained model

employed; (4) quantitative wood anatomical traits matrix; and (5) maximum likelihood phylogenetic tree with multiple *C. tortuosa* and *R. herbanica* accessions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Voucher information of specimens used in phylogenetic and anatomical studies of tribe Apieae and the outgroup. The accessions used to obtain new sequences are provided with detailed voucher information and accession ID, whereas accessions retrieved from GenBank are provided only with taxonomic information and GenBank reference numbers. All herbarium acronyms follow *Index Herbariorum* (Thiers, 2013). The letter 'A' following an accession ID denotes a specimen used in the anatomical study.

Figure S1. Dated maximum clade credibility tree from Bayesian MCMC analysis with the complete results of dispersal–extinction–cladogenesis (DEC) estimation of biogeographical scenarios.