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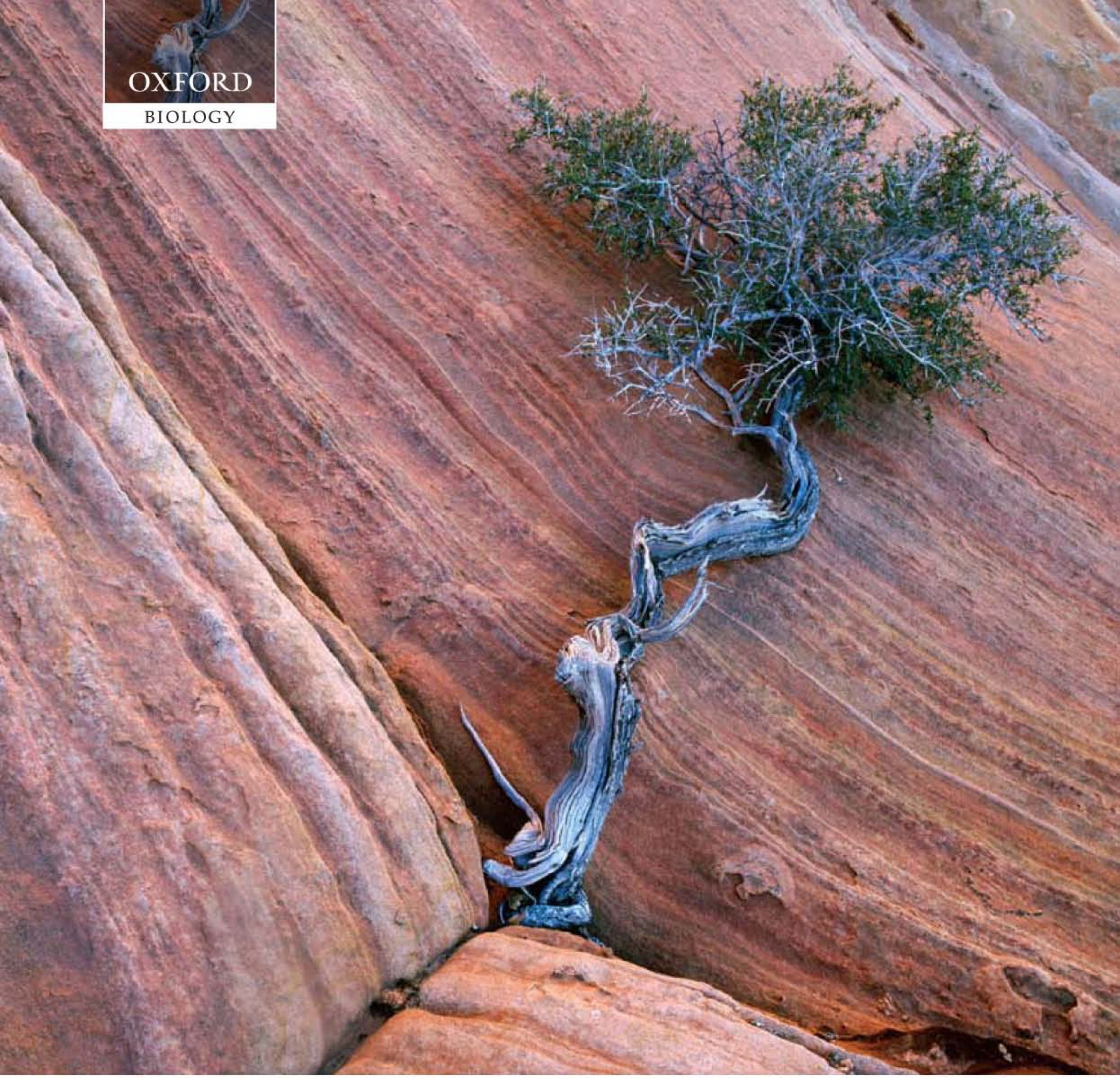

the TIMETREE of LIFE

edited by **S. BLAIR HEDGES** and **SUDHIR KUMAR**
foreword by James D. Watson

Eurosid II

Félix Forest and Mark W. Chase*
Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3DS, UK
*To whom correspondence should be addressed (f.forest@kew.org)

Abstract

Rosids are divided into two main assemblages, Eurosid I and II, and a certain number of unplaced families and orders. This chapter deals with Eurosid II (malvids) and the putatively closely related families and orders (Geraniales, Crossosomatales, Aphloiaceae, Ixerbaceae, Strasburgeriaceae). Eurosid II comprises the Orders Sapindales, Malvales, Brassicales, and Huerteales, and the small Family Gerrardinaceae of uncertain position within the group. Eurosid II was established based on DNA sequence studies whereas morphological characters uniting it remain elusive. They diverged from their closest relatives 104–97 million years ago (Ma) and representatives of each order were present from the early Paleocene (66–56 Ma).

Eurosid II (~15,000 sp.) is smaller than its counterpart in the rosids, Eurosid I (>40,000 sp.) (*1*). Several studies have provided robust support for Eurosid II (*2–6*); Dipentodontaceae and Gerrardinaceae were only recently included in molecular-based analyses. Here, relationships and divergence times within Eurosid II are reviewed as well as for the putatively closely related families (Aphloiaceae, Ixerbaceae, and Strasburgeriaceae) and orders (Geraniales and Crossosomatales).

Despite the strong support recovered for Eurosid II in numerous phylogenetic analyses, relationships within this group remain unclear with most possible arrangements retrieved by at least one study. In some studies, Brassicales (Fig. 1) are found to be the closest relatives of Malvales, with Sapindales closely related to this duo (*6–8*), whereas others associate Malvales with Sapindales, together closely related to Brassicales (*9, 10*) or Brassicales plus Family Tapisciaceae (*3, 4*). The adjacent position of Brassicales and Tapisciaceae is also found elsewhere, but this time more closely related to Malvales alone, with Sapindales being the first lineage to diverge in the group (*11*). The early divergence within Eurosid II of Sapindales is also found in the only analysis comprising both Dipentodontaceae and Gerrardinaceae, in which these two families form an unresolved group with Brassicales and Malvales (*5*). In the timetree, Tapisciaceae is the first diverging lineage followed by Brassicales and the pair Sapindales–Malvales (Fig. 2). Based on these estimates, Eurosid II started to diverge 95–88 Ma ago, with the diversification of the three main orders, Brassicales, Malvales, and Sapindales, initiated 79–71, 71–67, and 62–57 Ma, respectively (*12*). The reader should be aware that, to date, phylogenetic relationships within Eurosid II remain poorly resolved, thus molecular estimates of divergence times can only be taken as preliminary results and viewed with caution; further analyses of the group could result in considerably different results.

Brassicales consist of 15 families, all characterized by the production of mustard oil glucosides (glucosinolates), a feature found only in Brassicales and one other family, Putranjivaceae (Malpighiales) (*13*). The most commonly known member of Brassicales is without doubt Brassicaceae, the cabbage family. Brassicaceae is by far the largest family in the order with about 4130 species of mostly annual and perennial herbs distributed in some 356 genera, representing more than 90% of the species found in the order. They are found

Fig. 1 A member of Brassicaceae (*Heliophila juncea*) growing near Springbok, South Africa. Credit: F. Forest.

F. Forest and M. W. Chase. Eurosid II. Pp. 197–202 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

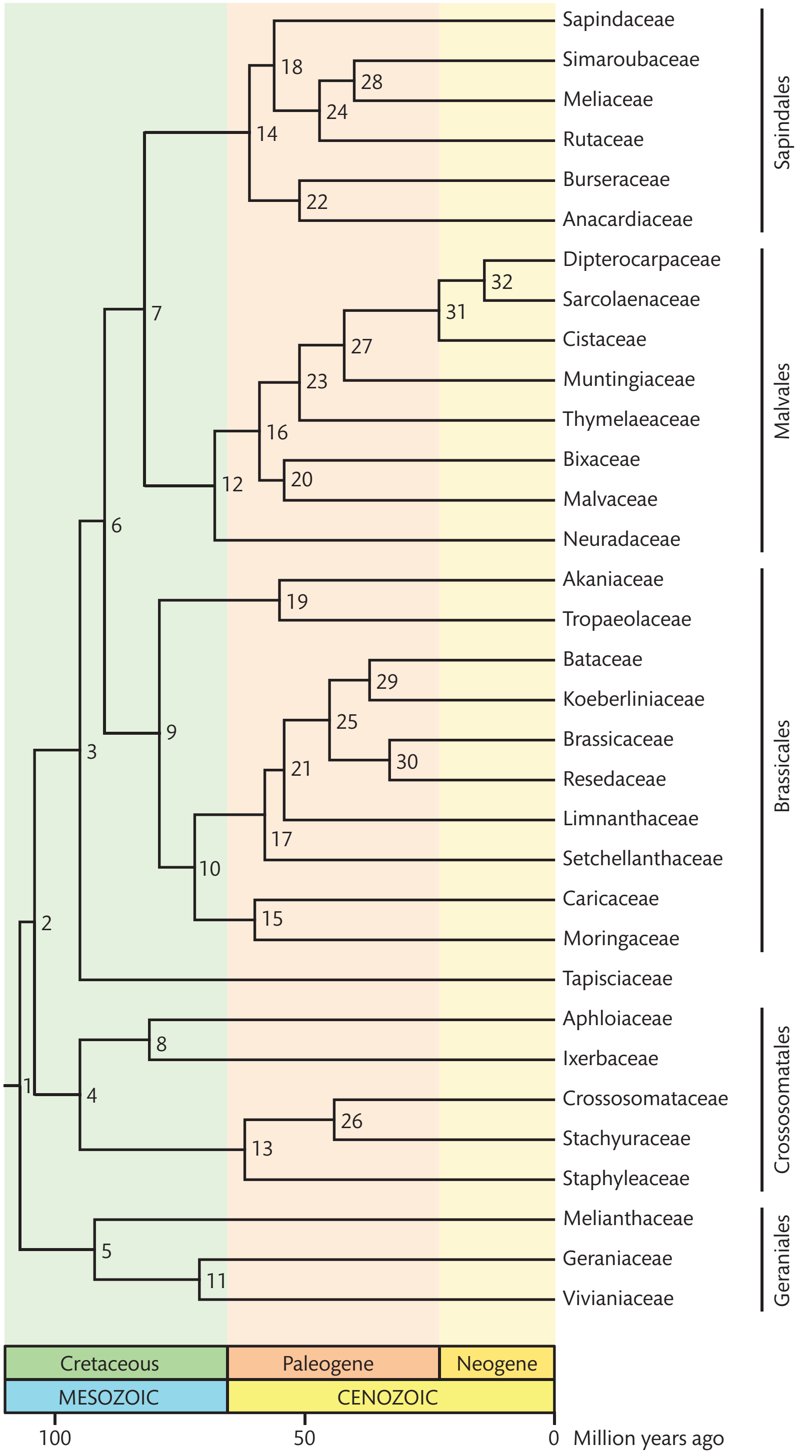

Fig. 2 A timetree of Eurosid II. Divergence times are shown in Table 1.

almost everywhere in the world, but are concentrated in the temperate zone of the Northern Hemisphere. This family comprises important crops including cabbage, broccoli, cauliflower (all from *Brassica oleracea*), rocket (*Hesperis*), and radish (*Raphanus*), to name just a few (*14, 15*). Brassicaceae also count among their members *Arabidopsis thaliana*, a model organism intensively used in molecular biology for the

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among families of Eurosid II.

Timetree		Estimates			
Node	Time	Ref. (*12*)(a)		Ref. (*12*)(b)	Ref. (*12*)(c)
		Time	CI	Time	Time
1	107	107	111–103	103	99
2	104	104	108–100	100	97
3	95	95	99–91	92	88
4	95	95	99–91	93	91
5	92	92	96–88	94	88
6	90	90	94–86	89	85
7	82	82	86–78	84	80
8	81	81	86–76	81	81
9	79	79	83–75	76	71
10	72	72	76–68	72	68
11	71	71	75–67	85	79
12	68	68	72–64	71	67
13	62	62	68–76	61	56
14	61	61	65–57	62	57
15	60	60	65–55	61	58
16	59	59	63–55	65	61
17	58	58	61–55	60	54
18	56	56	60–52	57	55
19	55	55	60–50	61	54
20	54	54	58–50	60	58
21	54	54	57–51	54	52
22	51	51	56–46	52	47
23	51	51	54–48	62	58
24	47	47	51–43	47	45
25	45	45	48–42	47	46
26	44	44	49–39	44	42
27	42	42	45–39	55	54
28	40	40	44–36	44	43
29	37	37	40–34	43	42
30	33	33	36–30	42	39
31	23	23	25–21	39	36
32	14	14	16–12	28	28

Note: Node times in the timetree are based on branch lengths computed using (a) ACCTRAN optimization in maximum parsimony in ref. (*12*). Estimates based on (b) DELTRAN optimization in maximum parsimony and (c) maximum likelihood method are also shown.

study of floral development, among many other purposes. Tropaeolaceae (nasturtium family) is the second largest family in Brassicales with some 90 species of herbs found in Central and South America followed by Resedaceae, which encompasses 70 species of herbs and shrubs, some of which are used as dye, perfume oil and cultivated as ornamental. Caricaceae (papaya family) consists of 34 species of small trees found mainly in Central and South America (one genus found in Africa) of which papaya is the best-known member. Limnanthaceae (poached egg plant) comprises 10 species of annual herbs divided into two genera found in seasonally wet areas across North America and widely used as ornamentals. The timetree comprises 10 of the 15 families assigned to Brassicales, and relationships among these families are representative of those found in more inclusive analyses (*10, 16*). Based on the timetree, Brassicales split from its closest relatives 90–85 Ma ago, an estimate in agreement with the fossil record of the group for which the oldest remains are from the Turonian (*17*). The pair Brassicaceae–Resedaceae, representing a large portion of the species in the Order Brassicales, diverged relatively recently, 42–33 Ma ago, a somewhat young age for such a species-rich group, suggesting a recent and rapid diversification.

Malvaceae (also sometimes called the core Malvales) is beyond doubt the largest of the 10 families currently placed in Malvales. It comprises about 2330 species of trees, shrubs, and herbs, cosmopolitan in distribution, and with many economically important representatives such as cotton (*Gossypium*), cola (*Cola*), chocolate (*Theobroma*), and also several members widely used as ornamentals (e.g., *Tilia*, *Hibiscus*). Thymelaeaceae is the second largest family in Malvales with about 800 species of shrubs and trees, but also lianas and herbs, of cosmopolitan distribution with greater numbers found in Africa and Australia. Dipterocarpaceae contains about 500 species of mostly large trees, often the dominant component of lowland tropical forests, especially in Southeast Asia. Many species are used as timber and also as source of oleoresins and as an alternative to cocoa butter (*14, 15*). Relationships within Malvales have been extensively investigated (*18–20*), and one of the most important results of these analyses is the expansion of Malvaceae to include several other families (Bombacaceae, Sterculiaceae, Tiliaceae; *20*). More recently, the placement of Cytinaceae, a family comprising 10 species of root parasites, which has been shown previously to be closely related to Malvales, was identified as the closest relative of Muntingiaceae (*21*). Based on the timetree, Malvales started to diverge at the end of the Cretaceous, an estimate consistent with the fossil record (*17*). The diversification of the expanded Family Malvaceae started 41–34 Ma ago following their split from their closest relatives, Bixaceae, between 60 and 54 Ma. The close relationship between Bixaceae and Malvaceae is not always recovered in other analyses; this estimate should therefore be viewed with caution.

Unlike Malvales and Brassicales, which are characterized by the presence of one large family and several smaller ones, Sapindales have several large families including Sapindaceae (2215 species), Rutaceae (930 species), Anacardiaceae (600 species), Burseraceae (500 species), and Meliaceae (550 species). The other four families, range in size from 5 to 115 species. Sapindaceae is the largest and most diverse family of the order. They comprise several well-known and economically important members such as maple (*Acer*), litchi (*Litchi*), horse chestnut (*Aesculus*), and *Sapindus,* used in the manufacture of soap. Representatives of the family are mainly trees and woody climbers found in several parts of the world, but concentrated in the tropics. Rutaceae is possibly the most economically important family of the order as they comprise the genus *Citrus* (e.g., lemon, orange, and grapefruit) and several species that are sources of essential oils (e.g., *Agathosma*). The family consists of trees, shrubs, climbers, and herbs found in the tropics, especially in the Southern Hemisphere (*14, 15*). Members of Anacardiaceae are shrubs and trees found mostly in the tropical areas of the world, but also in temperate regions. The family comprises many species with edible fruits such as mango (*Mangifera*), cashew (*Anacardium*), pistachio (*Pistacia*), and pink peppercorn (*Schinus*), and is also used as ornamentals (e.g., sumac) (*14*). The economic importance of Family Meliaceae resides in the fact that several of its representatives are valued timber trees, among which the most well known are mahoganies (*Swietenia* and *Khaya*). The family, pantropical in distribution, also comprises species of medicinal value and with edible fruits. Although most recent molecular studies strongly support Sapindales, the morphological characters defining this group are not obvious (*13*). Two main groups of families in Sapindales are consistently recovered, generally with strong support, one comprising Meliaceae, Rutaceae, and Simaroubaceae and the other Anacardiaceae and Burseraceae (*3, 7, 9, 22*). The relationships between these two groups in Sapindales vary between analyses (*3, 7, 9, 22, 23*). Nitrariaceae was found as the closest relative to Anacardiaceae and Burseraceae (*11*), Kirkiaceae as the closest relative to the remainder of the order (*22*), to Sapindaceae alone (*11*) or to Anacardiaceae + Burseraceae (*23*), and when included, Biebersteiniaceae was the earliest diverging lineage in Sapindales (*11, 23*). Aceraceae (maples) and Hippocastanaceae (horse chestnuts) were included in Sapindaceae based on both morphological and molecular investigations (*22, 24, 25*). Based on the timetree, Sapindales started to diverge in the early Paleocene

(62–57 Ma), an estimate concordant with fossil remains (the oldest are from the Maastrichtian–Paleocene boundary). Muellner *et al.* (*23*) obtained much older estimates for the first split in Sapindales, between 132.6 and 90.5 Ma, depending on the method used. All major families were present by the beginning of the Late Eocene (44–40 Ma) according to the timetree, while Muellner *et al.* place the origin of most families in the order in the Cretaceous and early Tertiary (*23*).

Tapisciaceae is a small family of only two genera of shrubs or small trees. *Tapiscia* with a single species is restricted to China whereas the four species *Huertea* are found in Central and South America (*14*). Tapisciaceae alone is most commonly placed as the closest relative to Order Brassicales (*3, 4, 11*), but also as the closest relative to the remainder of Eurosid II (*9*). A more recent study places it adjacent to Dipentodontaceae, with strong support, and both are found in a polytomy with Gerrardinaceae, Brassicales, and Malvales (*5*). Dipentodontaceae comprises a single species of small trees with a distribution restricted to south-central Asia and together with Tapisciaceae form the order Huerteales. Only Tapisciaceae is represented in the timetree. It diverged from the rest of Eurosid II 95–88 Ma (*12*), but its position is uncertain, and Dipentodontaceae is not represented in the timetree; thus, this estimate should be viewed with care.

The two species of *Gerrardina* are the only representatives of the newly described Family Gerrardinaceae (*5*). Based on various characters of the leaves, floral disk, and stamens, it was initially placed in Family Flacourtiaceae (now Achariaceae or Salicaceae) in Order Malpighiales, but subsequent molecular sequence analyses showed that it was better placed in Eurosid II, although the relationships of this small family with the other more species-rich members of this group are unclear (*5*). Gerrardinaceae was not included in the timetree analysis (*12*).

The second installment of the Angiosperm Phylogeny Group (*26*) placed Crossosomatales in the rosids, but their exact position within this group is not established. APGII recognized three families as members of this order, but four others were recently integrated (*13*). Crossosomataceae is a small family of nine species of shrubs endemic to North America. The ~15 species of shrubs and trees forming family Stachyuraceae are found mainly in China and Japan with some species cultivated as ornamentals. The largest family in Crossosomatales, Staphyleaceae, comprises about 46 species of shrubs and trees mostly distributed in the temperate regions of the Northern Hemisphere, but also in the northern parts of South America as well as Southeast Asia (*14*). The inclusion of four other families found to be part of Crossosomatales in various studies is not as well supported as the group formed by the three families mentioned earlier (*13*). The only species of Family Strasburgeriaceae is a tree endemic to New Caledonia whereas the single species of Geissolomataceae is confined to a few mountain slopes in the Cape region of South Africa. Aphloiaceae also comprises only one species of shrub or trees found in East Africa and Madagascar, the leaves of which are used as tea in the Mascarenes (*14, 27*). Likewise, Ixerbaceae consists of only one species, an evergreen tree endemic to New Zealand (*14*). An additional family, Guamatelaceae, was recently described to accommodate the genus *Guamatela*, a genus of one species found in Mexico and Central America once thought to be related to Rosaceae, but now found nested in Crossosomatales (*28*).

In most phylogenetic analyses based on DNA sequence data, Crossosomatales is found to be either the closest relative of Geraniales (*7*) or the closest relative of Eurosid II as a whole (*3, 9*). All families now consigned to Crossosomatales had an eventful past in terms of their systematics (*13, 14, 29*). Staphyleaceae, Stachyuraceae, and Crossosomataceae consistently form a well-supported group in which the former is the first diverging lineage (*3, 9, 11*). Aphloiaceae and Ixerbaceae are together the closest relatives of the rest of Crossosomatales in several studies, although this relationship is poorly supported (*3, 9, 11*). The only study including all eight families divided the order into two groups. In the first one, Staphyleaceae are the earliest lineage followed by the newly described Guamatelaceae and the pair Crossosomataceae + Stachyuraceae; these relationships are all well supported (*28*). In the second group, Geissolomataceae is the first diverging lineage followed by Aphloiaceae and the pair Strasburgeriaceae + Ixerbaceae; only the last are well supported (*28, 29*). These relationships are in general supported by floral characters except that based on these, the position of Geissolomataceae and Aphloiaceae would be inverted (*30*). Little can be said about the divergence times in this order since the fossil record is poor or absent, and only five of the eight families are included in the timetree. Nevertheless, Crossosomatales and related families would have started to diverge relatively early, 95–91 Ma ago (*12*), although these estimates are much older than those proposed by a subsequent study (47–40 Ma) (*31*).

The Order Geraniales comprises four families, of which Geraniaceae are by far the largest. Geraniaceae is widely distributed around the world with a concentration in temperate regions. Many of the ~800 species of herbs and shrubs are cultivated as ornamentals, such as genera *Pelargonium* and *Geranium* (*14*). The other three families are much smaller and less well known. Melianthaceae (including Greyiaceae and Francoaceae) comprises 18 species, all of them found on the African continent south of the Sahara, except for one species found in Chile and formerly assigned to Francoaceae; all 18 species of Vivianiaceae, mostly shrubs or herbs, are restricted to South America; Ledocarpaceae contains 12 species of shrubs all found in South America, mostly in the Andes. Apart from Geraniaceae and Vivianaceae, which were previously thought to be closely related, Geraniales, as defined by DNA-based studies, had never been proposed before. Furthermore, no known morphological character supports this assemblage (*13*). Geraniales did not always receive strong support (*7, 11*), although it is retrieved as a monophyletic group in most studies sometimes with strong or moderate support (*3, 7, 9, 11*). Relationships between Geraniaceae, Melianthaceae, and Vivianaceae are unclear; Geraniaceae is the closest relative to the pair Melianthaceae–Vivianaceae (all well supported) (*3*) or Melianthaceae are closely related to Vivianaceae and Geraniaceae (*9*). When Ledocarpaceae is included, it is found to be the closest relative of Vivianaceae, together closely related to Melianthaceae (*11, 13*). In our timetree, Melianthaceae is closely related to the pair Geraniaceae–Vivianaceae; Ledocarpaceae was not included (*12*). The first diversification in the order took place in the Late Cretaceous, 94–80 Ma (*12*), and Geraniaceae and Vivianaceae diverged 85–71 Ma. These estimates indicate that these families became established a relatively long time ago.

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