

**TAXONOMY AND EVOLUTION OF
THE BUCKTHORN FAMILY (RHAMNACEAE)
IN SOUTHEAST ASIA**

Daniel Cahen

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ABSTRACT

Southeast Asia is one of the world's most floristically diverse regions, with 50,000 flowering plant species recognised and an estimated 10,000 more that have yet to be scientifically documented. My research contributes to filling this knowledge gap by documenting plants in the Rhamnaceae family from Southeast Asia. Except for *Flora of Thailand*, which followed the conclusions of our publications, none of the region's major Flora initiatives have completed accounts for Rhamnaceae. Much of their diversity is still unknown, and species boundaries are unclear. A phylogeny-based tribal classification published in 2000 is the foundation of our current understanding of evolutionary relationships within the Rhamnaceae. The phylogenetic position of some genera is still uncertain. The family is thought to have originated in the Cretaceous and mostly diversified into its current tribes in Gondwana, based on fossil evidence. Recent discovery of older fossils suggest that it may have originated in the Jurassic. We have published taxonomic revisions and new species descriptions in four genera: *Ventilago*, *Smythea*, *Gouania* and *Ziziphus*. We revised the genus *Smythea* throughout its range, including six new species descriptions, described three new *Ventilago* species, plus two additional species in New Caledonia and Vanuatu, revised the genus *Gouania* in western Malesia, and contributed the first revision of *Ziziphus* in Borneo, including three new species and two new variety descriptions. This work, carried out between 2016 and 2021, lays the groundwork for a future revision of the entire family across the region. This research will help to understand the evolutionary history of the Rhamnaceae family. Almost all the plants I documented are woody climbers that either twine around the host plant (*Smythea* and *Ventilago*), use tendrils (*Gouania*) or spines along their stems to climb (*Ziziphus*). Some have wind-dispersed winged fruits (*Ventilago*, *Smythea*, and *Gouania*), while others have fleshy fruits dispersed by animals (*Ziziphus*). These different means of climbing and fruit dissemination may have affected the evolution and spread of the woody climbing species in different ways.

STATEMENT OF AIMS

The aims of the research here are to study the Rhamnaceae family in Southeast Asia. A phylogeny-based classification was published in 2000, providing us with our current understanding of evolutionary relationships within the family; however, much of the diversity within the family remains undescribed, species boundaries are unclear, and the phylogenetic placement of some genera is still uncertain. Except for *Flora of Thailand*, which followed the conclusions of our publications, none of Southeast Asia's Flora initiatives have completed Rhamnaceae accounts. This work lays the groundwork for a revision of the family across the whole region, contributing to understanding the evolutionary history of the entire family.

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1. RHAMNACEAE DIVERSITY

1.1. Family size and distribution

The buckthorns (Rhamnaceae Juss.) are a medium-sized flowering plant family with c. 60 genera and 1,200 species (WCVP 2022). To put these figures into context, the average vascular plant family has 31 genera and 775 species, although the majority are much smaller, with median values of three genera and 57 species per family (WCVP 2022). It mostly consists of shrubs but also includes trees, woody climbers, and a single known herbaceous genus (*Crumenaria* Mart.). Onstein & Linder (2016) characterise it as a family of ‘predominantly warm-temperate woody shrubs’. While the family is cosmopolitan, it is most diverse in Mediterranean-type ecosystems (POWO 2022), with significant radiations occurring in the Cape region of South Africa, south and southwestern Australia, and California in particular. Rhamnaceae is especially diverse in Australia, where it is one of the 20 largest plant families (Kellermann & Thiele 2008), with c. 250 species, accounting for over a fifth of all Rhamnaceae species. The family is also diversified in the tropics and subtropics, with over 200 species occurring in the Neotropics, and c. 180 species in tropical Asia (POWO 2022) (Table 1). Tropical Africa has fewer Rhamnaceae species than other tropical regions, with c. 55 species (POWO 2022).

Table 1. The number of accepted Rhamnaceae species by region (POWO 2022). Regions are defined following WGSRPD (Brummitt 2001).

Region	Rhamnaceae species
Europe	29
Africa	242
<i>incl. Southern Africa</i>	<i>158</i>
Asia-Temperate	207
Asia-tropical	181
<i>incl. Indian Subcontinent</i>	<i>70</i>
<i>incl. Indochina</i>	<i>83</i>
<i>incl. Malesia</i>	<i>70</i>
<i>incl. Papuasia</i>	<i>24</i>
Australia	244
Pacific	41
Northern America	193
Southern America	208
World	1181

Outside of Mediterranean-type ecosystems, Rhamnaceae are less diverse in temperate regions, particularly in Europe, with only two species occurring in northern Europe, buckthorn (*Rhamnus cathartica* L.) and alder buckthorn (*Frangula alnus* Mill.), and less than ten species occurring in non-Mediterranean parts of Europe overall. The numbers above are provisional, however, as many groups of plants within the family have yet to be systematically documented and there are significant gaps in knowledge for several genera (Medan & Schirarend 2004).

1.2. Classification

A phylogeny-based classification of the family has been produced (Richardson et al. 2000a, 2000b) and one of the key findings is that the family is divided into three clades: the species-rich ziziphoids (over 600 species) and rhamnoids (over 300 species), and the species-poor ampeloziziphoids (c. 15 species). These clades have strong support in the original study and every subsequent family-wide analysis (Islam & Simmons 2006; Onstein et al. 2015; Hauenschild et al. 2016b; Wang et al. 2021; He & Lamont 2022),

although no morphological characters can be used to define them reliably and they are generally treated as informal clades rather than subfamilies. Ziziphoids and rhamnoids both have cosmopolitan distributions; ampeloziziphoids have a disjunct distribution with species occurring in Brazil (*Ampelozizyphus* Ducke), Cuba (*Doerpfeldia* Urb.), Madagascar (*Bathiorhamnus* Capuron) and Africa (*Ziziphus pubescens* Oliv., *Z. rivularis* Codd, and *Z. robertsoniana* Beentje).

The family is further divided into 11 tribes following a tribal classification based on molecular and morphological evidence (Richardson et al. 2000b); most of these tribes have been well-supported as monophyletic in more recent analyses (e.g., Hauenschild et al. 2016b). Several genera, however, cannot currently be confidently placed in a tribe (Table 2).

Table 2. The genera of Rhamnaceae and their tribal classification (Richardson et al. 2000b; Hauenschild et al. 2016b; Wang et al. 2021; WCVP 2022).

Clade	Tribe	Genera
ampeloziziphoids	<i>unplaced</i>	<i>Ampelozizyphus, Bathiorhamnus, Doerpfeldia</i>
rhamnoids	Maesopsidaeae	<i>Maesopsis</i>
rhamnoids	Rhamneae	<i>Auerodendron, Berchemia, Berchemiella, ConDALIA, Frangula, Karwinskia, Krugiodendron, Oreorhamnus, Phyllogeiton, Pseudozizyphus, Reynosia, Rhamnella, Rhamnidium, Rhamnus, Sageretia, Scutia</i>
rhamnoids	<i>unplaced</i>	<i>Fenghwaia</i>
rhamnoids	Ventilagineae	<i>Smythea, Ventilago</i>
ziziphoids	Colletieae	<i>Adolphia, Colletia, Discaria, Kentrothamnus, Ochetophila, Retanilla, Trevoa</i>
ziziphoids	Gouanieae	<i>Alvimiantha, Crumenaria, Gouania, Helinus, Johnstonalia, Reissekia</i>
ziziphoids	Paliureae	<i>Hovenia, Paliurus, Sarcomphalus, Zizyphus</i>
ziziphoids	Phyliceae	<i>Nesiota, Noltea, Phylica, Trichocephalus</i>
ziziphoids	Pomadereae	<i>Blackallia, Cryptandra, Papistylus, Polianthion, Pomaderris, Serichonus, Siegfriedia, Spyridium, Stenanthemum, Trymalium</i>
ziziphoids	<i>unplaced</i>	<i>Alphitonia, Ceanothus, Colubrina, Emmenosperma, Granitites, Jaffrea, Lasiodiscus, Schistocarphaea</i>
<i>unknown</i>	<i>unknown</i>	<i>Araracuara</i>

1.3 Uses

There are few plants of economic value in Rhamnaceae. *Zizyphus* Mill. Species produce edible fruits, of which Chinese jujube (*Z. jujuba* Mill.) and Indian jujube (*Z. mauritiana* Lam.) are the only two that are grown commercially at scale. Japanese raisin trees (*Hovenia dulcis* Thunb.) are also widely cultivated for their fleshy, edible rachis and inflorescence branches. *Rhamnus* L. species from the Old World produce yellow and

green dyes, and species from other genera, particularly *Ventilago* Gaertn., are also sources of dyes (see also Cahen et al. 2020b). Medan & Schirarend (2004) list *Maesopsis eminii* Engl. (house and boat building), *Ziziphus*, *Reynosa* Griseb., *Krugiodendron* Urb., *Hovenia* Thunb., and *Colubrina* Rich. Ex Brongn. (construction, fine furniture, carving, lathework, and musical instruments) as sources of timber. Some shrubs are cultivated as ornamental plants in temperate regions, particularly species of *Ceanothus* L. and *Colletia* Comm. Ex Juss., but also species of *Hovenia*, *Noltea* Rchb., *Paliurus* Mill., *Phyllica* L., *Pomaderris* Labill., and *Rhamnus* (Medan & Schirarend 2004).

1.4 Rhamnaceae in the angiosperm phylogeny

1.4.1 Historical context

During the 20th century, with fewer fossils available, and before the possibility to compare DNA sequences, several botanists attempted to infer angiosperm evolution and relationships in big-picture classification systems (e.g., Cronquist 1968; Takhtajan 1980; Thorne 1992). These were ultimately based on the investigator's broad knowledge of plant diversity and his intuitions about the bigger picture of angiosperm relationships based on characters considered informative (Soltis et al. 2018).

As noted by Richardson et al. (2000b), these classifications typically had Rhamnaceae placed with families such as Vitaceae on the basis of shared floral traits (Cronquist 1968; Takhtajan 1980) or with Elaeagnaceae on the basis of shared vegetative characteristics (Thorne 1992; Takhtajan 1997). Stamens opposite the petals is an uncommon trait in angiosperms, hence why Rhamnaceae was often grouped with Vitaceae. Harms in Suessenguth (1953) examines the two families' relationship and history of being associated. He observes that their relationship is not obvious, owing to the shrubby or tree-like habit of Rhamnaceae species versus climbing in Vitaceae, as well as the varying position of the ovary in Rhamnaceae versus the consistently superior ovary in Vitaceae.

As DNA-based classifications became available, Rhamnaceae were soon shown to clearly belong to the order Rosales (e.g., Soltis et al. 2000), confirming that the family is closely related to Elaeagnaceae but not to most of the other families previously associated with it such as Vitaceae and Celastraceae.

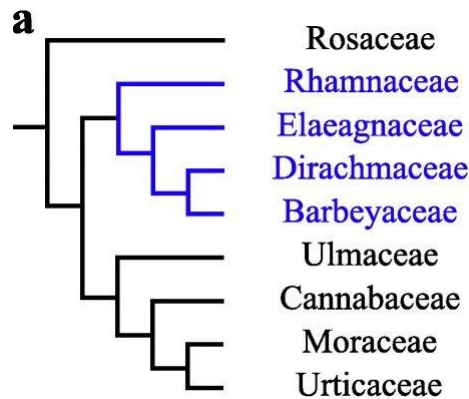
1.4.2. Rosales

The order Rosales is widely accepted to be monophyletic (e.g., Sun et al. 2016). With nine families, over 290 genera, and over 10,000 species, it accounts for over 2% of all vascular plant diversity (WCVP 2022). Judd et al. (2016) suggest that the presence of a hypanthium may be a synapomorphy of the order; it can be found in Rosaceae, Rhamnaceae, and some Ulmaceae, and may have been lost in more derived families with smaller flowers, such as Urticaceae, Moraceae, and Cannabaceae. Other possible synapomorphies include a reduced or absent endosperm, a valvate calyx and clawed petals (Stevens 2001 onwards; Judd et al. 2016). Molecular studies (e.g., Wang et al. 2009; Sun et al. 2016), support three major clades in Rosales: Rosaceae, Rhamnaceae and its related families (Elaeagnaceae, Barbeyaceae and Dirachmaceae), and Ulmaceae and its related families (Cannabaceae, Moraceae and Urticaceae).

Rosaceae is strongly supported as a sister to the rest of the family and is distinguished by flowers with many stamens and distinct carpels. Ulmaceae and its related families comprise a clade that is highly supported by molecular evidence and corresponds to the formerly recognised order Urticales, which is distinguished by the presence of cystoliths and 2-carpellate flowers. Cannabaceae, Moraceae, and Urticaceae also form a well-supported clade nested within this group, characterised by much reduced unisexual flowers. Finally, Cannabaceae is a sister to the clade comprising Moraceae and Urticaceae, well supported by DNA sequences and the presence of laticifers (Stevens 2001–onwards; Judd et al. 2016).

While most analyses conclude that a clade composed of Rhamnaceae, Elaeagnaceae, Barbeyaceae, and Dirachmaceae is well supported—Thulin et al. (1998) even argue that it is compatible with the circumscription of an order Rhamnales, recognised by Thorne (Thorne 1992; Thorne & Reveal 2007) and Takhtajan (2009)—the relationships between these families within the clade are not as strongly supported and remain more tentative. Zhang et al. (2011) examined the variation in 12 genes (including ten from plastids) in 25 Rosales taxa and concluded that Rhamnaceae could be a sister to a clade of Elaeagnaceae and (Barbeyaceae + Dirachmaceae). Support for some of these clades was weak, with a maximum likelihood bootstrap value of only 67% for the 'Elaeagnaceae and (Barbeyaceae + Dirachmaceae)' node. This topology, however, was also obtained, and with better support, by Li et al. (2021) in their angiosperm-wide phylogenomic analysis of 80 plastid genes (Fig. 1).

Figure 1. Phylogenetic relationships in Rosales. Based on plastid genes retrieved by Li et al. (2021). Every node has a bootstrap percentage of 100. The blue lines represent differences in phylogenetic positions between the authors' phylogeny and those presented on the Angiosperm Phylogeny Website (Stevens 2001 onwards). Rhamnaceae forms a clade with Elaeagnaceae, Dirachmaceae, and Barbeyaceae. Figure from Li et al. (2021).



1.4.3. Nitrogen-fixing clade

DNA analysis strongly supports a clade formed by Rosales, Fabales, Cucurbitales, and Fagales (e.g., Li et al. 2015) and these orders share a genetic predisposition for nitrogen fixation via root nodules. This may represent a synapomorphy for this clade, which is referred to as the ‘nitrogen-fixing clade’. This symbiotic relationship occurs in just ten angiosperm families: Betulaceae, Cannabaceae, Casuarinaceae, Coriariaceae, Datisceae, Elaeagnaceae, Fabaceae, Myricaceae and Rhamnaceae, all of which are included in these four orders. As noted by Soltis et al. (2018), these families were considered distantly related in traditional morphology-based classifications (e.g., Cronquist 1968; Takhtajan 1980), and their presence in a single well-defined clade is a remarkable insight derived from molecular phylogenetics.

In Rhamnaceae, the ability to form root nodules and fix nitrogen in symbiosis with *Frankia* actinomycete bacteria occurs in the tribe Colletieae and in the genus *Ceanothus*. The latter is phylogenetically close to Colletieae in the ziziphoids, but there is no strong evidence that they form a monophyletic group together (e.g., Richardson et al. 2000b; Hauenschield et al. 2016b; Wang et al. 2021). Richardson et al. (2000b) suggest that the ability to fix nitrogen in ziziphoid genera evolved twice independently or was an ancestor state that was lost as the group diversified, in which case *Ceanothus* and Colletieae could end up as sister taxa. They also mention that nitrogen-fixing has not been extensively

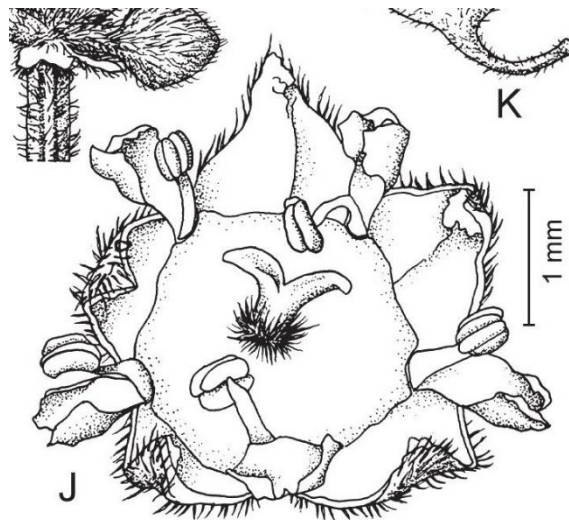
explored across Rhamnaceae and that other nitrogen-fixing groups may be discovered in the future.

1.5. Rhamnaceae delimitation and historical concepts

1.5.1. Recognition by Robert Brown

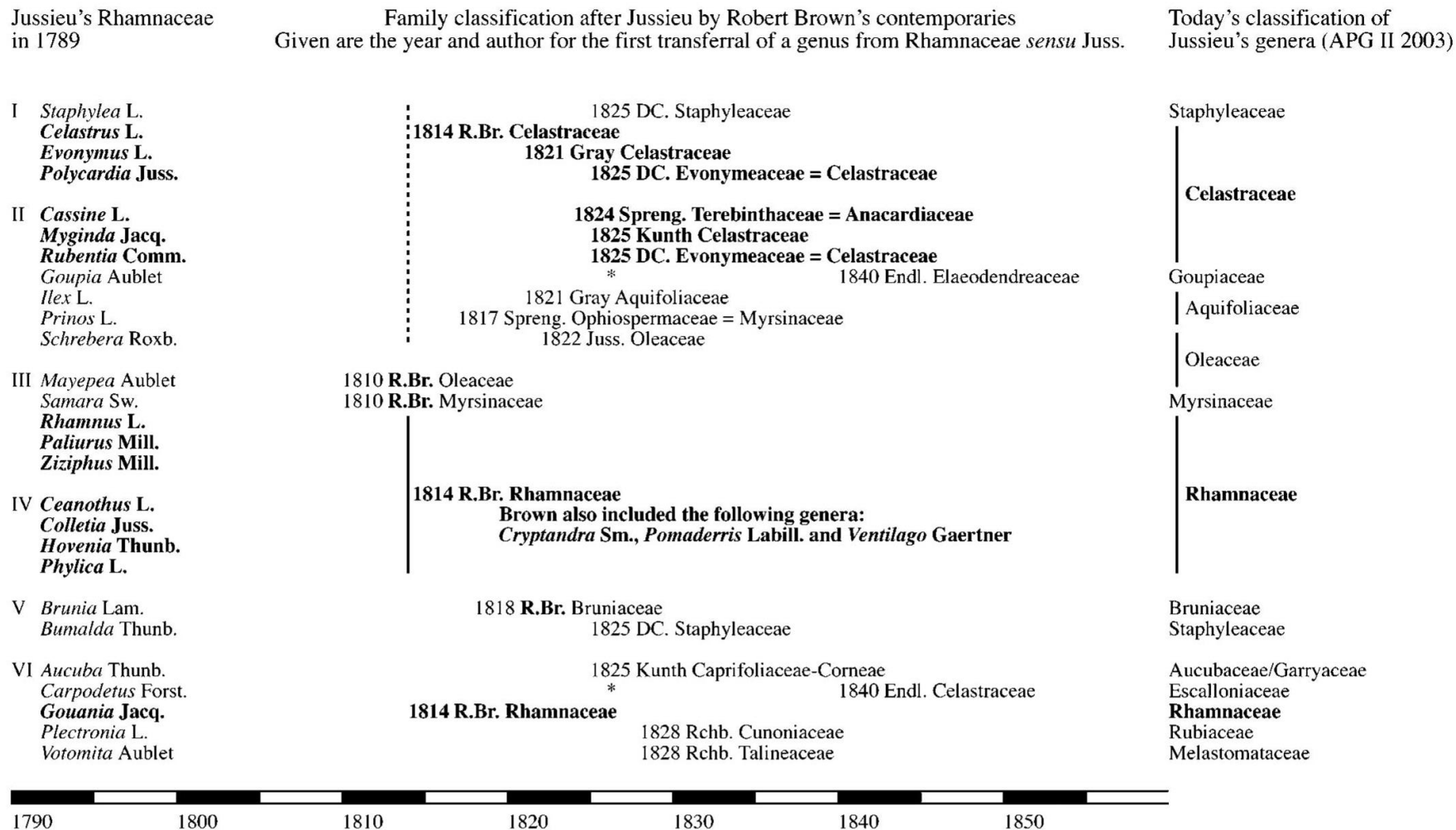
The family is strongly supported as monophyletic (Sun et al. 2016), and straightforward to recognise thanks to its unmistakable flowers, which are hypanthia with a fleshy nectar disk and, diagnostically, valvate calyx lobes and the stamens opposite the petals (Fig. 2). Despite this morphological uniformity, the family was not accurately recognised until Robert Brown emphasised the diagnostic importance of these flower characters (Brown & Bauer 1814).

Figure 2. *Ventilago vanuatuana* Cahen, Toussiroto & Pillon (Rhamnaceae) flower. Face view; the valvate calyx lobes and stamens opposite the petals are diagnostic of Rhamnaceae. Illustration by Andrew Brown. Figure from Cahen et al. (2020b).



The family had previously been established by Antoine-Laurent de Jussieu as ‘Rhamni’ (de Jussieu 1789), and even earlier by Michel Adanson who had named the clade ‘Ziziphi’ (Adanson 1763). However, de Jussieu and Adanson’s groups included plants now belonging to several families, in particular Celastraceae, which Robert Brown split from de Jussieu’s ‘Rhamni’, recognising that Celastraceae flowers have stamens that alternate with the petals (Table 3). Robert Brown revolutionised the Rhamnaceae family concept, and his new definition is still valid and in use today.

Table 3. Genera included in de Jussieu's 'Rhamni' and their subsequent transfers to other families. Asterisks indicate genera transferred out of Jussieu's 'Rhamni' by Brongniart (1826) without mentioning a new family placement. The table shows how Robert Brown recognised the boundaries of Rhamnaceae from within a group that previously included genera from many unrelated families. Table from Kellermann (2004).



1.5.2. Brongniart's monograph (1826)

Brown's concept of Rhamnaceae was adopted in subsequent classifications, such as in de Candolle's *Prodromus* (de Candolle 1825), which also provides the first review of the family following Brown's concept with a description of every then-known genus and species. Brongniart published the first detailed monographic work on the family the following year (Brongniart 1826). Miers (1860) described it as 'the best monograph of the family that has yet been published, where its affinities are well discussed, and where ample characters of the genera are given'.

Brongniart's work begins with the morphological evidence demonstrating why the split of de Jussieu's 'Rhamni' and Brown's delimitation of the family should be accepted; this includes the valvate calyx lobes and the stamens being placed opposite the petals as mentioned above. He also noted that the position of the nectar disk, the ovary's structure, the position and number of ovules in each locule, and the seed's structure are all quite consistent across the family. The tribes and genera of the family are mostly recognised based on fruit characteristics, a pattern that Brongniart had already identified, emphasising the value of fruits in distinguishing different members of the family. The North American Rhamnaceae genus *Adolphia* Meisn. (Colletieae) is dedicated to Adolphe Brongniart.

1.5.3. Major works following Brongniart's monograph

Since Brongniart's original monographic treatment of the family, the most thorough, in-depth studies of Rhamnaceae were published by Baillon (1875, 41 pages) and then in *Die Natürlichen Pflanzenfamilien*, with Weberbauer's initial treatment (1895, 34 pages) serving as the foundation but being considerably augmented by Suessenguth (1953, 173 pages). The latter work is the most recent revision of the entire family, as well as the most ambitious effort to date to cover the entire known diversity of the family at the species level. The most recent encyclopaedia-like review of the family was published in *The Families and Genera of Vascular Plants* (Medan & Schirarend 2004, 18 pages), which, while encompassing all of the then-known diversity of Rhamnaceae, is much more synoptic than Suessenguth's revision and covers the family's diversity at the genus level but not the species level.

The low variability of flower characters in Rhamnaceae is an obstacle to studying its taxonomy (although floral nectary disks have been used for diagnosis in *Gouania* and Colletieae and other genera—see Ribeiro et al. 2021 for full references). This morphological uniformity of the flowers is a striking feature of the family that contrasts with the comparatively great morphological diversity of the fruits, which serve more in delimiting genera, as already mentioned, and was the basis of the tribal classifications by Endlicher (1840), Hooker (1862), Weberbauer (1895) and Suessenguth (1953), before the additional use of molecular characters by Richardson et al. (2000a, 2000b).

Fruit characters alone, however, are not sufficient in characterising many clades within the family. For example, as noted by Richardson et al. (2000b), *Berchemia* Neck. Ex DC., a rhamnoid, was placed with *Ziziphus*, a ziziphoid, in Zizipheae (= Paliureae) by Hooker (1862) and Suessenguth (1953), and while both have drupaceous fruits, this does not reflect their phylogenetic relationship, as would have been inferred when looking at other morphological characters such as the ovary position (partially immersed in the nectar disk in *Berchemia* versus superior in *Ziziphus*), and leaf venation (pinnate in *Berchemia* versus triplinerved in *Ziziphus*). In other cases, like between genera within Ventilagineae or between those within Gouanieae, the shared character of winged and wind-dispersed fruits does reflect that genera within these tribes are closely related, even though the tribes Ventilagineae (rhamnoids) and Gouanieae (ziziphoids) are themselves not closely related.

1.6. Rhamnaceae phylogeny and current concepts

1.6.1 Foundation phylogenetic analysis: Richardson et al. (2000)

The first family-wide molecular phylogenetic study was undertaken by Richardson et al. (2000a), which led to a revision of the family's tribal classification (Richardson et al. 2000b). In a total evidence approach, the authors also included morphological characters in their analysis, mostly based on those suggested to be diagnostic for genera or tribes by Suessenguth (1953). This research forms the basis of current understandings of evolutionary relationships within Rhamnaceae.

Richardson et al. (2000b) summarised the taxonomic history of suprageneric classifications in Rhamnaceae prior to their work. Endlicher (1840) recognised Colletieae, Gouanieae, and Pomaderreae, and included genera that are still placed in these

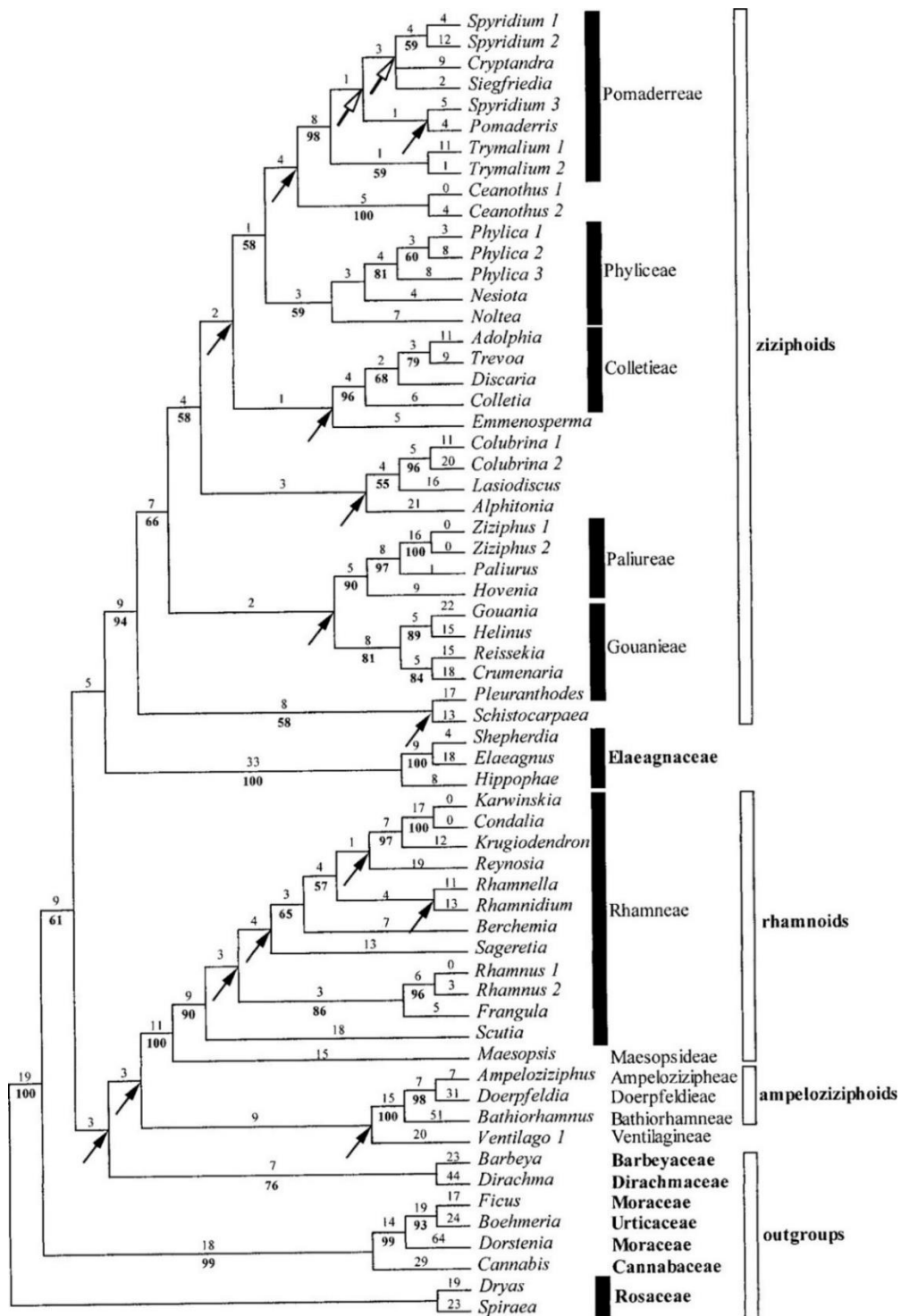
tribes; however, the composition of Phylliceae and Paliureae, also tribes that are still recognised, has since been overhauled. Hooker (1862) followed Endlicher's system but removed *Ventilago* from Endlicher's Paliureae and placed it alongside the newly described *Smythea* Seem. In the newly recognised Ventilagineae, which still includes the same two genera. Suessenguth (1953) recognised the same five tribes as Hooker (1862), and his classification served as the basis for the revision by Richardson et al. (2000b) (Table 4).

Table 4. Suessenguth's tribal classification of Rhamnaceae. Only Colletieae, Gouanieae and Ventilagineae were retained as monophyletic in the analysis by Richardson et al. Rhamneae and Zizipheae contain genera belonging to a diverse set of clades across the family tree. Asterisks indicate genera sampled by Richardson et al. for their tribal classification. Table from Richardson et al. (2000b).

<i>Colletieae</i>	Adolphia* , Colletia* , Discaria* , Kentrothamnus , Retanilla , Talguenea , Trevoa*
<i>Gouanieae</i>	Crumenaria* , Gouania* , Helinus* , Pleuranthodes* , Reissekia*
<i>Rhamneae</i>	Ampelozizphus* , Alphitonia* , Ceanothus* , Colubrina* , Cormonema , Cryptandra* , Emmenosperma* , Hovenia* , Hybosperma , Lasiodiscus* , Macrorhamnus , Nesiota* , Noltea* , Oreorhamnus , Phyllica* , Pomaderris* , Rhamnus* , Sageretia* , Schistocarpha* , Scutia* , Siegfriedia* , Spyridium* , Trymalium* , <i>Tzellemtinia</i>
<i>Ventilagineae</i>	Smythea , Ventilago*
<i>Zizipheae</i>	Auerodendron , Berchemia* , Berchemiella , Chaydaia , Condalia* , Condaliopsis , Dallachya , Doerpfeldia* , Lamellisepalum , Microrhamnus , Karwinskia* , Krugiodendron* , Maesopsis* , Paliurus* , Phyllogeiton , Reynosia* , Rhamnella* , Rhamnidium* , Sarcomphalus , Ziziphus*

Suessenguth's (and, by extension, Hooker's) Rhamneae and Zizipheae tribes were large and morphologically diverse, and the analysis by Richardson et al. (2000b) revealed that they were polyphyletic. Only Ventilagineae, Colletieae, and Gouanieae were previously identified as having more or less the same genera as those placed in these tribes by Richardson et al. (2000b). The authors elucidated phylogenetic relationships using the plastid genes *rbcL*, *trnL-F*, and a combination of *rbcL+trnL-F*. The *trnL-F* and *rbcL+trnL-F* topologies were more strongly supported by bootstrap than the *rbcL* tree, which the author notes misses more homoplasious changes and has a less accurate overall topology. The combined *rbcL+trnL-F* tree is the one most used to interpret phylogenetic relationships in the analyses by Richardson et al. (Fig. 3).

Figure 3. Rhamnaceae tribal classification phylogeny by Richardson et al. (2000a). Successive approximations weighting tree obtained by parsimony analysis of *rbcL* sequences. Fitch lengths are indicated above branches and bootstrap values below. Solid arrows indicate branches not present in the Fitch strict consensus tree, while open arrows indicate those not present in the successive approximations weighting strict consensus tree. This research forms the basis of current understandings of evolutionary relationships within Rhamnaceae. Figure from Richardson et al. (2000a).



The authors warn that a ‘classification based solely on DNA sequence data should be treated with caution unless corroborated by evidence from other sources, but the *rbcL/trnL-F* data have indicated patterns that were not apparent from previous non-phylogenetic studies of morphology and anatomy’. Indeed, their research has yielded important insights into relationships within Rhamnaceae.

Apart from the key result of revealing the existence of the three strongly supported ziziphoid, rhamnoid and ampeloziziphoid clades, other significant findings include:

- Three of the five tribes recognised by Suessenguth (Gouanieae, Colletieae and Ventilagineae) are supported as monophyletic; Suessenguth’s remaining two tribes, Rhamneae and Zizipheae, were not monophyletic and included genera belonging to several tribes.
- Pomaderreae is supported as monophyletic and is reinstated.
- Paliureae, when restricted to *Ziziphus*, *Paliurus* and *Hovenia*, is supported as monophyletic.
- *Ceanothus* is supported as monophyletic but its placement in a tribe is not clear
- Phyliceae is supported as monophyletic but is emended to include different genera.
- *Colubrina* is supported as monophyletic but its placement in a tribe is not clear.
- *Maesopsis* is supported as sister to a much-emended Rhamneae tribe including *Karwinskia* Zucc., *Condalia* Cav., *Krugiodendron*, *Reynosia*, *Rhamnella* Miq., *Rhamnidium* Reissek, *Berchemia*, *Sageretia* Brongn., *Rhamnus*, *Frangula* Mill., and *Scutia* (Comm. ex DC.) Brongn.
- *Ampelozizyphus*, *Doerpfeldia*, and *Bathiorhamnus* form a clade despite no clear morphological similarities and very disjunct distributions (Brazil, Cuba, and Madagascar), implying that they are remnants of groups that were once more diverse and widespread.
- *Colubrina* and *Lasiodiscus* Hook.f., two morphologically similar genera, may eventually be treated as a distinct tribe, but there is insufficient molecular evidence to recognise this clade.
- *Alphitonia* Reissek ex Endl. and *Emmenosperma* F.Muell. are similar because they have red arillate seeds persisting on the receptacle after dehiscence and may eventually be placed in a single tribe but there is insufficient molecular evidence to recognise this clade.

- *Schistocarpha* F.Muell. appears to be closely related to Colletieae, despite sharing few obvious morphological characters, but its placement in a tribe is not well supported.
- *Ceanothus* is placed not too distant from Colletieae in the phylogenetic tree, and both engage in nitrogen fixation via root nodules; they could end up as sister taxa but there is insufficient evidence to recognise this.

Currently accepted new genera have been described since the revised tribal classification by Richardson et al. (*Johnstonalia* Tortosa and *Polianthion* K.R.Thiele in 2006, *Serichonus* K.R.Thiele and *Papistylus* Kellermann, Rye & K.R.Thiele in 2007, *Araracuara* Fern.Alonso in 2008, *Jaffrea* H.C.Hopkins & Pillon in 2015, *Pseudoziziphus* Hauenschild in 2016, and *Fenghwaia* G.T.Wang & R.J.Wang in 2021) or been reinstated (e.g., *Sarcomphalus* P.Browne in Hauenschild et al. 2016b and *Phyllogeiton* Herzog in Huang et al. 2021) and more recent molecular analyses slightly refined this phylogenetic backbone. However, the basic structure of the classification by Richardson et al. has not changed, and no new tribe has been described or significantly redefined since the 11 they recognised.

1.6.2. Uncovering the polyphyly of *Ziziphus*

In the second family-wide phylogenetic analysis, Islam & Simmons (2006) re-examined the intrageneric phylogenetic relationships of two species cultivated for their edible fruits, *Ziziphus jujuba* and *Z. mauritiana*, in order to identify their closest relatives. Their main finding was that *Ziziphus* species from the Old and New Worlds formed two distinct and well-supported clades with the Old World species more closely related to *Paliurus* than to New World *Ziziphus*, rendering the genus as they accepted it non-monophyletic. The authors decided to transfer *Sarcomphalus* to *Ziziphus* because *Sarcomphalus* species were nested within the New World *Ziziphus* clade. Hauenschild et al. (2016b) later decided to reinstate *Sarcomphalus* and transfer New World *Ziziphus* species to *Sarcomphalus*. This remains the most significant modification to the original classification by Richardson et al. (2000b).

The family-wide molecular phylogenetic analysis by Onstein et al. (2015) included the most extensive sampling of the family at the time, with samples from 50 Rhamnaceae genera, but its goal was to compare diversification rates in Rhamnaceae

across different Mediterranean-type ecosystems rather than to solve taxonomic problems. The tree they produced is mostly consistent with the findings of Richardson et al. (2000b). With high posterior probabilities, all 11 original tribes were confirmed to be monophyletic. Onstein et al. found distinct Old World and New World *Ziziphus* clades, confirming the findings of Islam & Simmons (2006). The positions of *Ziziphus celata* Judd & D.W.Hall (in Rhamnaceae) and *Z. pubescens* (in ampeloziziphoids) are also consistent with Islam & Simmons's results. *Ziziphus rivularis* (which was not sampled in subsequent analyses) was included in their sampling and is classified as an ampeloziziphoid alongside *Z. pubescens*.

1.6.3. A new reference Rhamnaceae phylogeny: Hauenschild et al. (2016b)

The largest data set used for phylogenetic reconstruction of the family to date was generated by Hauenschild et al. (2016b), who included plastid, mitochondrial, and nuclear markers in 57 Rhamnaceae genera. This marks a slight increase over the original tribal classification analysis by Richardson et al. (2000b) that was based on two plastid markers in 42 genera. The authors also specify that they gathered data from samples reflecting the distribution of cosmopolitan groups and checked the identification of the vouchers used for sampling.

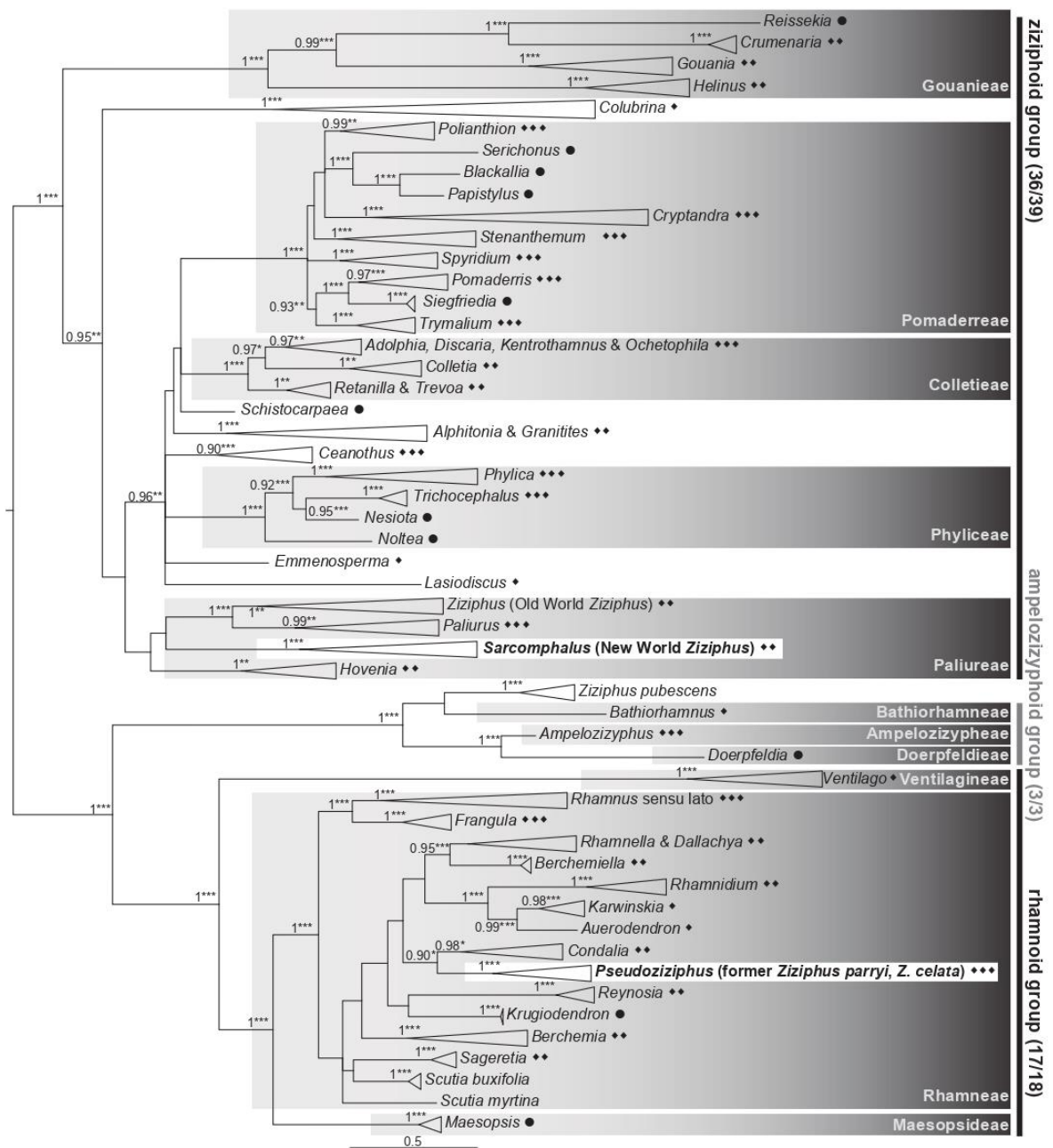
The goal of this study was to elucidate relationships in the family that remained obscure in the analysis by Richardson et al. (2000b). The authors state the aims of their research in four questions: '(1) Is the most recent tribal classification by Richardson et al. (2000b) supported by our analyses? (2) Which are the remaining uncertainties concerning tribal phylogenetic relationships in Rhamnaceae? (3) Are all accepted Rhamnaceae genera monophyletic? (4) If not, which taxonomic treatments can be suggested to arrive at a sound classification of the buckthorn family?'

The answers to these questions based on their results can be summarised as follows: (1) The three main clades recognised by Richardson et al. (ziziphoids, rhamnoids and ampeloziziphoids) are all clearly monophyletic; ampeloziziphoids are closely related to the rhamnoids, and together they are the sister clade to the ziziphoids. The tribes recognised by Richardson et al. are placed in the same clades in this analysis, and their composition is mostly unchanged. (2) Genera that could not confidently be placed in a tribe by Richardson et al. also could not be placed in a tribe following this analysis; *Colubrina*, *Alphitonia*, *Ceanothus*, *Emmenosperma*, *Granitites*, *Lasiodiscus* and

Schistocarpha remain tribeless. (3) *Ziziphus* as previously defined was polyphyletic; two former *Ziziphus* clades are within the ziziphoids: Old World *Ziziphus*, retained as *Ziziphus*, and New World *Ziziphus* transferred to the reinstated *Sarcomphalus*; a third clade of former *Ziziphus* taxa are nested in the rhamnoids and transferred to the new genus *Pseudoziziphus*, weakly supported as sister to *Condalia*; The fourth clade consists of *Z. pubescens* and is nested in the ampeloziziphoids, although the authors did not describe a new genus to accommodate it, or expand *Bathiorhamnus* to include it. Other genera not supported as monophyletic include *Rhamnella* and *Scutia*. (4) The authors do not explicitly answer this question, although they imply that *Colubrina* might be closely related to Paliureae or could represent an independent section and that increased sampling might help address this question (only four of c. 30 *Colubrina* species were sampled). Only a single species of *Lasiodiscus* (of 11 accepted) and *Emmenosperma* (of six accepted) were included in the study, and more extensive sampling might help determine their position in the phylogeny.

Despite the inclusion of more taxa and markers, this analysis mostly replicates the results obtained by Richardson et al. (2000b) and could not settle the status of their unplaced genera (Fig. 4). The authors, however, specify that they used topological constraints to build their trees wherever nodes had previously been consistently supported. In addition, about half of the samples included in their study had been used in the original analysis by Richardson et al. (2000b), which could carry over biases. Overall, more than half of the sequences included in their analysis were obtained on GenBank from previous phylogenetic analyses.

Figure 4. Rhamnaceae phylogeny by Hauenschield et al. (2016b). Based on combined nuclear ribosomal internal transcribed spacer (ITS) and *trnL-trnF* data. Majority-rule consensus tree (Bayesian analysis). The family's three informal clades are labelled on the right (numbers in brackets: genera included in this study / genera). Numbers at nodes represent posterior probabilities. The stars after the numbers refer to fasttree-like searches and maximum likelihood estimates: * node present in all analyses (ITS, *trnL-trnF*, combined), but not supported; ** node present and supported in two of three analyses; * node present and supported in all analyses. Genera newly recognised by the authors are highlighted. Species sampling: ● genus monotypic, ◆ less than 20% included, ◆◆ 20%–49% included, ◆◆◆ 50% or more of species included. This research mostly confirmed the results of Richardson et al. (2000a) but addressed the polyphyly of *Ziziphus*. Figure from Hauenschield et al. (2016b).**



One of the primary outcomes of this study was the publication of a formalised solution to the polyphyly of *Ziziphus*, first supported by molecular evidence by Islam & Simmons (2006) and confirmed by Onstein et al. (2015) and Islam & Guralnick (2015), but was missed by Richardson et al. (2000a, 2000b), who only included two *Ziziphus* samples, both of which belonged to the Old World clade. In summary, Hauenschild et al. believe that the concept of three distinct genera (*Pseudoziziphus* gen. nov., *Sarcomphalus*, and *Ziziphus*) is the most conservative solution to the polyphyly of *Ziziphus* as previously defined.

However, they did not decide which genus *Ziziphus pubescens* should belong to, and it will inevitably be assigned to a different genus in a future publication given its strongly supported placement in the ampeloziziphoids. The authors note that *Z. pubescens* and *Z. robertsoniana* are morphologically similar to *Bathiorhamnus* and that additional research involving more genetic data will be required to determine whether *Bathiorhamnus* should be expanded to include these species, or if the description of a new genus is preferable.

1.6.4. Other Rhamnaceae phylogenies

In addition to presenting one of the most morphologically unique new Rhamnaceae species discoveries in recent decades, Wang et al. (2021) reconstructed a family-wide phylogeny, mostly based on data available on GenBank from the analysis by Hauenschild et al. (2016b). The new genus, *Fenghwaia*, has cylindrical drupaceous fruits with an inferior ovary that are distinct from all other fruits in the family. Although there are some differences that could eventually lead to a more accurate understanding of tribal limits, the topology of their Rhamnaceae phylogeny is mostly like those obtained by previous authors (Richardson et al. 2000a, 2000b; Onstein et al. 2015; Hauenschild et al. 2016b), which is not surprising as it is largely based on the same sequences.

The most recent Rhamnaceae phylogeny was included in an article focusing on the implications of recalibrating the molecular clock by including a 99-million-year-old fossil attributed to *Phyllica* to estimate when Rhamnaceae first appeared (He & Lamont 2022). The authors included one or two GenBank sequences from 48 Rhamnaceae genera (five sequences for *Phyllica*). Their phylogeny surprisingly includes a split of Colletiae, as well as the placement of *Maesopsis* within Rhamneae. The sampling was not as extensive as in previous studies, and the authors did not provide support values for their

clades. Although the focus of this article was molecular dating rather than providing a high-resolution phylogeny of the family, these findings are an additional data point that may eventually provide further evidence for more robustly supported topologies.

Apart from the family-wide phylogenies discussed above, additional phylogenies for a subset of the family were recently published in publications focusing on a particular genus, notably *Ceanothus* (Burge et al. 2011), *Ziziphus sensu lato* (Islam & Guralnick 2015), *Sageretia* (Yang et al. 2019), *Phyllica* (van Santen & Linder 2020) and *Berchemia* (Huang et al. 2021).

Yang et al. (2019) used five molecular markers and a large sample of rhamnoids (23 species of *Sageretia* and 11 other genera) and mostly confirmed the topology obtained by Hauenschild et al. (2016b), which was used as a reference point in this study. Both phylogenies support a clade composed of *Karwinskia*, *Auerodendron* Urb., *Rhamnidium*, *Rhamnella* (including *Dallachya vitiensis* (Benth.) F.Muell.), *Berchemiella* Nakai, *Condalia*, *Pseudoziziphus*, *Krugiodendron*, *Reynosia*, and *Berchemia* (dubbed the ‘*Berchemia* Alliance’ by these authors). Significant differences include the better-supported monophyly of *Scutia* (polyphyletic in Hauenschild et al. 2016b) and the non-monophyly of *Berchemia*, with *B. discolor* (Klotzsch) Hemsl. and *B. zeyheri* (Sond.) Grubov placed in a different clade than other *Berchemia* species. The authors were unable to provide strong support for the position of *Sageretia* position within Rhamnaceae, which was tentatively assigned as a sister to the ‘*Berchemia* Alliance’ and *Scutia*; previous research had identified *Sageretia* as a sister group to *Scutia* (Richardson et al., 2000b), a clade consisting of *Scutia* and *Rhamnus* (Islam & Guralnick, 2015), and *Scutia buxifolia* Reissek (Hauenschild et al., 2016b), but all of these results were also poorly supported.

Huang et al. (2021) confirmed the non-monophyly of *Berchemia* and reinstated the genus *Phyllogeiton* to accommodate *B. discolor* (= *Phyllogeiton discolor* (Klotzsch) Herzog) and *B. zeyheri* (= *Phyllogeiton zeyheri* (Sond.) Suess.). The topology they obtained was nearly identical to that obtained by Yang et al. (2019) and provides no additional information.

1.7. Contributions by Cahen et al.

Many taxonomic groups in Rhamnaceae require revision, with poorly defined genus and species boundaries and much-undescribed diversity. Generic limits in the tribe Rhamneae, for example, between *Reynosia*, *Rhamnidium*, *Auerodendron*, and *Karwinskia* need investigating (Medan & Schirarend 2004). Much of the diversity of Southeast Asia's *Ventilago* and *Gouania* species has yet to be described, with herbarium specimens that do not match well with the type material of currently recognised species (Cahen, pers. obs.).

Rhamnaceae have several genera with wide distributions, e.g., *Berchemia*, *Colubrina*, *Gouania*, *Rhamnus*, *Sageretia*, *Scutia*, *Ventilago* and *Ziziphus*. While *Berchemia* (Huang et al. 2021), *Rhamnus* (Hauenschild et al. 2016a) and *Sageretia* (Yang et al. 2019) were recently included in revisions that incorporated DNA sequencing and biogeographic assessments, this remains to be done at a fine scale in all the other listed genera.

Much of the research on which this publication is based was done expressly to address the issue of revising the taxonomy of genera with uncertain species limits and a much remaining undescribed diversity, with a focus on Southeast Asia (as well as New Caledonia and Vanuatu for *Ventilago*).

1.7.1. Ventilagineae

Ventilagineae currently consists of two genera, *Ventilago*, a genus of c. 40 species of Old World tropical climbing shrubs, lianas and, rarely, small trees, and *Smythea*, a group of 12 species of mostly South-East Asian tropical climbers (POWO 2022; Cahen & Utteridge 2017; Cahen & Utteridge 2018; Cahen et al. 2020b). Members of the tribe are easily recognised by their fruits having an oblong wing-like apical appendage. Ventilagineae is consistently supported as belonging to the rhamnoids as a sister group to the rest of the clade, which consists of *Maesopsis*, *Fenghwaia* and Rhamneae (Richardson et al. 2000a, 2000b; Wang et al. 2021) (Fig. 3). Surprisingly, no *Smythea* species have ever been successfully sequenced and incorporated into phylogenetic analyses. Richardson et al. (2000a, 2000b) did not sample the genus in their tribal classification, although it was placed in Ventilagineae alongside *Ventilago* due to their similar morphology.

1.7.2. *Smythea* and *Ventilago*

Smythea was revised based on morphological characters across its entire range, in a publication that also included the description of five new species (Cahen & Utteridge 2018). Generic limits are discussed in detail in this publication. To summarise, *Smythea* was originally based on a single species, *S. lanceata* (Tul.) Summerh., a coastal species with inflated fruits that are dispersed by water and where the appendage above the seed chamber is rarely planar and wing-like. Later authors, such as Weberbauer (1895), Ridley (1922), Suessenguth (1953), and Banerjee & Mukherjee (1970), recognised that some Ventilagineae species have fruits with a conspicuous globose seed chamber clearly differentiated from the wing (placed in *Ventilago*) as opposed to other species that have fruits with a laterally compressed seed chamber graduating into the wing (placed in *Smythea*, alongside *S. lanceata* despite the difference in fruit morphology).

While revising *Smythea*, Cahen & Utteridge found additional characters that may help distinguish the two genera: *Smythea* fruits, except for *S. lanceata* and *S. poomae* Cahen & Utteridge, are slightly twisted around the base, which is not the case with *Ventilago*. In *Ventilago*, the fruit base is frequently covered by the persistent calyx, but not in *Smythea*. In *Smythea*, leaves are almost always asymmetrical at the base, and leaf margins are at least obscurely crenate-serrate, whereas many *Ventilago* species have symmetrical leaves with entire leaf margins; lateral pairs of secondary veins are generally fewer in *Smythea* than in *Ventilago*, and domatia are more common. Most *Smythea* species have flowers borne in fascicles in the axils of persistent leaves, whereas in *Ventilago*, the fascicles are mostly arranged in leafless racemes or panicles. Furthermore, unlike in *Ventilago*, some species of *Smythea* have flowers with clearly papillate nectary discs.

Ventilagineae with laterally compressed seed chambers, fruit slightly twisting near the base, and papillate nectary discs may form a separate genus from *Ventilago* and *Smythea sensu stricto* (if restricted to *S. lanceata* and *S. poomae*). The morphology-based concepts of *Smythea* and *Ventilago*, as well as this hypothesis of well-differentiated clades leading to a different circumscription of species, are currently being investigated using DNA evidence by Henry Miller, an MSc student at Kew, who is supervised by Tim Utteridge, Félix Forest, and Daniel Cahen.

1.7.3. Contribution to the knowledge of *Smythea*

The genus *Smythea*, named after William James Smythe (1816 – 1887), general and colonel-commandant of the Royal Artillery, first appeared in a list of plants gathered in the Fiji Islands by Berthold Seemann (Seeman 1861). The following year, Asa Gray (1862) published ‘Remarks’ on the plants collected by Seemann, noting that *S. pacifica* Seem. had axillary flowers like *Ventilago bombaiensis* Dalzell (= *S. bombaiensis* (Dalzell) S.P.Banerjee & P.K.Mukh.) and fruits similar to *Ventilago lanceata* Tul. (= *S. lanceata*). Seemann (1862) validly published the genus the following month, which contained only *S. pacifica* (= *S. lanceata*). Regional revisions have since been published in local Floras, such as King (1896) and Ridley (1922) for the Malay Peninsula, and Banerjee & Mukherjee (1970) for India.

The revision of *Smythea* (Cahen & Utteridge 2018) not only clarified what morphological characters are used to delimit it from *Ventilago* but included the description of five new species and six new synonyms. A new combination for one of the most common species was also established (*S. oblongifolia* (Blume) Cahen & Utteridge). This revision covers the known global diversity of *Smythea* species, includes distribution maps and tentative conservation assessments, and lays the framework for future research into the group’s diversity. Results from this publication have already been used to inform the Flora of Thailand account of Rhamnaceae (Norsaengsri et al. 2020) and to update Co’s Digital Flora of the Philippines (Pelzer et al. 2011 onwards).

Timothy Utteridge recently discovered a specimen of an undescribed *Smythea* species (*S. papuana* Utteridge & Cahen) while visiting the Australian National Herbarium. Its description completes the account of the currently known diversity of species in the genus (Utteridge & Cahen 2021).

1.7.4. Contributions to the knowledge of *Ventilago* in Southeast Asia

Regional revisions of *Ventilago* were published in local Floras, most notably by Pierre (1894), who revised the genus for Cochinchina; King (1896), and Ridley (1922) for the Malay Peninsula; Pitard (1907 – 1912) and Tardieu-Blot (1948) for Indochina; and Guillaumin (1926) for New Caledonia. Merrill presented an enumeration of *Ventilago* species from the Philippines (Merrill 1923), while Banerjee & Mukherjee (1970) revised the genus for India, and Chen & Schirarend (2007) for China.

However, unlike *Smythea*, *Ventilago* has not yet been revised across its distribution, and there are certainly more species to describe, particularly in Southeast Asia (Cahen, pers. obs.), despite the description of three new species from Malesia and New Guinea, including two from Borneo that were previously recognised as the much-different *V. dichotoma* (Blanco) Merr. (Cahen & Utteridge 2017). This publication also includes a key to the known *Ventilago* species of Borneo, a preliminary IUCN conservation status assessment, and a distribution map for each new species, all of which contribute to a better understanding of the species diversity in this genus and could form the basis of the future *Flora Malesiana* account.

Another novel observation in Cahen & Utteridge (2017) was that the name *V. madraspatana* Gaertn. is widely misapplied. Gaertner originally used it to describe a *Ventilago* species based on Rumphius's *Funis viminalis* from Ambon (Rumphius 1747). However, the name has since been widely and incorrectly applied to a commonly collected species from India. This issue, however, has not yet been formally addressed, and the Indian species may eventually need to be placed under a new name. *Ventilago madraspatana* sensu Gaertn. is more closely related to a group of species that includes *V. papuana* Merr. & L.M.Perry, *V. borneensis* Ridl., and *V. microcarpa* K.Schum. and is distinguished by broad leaves with entire margins, 6—8 pairs of abaxially almost flat secondary veins, no domatia at secondary vein axils, and flowers with hairy nectary discs (Cahen, pers. obs.).

1.7.5. Contributions to the knowledge of *Ventilago* in the Pacific

Ventilago was also revised for New Caledonia and Vanuatu (Cahen et al. 2020b). The revision clarified the distinctions between previously muddled species concepts. Four specimens had originally been used to describe *V. pseudocalyculata* Guillaumin. The species is now thought to be restricted to the Loyalty Islands, with specimens from New Caledonia's main island being treated as a new species, *V. tinctoria* Cahen, Toussirot & Pillon. The plants from Vanuatu, previously identified as *Ventilago neocaledonica* Schltr., are now considered a new species endemic to the archipelago (*V. vanuatuana* Cahen, Toussirot & Pillon). This work contributed to a better understanding of Ventilagineae diversity as well as helped determine what the correct scientific name (*V. vanuatuana*) is for the climber whose bark is traditionally used to prepare the red dye of ceremonial mats in Vanuatu.

1.7.6. *Gouania* in western Malesia

Gouania is a pantropical genus of over 50 woody climber species distinguished by circinnate tendrils and 3-winged dry schizocarps that separate into three 2-winged indehiscent mericarps (Medan & Schirarend 2004). The only Gouanieae members found in the Old World are *Gouania* and *Helinus* E.Mey. ex Endl. The latter genus also comprises climbers with tendrils, but its fruits are unwinged capsules, and its range is limited to Eastern and Southern Africa, Madagascar, the Arabian Peninsula's southern tip, and the Indian subcontinent. *Gouania* has never been revised across its range, and most of its diversity remains undocumented, however, revisions for the Western Indian Ocean (Buerki et al. 2011) and North America were recently published (Pool 2014), in addition to our revision for western Malesia (Cahen et al. 2020a).

Lauterbach (1922) provided the most comprehensive survey of Asian *Gouania* species to date, with some minor changes made by Suessenguth (1953) in what is the most recent attempt at a complete study at the species level. The taxonomic history of the genus in western Malesia is complex and summarised by Cahen et al. (2020a).

Going through the taxonomic literature and studying herbarium specimens helped to clarify species concepts. Lauterbach (1922) published two endemic new species to the Philippines: *G. fimbriata* Reissek ex Lauterb. and *G. nematostachya* Reissek ex Lauterb., both of which were retained by Suessengueth (1953) but had not appeared in checklists or taxonomic descriptions thereafter. Cahen et al. recognised them as distinct species after study of herbarium material and found that Sulawesi and Borneo are also home to *G. nematostachya*. It is the only species of *Gouania* known to grow in Borneo, where it was recognised as *G. microcarpa* by numerous authors (e.g., Merrill 1921; Masamune 1942; Beaman & Anderson 2004), however, it differs from *G. microcarpa* DC. in several morphological characters discussed in the revision. Specimens from Philippine islands south of Luzon, with densely hairy leaves and peduncles longer than in *G. fimbriata*, are described in the revision as belonging to a new species: *G. longipedunculata* Cahen, Stenn & Utteridge.

Another finding was that *Gouania obtusifolia* Vent. ex Brongn. is restricted to western Malesia and that its synonym, *G. javanica* Miq., is still used to refer to plants found in southern China and parts of Southeast Asia found north of the Malay Peninsula. These share several characters with *G. obtusifolia*, including stipule and disk features.

However, *G. obtusifolia* is distinguished by prominently crenate-serrate leaf margins, as noticed by Kurz (1871, 1875), Hasskarl (1871), and Lauterbach (1922) and other characters listed by Cahen et al. (2020a). The taxonomic status of the plants north of the Malay Peninsula referred to as *G. javanica* will need to be addressed in a future publication.

The revision of *Gouania* in western Malesia (Cahen et al. 2020a) helped resolve a confusing taxonomic situation characterised by many misapplied names. Five species were recognised and distribution maps, and preliminary IUCN conservation status assessments were provided for each species, helping document the diversity of species in this genus. Results from the revision form the basis of the *Gouania* treatment in Co's Digital Flora of the Philippines (Pelzer et al. 2011 onwards).

1.7.7. *Ziziphus* in Borneo

Ziziphus includes over 80 species of deciduous and evergreen shrubs, climbers, and trees found across the Old World tropics, subtropics, and warmer temperate regions. Despite being widely distributed, questions remain around the age, dispersal, and morphological adaptations of the genus. In Malesia, the genus is especially diverse, with over 25 currently recognised species (Cahen et al. 2021; POWO 2022). There was no complete taxonomic treatment of *Ziziphus* on Borneo before the revision by Cahen et al. (2021), but checklists for the island (Merrill 1929; Masamune 1942) and the Mount Kinabalu area (Beaman & Anderson 2004) are available, with Merrill listing five species, Masamune listing 11, and Beaman & Anderson listing eight. The most complete overview of *Ziziphus* species occurring in Borneo was restricted to Sabah and Sarawak (Schirarend 1995). It includes a detailed account of *Z. angustifolia* (Miq.) Hatus. ex Steenis and recorded seven climbing species in the key only.

The revision by Cahen et al. (2021) revealed that Borneo is the island with the greatest known diversity of *Ziziphus* species in the world with 13 recognised species. Many of the species occurring in Borneo were found to have a small distribution range: five are endemic to the island and four are restricted to the Philippines, Borneo, and Sulawesi. The area surrounding Mount Kinabalu is particularly diverse with nine species recorded for Ranau, including two local endemic varieties.

The revision by Cahen et al. (2021) includes the description of three new endemic species and two new varieties. In addition, four new synonyms were established and *Z.*

elmeri Merr. a tree species with pinnate venation was placed as a synonym of *Colubrina beccariana* Warb. following the study of herbarium material (Cahen, pers. obs.). A taxonomic treatment was provided for each species, as well as distribution maps and preliminary IUCN conservation status assessments, helping document the diversity of this genus in Southeast Asia. Results from the revision were already used to update the *Ziziphus* data in Co's Digital Flora of the Philippines (Pelzer et al. 2011 onwards) and Wilf et al. (2022) used it to accurately identify a fossil leaf from Brunei.

1.8. Conclusion and challenges

Our current understanding of relationships in Rhamnaceae is due to the first family-wide molecular analysis by Richardson et al. (2000a) It revealed the existence of three well-supported clades (ziziphoids, rhamnoids and ampeloziziphoids). However, no morphological characters could be used to support a formal taxonomic description of the clades as subfamilies; therefore, Richardson et al. (2000b) refer to them as 'cryptic clades'. The only possible apomorphy they hypothesise, but for which there is insufficient data, is in gynoeceum ontogeny: in the rhamnoid genera examined by Medan (1988), e.g., in *Condalia* and *Rhamnus*, the floral apex is more or less flat at the time of primordia differentiation, and usually leads to superior ovaries, whereas in ziziphoid genera, e.g., *Colletia*, *Noltea*, *Phyllica*, and *Pomaderris*, the floral apex shows a circular depression at the time of primordia differentiation, and usually leads to inferior or semi-inferior ovaries.

Chemical and metabolic characters may prove to be stronger synapomorphic signals, in particular the presence of nitrogen-fixing symbioses seems to be restricted to ziziphoids, and a comprehensive mass spectrometry-guided phenotyping of Rhamnaceae metabolites revealed that only the ziziphoids developed the triterpenoid biosynthetic pathway, whereas the rhamnoids predominantly developed diversity in flavonoid glycosides (Kang et al. 2019).

While the split of the family in three informal clades is strongly supported by molecular evidence (Richardson et al. 2000a, 2000b; Onstein et al. 2015; Hauenschield et al. 2016b), uncertainties remain in the relationship between tribes and genera within these clades and several genera have not been confidently ascribed to a tribe (Table 2).

The topology of the combined *rbcL+trnL-F* tree generated by Richardson et al. (Fig. 3) as well as the tribes they recognised have not been much affected by future analyses, a notable exception being the polyphyly of *Ziziphus*, revealed to be spread

across all three clades, and partially resolved by Hauenschield et al. (2016b) who reinstated *Sarcomphalus* and described *Pseudoziziphus* (Fig. 4); the *Ziziphus* species related to *Bathiorhamnus* still need to be placed in a different genus.

While results have been inconsistent, most analyses place Pomaderreae, Colletieae, the group of genera called the ‘*Alphitonia* Group’ by Kellermann (2020) (*Alphitonia*, *Granitites*, *Emmenosperma* and *Jaffrea*), *Ceanothus* and *Schistocarpea* in close vicinity. It is possible that currently unplaced genera in this list will eventually successfully be placed in a tribe either by the formation of new tribes or the redefinition of existing tribes.

In their work leading to the tribal classification of the family, Richardson et al. (2000a) also generated phylogenetic trees based on morphological characters and comparing them to those obtained using molecular characters provides some insight. In particular, the morphological trees do not support the three major clades (ziziphoids, rhamnoids, and ampeloziziphoids) that the molecular trees strongly support. The authors believe this is because convergent evolution would obscure the relationships that molecular characters reveal. Furthermore, they highlight broader issues with the use of morphological characters, such as the reliance on a small number of characters, primarily fruit characters in the case of how Rhamnaceae tribes are delimited. In addition, many characters, such as the position of the disk and ovary, are variable and continuous rather than discrete. Richardson et al. only formally recognised groups defined by morphological characters in addition to molecular evidence in their classification.

Contributions by Cahen et al. helped better understand the diversity of Ventilagineae (Cahen & Utteridge 2017, 2018; Cahen et al. 2020b; Utteridge & Cahen 2021), *Gouania* (Cahen et al. 2020a) and *Ziziphus* (Cahen et al. 2021) in Southeast Asia and the Pacific. However, groups of morphologically similar species still require work to tell apart. This includes a group of species of *Ventilago* with broad leaves with entire margins, 6–8 pairs of abaxially almost flat secondary veins, no domatia at secondary vein axils, and flowers with hairy nectary discs (*V. papuana*, *V. borneensis*, *V. microcarpa* and *V. madraspatana* sensu Gaertn.) (Cahen, pers. obs.). There is also a set of *Ventilago* specimens with glabrous fruit wings and the calyx remains covering less than a quarter of the seed chamber at the base of mature fruits that seem to form a morphological continuum without well-defined and clearly identifiable species (*V. maingayi* M.A.Lawson, *V. dichotoma*, *V. harmandiana* Pierre, *V. sororia* Hance, etc.) (Cahen, pers. obs.); whether these should be recognised as separate or lumped together should be

investigated using different approaches. There is also a morphological continuum without easily distinguished species in *Gouania*, especially those in New Guinea referred to by Lauterbach (1922) as varieties of *G. microcarpa* (Cahen, pers. obs.). And while *Ziziphus* is now revised for Borneo (Cahen et al. 2021), it remains to be seen whether *Z. angustifolia* and *Z. ridleyana* Rasingam & Karthig. two species that differ morphologically in significant ways (e.g., tall, unarmed trees when all other species in Borneo are spiny climbers), belong to a distinct clade.

A short-term goal in documenting Rhamnaceae diversity in Southeast Asia would be to produce flora accounts for all Rhamnaceae species in the region (in *Flora Malesiana*, in particular). Another necessary step in understanding the diversity in these genera and how they diversified is to produce phylogenetic analyses and biogeographic reconstructions supported by a well-resolved taxonomy and DNA evidence from a well-sampled set of specimens.

How might the family's current taxonomic issues be resolved? Sequencing many well-identified specimens would certainly yield insights. Although some groups have been revised, their species have yet to be sequenced (e.g., Ventilagineae, many species in Gouanieae, *Lasiodiscus*, *Colubrina*, and *Alphitonia*). Regardless, a phylogeny is only as good as the level of resolution of the underlying taxonomy, and much work remains to be done to recognise and describe species before the family can be considered taxonomically well understood. This is true for many plant groups, particularly those that are diverse in the tropics and in areas with low collection densities.

The long-term goal of documenting plant diversity and understanding evolutionary relationships is dependent on having material to study, the means, and personnel to conserve and study this material, the expertise to recognise and describe relevant taxonomic units, and the ability to generate phylogenetic trees using molecular evidence. Every stage has its own set of challenges. The following chapter will provide an overview of what is known and hypothesised about Rhamnaceae diversification. The same challenges apply here because biogeographic scenarios rely on robust phylogenies supported by a well-resolved taxonomy; additional challenges include the reliance of such scenarios on the fossil record and how it is interpreted, as well as well-adjusted molecular clocks, which can both be sources of errors.

2. RHAMNACEAE DIVERSIFICATION

2.1. Angiosperms

In a well-known 1879 letter to J. D. Hooker, Darwin wrote that ‘the rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery’. Despite advances in palaeobotany, molecular systematics, genomics, and developmental genetics since Darwin’s time, the relationship of angiosperms with other seed plants remains elusive; his comments still apply as flowering plants and their extant families seem to have burst on the scene without evidence of a gradual assembly of the angiosperm body plan (Soltis et al. 2018; Silvestro et al. 2021).

The earliest fossils thought to unequivocally belong to crown angiosperms are from the Early Cretaceous. Molecular dating methods suggest an earlier origin of angiosperms in the Jurassic, Triassic, or even the Permian if Jurassic-Triassic pollen records are accepted as valid (Magallón et al. 2015; Smith et al. 2010; Li et al. 2019; Silvestro et al. 2021).

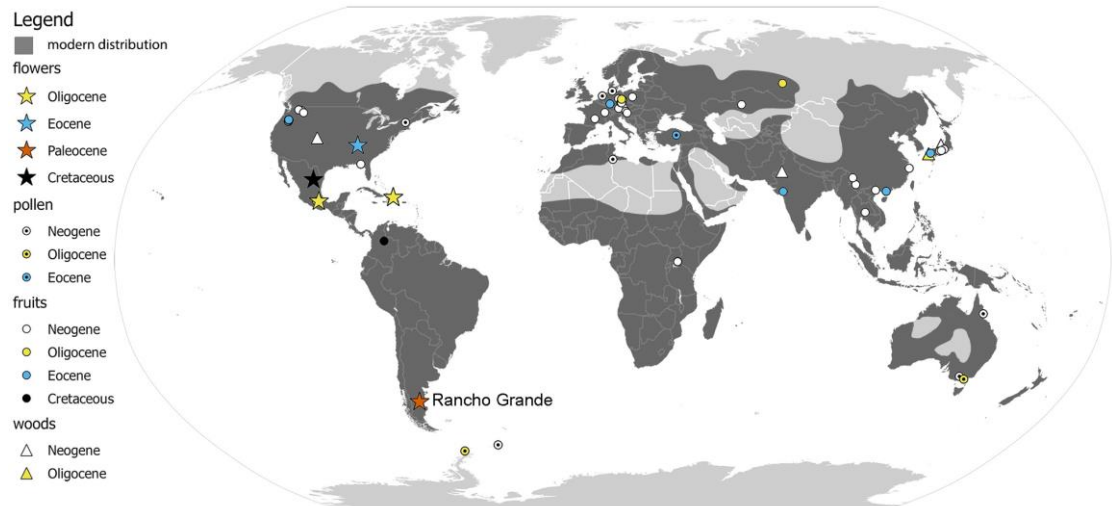
Sauquet et al. (2022) most recently argued that ‘the age of angiosperms is best described as largely unknown (140–270 Ma)’ because interpretations of the fossil record and fossil-calibrated molecular dating analyses support both the Early Cretaceous and Permian ends of the time spectrum. Current molecular dating analysis methods base angiosperm age estimates on the Bayesian prior probability distribution for this age, which is dependent on assumptions about the fossil record and angiosperm evolution that have yet to reach any form of consensus (Sauquet et al. 2022).

2.2. Rhamnaceae fossil record

The majority of Rhamnaceae fossils have been found in Eocene and younger deposits in the Northern Hemisphere (Fig. 5). In comparison, the Southern Hemisphere fossil record is relatively sparse, which was thought to reflect the family’s Laurasian origin and subsequent expansion into Gondwana, as proposed by Gentry (1982); however, Jud et al. (2017) argue that this pattern could be driven by a geographical sampling bias. Raven & Axelrod (1974) estimated that ‘Rhamnaceae are so well represented both in tropical and temperate regions that it is difficult to trace the history of the family’. Recent Rhamnaceae biogeographic discussions, however, have concluded

that the family originated in Gondwana (Richardson et al. 2004; Jud et al. 2017; Hauenschild et al. 2018a; He & Lamont 2022).

Figure 5. Distribution of modern and fossil Rhamnaceae. The dark grey area indicates the distribution of extant Rhamnaceae. The majority of the fossils were found in the Northern Hemisphere, leading some authors to believe the family originated in Laurasia; however, recent biogeographic discussions have concluded that the family originated in Gondwana. Figure from Jud et al. (2017).



Rhamnaceae are thought to have originated in the Cretaceous, according to most recent studies (e.g., Onstein et al. 2015; Hauenschild et al. 2018a), based on the previously oldest known Rhamnaceae fossils, which are approximately 80 million years old (Table 5). The currently oldest known Rhamnaceae fossils are between 110 and 99 million years old (Shi et al. 2022), but because their interpretation may be contentious, prior Rhamnaceae age estimates and inferred diversification scenarios should not be dismissed just yet.

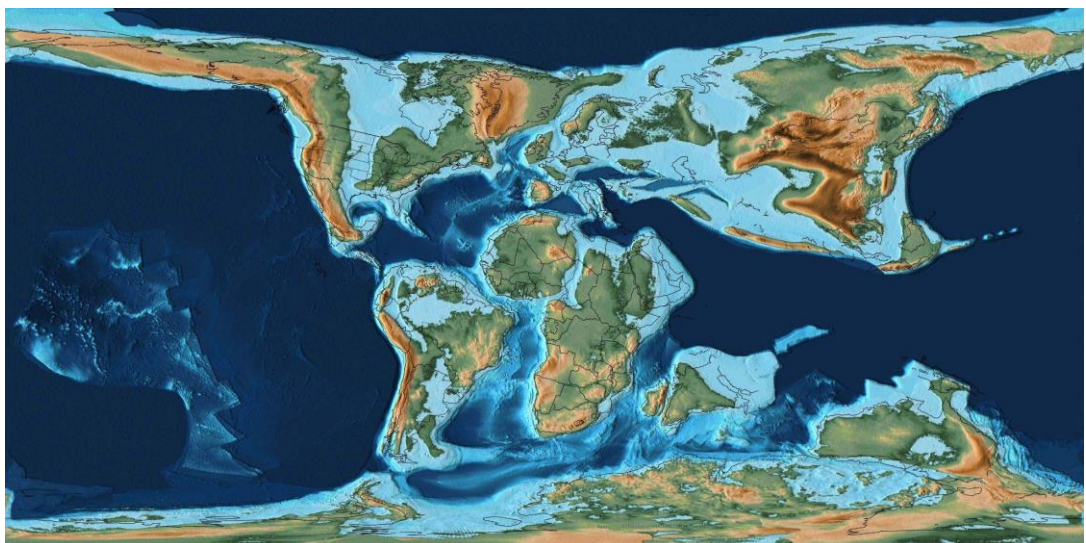
Table 5. Oldest Rhamnaceae fossils. The family likely originated in the Cretaceous.

Taxon	Location	Approximate age (Ma)
<i>Eophylica</i> and <i>Phylica</i>	Myanmar	99—110
<i>Coahuilanthus</i>	Mexico	80
<i>Archaeopaliurus</i> and <i>Berhamniphyllum</i>	Colombia	70
<i>Nothiantha</i> and <i>Suessenia</i>	Argentina	65

2.3. Rhamnaceae biogeographical scenarios before the discovery of the Myanmar fossils

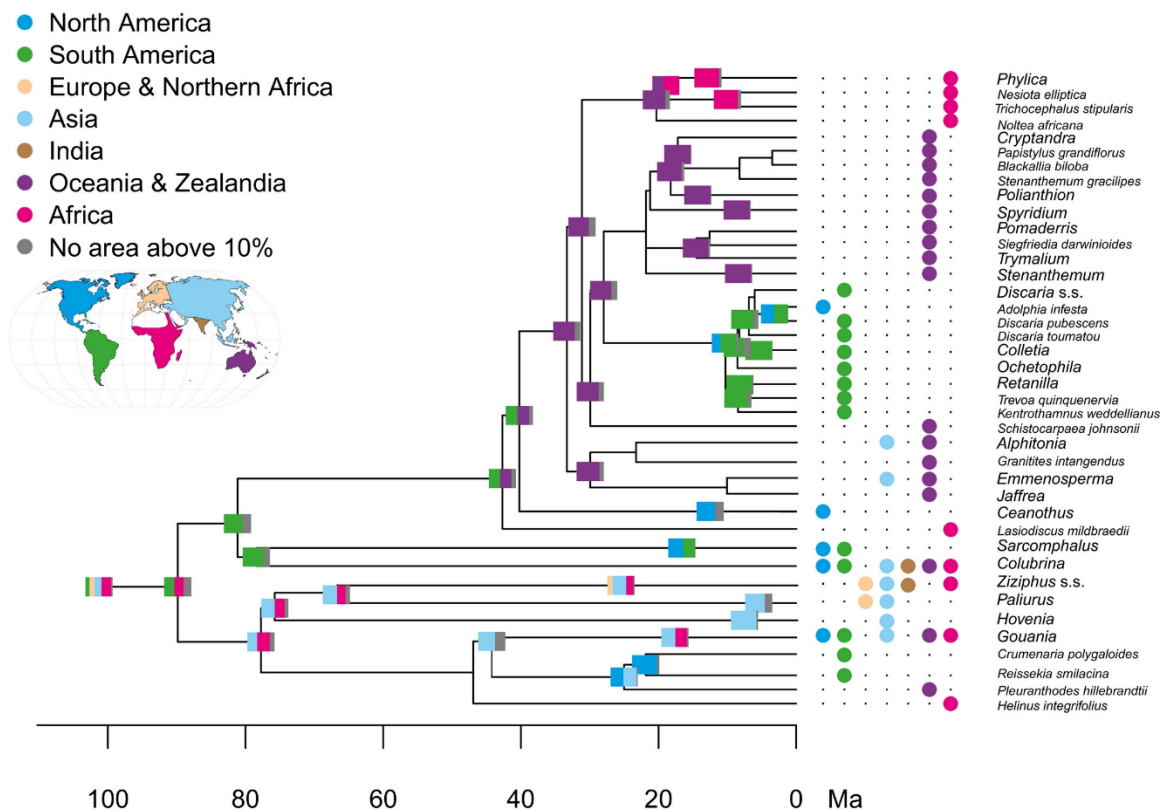
Hauenschield et al. (2018a) found that the most recent common ancestor of all extant Rhamnaceae lived between 91.4 and 102.6 million years ago. This loosely corresponds to the Cenomanian period (c. 100.5–93.9 Ma), in the early Late Cretaceous when the breakup of Gondwana was well underway (Fig. 6). They proposed that the common ancestor of all extant ziziphoids lived in Africa and/or South America during the Late Cretaceous by calibrating seven nodes in their phylogeny using fossils, including the two oldest then-known Rhamnaceae fossils (*Coahuilanthus belindae* Calvillo-Canadell & Cevallos-Ferriz and *Archaeopaliurus boyacensis* Correa, Manchester, Jaramillo & Gutierrez).

Figure 6. Map of the world during the Cenomanian (c. 100.5–93.9 Ma), which loosely corresponds to when Rhamnaceae may have originated according to Hauenschield et al. (2018a). Figure from Scotese & Wright (2018).



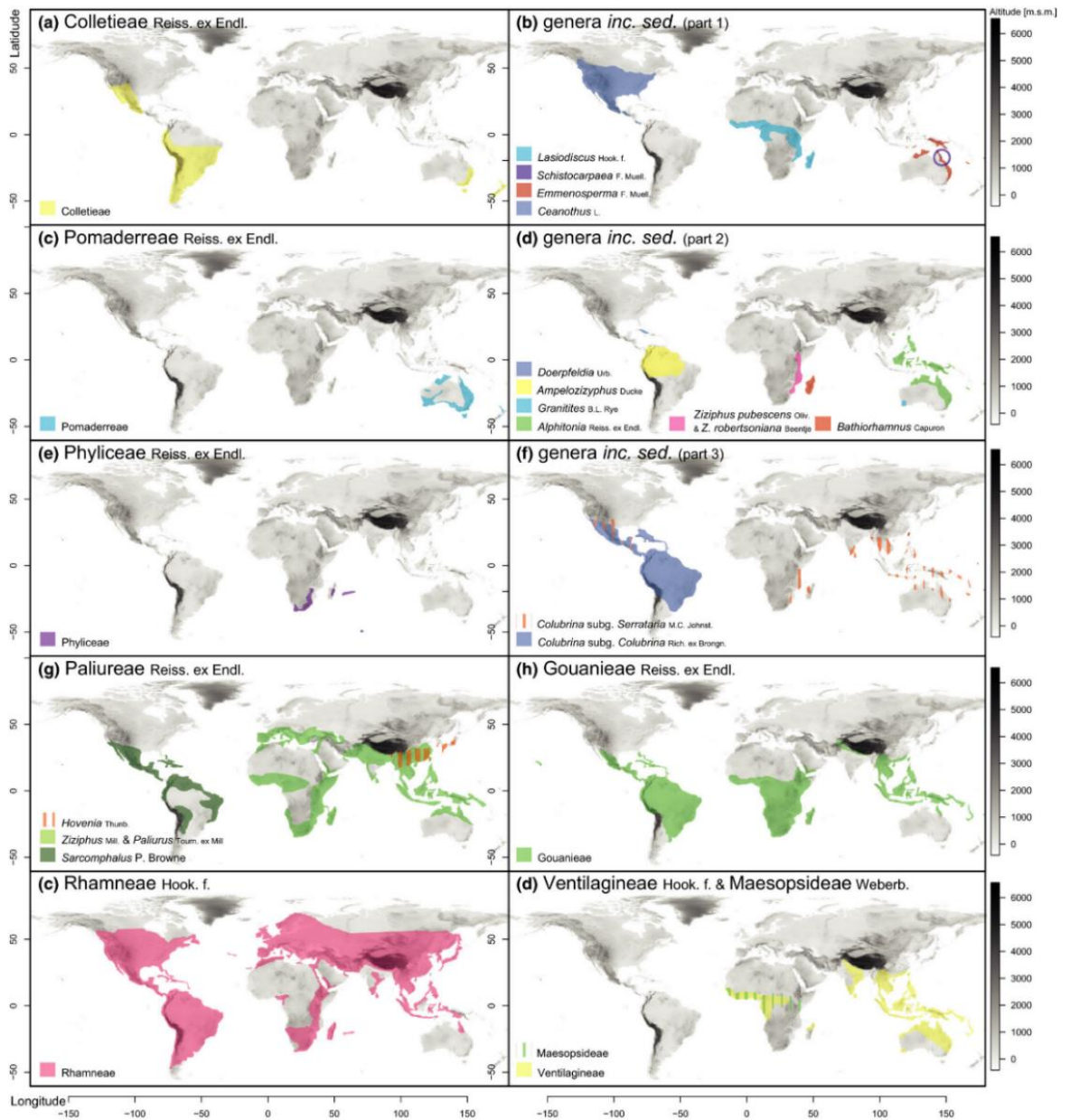
The results of Hauenschild et al. (2018a) suggest Paliureae (excluding *Sarcomphalus*) and Gouanieae (except *Helinus*) originated in Africa before extending to Asia (Fig. 7). All other ziziphoid taxa would have shared a common ancestor in South America and remained on the southern Gondwanan fragment of Australia, Antarctica, and South America during the Palaeogene. Among these, *Colubrina* and *Sarcomphalus* remained in South America at first, while the other genera migrated towards Australia. In their reconstruction, the common ancestor of Colletieae, Phyliceae, Pomaderreae and *Schistocarphaea* occurred in Australia in the early Cenozoic. The ancestor of *Alphitonia* and its related genera (*Emmenosperma*, *Granitites* and *Jaffrea*) would have become extinct in South America, and the distribution of this group became limited to Australia; later, when the Australian plate made contact with Southeast Asia, *Alphitonia* and its relatives dispersed into Wallacea, the Philippines and the Asian continent (Hauenschild et al. 2018b).

Figure 7. Phylogeny of the ziziphoids with molecular clock date estimates and ancestral area analysis results. Mixed colours refer to potentially combined areas. Species names on branches leading to single species are written in smaller font than genera with multiple species. The results suggest the clade mostly originated and diversified in Gondwana. Figure from Hauenschild et al. (2018a).



While their interpretation places a lot of weight on vicariance associated with the breakup of Gondwana, long-distance dispersal events are still thought to be the most likely explanation for the current distribution of several Rhamnaceae groups (Fig. 8). Long-distance dispersal events during the Neogene would explain the pantropical distribution of Gouanieae in particular. The authors also propose that Phyliceae spread from Australia to Africa and the Antarctic Islands. Colletieae are hypothesised to have extended their range from Australia to South America by long-distance dispersal events in the Late Eocene, Oligocene, and Miocene. Finally, *Ceanothus*, *Sarcomphalus* and *Colubrina*, would have first diversified in South America and then recolonised Africa and Australia or dispersed into North America, via long-distance dispersal events from the Oligocene onwards.

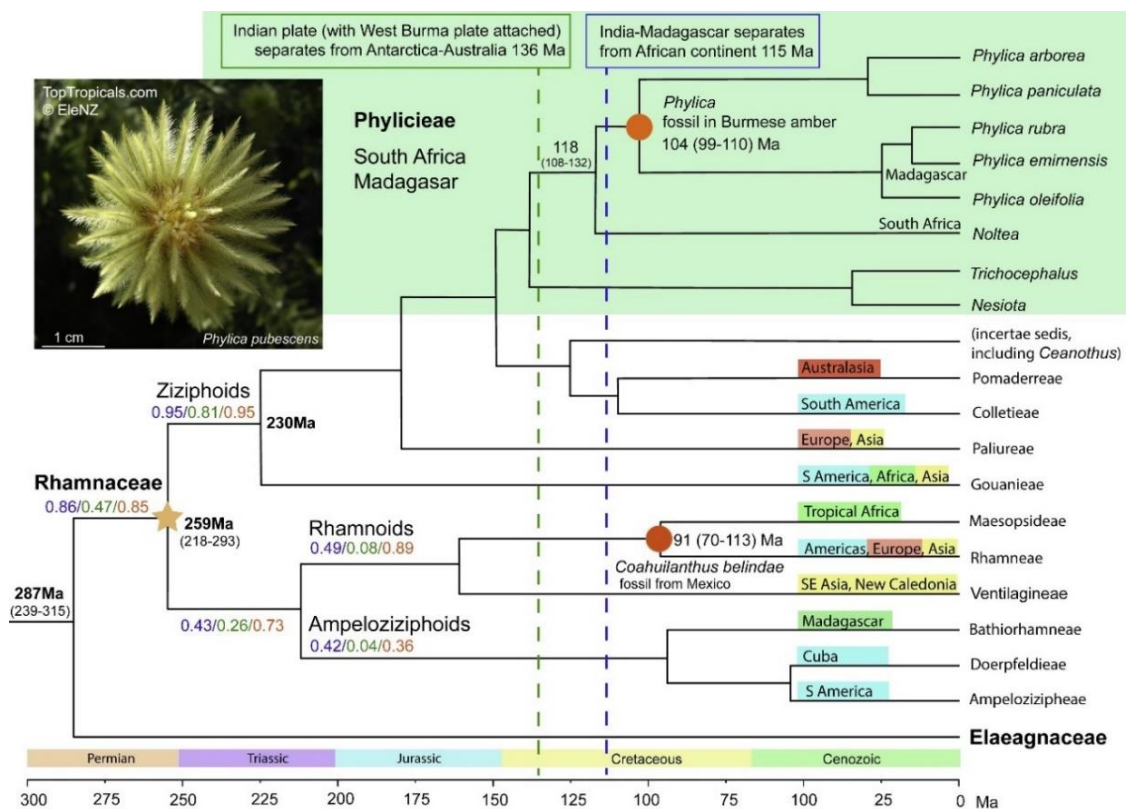
Figure 8. Current distribution of Rhamnaceae taxa. While vicariance associated with the breakup of Gondwana is likely to explain much of the diversification in the family, long-distance dispersal events explain some widespread distributions such as in Gouanieae. Figure from Hauenschild et al. (2018a).



2.4. Rhamnaceae biogeographical scenarios including the Myanmar fossils

The discovery of c. 110 and c. 99-million-year-old fossils from Myanmar (Shi et al. 2022), and their identification as Phylicae, imply that the Rhamnaceae diverged much earlier than previously thought. He & Lamont (2022) published the first dated phylogeny of the family since the discovery of the Myanmar fossils, using these to calibrate the crown age of *Phylica* to 104 million years (Fig. 9). They date the origin of Rhamnaceae to c. 259 million years ago, in the late Permian, which is not only very old in comparison to previous estimates of the age of Rhamnaceae, but also very old in absolute terms, given that the earliest fossils thought to unequivocally belong to crown angiosperms are from the Early Cretaceous (Silvestro et al 2021).

Figure 9. Rhamnaceae phylogeny with date estimates obtained using a molecular clock calibrated with the fossils from Myanmar. Ages are given as the median \pm 95% highest posterior density interval. The crown age of Rhamnaceae is marked by a light orange star. Probability values at a given stem in blue represent hard-seededness (water impermeability), in green fire-stimulated germination (specifically heat-released dormancy), and in red fire-proneness (vegetation likely to burn within its lifetime). The old ages obtained challenge the theory of flowering plants diversifying in the Cretaceous. Figure from He & Lamont (2022).



The implications of the ages obtained by He & Lamont (2022) on our understanding of the diversification of Rhamnaceae would be profound; the authors note that ‘the effect on the estimated age of Rhamnaceae is even more remarkable: it is in the order of 150 My compared with that previously reported’ and that ‘any past statistical concerns about large levels of uncertainty surrounding the means pale into insignificance compared with the effect of the ad hoc presence/absence of fossils used to set the molecular clock’. While the age and identification of the Myanmar fossils as belonging to *Phyllica*, as well as the molecular clock estimates obtained by He & Lamont, cannot be dismissed on the grounds that a Permian origin of Rhamnaceae seems unlikely, we must wait for the discovery of additional fossil evidence that backdates other crown angiosperm clades before accepting their hypotheses without reservations.

Using the Myanmar fossils to calibrate the crown of *Phyllica* further supports that Rhamnaceae originated in Gondwana (He & Lamont 2022). It also suggests that ancestors of extant Rhamnaceae tribes may have already occurred in Africa, Australasia, the Americas, Europe, and Asia before the separation of Antarctica and Australia from the rest of Gondwana during the Cretaceous. According to He & Lamont (2022), *Phyllica* split from *Noltea* around 118 million years ago, and they suggest that if the genus appeared in the Cape, it is possible that it would have reached the West Burma plate where the fossils were discovered via Madagascar and India before India rafted towards Asia during the Cretaceous and early Cenozoic. This contradicts the earlier hypothesis by Hauenschield et al. (2018a) of Phyliceae spreading from Australia to Africa.

Other implications of attributing the Myanmar fossils to *Phyllica* are not discussed in detail by He & Lamont (2022) although they do note that the ages they retrieved for the common ancestor of Pomaderreae and Colletieae, around 150 million years, would explain that these groups diversified concurrently with the breakup of Gondwana, leading to their modern distributions (mostly Australia for Pomaderreae and South America for Colletieae). Similarly, they point out that the ages they obtained would explain the disjunction of the ampeloziziphoids between Madagascar and South America.

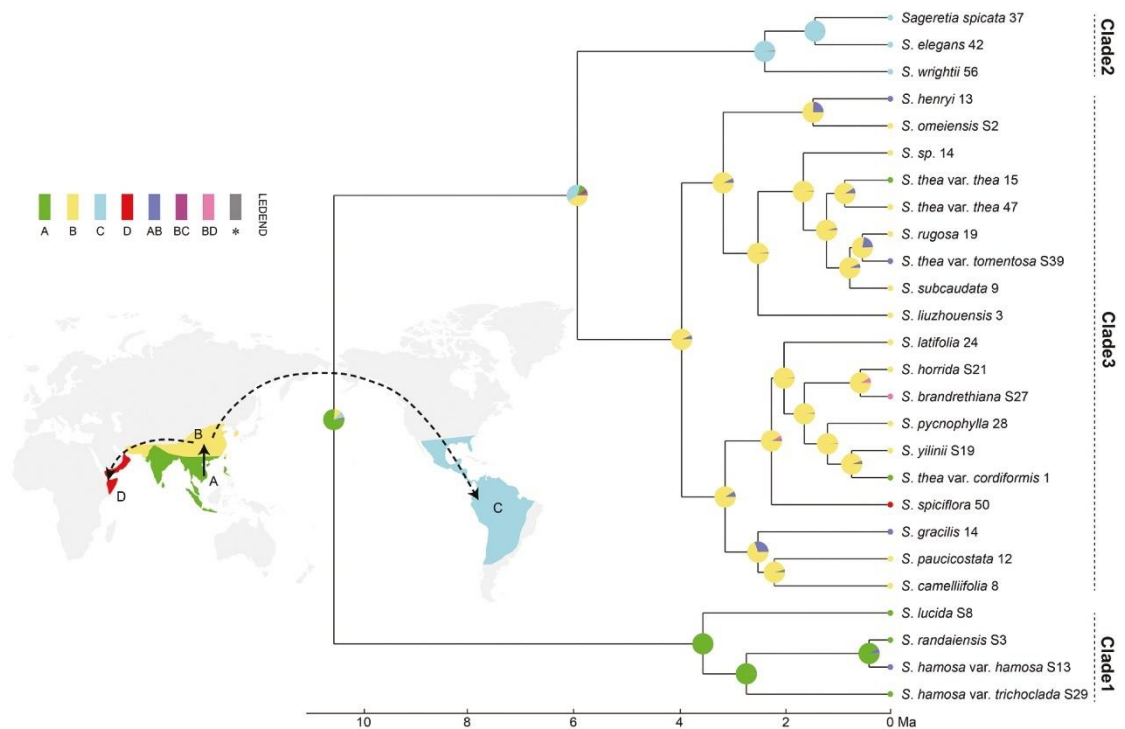
He & Lamont (2022) also speculate that the widespread distribution of *Colubrina* on all continents could be explained by its diversification concurrent with the breakup of Gondwana, with a most recent common ancestor estimated to be around 110 million years old. The distribution of the genus has previously been explained because of long-distance dispersal events: Richardson et al. (2004) noted that dispersal capabilities in the genus are evident based on the occurrence of *C. asiatica* (L.) Brongn. all around the Pacific rim,

while the results from Hauenschild et al. (2018a) suggest that *Colubrina* remained in South America during the breakup of Gondwana and later recolonised Africa and Australia before dispersing into North America in the Oligocene.

2.5. Biogeographical scenarios in the rhamnoids

In addition to the analysis by Hauenschild et al. (2018a), which focused on the ziziphoids, the diversification of the rhamnoid genera *Sageretia* and *Berchemia* was recently investigated (Yang et al. 2019; Huang et al. 2021). *Sageretia* most likely originated in tropical Asia during the Eocene and likely spread north until the Miocene, colonising areas that became suitable as the arid belt receded, and then dispersed to North America via the Beringian Land Bridge, and to Africa via Arabia (Yang et al. 2019) (Fig. 10). *Berchemia*, on the other hand, most likely originated in the Western Tethys during the middle Eocene, before forming a tropical Asia and tropical America disjunction during the Oligocene and diversified further in Asia from the early Miocene onward (Huang et al. 2021).

Figure 10. Biogeographic inferences for *Sageretia*. Results obtained from a Bayesian binary MCMC method conducted in RASP software; outgroups pruned. Letters on the map represent the current distribution areas of *Sageretia*. Pie charts show probabilities of ancestral area reconstructions. The arrows represent assumptions of three plausible dispersal event (events showed with a solid arrow happened earlier than that with dashed ones). *Sageretia* most likely evolved in tropical Asia during the Eocene, spread north until the Miocene, and spread to North America via the Beringian Land Bridge, and Africa via Arabia. Figure from Yang et al. (2019).



The study of *Sageretia* (Yang et al. 2019), a genus of c. 35 species, showed tropical Asia to be the ancestral area of diversification. The authors propose that the distribution of the genus in tropical Asia may correspond to the ‘dying embers’ hypothesis (Spriggs et al. 2015), which suggests that *Sageretia* did not thrive in the lowland tropical forests where it evolved, but rather in warm temperate or colder forests where it later moved. This would explain why the genus is now more diverse in more northern, temperate parts of Asia. In the Americas, a similar pattern can be seen to a lesser extent, with a single species, *Sageretia elegans* (Kunth) Brongn., occurring in tropical South America versus three in North America (POWO 2022).

The phylogenetic analysis of *Berchemia* (Huang et al. 2021), a genus of also c. 35 species native to Asia, the central and south-eastern United States, and Central America, did not include Malesian species (e.g., *B. cinerascens* (Blume) Miq. and *B. pubiflora* (DC.) Miq.), which may have affected the results. The crown of the Asian clade of

Berchemia was dated to the early Miocene, coinciding with a significant period of Himalayan uplift, and the majority of Asian *Berchemia* diversification occurred less than ten million years ago, coinciding with the onset of the Indian and East Asian monsoon regimes.

The findings of these biogeographic analyses of *Berchemia* and *Sageretia* could shed light on how other Asian Rhamnaceae groups, including those studied by Cahen et al., diversified. Other genera, which are now more diverse and widespread in temperate regions, may have first diversified in tropical Asian forests before migrating to and diversifying in temperate regions (e.g., Paliureae, discussed below). Similarly, climate change linked to Himalayan uplift and the establishment of Asian monsoons may have resulted in the diversification of *Rhamnus* in temperate Asia.

These findings could also imply that rhamnoids evolved primarily in Laurasian regions. However, Ventilagineae are found throughout the Old World tropics, including Madagascar and Australia, and *Maesopsis* is found in tropical Africa. These groups are considered sister groups to the other rhamnoids (e.g., Hauenschild et al. 2018a). Therefore, regardless of where they diversified, rhamnoids likely shared a common ancestor in Gondwana. In addition, some Rhamneae genera have a more typically Gondwanan distribution, such as *Scutia*, which is found in South America, Africa, Madagascar, India, and Eastern Asia.

When more phylogenetic analyses become available, and relationships within rhamnoids become better understood, it may be possible to see where other genera may have originated and later diversified. According to current evidence, rhamnoids originated in Gondwana, but some Rhamneae genera such as *Berchemia* and *Sageretia* arose in Eurasia after India had already collided with it, and later dispersed and diversified across the temperate Northern Hemisphere.

2.6. Groups examined by Cahen et al.

2.6.1. Ventilagineae

A fossilised Ventilagineae fruit from the Middle Eocene from Central Tibet, is the earliest known fossil of the tribe (Del Rio et al. 2021). The authors propose that the Indo-Tibetan region may be the origin of the genus, and they explain the presence of an Oligocene fossil attributed to *Ventilago* in Puebla, Mexico (Calvillo-Canadell &

Cevallos-Ferriz 2007), by dispersal occurring via the Bering Land Bridge during the Eocene.

Del Rio et al. (2021) published their biogeographic discussion prior to the discovery of the 99-million-year-old Myanmar fossil attributed to *Phyllica* (Shi et al. 2022), which when used to calibrate molecular clocks significantly pushes back ages in the Rhamnaceae phylogeny and places the most recent common ancestor of Ventilagineae and other rhamnoids in the Jurassic (He & Lamont 2022).

Even if Ventilagineae diversified tens of millions of years later, it would have occurred during the Cretaceous period, favouring the scenario of the tribe diversifying concurrently with the breakup of Gondwana. This is consistent with the hypothesis by Richardson et al. (2000a) that Ventilagineae originated in Gondwana and spread into Asia when India collided with Asia, with India serving as a raft. Richardson et al. (2004) later speculated that Ventilagineae dispersed from Africa to India only after India had already split from Africa, but this was based on age estimates that are now considered too young (Hauenschild et al. 2018a).

Smythea lanceata is a widespread coastal species whose seeds float in the sea. Could long-distance seed dispersal in species like *S. lanceata* have played a role in the current distribution of Ventilagineae? A dated phylogenetic analysis would help determine whether the more narrowly distributed wind-dispersed *Ventilago* and *Smythea* species evolved from a clade that included species prone to long-distance dispersal, or whether *S. lanceata* evolved from the wind-dispersed Ventilagineae and is on its separate evolutionary branch. This would reveal whether long-distance dispersal events played a role in the diversification and distribution of the tribe or whether these are best explained by vicariance events related to the breakup of Gondwana.

The position in a dated Ventilagineae phylogeny of the tribe's only tree, *Ventilago viminalis* Hook., endemic to Australia, would also yield insights. Were its ancestors already in Australia when Gondwana was breaking apart or did they travel across Asia to get to Australia? When did the tree habit appear in their diversification history? A phylogeographic study of the tribe would not only help clarify generic boundaries and define clades but might also reveal where and when these clades originated and diversified.

2.6.2. Ventilagineae in New Caledonia and Vanuatu

The flora of New Caledonia is thought to be younger than the island's separation from Australia in the late Mesozoic (c. 80 million years ago) and to have been assembled through colonisation by dispersal over water following the island's re-emergence, c. 37 million years ago, after a long period of immersion (Pillon 2012). All the *Ventilago* species known to occur there are endemic, as is *V. vanuatuana* in Vanuatu. Furthermore, *V. pseudocalyculata* was found to be endemic to New Caledonia's Loyalty Islands (Cahen et al. 2020), indicating a proclivity for Ventilagineae to form endemic species on different islands.

Ventilago buxoides Baill., also endemic to New Caledonia, differs from other Southeast Asian Ventilagineae species in that its leaves, inflorescences, and fruits are smaller, possibly as an adaptation to ultramafic conditions. There is no available phylogenetic analysis to determine whether this habit evolved from the typical Ventilagineae habit after the island was colonised or from a morphologically similar ancestor that was well adapted to occupy this ecological niche. The only other Ventilagineae species with this diminutive habit is *Ventilago elegans* Hemsl., which is endemic to Taiwan, but the relationship between *V. buxoides* and this species has not yet been investigated in any phylogenetic analysis.

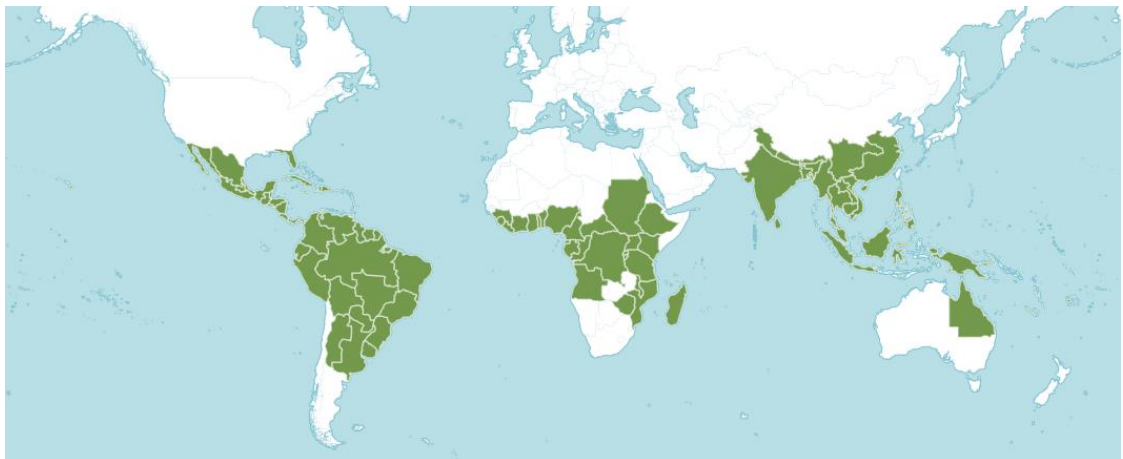
Most plants in Vanuatu likely came from Malesia via New Guinea and the Solomon Islands, as well as Fiji (Ramon & Sam 2015). The archipelago, however, is close to New Caledonia, with Aneityum, the southernmost island, just over 200 km northeast of the Loyalty Islands and 350 km from the main island, Grande Terre. Another question that a phylogenetic analysis would help answer is whether *Ventilago vanuatuana* is more closely related to New Caledonian or New Guinean species of *Ventilago*.

2.6.3. *Gouania*

Not much has been written about the biogeography of Gouanieae in general or *Gouania* in particular. The genus is notable among tropical Rhamnaceae for its unusually broad distribution (Fig. 11). *Gouania* lianas reach the forest canopy (Reissek 1861) and their fruits are wind-dispersed, and possibly also water-dispersed (Carlquist 1966), which may make them particularly well-suited for long-distance dispersal. It is one of the few Rhamnaceae genera found in Hawaii; the presence of *Pleuranthodes hillebrandtii* (Oliv.

ex Hillebr.) Weberb (= *Gouania hillebrandii* Oliv. ex Hillebr.) in Hawaii was highlighted by Richardson et al. (2004) to illustrate the high dispersal capability of Gouanieae. The presence of *G. mangarevica* Fosberg in the remote French Polynesian Gambier Islands demonstrates this ability even further.

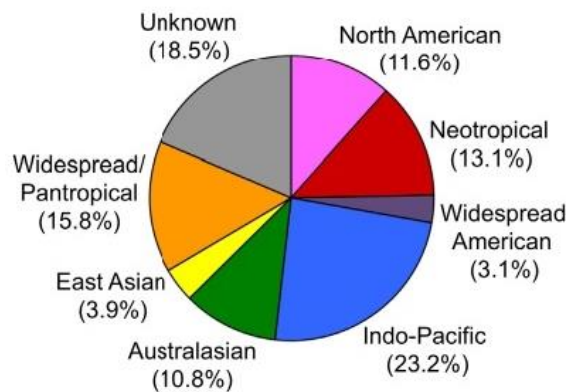
Figure 11. Distribution of *Gouania*. The genus has an unusually wide distribution for the family, possibly due to its wind- and possibly also water-dispersed fruits. Figure from POWO (2022).



Hawaii's isolated location in the middle of the Pacific makes it an appealing case study for oceanic island evolutionary studies, and Price & Wagner (2018) compiled a list of the geographic source regions of the plants that grow there (Fig. 12). Among the Rhamnaceae, *Alphitonia ponderosa* Hillebr. is thought to have arrived from Australia via other Pacific Islands by bird dispersal, *Colubrina asiatica* by floating on water from Australia, Indomalaya, and/or the Pacific Islands, and *C. oppositifolia* Brongn. ex H.Mann by floating on water from the Neotropics. On the other hand, the authors do not speculate on how the three *Gouania* species found in Hawaii arrived, though Carlquist (1966) hypothesised that the species arrived by floating on water.

In any case, the widespread distribution of *Gouania* and its presence on many Pacific islands suggest that long-distance dispersal events, as proposed by Hauenschild et al. (2018a), played a significant role in explaining their current distribution, and that vicariance may not have been the dominant mechanism at work.

Figure 12. Geographic origin of the plant species occurring in Hawaii. ‘Indo-Pacific’ includes all lineages originating in the Indo-Malayan region, including those arriving via stepping-stone dispersal via Pacific Islands. The Hawaiian flora is the result of migrations from many source areas around the Pacific. Among the Rhamnaceae, *Alphitonia ponderosa* is thought to have arrived from Australia via other Pacific Islands by bird dispersal, *Colubrina asiatica* by floating on water from Australia, Indomalaya, and/or the Pacific Islands, and *C. oppositifolia* by floating on water from the Neotropics. Figure from Price & Wagner (2018).



The oldest known *Gouania* fossils were discovered in Mexico and date back c. 23 million years (de Jesús Hernández-Hernández & Castañeda-Posadas 2018), similar to the c. 23-million-year-old crown age of Gouanieae obtained by Richardson et al. (2004). This suggests that southern Mexico may have been the centre of diversification of the genus. However, the age estimates of Richardson et al. are now considered too young, and a Gondwanan origin appears more likely given crown ages obtained in recent analyses (e.g., Hauenschild et al. 2018a; He & Lamont 2022).

One of the findings by Cahen et al. (2020a) is that *Gouania nematostachya* Reissek ex Lauterb. is not restricted to the Philippines but also occurs in Borneo and Sulawesi. This distribution pattern is not particularly common, as non-endemic species found in Borneo are more frequently found in other parts of Sundaland, particularly the Malay Peninsula and Sumatra rather than Sulawesi, whereas non-endemic plants of Sulawesi, while frequently found in the Philippines, are more commonly also found in the Moluccas than Borneo (van Welzen et al. 2011).

The nectar discs of *G. nematostachya* have a wrinkled surface and no lobes opposite the sepals, like *G. microcarpa* var. *mollis* Lauterb. and *G. microcarpa* var. *rugulosa* Lauterb. in New Guinea (both these varieties would best not be placed in *G. microcarpa*, which has a densely hairy nectar disk, as discussed by Cahen et al. 2020a). *Gouania nematostachya* may be more closely related to these taxa than to the other west

Malesian species, all of which have smooth-surfaced nectar discs and lobes opposite the sepals. Sulawesi's flora is largely Australasian in origin (van Welzen et al. 2011), and phylogenetic analysis may reveal that the *G. nematostachya* lineage originated there rather than in Sunda. This hypothesis would be strengthened if this species were also discovered in the Moluccas, which share a sizeable portion of their flora with New Guinea (van Welzen et al. 2011).

2.6.4 *Ziziphus*

The oldest *Ziziphus* fossils are c. 53-million-year-old fruits from Gujarat (Singh et al. 2010). In addition, the oldest fossils of the closely related genus *Paliurus* are also from India and are c. 66 million years old (Manchester & Kapgate 2014). This supports the hypothesis by Hauenschild et al. (2018a) that Paliureae originated in Gondwana and later spread to Asia, presumably with diversification occurring on the Indian fragment of Gondwana prior to its collision with Eurasia, which is consistent with the Out-of-India hypothesis for the dispersal of *Paliurus* brought forward by Chen et al. (2017). The first reliable fossils of Rhamnaceae in Malesia, from Brunei, date from the Pliocene and consist of leaves that resemble *Ziziphus kunstleri* King (Wilf et al. 2022). Rhamnaceae fossils are common in South and East Asia, but none had been found in Malesia before these (Fig. 5).

Borneo has the greatest known diversity of extant *Ziziphus* species; the area surrounding Mount Kinabalu is especially diverse, with nine species occurring in Ranau (Cahen et al. 2021). This high concentration of species does not necessarily imply that this is where the genus evolved. The most complete *Ziziphus* phylogeny published to date (Hauenschild et al. 2016a) suggests that species included in their analysis only known to occur in Malesia (*Z. horsfieldii* Miq. and *Z. calophylla* Wall., both present in Borneo) belong to a clade distinct from clades with species from the Middle East and the Mediterranean, as well as clades including more temperate East Asian species. Making biogeographical inferences about the timing of events based on this phylogeny is difficult, but it does not seem to rule out the possibility that the clade that includes the Malesian endemics is sister to the rest of the genus, implying the genus first diversified in wet tropical environments and quickly spread to Southeast Asia after India made contact with Eurasia.

The flora of Mount Kinabalu was found to be younger than the mountain itself (6 million years), with a mix of immigrant pre-adapted lineages and descendants from local lowland ancestors, though significant shifts from lower to higher vegetation zones were uncommon (Merckx et al. 2015). This data suggests that the *Ziziphus* species endemic to the Mount Kinabalu region may have diversified there recently but most likely belong to lineages that were already adapted for such environments.

As previously discussed, *Ziziphus angustifolia* and *Z. ridleyana* differ morphologically from the other Sundaland species in that they are tall, unarmed trees, whereas the other species are spiny climbers. A phylogenetic analysis could help determine when the tree habit evolved and if it is the ancestral state of *Ziziphus*. The closest relatives of the genus, *Paliurus* and *Sarcomphalus*, are shrubs and small trees, implying that the climbing habitat in *Ziziphus* may be derived. If *Z. angustifolia* is shown to belong to the most ancient extant lineage of the genus, it might imply that the genus was originally non-climbing and adapted to tropical environments and that the rainforests of Southeast Asia may have served as a refuge for this lineage.

2.7. Conclusion and challenges

Prior to the development of molecular dating methods, biogeographic inferences were primarily based on the fossil record and the distribution of taxa. Although phylogenetic methods that integrate molecular clocks were designed to help compensate for data gaps in inferring the age of events, discovering when and how taxa diversified remains a major challenge (Richardson et al. 2012; Soltis et al. 2018). Since molecular clocks rely on fossils for their calibration, they cannot compensate for the limitations of an incomplete or incorrectly interpreted fossil record. De Baets et al. (2016) noted that ‘given that the molecular clock was developed explicitly to overcome the incompleteness of the fossil record, it is ironic that fossil evidence remains the literal rate-determining step in molecular clock analyses’. Contrasting age estimates in the literature mostly reflect conflicting Bayesian prior probability distributions (Sauquet et al. 2022).

While the phylogeny and biogeography of ziziphoids were studied by Hauenschild et al. (2018a), more sampling in specific genera, like work recently published in *Berchemia* (Huang et al. 2021) and *Sageretia* (Yang et al. 2019), is required to better understand the evolutionary history of many Rhamnaceae groups, including those studied by Cahen et al. An informative biogeographic analysis rests on an accurate

phylogeny which is itself dependent on well-identified samples and a resolved taxonomy. The contributions by Cahen et al. help in achieving this objective because it improved the description of the diversity in several groups. This research has already yielded results, as Del Rio et al. (2020) used their revision of *Smythea* (Cahen & Utteridge 2018) to interpret the *Ventilago* fossil from Tibet, and Wilf et al. (2022) used their revision of *Ziziphus* in Borneo (Cahen et al. 2021) to accurately identify a fossil leaf from Brunei.

Rhamnaceae are thought to be Gondwanan in origin (Richardson et al. 2004; Jud et al. 2017; Hauenschild et al. 2018a; He & Lamont 2022). All the Rhamnaceae tribes for which biogeographic inferences have recently been made appear to have originated in Gondwana (Hauenschild et al. 2018a; He & Lamont 2022), although a Laurasian origin for some lineages is possible. The Paleocene/Eocene thermal maximum allowed the spread of tropical megathermal groups across the Northern Hemisphere's higher latitudes, and the current distribution of some Rhamnaceae clades could be the result of the breakup of this Northern Hemisphere megathermal rainforest belt later in the Cenozoic (Richardson et al. 2004; Richardson et al. 2012). Some extant genera, such as *Berchemia* (Huang et al. 2021) and *Sageretia* (Yang et al. 2019), were recently inferred to have originated in Eurasia during the Eocene and diversified and dispersed after the early Cenozoic thermal maximum. Most estimates place the family's origin in the Cretaceous (e.g., Onstein et al. 2015; Hauenschild et al. 2018a), but recent fossil evidence has called that into question (Shi et al. 2022), leading some authors (He & Lamont 2022) to suggest that its age is on the order of 150 million years older than previously reported, such that age estimates for Rhamnaceae parallel estimates for angiosperms, which Sauquet et al. (2022) recently argued is 'best described as largely unknown (140-270 Ma)'.

3. THE STATE OF KNOWLEDGE OF SOUTHEAST ASIA'S PLANT DIVERSITY AND THE CASE OF RHAMNACEAE

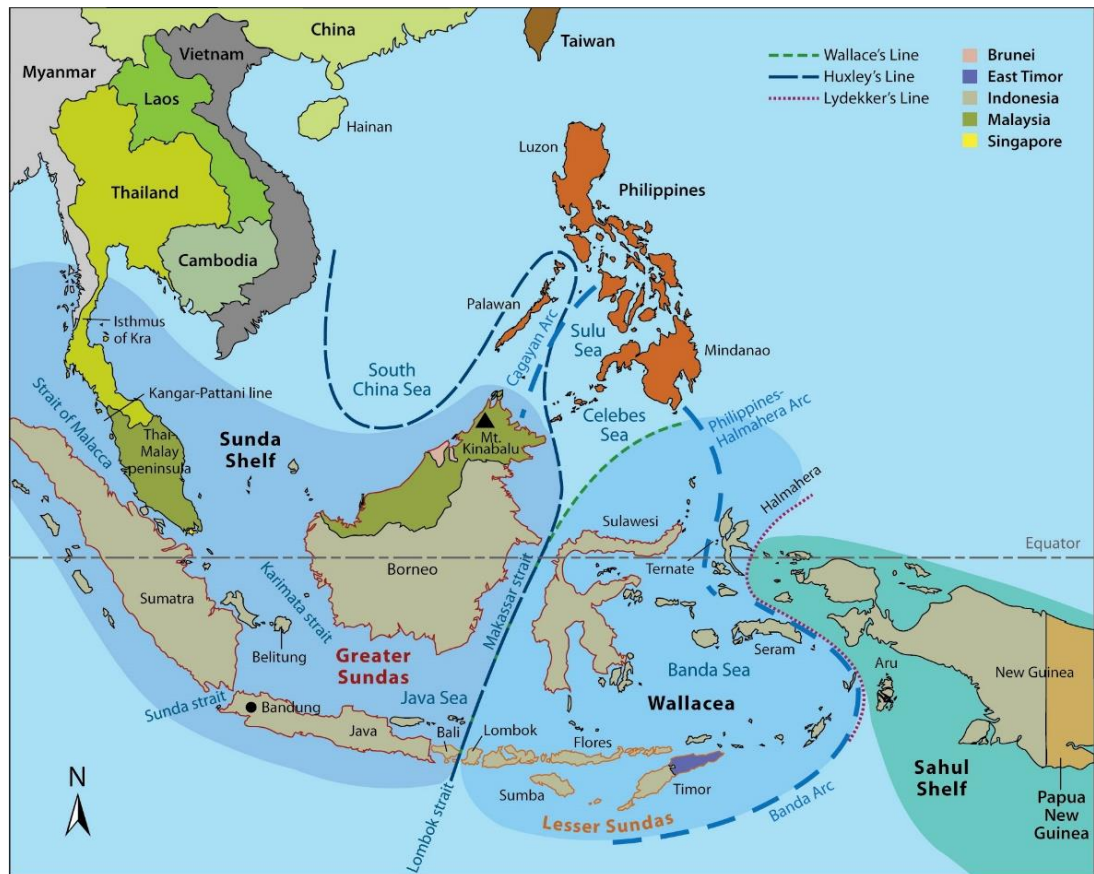
3.1. Introduction

Much of the world's plant diversity has yet to be scientifically documented, particularly in tropical areas, with some estimates suggesting that up to 100,000 species have yet to be located, described, and named (Corlett 2016). And when a species is invisible to the scientific community, it is impossible to study its ecology and phylogenetic placement, and it cannot be considered in conservation planning, reducing its chances of survival. It also makes it difficult to assess its potential for use as food, medicine, and other products that benefit both people and the planet. (Antonelli et al. 2020; Cheek et al. 2020; Grace et al. 2021).

Middleton et al. (2019) provided an update on the current state of knowledge regarding the flora of Southeast Asia's various countries: Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Papua New Guinea, the Philippines, Singapore, Thailand, Timor-Leste, and Vietnam. The region is home to about 50,000 species of flowering plants so far described, but much of the area remains botanically unexplored and many of the collected specimens have not yet been scientifically studied. This represents about 15% of the estimated 369,000 described species worldwide (Royal Botanic Gardens, Kew 2016).

Within Southeast Asia, Malesia is particularly species-rich and contains important levels of endemism. Its complex geological history resulted in its current division into three main biogeographic regions: Sunda, Wallacea and Sahul (van Welzen et al. 2005; Lohman et al. 2011, Richardson et al. 2012) (Fig. 13). Rising and falling sea levels caused islands on the Sunda Shelf to form a single land mass with the Asian continent during the Pleistocene. Similarly, when sea levels fell, New Guinea and Australia were linked leading to species exchanges. Deep marine areas, however, remained between the Sahul and Sunda shelves, and there was no land connection between them (Lohman et al. 2011).

Figure 13. Map of Malesia showing biogeographic demarcation lines. The major islands are labelled, and the various Malaysian countries are indicated by colour. The presence of red or orange borders around an island indicates it belongs in the Greater or Lesser Sundas, respectively. Malesia is divided into three broad biogeographical regions, one associated with the Sunda Shelf, another with the Sahul Shelf, and Wallacea in between. The significance of a plant equivalent of Wallace's Line has proven to be less obvious than that of animals; instead, Wallace's Line for plants could be compared to a filtering zone that spans Wallacea, inhibiting the distribution of some lineages but not others. Figure from Lohman et al. (2011).



The biogeographic demarcation line between Indomalayan and Australasian species assemblages, beginning with the famous faunal boundary known as ‘Wallace’s Line’, has been the subject of many papers (e.g., van Welzen et al. 2011, and references therein). The significance of an equivalent of Wallace’s Line for plants has proven less obvious than for animals (Richardson et al. 2012). Instead, Wallace’s Line for plants could be compared to a zone that spans Wallacea, with the exact location of the line changing depending on the taxonomic group studied, and with several plant lineages seemingly unaffected by it; therefore, it could be thought of as a filtering zone, spanning Wallacea and inhibiting the distribution of some lineages but not others (van Welzen et al. 2005; Richardson et al. 2012). Java, on the Sunda Shelf and west of Wallace’s Line,

Huxley's Line, and Lydeker's Line (Fig. 13), is regarded as having a plant assemblage more like Wallacea than the rest of Sunda because of the presence of a pronounced dry season on much of the island (van Welzen et al. 2011).

While plants in western Malesia are predominantly Asian and become proportionately more Australasian as they approach New Guinea, there is an asymmetric relationship; Asian groups from the lowlands have expanded their range from west to east into the Wallacea and even New Guinea and Australia, whereas Australasian lowland plants have colonised westwards to a much lesser extent. It is estimated that eastward migration into Sahul outnumbers westward migration by a factor of 2.4 (Crayn et al. 2015). The distribution of mountain species is an exception to this general trend. Mount Kinabalu has significantly more Australasian temperate plants than Timor. And Sumatra's montane flora shares less in common with eastern Malesia, Sulawesi, and the Moluccas than with Australia and New Guinea, suggesting a westward flow of Australasian taxa across the montane regions of Malesia (Richardson et al. 2012, and references therein).

The flora of Southeast Asia is still poorly documented, although there are significant differences between localities and taxonomic groups. Collection patterns differ between countries. Only ten plant specimens per 100 km² were collected in Laos, 16 in Cambodia, 20 in Myanmar, in comparison to 200 in Peninsular Malaysia or 5721 in Singapore (Middleton et al. 2019; Niissalo et al. 2014). Within Indonesia, the collection density is five times higher in Java than in Sumatra and a substantial number of the archipelago's 17,000 islands have likely had no specimen collected at all. In Thailand, a single province (Chiang Mai) accounts for 20% of total collections, while half of all provinces combined account for less than 10% (Parnell et al. 2003).

In addition, only one-fifth of herbarium specimens from Tropical Asia are available through the Global Biodiversity Information Facility (GBIF 2022), which is the primary resource used by scientists to get species occurrence data (Paton et al. 2020). Accelerating collection digitisation and making data available through aggregators such as GBIF is a priority (Paton et al. 2020).

Flora accounts are not available for many plant groups in Southeast Asia, particularly the largest plant families and genera. The major Floras in Southeast Asia are *Flora of Thailand*, *Flore du Cambodge*, *du Laos et du Viêt Nam*, *Flora Malesiana*, *Flora of Peninsular Malaysia*, *Tree Flora of Sabah and Sarawak*, *Flora of Singapore*, and *Flora of Vietnam*; and none these Floras has yet been completed (Middleton et al. 2019).

3.2. Rhamnaceae in Southeast Asia

Rhamnaceae has c. 140 accepted species in the region (POWO 2022) but, except for *Flora of Thailand* (Norsaengsri et al. 2020), no treatment for the family is available in the region's major Floras yet aside from the *Tree Flora of Sabah and Sarawak* (Schirarend 1995), which only covers a small proportion of the Rhamnaceae taxa because most species are climbers and shrubs. *Flora of Thailand* contains the most up-to-date account of Rhamnaceae for any region in Southeast Asia. The authors recognise 11 genera and 32 species. Their treatment includes *Smythea poomae* and accepts *Gouania obtusifolia* and *Smythea oblongifolia*, following the conclusions of Cahen et al. (Cahen & Utteridge 2018; Cahen et al. 2020a). Species concepts in *Ventilago* in *Flora of Thailand* may need to be reconsidered after further analysis, particularly for the set of specimens with glabrous fruit wings and calyx remains that cover less than a quarter of the seed chamber at the base of mature fruits (Cahen, pers. obs., see also Section 1.8. Conclusions and challenges). Nonetheless, the Rhamnaceae treatment in *Flora of Thailand* will serve as a foundation for future Southeast Asian Rhamnaceae Flora accounts.

Malesia's main Flora project, *Flora Malesiana* began in the 1940s, but it still only covers about a third of the region's vascular plant species diversity; this incompleteness, combined with its slow progress, has limited its impact on issues like conservation and land use planning in the region (Middleton et al. 2019). Many of the larger families and genera have received insufficient attention, and some accounts published in the 1960s and 1970s are out of date (Johns 1995). While recent progress has been made in documenting Malesian Rhamnaceae taxa, e.g., *Smythea* (Cahen & Utteridge 2018), *Ventilago* for Borneo (Cahen & Utteridge 2017), *Gouania* for the Philippines and Sunda (Cahen et al. 2020a), *Ziziphus* for Borneo (Cahen et al. 2021), work remains to complete the *Flora Malesiana* account for the entire family. There are uncertain species concepts in *Ventilago* and *Gouania* to sort out (see also Section 1.8. Conclusion and challenges), as well as in *Alphitonia* (Hauenschild et al. 2018b).

Among the Rhamnaceae within Malesia, *Alphitonia* and the related *Emmenosperma* are thought to be Australasian (Hauenschild et al. 2018b) and while *Emmenosperma* is most abundant in New Guinea and does not extend beyond Wallacea, *Alphitonia* extends to Borneo and the Philippines (and even further into Hainan) but is absent from Sumatra and the Thai-Malay Peninsula. Similarly, *Rhamnella vitiensis* (Benth.) A.C.Sm., has an Australasian distribution, being only known to occur in

Australia and New Guinea. *Gouania* has a pantropical distribution and seems unaffected by Malesian biogeographic boundaries. Similarly, coastal species like *Smythea lanceata* and *Colubrina asiatica* are found throughout the region with no discernible biogeographic influence.

Ventilago and *Smythea*, on the other hand, appear to be more diverse in western Malesia than in eastern Malesia, with at least nine species occurring in the Indo-Malay Peninsula compared to four in New Guinea (Cahen & Utteridge 2017; Cahen & Utteridge 2018; Cámara-Leret et al. 2020; Utteridge & Cahen 2021; see also Section 2.6.1 Ventilagineae). Except for *Sageretia hamosa*, which also occurs in northern Australia, *Sageretia* and *Berchemia* do not extend eastward beyond Wallacea. *Ziziphus* is found throughout Malesia, but Borneo has the greatest known diversity (Cahen et al. 2021), and Wallacea and Sahul have fewer species than Sunda. *Rhamnus* is found throughout Malesia, including four species in New Guinea (Cámara-Leret et al. 2020), but it is much more diverse in China, with over 50 species (Chen & Schirarend 2007). Only one species, *R. napalensis* (Wall.) M.A.Lawson, extends to Queensland, Australia. Overall, most Rhamnaceae species in Malesia appear to have arrived from Indo-Malaya and reach their greatest diversity in Sunda.

Cahen et al. found that most Malesian Rhamnaceae taxa they studied, namely *Smythea*, and *Ventilago* in Borneo and New Guinea, *Gouania* in Sundaland and the Philippines, and *Ziziphus* in Borneo, only occur in everwet lowland and lower montane forests. *Smythea lanceata*, a coastal species with sea-dispersed fruits, and *Smythea oblongifolia*, which occurs in both everwet and monsoon forests, such as in the Lesser Sunda Islands, are exceptions. Most species were collected only in lowland everwet rainforests (e.g., *Ziziphus kunstleri* King) or in both lowland and lower montane forests (e.g., *Ventilago ferruginea* Cahen & Utteridge). Rhamnaceae taxa that are only known to occur in montane forests are uncommon (e.g., *Ziziphus borneensis* var. *kinabalui* Suss.).

Only a few Rhamnaceae species, such as *Ziziphus oenoplia* (L.) Mill. in Java and the Lesser Sunda Islands, and *Z. timoriensis* DC. in the Lesser Sunda Islands, Sulawesi, and Queensland, Australia, appear to prefer monsoon environments with a dry season. However, many Southeast Asian Rhamnaceae species found in Indochina, such as *Ventilago denticulata* Willd. and *V. cristata* Pierre, live primarily in dry evergreen forests. These species occur north of the Isthmus of Kra and do not reach Malesia. *Ziziphus mauritiana*, an invasive thicket-forming species in many parts of the world, including Australia and the West Indies, appears to thrive in Malesia's drier, more open, and

disturbed habitats. To summarise, the majority of Rhamnaceae diversity in Malesia is concentrated in everwet, lowland and montane forests, with fewer species restricted to dry monsoon forests, and only a few species occurring in both everwet and dry forests.

3.3 Conclusion and challenges

Since botanists generally collect fertile material, it is likely that they have encountered several undescribed species that they either did not collect or that could not be used for a new species description because the material was sterile. In an analysis that included over 44,000 specimens from c. 30,000 species collected in 56 Southeast Asian locations, researchers assessed the total plant diversity of forest plots by collecting all vascular plant species, including sterile ones, and identifying them using DNA barcoding. In the specific case of Mt Bokor in Cambodia, 770 species were reported, with about a third with only sterile material available despite intensive collecting over seven surveys. Of the 770 species, 40 were new to science but remain scientifically undescribed because of the absence of flowers or fruits (Tagane et al. 2017; Yahara et al. 2012; Middleton et al. 2019). This shows how much plant diversity has been overlooked.

Collecting biases affect our understanding of the distribution of plant diversity and make subsets of plant species less well-represented in collections and the scientific literature than others. Montane habitats receive more attention than surrounding lowland habitats. An analysis of c. 8,000 collections from Mt Jaya, New Guinea, between 1903 and 1997 revealed that alpine and subalpine areas were more visited by collectors, who revisited already explored sites, only finding a few new species, whereas the surrounding lower elevation areas were much less explored but yielded more discoveries per visit (Utteridge & De Kok 2007). Middleton et al. (2019) made the following remarks: ‘It was clear from the Mt Jaya data that botanists love to climb mountains, and whilst the peaks of Southeast Asia are extremely species-rich and at threat from climate change, it is the lowland and montane [i.e., intermediate elevations] habitats that are most poorly collected and at most threat from immediate habitat conversion through logging and forest conversion to agricultural use such as oil palm’.

Another bias is that specimens are collected near roads. Based on specimen label locality and habitat information, this bias is clear in Southeast Asian Rhamnaceae collections (Cahen, pers. obs.). Roadside collections are likely to overrepresent species that tolerate disturbance and under-represent species of the forest interior. (Daru et al.

2018).

Even if they are well-versed in the flora, generalist collectors do not collect all species in an area and may overlook understudied species, whereas specialist collectors will home in on unusual species in taxonomically difficult groups they work on (Middleton et al. 2019). More targeted collecting of Rhamnaceae species from unresolved taxonomic groups, such as *Ventilago* plants with glabrous fruit wings and calyx remains that cover less than a quarter of the seed chamber could provide the data resolution needed to better understand species limits.

Tropical liana specimens are collected less frequently than tree specimens, making research about climbers more difficult because there are fewer specimens available to understand their diversity and species limits. As a result, even when a tropical flora is considered ‘well-known’, it usually refers to knowledge of the region’s trees, whereas herbaceous plants, epiphytes, climbers, understory trees, and shrubs are generally much less well known (Johns 1995). This problem is especially salient in Southeast Asian Rhamnaceae where most species are climbers.

Many herbaria struggle to balance competing claims for resources spent on databasing existing collections versus resources spent on collecting new material from underexplored regions (Middleton et al. 2019). Collecting specimens, as well as herbaria ensuring that material is properly processed and made available to researchers, are critical to species discovery and publication. According to one estimate, 47 to 66% of undescribed species have already been collected and are waiting to be studied and described in the world’s herbaria (Bebber et al. 2010; Middleton et al. 2019).

Despite these challenges and that no major Flora initiative in the region is yet complete, progress is being made in documenting Southeast Asia’s plant diversity. In the last ten years, nearly 3000 new species have been described for the region (Middleton et al. 2019). This appraisal is based on published work that contributed to this effort by revising the genus *Smythea*, including six new species descriptions, describing three new *Ventilago* species, plus two additional species in New Caledonia and Vanuatu, revising the genus *Gouania* in western Malesia and addressing its muddled species concepts, and contributing the first revision of *Ziziphus* in Borneo, including three new species and two new variety descriptions.

This research represents a significant step forward in our understanding of the diversity of Rhamnaceae in this part of the world, and it has laid the groundwork for the completion of Rhamnaceae accounts in the region’s Flora projects, particularly *Flora*

Malesiana. Completing these Flora projects is critical to ensuring that we have baseline data for future research, as well as a practical tool for identifying plants and informing conservation policies in the context of high deforestation and plant species extinction rates.

4. RHAMNACEAE CLIMBERS

4.1. Introduction

One of the most noticeable differences in composition between temperate and tropical forests, along with the presence of epiphytes, is the abundance of lianas; woody climbers account for a quarter of the woody stem biomass in lowland tropical forests. While the number of species increases from pole to equator in most groups of living organisms and most other types of plants, the increase in the diversity of lianas also occurs as a fraction of the total flora: climbers account for up to a quarter of all tropical forest species, a fivefold increase over lowland temperate forests (Schnitzer & Bongers 2002). Liana specimens are collected less frequently than tree specimens and, as a result, are less well-understood taxonomically than trees (Johns 1995). Describing tropical lianas is thus an especially important task in documenting the remaining plant species that have yet to be located, described, and named.

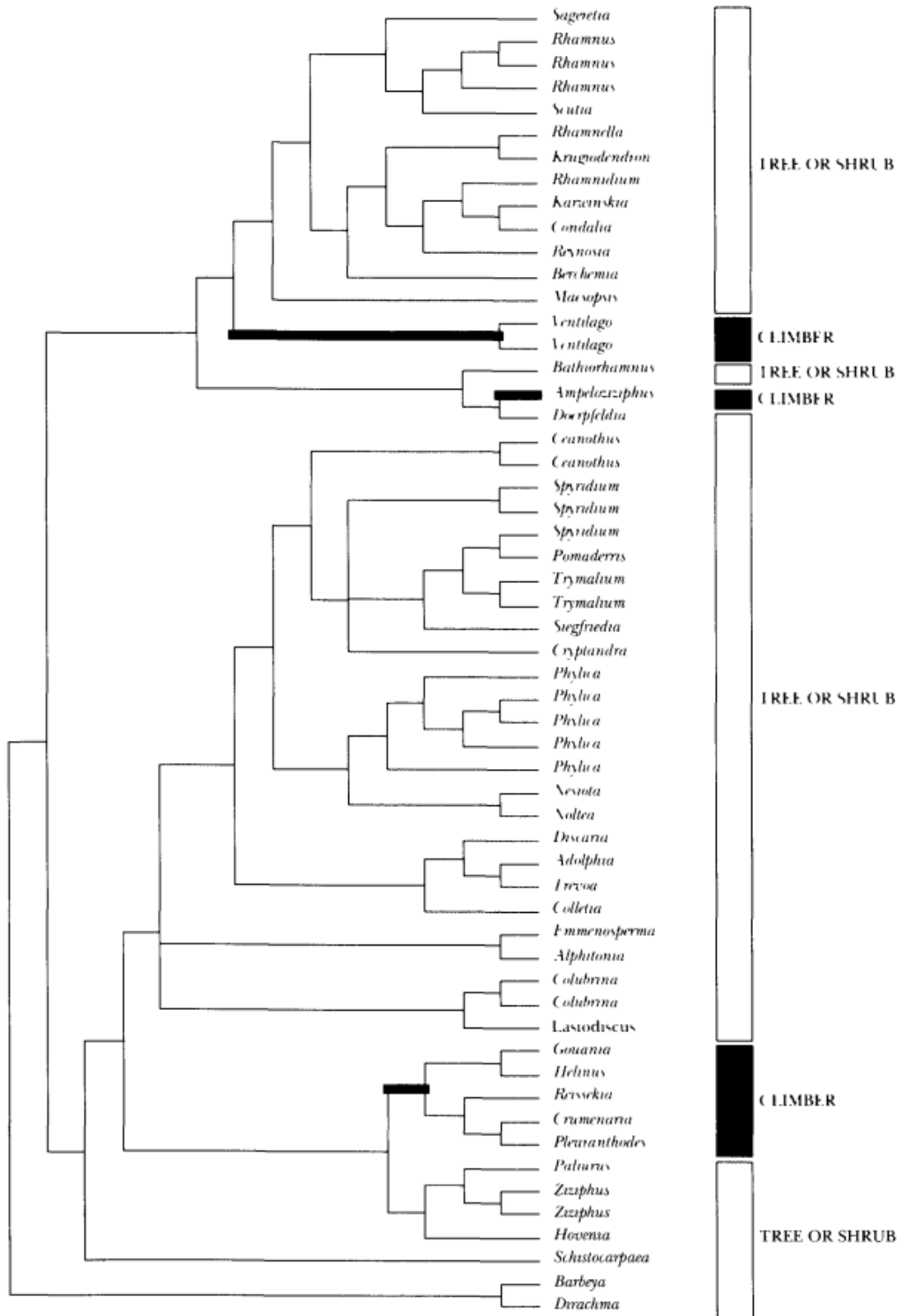
While Rhamnaceae mainly consists of shrubs and trees, it also includes many lianas, especially in tropical areas. The majority of Rhamnaceae species occurring in Southeast Asia are lianas; however, the distinction between a shrub and a liana is blurred in some species that climb more passively, such as *Sageretia thea* (Osbeck) M.C.Johnst, described as a ‘scrambler’, a ‘scandent shrub’, or a ‘climbing shrub’. Except for *Ziziphus ridleyana*, a large tree endemic to Sarawak, all the 13 new species described by Cahen et al. are woody climbers; and among the 36 taxa accounts included in their publications, only *Z. ridleyana* and *Z. angustifolia*, another large tree, are not climbers. Because Rhamnaceae climbers co-occur with Rhamnaceae shrubs and trees in Southeast Asia, and because they use different climbing mechanisms and vectors for fruit dispersal, they provide an informative case study for the ecology and diversification of climbing species.

4.2. Evolution and diversification

Richardson et al. (2000b) annotated whether lineages in the family are trees, shrubs, climbers, or herbs in their phylogenetic tree of Rhamnaceae (Fig. 14). According to their results, the climbing habit evolved three times from an arborescent ancestral state, and once in each of the family’s three broadest informal clades: Ventilagineae in the rhamnoids, *Ampelozizyphus* in the ampeloziziphoids, Gouanieae in the ziziphoids. In fact, the climbing habit has certainly evolved at least six times, given that *Berchemia*, *Ziziphus*,

and *Sageretia* belong to separate phylogenetic branches. The number would be even greater if including genera like *Colubrina* and *Rhamnus* that are occasionally scandent but lack specialised climbing mechanisms. Richardson et al. (2000b) described the phylogenetic trees at the genus level only and *Berchemia*, *Sageretia*, and *Ziziphus* contain both climbers and non-climbers.

Figure 14. Evolution of the climbing habit in Rhamnaceae. Phylogeny produced by Richardson et al. (2000b), obtained by a combined morphological and molecular analysis. Thick black bars represent character state changes. According to the annotations on this phylogeny, the climbing habit evolved three times from an arborescent ancestral state; however, given that *Berchemia*, *Ziziphus*, and *Sageretia* belong to distinct branches, the climbing habit has almost certainly evolved at least six times.



Climbing has appeared multiple times within genera containing both climbing and non-climbing species. There are climbing species in distinct clades of *Sageretia*, such as *S. hamosa* in ‘Clade 1’ (Old World tropics), *S. elegans* (Kunth) Brongn. in ‘Clade 2’ (Americas), and *S. thea* (Osbeck) M.C.Johnst. in ‘Clade 3’ (Asian temperate regions) (Yang et al. 2019). Similarly, climbing occurs in various well-supported *Berchemia* clades, such as *B. scandens* (Hill) K.Koch in ‘*Berchemia* clade I’ (North America), *B. kulingensis* C.K.Schneid. in ‘*Berchemia* clade III’ (Asia), and *B. floribunda* (Wall.) Brongn. in ‘*Berchemia* clade IV’ (Asia) (Huang et al. 2021). A more comprehensive phylogeny of *Ziziphus* has yet to be published to determine whether the climbing trait appeared independently multiple times in this genus as well.

The climbing habit more generally evolved independently in over 60% of dicotyledonous plant orders and about a quarter of all plant families, demonstrating how adaptive this trait has been throughout plant evolution (Gianoli 2015; Schnitzer & Bongers 2002). Climbing plants are found in six of the nine Rosales families and are present in all three major clades (Rosaceae, Rhamnaceae and its related families, and Ulmaceae and its related families; for notes on the Rosales phylogeny see Section 1.4.2. Rosales). They are particularly common in the former Urticales, with several climbers in Moraceae (notably *Ficus*, but also *Broussonetia*, *Maclura*, *Streblus*, and *Trophis*) and Urticaceae (notably *Urera*, *Nothocnide*, and *Poikilospermum*), as well as some in Cannabaceae (e.g., some species of *Celtis* and *Humulus*). Rosaceae contains some climbing shrubs, such as roses (*Rosa*) and brambles (*Rubus*). In the families most closely related to Rhamnaceae (Elaeagnaceae, Barbeyaceae and Dirachmaceae), climbers occur only in Elaeagnaceae, are rarer than in Rhamnaceae, and would be more accurately described as ‘scandent shrubs’ (e.g., *Elaeagnus latifolia* L.).

Climbing tends to increase diversity in the evolutionary groups where it appears regardless of the geographic region, and climbing taxa have more species than their non-climbing sister groups (Gianoli 2004). The trend in Rhamnaceae is unclear, in part because the sister groups to the only specialised climbing tribes, Gouanieae and Ventilagineae, contain so many genera, and Rhamnaceae is most diverse in drier Mediterranean-like ecosystems where climbers are scarce (e.g., Phyllicae in Southern Africa and Pomaderreae in Australia). When the analysis is restricted to tropical environments and lowland rainforests, particularly in Southeast Asia, the results confirm the trend of higher diversification in climbers than non-climbers, especially given the many potential undescribed species of *Ventilago* and *Gouania* (see also Section 1.8.

Conclusions and challenges). Regardless of this undocumented diversity, climbing is the most common Rhamnaceae habit in Malesia (Table 6).

Table 6. The habit of the Rhamnaceae genera in Malesia. Based on the accepted species list for Malesia in POWO (2022). Climbing is the most common habit for Rhamnaceae in this region, reflecting the tendency of climbing to increase diversification in the taxonomic groups where it appears.

Genus	Habit	Species
<i>Alphitonia</i>	Trees	2
<i>Berchemia</i>	Scandent shrubs	4
<i>Colubrina</i>	Trees and shrubs (sometimes scandent)	4
<i>Gouania</i>	Climbers	6
<i>Oreorhamnus</i>	Trees	1
<i>Rhamnus</i>	Shrubs (sometimes scandent)	7
<i>Sageretia</i>	Scandent shrubs	3
<i>Smythea</i>	Climbers	7
<i>Ventilago</i>	Climbers	14
<i>Ziziphus</i>	Climbers (mostly), trees and shrubs (sometimes scandent)	23

Another characteristic of Rhamnaceae in Malesia is the presence of several scandent plants belonging to genera that are mostly non-climbing throughout their global distribution, particularly in *Berchemia* (e.g., *B. floribunda*), *Colubrina* (e.g., *C. asiatica*), *Rhamnus* (e.g., *Rhamnus napalensis* (Wall.) M.A.Lawson) and *Sageretia* (e.g., *S. hamosa*). This reflects how high rainfall, and the presence of closed forested environments drive the distribution and diversification of lianas, where developing mechanisms for leaves to reach the canopy is adaptive (Rickenback et al. 2022).

4.3. Climbing mechanisms

When it comes to climbing mechanisms, Rhamnaceae lianas can be divided into two main groups: those that use tendrils and those that twine around a supporting substrate. Some species of *Sageretia* and *Ziziphus* also have hooks and spines that may help the climbing species attach themselves to their support (Table 7). Other adaptations

for climbing, such as downward-pointing adhesive hairs, and adhesive, adventitious roots are not known to occur in Rhamnaceae.

Table 7. Rhamnaceae genera with specialised climbing mechanisms. The recorded distribution of these genera is only for their climbing species. *Colubrina* and *Rhamnus* are not included because while some species can be scandent, they lack specialised climbing mechanisms. The two main types of climbing found in Rhamnaceae are twining around a support and using tendrils.

Genus	Tribe	Climbing mechanism	Distribution
<i>Alvimiantha</i>	Gouanieae	Tendrils	Neotropics
<i>Ampelozizyphus</i>	Ampelozizypheae	Twining	Neotropics
<i>Berchemia</i>	Rhamneae	Twining	Asia and North America
<i>Gouania</i>	Gouanieae	Tendrils	Pantropical
<i>Helinus</i>	Gouanieae	Tendrils	Paleotropics
<i>Johnstonalia</i>	Gouanieae	Tendrils	Neotropics
<i>Reissekia</i>	Gouanieae	Tendrils	Neotropics
<i>Sageretia</i>	Rhamneae	Scrambling (often with hooks or spines)	Asia, Africa, and Americas
<i>Smythea</i>	Ventilagineae	Twining	Paleotropics
<i>Ventilago</i>	Ventilagineae	Twining	Paleotropics
<i>Ziziphus</i>	Paliureae	Twining (with spines)	Southeast Asia

4.3.1. Tendrils

The presence of tendrils is a possible synapomorphy of Gouanieae (Fig. 14). It is the only Rhamnaceae tribe where tendrils occur and these are present in every genus except *Crumenaria*, which is also the only non-climbing genus of the tribe and the only herbaceous genus of the family. Richardson et al. (2000b) suggest that the herbaceous habit in *Crumenaria* could be a reduction from the climbing habit. The available information about the origin of tendrils in Gouanieae was compiled by Sousa-Baena et al. (2018) (Table 8).

Table 8. The origin of tendrils in Gouanieae. As summarised by Sousa-Baena et al. (2018).

Genus	Tendril origin
<i>Alvimiantha</i>	Modified stems
<i>Gouania</i>	Modified stems and inflorescence branches; also derived from peduncle
<i>Helinus</i>	Derived from peduncle
<i>Johnstonalia</i>	Modified stems
<i>Reissekia</i>	Modified stems

Tendrils in Gouanieae have a simple structure, consisting in simple-ended coiled structures (Fig. 15). This contrasts with more complex structures found in other plant families, such as tendrils that are branched (e.g., *Cobaea*, Polemoniaceae), coiled in a spring-like shape (e.g., *Fevillea*, Cucurbitaceae), end with a hook (e.g., *Dolichandra unguis-cati* (L.) L.G.Lohmann, Bignoniaceae), end with adhesive pads (e.g., *Cissus*, Vitaceae) or become lignified over time (e.g., *Strychnos*, Loganiaceae) (Sperotto et al. 2020).

Figure 15. *Gouania* sp. with visible tendrils. Observed and photographed in Sandoval, Peru by Ruth Ripley (CC BY-NC).



The most detailed study of the origin and development of tendrils in Gouanieae was by Tortosa (2005). He observed that in *Gouania*, the distal bud in an axillary cluster of buds gives rise to a stem with determinate growth that bears two prophylls, and a foliage leaf, in the axil of which the inflorescence and the tendril develop; he also noted that tendrils occur in the axis of inflorescences. He noted that tendrils emerge at the nodes of plagiotropic shoots (horizontal shoots) in *Johnstonia* (= *Johnstonalia*), *Alvimiantha*, and *Reissekia*, other members of Gouanieae, but tendrillate shoots develop at the nodes of orthotropic shoots (erect, vertical shoots) in *Gouania* (Fig. 16).

Figure 16. Tendril position in Gouanieae. In *Gouania* (A, B), a stem with determinate growth that bears two prophylls and a foliage leaf develops from the distal bud in an axillary cluster of buds; the inflorescence and tendril develop in the axil of the foliage leaf. Tendrils occur in the axis of inflorescences. In *Johnstonia* (= *Johnstonalia*) (C), and *Alvimiantha* (E), tendrils emerge at the nodes of plagiotropic shoots (horizontal shoots), whereas tendrillate shoots develop at the nodes of orthotropic shoots (erect, vertical shoots) in *Gouania*. Figure from Tortosa (2005).

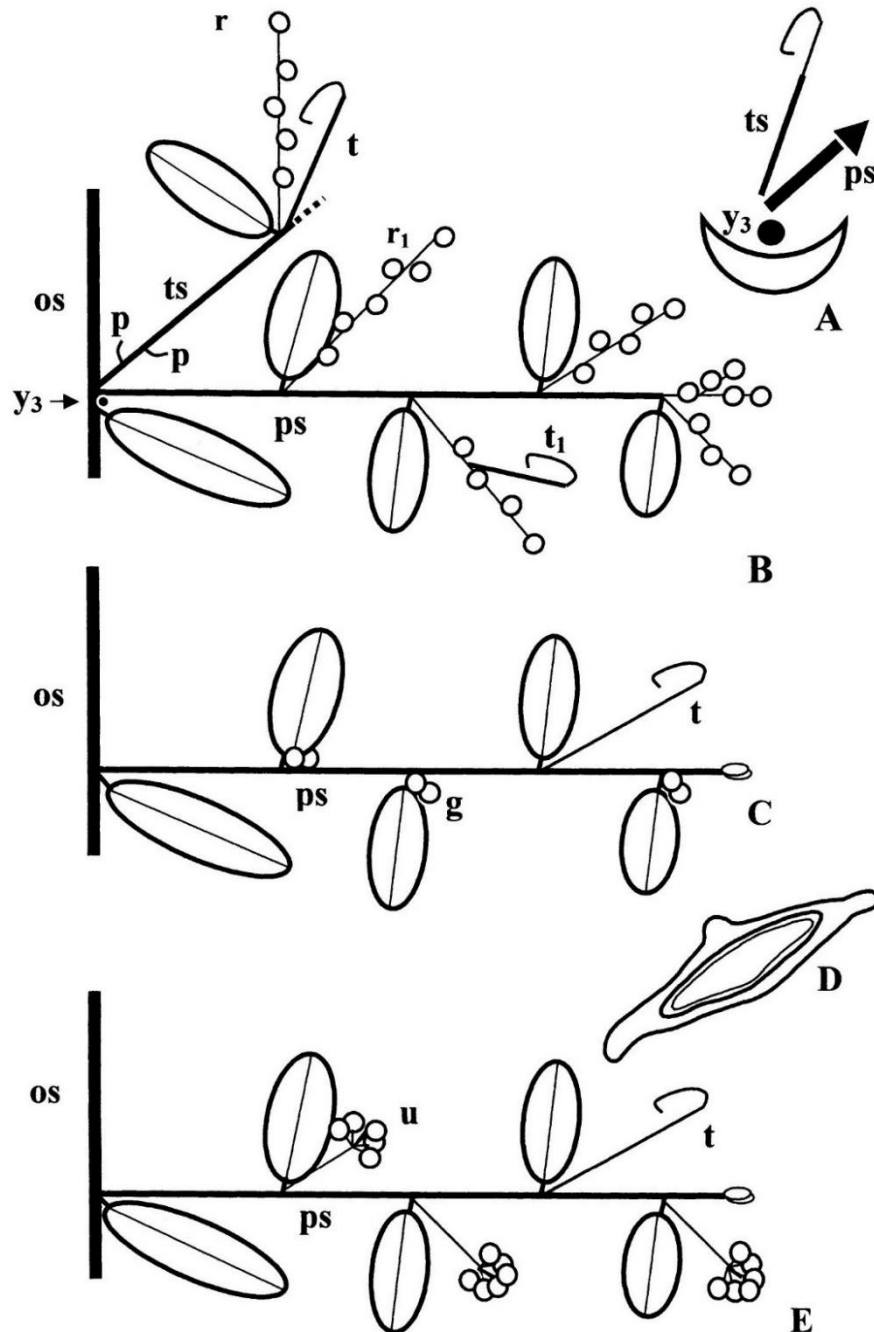


Figure 1. A, B, *Gouania*.—A. Axillary complex. —B. Vegetative and reproductive structures at a node. C, D, *Johnstonia axilliflora*.—C. Vegetative and reproductive structures at a node. —D. Cross section of a mericarp (from Smith & Vásquez 3396, holotype, TEX). —E. *Alvimiantha tricamerata*. Vegetative and reproductive structures at a node. References: g, 2-flowered glomerule; os, orthotropic shoot; p, prophyll; ps, plagiotropic shoot; r and r₁, spike-like raceme; t and t₁, tendril; ts, tendril shoot; u, umbellate-pedunculate inflorescence; y₃, dormant proximal bud.

Putz (1991) mentioned that the number of *Gouania* species is small in the context of increased speciation levels in groups of plants that developed specific climbing mechanisms, particularly those with tendrils like *Gouania*. However, *Gouania* is a genus that needs to be revised across its distribution (Medan & Schirarend 2004; Cahen et al. 2020a). Many new species have been described recently, particularly following revisions for Madagascar and its neighbouring islands (Buerki et al. 2011) and North America (Pool 2014) and there may be several more species to describe in addition to the c. 70 currently accepted species (POWO 2022).

There is a morphological continuum with difficult-to-distinguish species in some sets of specimens of *Gouania* from Southeast Asia, and more extensive sampling and research will certainly yield new discoveries. Furthermore, some current species concepts in the genus are broad, such as *Gouania microcarpa* DC., which is restricted to India and Sri Lanka as discussed by Cahen et al. (2020a) but was previously thought to occur in various parts of Malesia, including New Guinea, by authors such as Lauterbach (1922), who recognised four endemic varieties of *G. microcarpa* in New Guinea. Because they are likely only distantly related to *G. microcarpa*, these varieties may be elevated to the species level (Cahen, pers. obs.).

In the end, even excluding undescribed Gouanieae species, the tribe accounts for more species than less specialised twining groups in the family like Ventilagineae. As a result, contrary to the comments by Putz (1991), the trend of increased speciation levels in climbers with tendrils versus less specialised climbers like twiners seems to hold true in Rhamnaceae.

Climbers with tendrils have been observed to prefer sites with an abundance of thin supporting stems and are thus considered early succession specialists (Wyka et al. 2013). This is consistent with the habitat description data for Southeast Asian *Gouania* herbarium specimen labels, which show plants growing at the edge of a forest, on slopes, in open areas, or in disturbed habitats, e.g., ‘Hill forest with some anthropogenic disturbance. At edge of old garden.’ (*Takeuchi* 11711, Chimbu Province, Papua New Guinea), or ‘Along side of the lake. Disturbed forest.’ (*Reynoso* PPI 7268, Luzon, Philippines).

4.3.2. Twiners

In contrast to the presence of tendrils, which is restricted to the single tribe Gouanieae, twining is found independently in several distantly related Rhamnaceae clades, including *Berchemia* in Rhamneae, *Ziziphus* in Paliureae, and *Ventilago* and *Smythea* in Ventilagineae (Fig. 17). Twining is also found in *Ampelozizyphus*, but this is not mentioned in *The Families and Genera of Vascular Plants* (Medan & Schirarend 2004), where the plants in the genus are described as ‘unarmed climbers without tendrils’. The twining habit of *Ampelozizyphus amazonicus* Ducke is visible in photographs (Leitão et al. 2022), even though the species is more commonly described as scrambling (e.g., Acevedo-Rodriguez 2020). The genus now has three accepted species, including two new tree species described after the tribal analysis by Richardson et al. (2000b), where the *Ampelozizyphus* branch of the phylogeny was marked as a clade of climbers (Fig. 14). This provides more evidence that the climbing habit can appear or disappear secondarily within Rhamnaceae genera.

Figure 17. Twining stem of *Ventilago pubiflora* W.D.Francis. Observed and photographed in Queensland, Australia by Tony van Kampen (CC-BY).



Climbing with twining stems is a likely synapomorphy of the Ventilagineae, which evolved from a non-climbing ancestral state within the rhamnoids (Richardson et al. 2000b, see also Fig. 14). If this is the case, *Ventilago viminalis*, the only known tree species in the tribe, transitioned back from the climbing habit to an arborescent state (see also Section 2.6.1. Ventilagineae).

Twining lianas, like climbers with tendrils, are more commonly found growing along small-diameter supporting stems. They are not, however, as much of an early succession specialist as tendril climbers, and their relative importance has been found to increase with forest age, whereas the relative importance of tendril climbers has been found to decrease with forest age (Dewalt et al. 2000). Twining climbers are thus intermediate between tendril climbers, which have a lower upper limit of the supporting tree's trunk diameter, and root climbers, which are not constrained by large support diameters and can occur in more shaded areas of the forest (Gianoli 2015). This intermediate position is consistent with the herbarium label data of Ventilagineae specimens, which reflects a capacity to thrive in both later-succession (e.g., 'large climber on tree in primary-forest', *Shea & Aban* SAN 77250, Ranau, Sabah) and early-succession stage habitats ('hill side, logged over area', *Sundaling* SAN 93192, Tongod, Sabah).

Lianas, particularly twiners, are likely to expand their distribution range with global warming. The small number of lianas in colder regions can be attributed in part to the vulnerability of their larger vessels to freezing-induced embolism; this contrasts with the comparatively smaller decrease in the proportion of herbaceous climbing species, which have smaller vessels and are less susceptible to temperature oscillations (Durigon et al. 2014). Thus, as temperatures rise and the risk of freeze-induced embolism decreases, the distribution range of lianas is likely to expand to higher latitudes and altitudes provided their potential new habitats are not converted for agriculture or other uses.

4.3.3. Spiny climbers

Spines are present in most Rhamnaceae tribes (some notable exceptions are Gouanieae, Phyllicae and Ventilagineae). They are most common and impressive in Colletieae (e.g., *Colletia paradoxa* (Spreng.) Escal.) and are especially common in shrubs in drier Mediterranean-type ecosystems (e.g., *Paliurus spina-christi* Mill.). This spiny shrubby habit is the one most associated with Rhamnaceae plants in general; such spines in shrubs are thought to serve as a defence against grazing herbivores (Osborne et al.

2018). Despite having spiny and thorny species in other parts of the world (e.g., *Colubrina verrucosa* (Urb.) M.C.Johnst. and *Rhamnus oleoides* L.), *Colubrina* and *Rhamnus* are occasionally scandent in Southeast Asia, but these ‘scandent shrubs’ are unarmed.

Sageretia and *Ziziphus* are the only two Rhamnaceae genera with lianas that use spines to facilitate climbing. The climbing species of *Sageretia* are described as ‘scandent shrubs’ in *Flora of China* (Chen & Schirarend 2007) and as ‘climbing by thorns’ with no mention of twining shoots in *The Families and Genera of Vascular Plants* (Medan & Schirarend 2004). However, herbarium label descriptions suggest that at least some species, such as *S. hamosa*, reach the canopy of trees like lianas (e.g., ‘vine in tops of medium sized trees’, *Kairo* 484, Morobe Province, Papua New Guinea). Hooks are especially noticeable in *S. hamosa*, which is described as having ‘hooklike stout spines’ in *Flora of China* (Chen & Schirarend 2007); the species was also described as a ‘woody vine climbing by backward pointing woody hooks, which are capable of ripping open shirts’ (*Ford* 5248, Queensland, Australia).

Whereas climbing specialists account for a small proportion of all *Sageretia* species, lianas account for at least one-third of all *Ziziphus* species. Despite the widespread distribution of the genus across all Old World continents and biomes, *Ziziphus* lianas are only found in Southeast Asia’s high-rainfall forests (Rickenback et al. 2022), where they can reach a height of at least 30 metres, e.g., in *Z. havilandii* Ridl. (*Wong* WKM 1598, Brunei) (Suessengueth 1953; Cahen et al. 2021).

The spines in *Ziziphus* are modified stipules. In most of the spiny *Ziziphus* lianas, one stipule aborts or remains membranous and deciduous, while the other changes into a strong and curved spine (Cahen et al. 2021). In other spiny *Ziziphus* species, particularly in the spiny shrubs of drier, more open areas such as *Z. mucronata* Willd., both stipules are modified into spines; those on the side of the branch that corresponds to the upper surface of the leaves are usually straight and long, whereas those on the opposite side are shorter and recurved (Brongniart 1826).

4.4. Fruit dispersal

When compared to trees or shrubs, lianas tend to have relatively small, wind-dispersed seeds (Schnitzer & Bongers 2002). This pattern is consistent with traits observed in Rhamnaceae, where wind-dispersed fruits are much more common among the climbing genera than in the rest of the family. *Alvimiantha* (winged hemicarps), *Gouania* (3-winged schizocarps splitting into three 2-winged mericarps), *Johnstonalia* (schizocarps splitting into three mericarps with a winged margin), *Smythea* and *Ventilago* (samaras with elongate terminal wing) are all climbing genera with winged fruits. In comparison, *Paliurus* (shrubs with dry fruits with a hemispherical wing) and *Crumenaria* (herbs with 3-winged schizocarps splitting into three 2-winged mericarps) are the only non-climbing genera with winged fruits (Medan & Schirarend 2004).

The two specialised Rhamnaceae climbing tribes, Gouanieae and Ventilagineae mostly have winged fruits that are adapted for wind dispersal. This is unlike in the genera that include both climbing and non-climbing species, such as *Berchemia*, *Sageretia*, and *Ziziphus*, all of which have fleshy fruits. Climbing appears to be a synapomorphy in Gouanieae and Ventilagineae rather than a trait that evolved secondarily within groups of trees and shrubs as in other genera, implying that the lianescent habit co-evolved preferentially with wind dispersal.

It is difficult to assess whether the presence of wind-dispersed versus fleshy fruits predicts a larger or smaller distribution range, but, based on distribution maps, small ranges occur among the wind-dispersed Gouanieae (e.g., *Gouania fimbriata* Reissek ex Lauterb.) and Ventilagineae (e.g., *Smythea crenata* Cahen & Utteridge) as well as among the fleshy-fruited *Ziziphus* (e.g., *Ziziphus puberula* Cahen & Utteridge), but broad distributions are more common in the wind-dispersed genera. *Gouania leptostachya* DC. is distributed in much of Asia, from India, through the Himalayas to China and across much of Malesia, and *Gouania obtusifolia* and *Smythea oblongifolia* are also distributed across much of Malesia. In comparison, no climbing *Ziziphus* species (all fleshy-fruited) has such a broad distribution, and span at most western Malesia without venturing north of the Isthmus of Kra (e.g., *Z. calophylla*, *Z. horsfieldii* and *Z. kunstleri*). Of the 13 *Ziziphus* species found in Borneo, five are endemic to the island and three are restricted to Borneo and the Philippines (Cahen & Utteridge 2017, 2018; Cahen et al. 2020b, 2021).

It is unclear why wind-dispersed fruits in climbers would result in broader distribution ranges. In a closed canopy forest in Cameroon, animal-dispersed species had

longer mean dispersal distances than wind-dispersed species, but lower fecundities (Clark et al. 2005). One possibility is that wind-dispersed species rely less on the presence of specific types of animals to disperse their fruits, allowing them to spread more easily in new environments. Another explanation is that *Ziziphus* climbers do not thrive outside of everwet forest plant communities, whereas Ventilagineae and *Gouania* climbing species can survive in a wider range of environments, including those with a prolonged dry season (e.g., *Ventilago denticulata*). Shrubby *Ziziphus* species adapted to drier and more open conditions, such as *Z. mauritiana*, have an extremely broad distribution, as does the tree species *Z. angustifolia*, which occurs throughout Malesia, implying that it is not the presence of fleshy fruits that explains the narrow range of *Ziziphus* climbers in Southeast Asia.

It is noteworthy here that *Smythea lanceata* and *Colubrina asiatica*, the two scandent Southeast Asian Rhamnaceae species with the broadest distribution range, are mainly coastal species with water-dispersed seeds that can float in seawater and remain viable for months (Guppy 1906).

4.5. Trends

Some of these Rhamnaceae climbers are likely to thrive and expand their range in the face of forest fragmentation and global warming. Because many lianas are early-succession specialists, the observed increase in the abundance of liana species has been attributed to increased forest disturbance and fragmentation (Schnitzer & Bongers 2002; Schnitzer 2005). While lianas have been shown to have a negative impact on the reproduction, growth, and survival of trees, as well as to sequester less carbon due to their relatively slender stems and low wood density, they also appear to contribute positively to overall forest plant diversity and to the diversity of various animal groups (Schnitzer & Bongers 2002; Estrada-Villegas & Schnitzer 2018).

The current low presence of lianas in temperate forests has been attributed to the vulnerability of their large vessels to freezing-induced embolism (Durigon et al. 2014). The only data available on the potential response of Rhamnaceae climbers to warmer winters in temperate regions suggests that while winter warm spells have no effect on the germination rates of the North American twining liana *Berchemia scandens*, they do lead to earlier germination and increased germination rates in other climbing species, giving

them a competitive advantage over spring-emerging seedlings (Flanigan et al. 2020).
Lianas may expand their range to higher latitudes if winters become warmer.

5. CONCLUSION

Our current understanding of evolutionary relationships in Rhamnaceae is primarily based on an early family-wide molecular analysis (Richardson et al. 2000a, 2000b), which revealed the existence of three well-supported clades: the species-rich rhamnoids and ziziphoids and the species-poor ampeloziziphoids. Uncertainties persist regarding the relationship between tribes and genera within these clades, and several genera, including *Alphitonia*, *Ceanothus*, *Colubrina*, and *Lasiodiscus*, have yet to be confidently assigned to a tribe. This research helped better understand the diversity of Ventilagineae (rhamnoids), *Gouania* and *Ziziphus* (ziziphoids) in Southeast Asia and the Pacific. And once species are well-defined, and tools such as taxonomic revisions are available to correctly identify them, phylogenetic analyses and biogeographic reconstructions can be performed on a well-sampled set of specimens to investigate how they diversified. However, some taxonomic issues in these genera remain unresolved. Are *Smythea* as currently recognised and *Ventilago* monophyletic? What morphological characters can be used to distinguish species that appear to form a morphological continuum without clearly identifiable taxa in *Gouania* and *Ventilago*?

Based on fossil evidence, the family is thought to have originated in the Cretaceous and mostly diversified into its current tribes in Gondwana. The discovery of older fossils in Myanmar, however, has called the age of the family's early diversification events into question. Although long-distance dispersal events are thought to better explain the distribution of widespread genera like *Gouania*, the current distribution of extant Rhamnaceae tribes and genera is primarily attributed to vicariance events related to the breakup of Gondwana. While Hauenschield et al. (2018a) studied the phylogeny and biogeography of ziziphoids, more sampling in specific genera, such as work recently published in *Berchemia* (Huang et al. 2021) and *Sageretia* (Yang et al. 2019), is needed to better understand the evolutionary history of many Rhamnaceae groups, including those we studied. Did the water-dispersed *Smythea lanceata* evolve from the wind-dispersed Ventilagineae, or does it belong to a different evolutionary branch? What is the phylogenetic position of *Ventilago viminalis*, the only tree in Ventilagineae, and when did the tree habit appear in the tribe's diversification history? Similarly, what is the evolutionary relationship between the Malesian climbing species of *Ziziphus* and the two Malesian tree species, *Z. angustifolia* and *Z. ridleyana*?

A substantial portion of Southeast Asia's plant diversity is unknown, and tropical climbers have received little attention in comparison to other plant groups. This research expands our understanding of the diversity of Rhamnaceae in this region of the world, and it lays the groundwork for the completion of Rhamnaceae accounts in the region's Flora projects, particularly *Flora Malesiana*. Completing these projects is critical for ensuring baseline data for future research as well as a practical tool for identifying plants and informing conservation policies in the context of high deforestation and plant species extinction rates.

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APPENDIX 1. STATEMENTS OF CONTRIBUTION OF THE PAPERS PRESENTED FOR THIS THESIS

Paper 1. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Cahen, D. & Utteridge, T. M. A. (2017). Three new species of *Ventilago* (Rhamnaceae) from South-East Asia. *Phytotaxa* 307(3), 171—182.

Background: The tribe Ventilagineae (Rhamnaceae) includes two genera, *Smythea* and *Ventilago*, which are mostly climbers with winged fruits that grow in the Old World tropics. In Southeast Asia, the genus *Ventilago* has yet to be revised. This study contributed to this by identifying three new Malesian species: *V. crenata* from New Guinea, *V. ferruginea* from Borneo, Singapore, and Sumatra, and *V. flavovirens* from Borneo. Herbarium sheets of the two new species occurring in Borneo had previously identified as *V. dichotoma* and morphological differences are clarified here. A key to the *Ventilago* species in Borneo is also provided.

Contribution of the candidate: I, Daniel Cahen, took the leading role in this study and in the preparation of the manuscript by making the following contributions:

- I determined three new species to science, in concertation with Tim Utteridge
- I wrote the introduction, which Tim Utteridge revised, as well as the key to the five species of Borneo
- I created the comparative table of morphological characters between *Ventilago dichotoma*, *V. ferruginea* and *V. flavovirens*
- I wrote all three species descriptions
- I studied all cited herbarium specimens, designated the type specimens, and prepared all three distribution maps
- I prepared all three species conservation assessments
- I, along with Tim Utteridge, collaborated with the botanical artist, who prepared three line drawings

Statement of contribution: As co-author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

Name, institute, email address

Signature

Date

Dr Timothy Utteridge
Royal Botanic Gardens, Kew
t.utteridge@kew.org



6th June 2022

Paper 2. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Cahen, D. & Utteridge, T. M. A. (2018). A synopsis of the genus *Smythea* (Rhamnaceae). *Kew Bulletin* 73(1), 1—29.

Background: The tribe Ventilagineae (Rhamnaceae) includes two genera, *Smythea* and *Ventilago*, which are mostly climbers with winged fruits that grow in the Old World tropics. While the delimitation between the two genera is still to be evaluated using molecular evidence, taxonomists have used the shape of the seed chamber, namely flattened and slightly twisted in *Smythea* versus globose in *Ventilago*, as a diagnostic character since Weberbauer first proposed it in 1895. This work discusses this generic delimitation and, for the first time, revises the genus *Smythea*, recognising 11 species, five of which are scientifically described and illustrated for the first time. Distribution maps and a conservation status assessment are given for each species.

Contribution of the candidate: I, Daniel Cahen, took the leading role in this study and in the preparation of the manuscript by making the following contributions:

- I determined five new species to science, in concertation with Tim Utteridge
- I established six new synonyms as well as the new combination: *Smythea oblongifolia*
- I wrote the introduction, which Tim Utteridge revised, as well as the key to the eleven species
- I wrote the section on the generic delimitation between *Smythea* and *Ventilago* as well as the section on the key morphological characters within the genus, which Tim Utteridge both revised
- I wrote all five species descriptions
- I studied all cited herbarium specimens, worked on determining the type specimens with Tim Utteridge, and prepared all five distribution maps
- I prepared all 11 species conservation assessments
- I, along with Tim Utteridge, collaborated with the botanical artists, who prepared six line drawings

Statement of contribution: As co-author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

Name, institute, email address

Dr Timothy Utteridge
Royal Botanic Gardens, Kew
t.utteridge@kew.org

Signature



Date

6th June 2022

Paper 3. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Cahen, D., Toussiro, M. & Pillon, Y. (2020). A revision of *Ventilago* (Rhamnaceae) in New Caledonia and Vanuatu with notes on dyeing properties. *Willdenowia* 50(2), 253—266.

Background: *Ventilago* represents most of the diversity in the Ventilagineae tribe of Rhamnaceae in Eastern Melanesia. *Smythea lanceata*, a primarily coastal species with water-dispersed fruits and a wide distribution, is the only species of *Smythea*, the tribe's other genus, known to occur in this region. Guillaumin wrote identification keys for *Ventilago* species in New Caledonia, as well as described *V. pseudocalyculata* based on four syntypes. Yohan Pillon noticed that its specimens from the Loyalty Islands and those from Grande Terre differed. As a result, the name *V. pseudocalyculata* is lectotypified with a specimen from the Loyalty Islands in this publication, while the specimens from Grande Terre are regarded as a new species, *V. tinctoria*. Furthermore, plants previously labelled as *V. neocaledonica* in Vanuatu were found to differ from this species and are now recognised as *V. vanuatuana*, a new species also described in this work. This made it possible to elucidate what species, known as *laba* in Vanuatu, is the responsible of the red colour traditionally used as a dye for ceremonial mats. We revised the genus *Ventilago* for New Caledonia and Vanuatu, recognising four species in New Caledonia and one in Vanuatu and discussed the dyeing properties of *Ventilago* and identity of *laba*. Both new species are illustrated, and distribution maps and conservation status assessments are presented for each species.

Contribution of the candidate: I, Daniel Cahen, contributed to the manuscript's preparation by making the following contributions:

- I wrote all five species descriptions with input from Yohan Pillon
- I prepared all five distribution maps
- I wrote the section on the key morphological characters within the genus as well as those that separate *Ventilago* from other Rhamnaceae genera in this area
- I reviewed what characters distinguished the new species from previously described ones with Yohan Pillon, who first observed discrepancies between the new species and previously described ones
- I wrote the identification key in collaboration with Yohan Pillon
- I collaborated with the botanical artist, who prepared two line drawings
- I communicated with the journal and addressed the comments of the reviewers

Statement of contribution: As co-author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

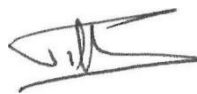
Name, institute, email address

Signature

Date

Dr Yohan Pillon

Institut de Recherche pour le Développement
yohan.pillon@ird.fr



09/06/2022

Paper 4. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Cahen, D., Stenn, K. S. & Utteridge, T. M. A. (2020). A revision of the genus *Gouania* (Rhamnaceae) in the Philippines and Sundaland. *Kew Bulletin* 75(1), 1—24.

Background: The pantropical genus *Gouania* (Rhamnaceae) consists of climbers with tendrils and fruits that split in three winged mericarps. The genus has yet to be revised for the entirety of Southeast Asia. This work contributes significantly to that goal by covering western Malesia, including the Philippines. The genus' taxonomic history in this region is complicated, with misapplied names and the grouping of distinct species into *G. microcarpa*, which seems to be restricted to India and Sri Lanka. This study clears up the confusion by recognising and clarifying the diagnostic characters of *G. fimbriata* and *G. nematostachya*, two species published by Lauterbach in 1922 that had not been mentioned in the literature since. A new species, *G. longipedunculata*, is described from the Philippine islands south of Luzon; it differs from *G. fimbriata* in having densely hairy leaves and longer peduncles. The priority of the name *G. obtusifolia* over *G. javanica* is also discussed, as are the morphological differences between specimens that had been referred to as *G. javanica* found north of the Malay Peninsula and in Malesia.

Contribution of the candidate: I, Daniel Cahen, took the leading role in this study and in the preparation of the manuscript by making the following contributions:

- I recognised a new species to science, *Gouania longipedunculata*, and the validity of Lauterbach's morphological species concepts of *G. fimbriata* and *G. nematostachya*
- I disentangled previous taxonomic confusions around *G. microcarpa* for plants occurring in this region
- I established two new synonyms
- I wrote the introduction, which Tim Utteridge revised, as well as the key to the five species
- I wrote the section on key morphological characters within the genus
- I wrote all five species descriptions with input from Kurt Stenn
- I studied all cited herbarium specimens with the help of Kurt Stenn, designated the type specimens with Tim Utteridge and the help of a manuscript reviewer, and prepared all five distribution maps
- I prepared all five species conservation assessments
- I collaborated with the botanical artists, who prepared two line drawings
- I communicated with the journal and addressed the comments of the reviewers

Statement of contribution: As co-author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

Name, institute, email address

Signature

Date

Dr Timothy Utteridge
Royal Botanic Gardens, Kew
t.utteridge@kew.org

A handwritten signature in black ink, appearing to read 'T Utteridge', written in a cursive style.

6th June 2022

Paper 5. Statement of contribution

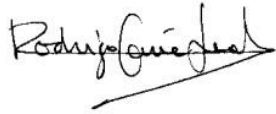

Paper to be considered as part of the PhD by Published Work:

Cámara-Leret, R., Frodin, D. G., ..., Cahen, D., ... & van Welzen, P. C. (2020). New Guinea has the world's richest island flora. *Nature* 584(7822), 579—583.

Background: This paper is the first published attempt to catalogue the entire vascular plant diversity of New Guinea in an expert-verified checklist.

Contribution of the candidate: I, Daniel Cahen helped to the checklist's preparation by cataloguing the Rhamnaceae species found on the island of New Guinea alongside Timothy Utteridge. I added the species of *Gouania* known to occur on the island (*G. exilis* and *G. microcarpa*), as well as the small tree *Dallachya vitiensis* and the climber *Ventilago microcarpa*, while Dr Utteridge included all the remaining Rhamnaceae species.

Statement of contribution: As author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

Name, institute, email address	Signature	Date
Dr Rodrigo Cámara Leret (first author) University of Zurich rodrigo.camaraleret@ieu.uzh.ch		5 May 2022
Dr Timothy Utteridge (co-author) Royal Botanic Gardens, Kew t.utteridge@kew.org		5 May 2022

Paper 6. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Cahen, D., Rickenback, J. & Utteridge, T. M. A. (2021). A revision of *Ziziphus* (Rhamnaceae) in Borneo. *Kew Bulletin* 76(4), 767—804.

Background: The jujube genus *Ziziphus* consists of approximately 80 species of mostly shrubs and climbers with edible drupes found in the Old World tropics, subtropics, and warmer temperate regions. The genus as previously defined was polyphyletic and included New World species that have since been reattributed to the genera *Sarcomphalus* and *Pseudoziziphus*. This is the first revision of the genus for all of Borneo, and it recognises 13 species, three of which are newly described endemics. It also recognises two newly described varieties and establishes five new synonyms, including *Ziziphus elmeri* as a synonym of *Colubrina beccariana*. This revision reveals that Borneo is the island with the greatest known diversity of species in the entire genus, with a particularly high concentration of species in the area surrounding Mount Kinabalu. For each species, distribution maps and a conservation status assessment are provided.

Contribution of the candidate: I, Daniel Cahen, took the leading role in this study and in the preparation of the manuscript by making the following contributions:

- I determined three new species and two new varieties to science, in concertation with Tim Utteridge
- I established five new synonyms
- I wrote the introduction, which Tim Utteridge revised, except for Jessica Rickenback's section on ecology, functional traits, and possible diversification of the genus in Asia
- I wrote the key to the thirteen species as well as the key to the four varieties of *Ziziphus borneensis*
- I wrote the section on the key morphological characters within the genus
- I wrote all thirteen species descriptions
- I studied all cited herbarium specimens, worked on determining the type specimens with Tim Utteridge, and prepared all thirteen distribution maps
- I prepared all 17 conservation assessments
- I collaborated with the botanical artist, who prepared four line drawings
- I communicated with the journal and addressed the comments of the reviewers

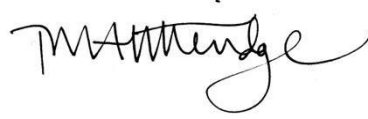
Statement of contribution: As co-author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

Name, institute, email address

Signature

Date

Dr Timothy Utteridge
Royal Botanic Gardens, Kew
t.utteridge@kew.org

A handwritten signature in black ink, appearing to read 'T Utteridge', written in a cursive style.

6th June 2022

Paper 7. Statement of contribution

Paper to be considered as part of the PhD by Published Work:

Utteridge, T. M. A. & Cahen, D. (2021). A new species of *Smythea* (Rhamnaceae) from New Guinea. *Phytotaxa* 498(3), 152—158.

Background: During a visit to the Australian National Herbarium, the first author discovered a specimen of an undescribed species of *Smythea* from Papua New Guinea. This article describes the new taxon, which is the first inland species of the genus to be described. This article completes the account of the known diversity of species in *Smythea* by including an amendment to the key to the genus originally published in ‘A synopsis of the genus *Smythea*’ by Cahen & Utteridge (2018).

Contribution of the candidate: I, Daniel Cahen, contributed to the manuscript's preparation by making the following contributions:

- In the Taxonomic treatment, I wrote the species diagnosis, describing how the newly described *Smythea papuana* differs from the morphologically similar *S. bombaiensis* and *S. oblongifolia*.
- In the Discussion, I specified which morphological characteristics are unique to the newly described species.
- In the Discussion, I highlighted how the newly described species differs vegetatively from the *Ventilago* species found in New Guinea.
- In the Discussion, I explained how the specimen *Pullen 8188* identified as *Ventilago crenata* in ‘Three new species of *Ventilago* (Rhamnaceae) from South-East Asia’ by Cahen & Utteridge (2017) differs from the type specimen and shares many vegetative characters with *Smythea papuana*, but lacks domatia, and that fruiting material would be needed to confirm the identity of *Pullen 8188*.
- In the key to species, I added leaf characters to further distinguish the newly described species from *Smythea bombaiensis*.

Statement of contribution: As first author of the listed paper, I hereby endorse this statement of contribution by Daniel Cahen.

Name, institute, email address

Signature

Date

Dr Timothy Utteridge
Royal Botanic Gardens, Kew
t.utteridge@kew.org



5 May 2022