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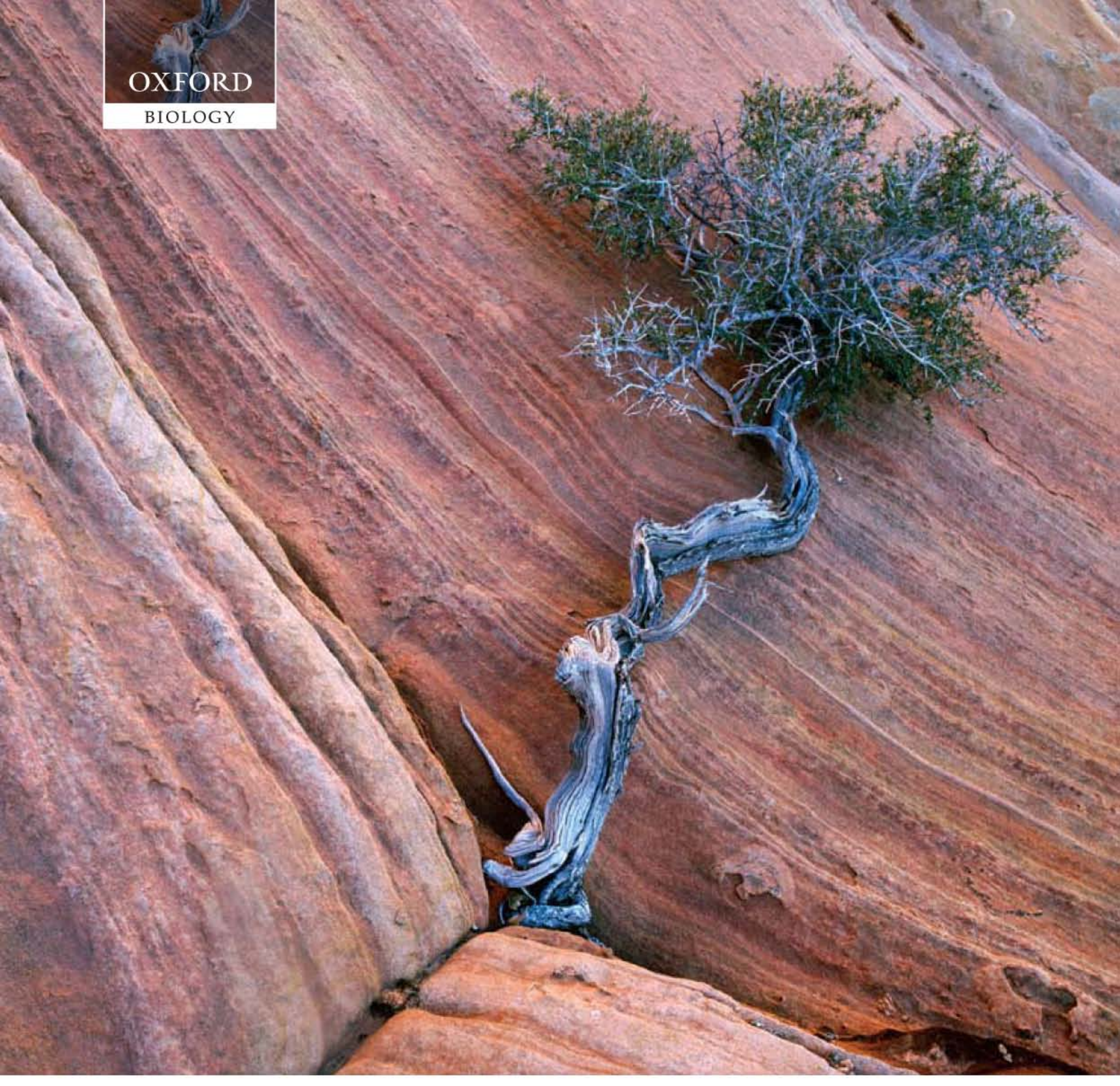

the TIMETREE of LIFE

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Eurosid I

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Abstract

About one-quarter of all flowering plant (angiosperm) species are assigned to rosids, which contains many economically important families such as the rose (Rosaceae), bean (Fabaceae), and cabbage (Brassicaceae) families. Here we consider Eurosid I, one of the two main assemblages of rosids. Eurosid I consists of seven orders that are divided into two informal groups: COM clade (Orders Celastrales, Oxalidales, and Malpighiales) and the nitrogen-fixing clade (Orders Rosales, Fabales, Fagales, and Cucurbitales). Eurosid I diverged from its closest relatives 121–111 million years ago (Ma) and rapidly started to diversify 117–108 Ma.

Rosids represent another example of a group vastly reorganized following the influx of DNA sequence data in phylogenetic analyses and angiosperm classification. To a group known as Subclass Rosidae or Superorder Rosanae in earlier classifications (*1–3*) were added some former members of Magnoliidae, Dilleniidae, and Hamamelidae. Additionally, some families previously thought to be of rosid affinity were found to be better placed within asterids (*4*). Although strong support is found for the rosid group as a whole (*5, 6*), deeper relationships within rosids remain unclear despite considerable additional data and efforts. In addition, morphological characters uniting rosids have yet to be identified (*4*). The ca. 68,000 species assigned to rosids, which represent about a quarter of all angiosperm species and 39% of all eudicots (*7*), are divided into seven orders and 124 families (*8*). The great majority of the species are assigned to two main groups, Eurosid I and Eurosid II, also known as fabids and malvids, respectively. Species not included in the two eurosid groups are found in three orders (Myrtales, Geraniales, and Crossosomatales) and six families (Aphloiaceae, Geissolomataceae, Ixerbaceae, Picramniaceae, Strasburgeriaceae, and Vitaceae) of uncertain placement within rosids. Here, relationships and divergence times of the first group, Eurosid I, are reviewed. Myrtales will be discussed with Eurosid I because it has been placed in some studies as the closest relative to this group (*5*), as well as in the timetree considered here based on the study by Wikström *et al.* (*9*).

Vitaceae is a cosmopolitan family with the greatest diversity in the tropics. It comprises 12–14 genera and about 800 species of mostly climbers and shrubs among which the most well-known member is the grapevine (*Vitis vinifera*) (*10*). This family, placed in rosids by the Angiosperm Phylogeny Group (*8*) but not assigned to any order, has been shown by several studies to be the closest relative of the remainder of rosids, but generally this placement is not strongly supported (*5, 6, 11*) and sometime contradicted (*12*). The position of Vitaceae as the closest relative of the rest of rosids was supported by an analysis based on 61 coding region sequences and 29 taxa, which was performed following the sequencing of the complete plastid genome of *V. vinifera* (*13*). The addition of several taxa in such genome-scale analyses further confirmed the position of Vitaceae as the closest relative to the rest of the rosids (*14–16*).

Eurosid I comprises seven orders that can be divided into two informal groups, the first one comprising the Orders Celastrales (three families), Oxalidales (six

Fig. 1 *Oxalis namaquana* (Oxalidaceae), growing in the Kamiesberg, South Africa. Credit: F. Forest.

F. Forest and M. W. Chase. Eurosid I. Pp. 188–196 in *The Timetree of Life*, S. B. Hedges and S. Kumar, Eds. (Oxford University Press, 2009).

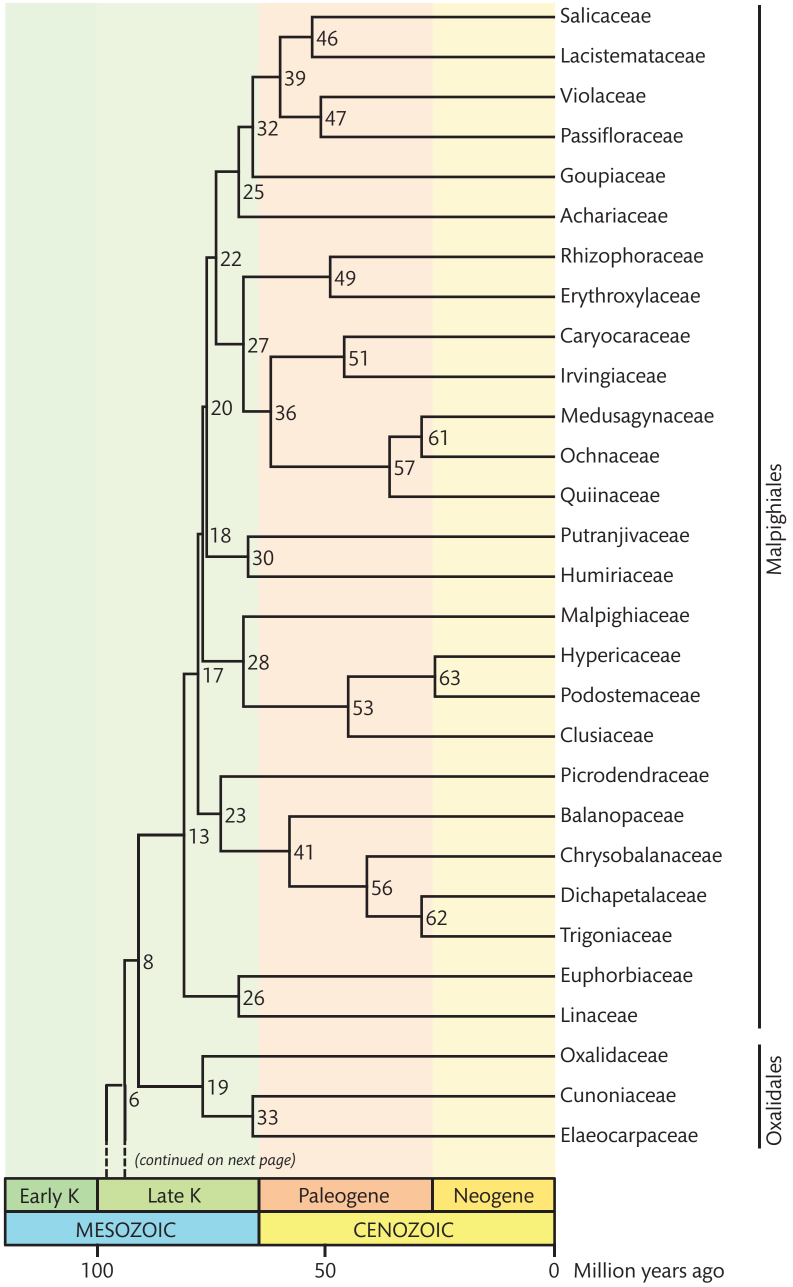

Fig. 2 *Continues*

families, Fig. 1), and the large order Malpighiales (28 families), and the second consisting of Orders Rosales (nine families), Fabales (four families), Fagales (seven families), and Cucurbitales (seven families), which is also referred to as the nitrogen-fixing clade (*17*). These two groups are generally only weakly supported (*5, 18–20*). However, high posterior probabilities from a three-gene study (*6*) and strong support from a four-gene analysis (*11*) were found for both assemblages. Both groups are discussed in more detail later.

Zygophyllaceae and Huaceae are also included in Eurosid I, but their exact placement in relation to the other members of this group is unclear. Huaceae is a small family of two genera of evergreen trees found in tropical Africa, some of which are used as condiments and medicine (*10*). Zygophyllaceae (creosote bush

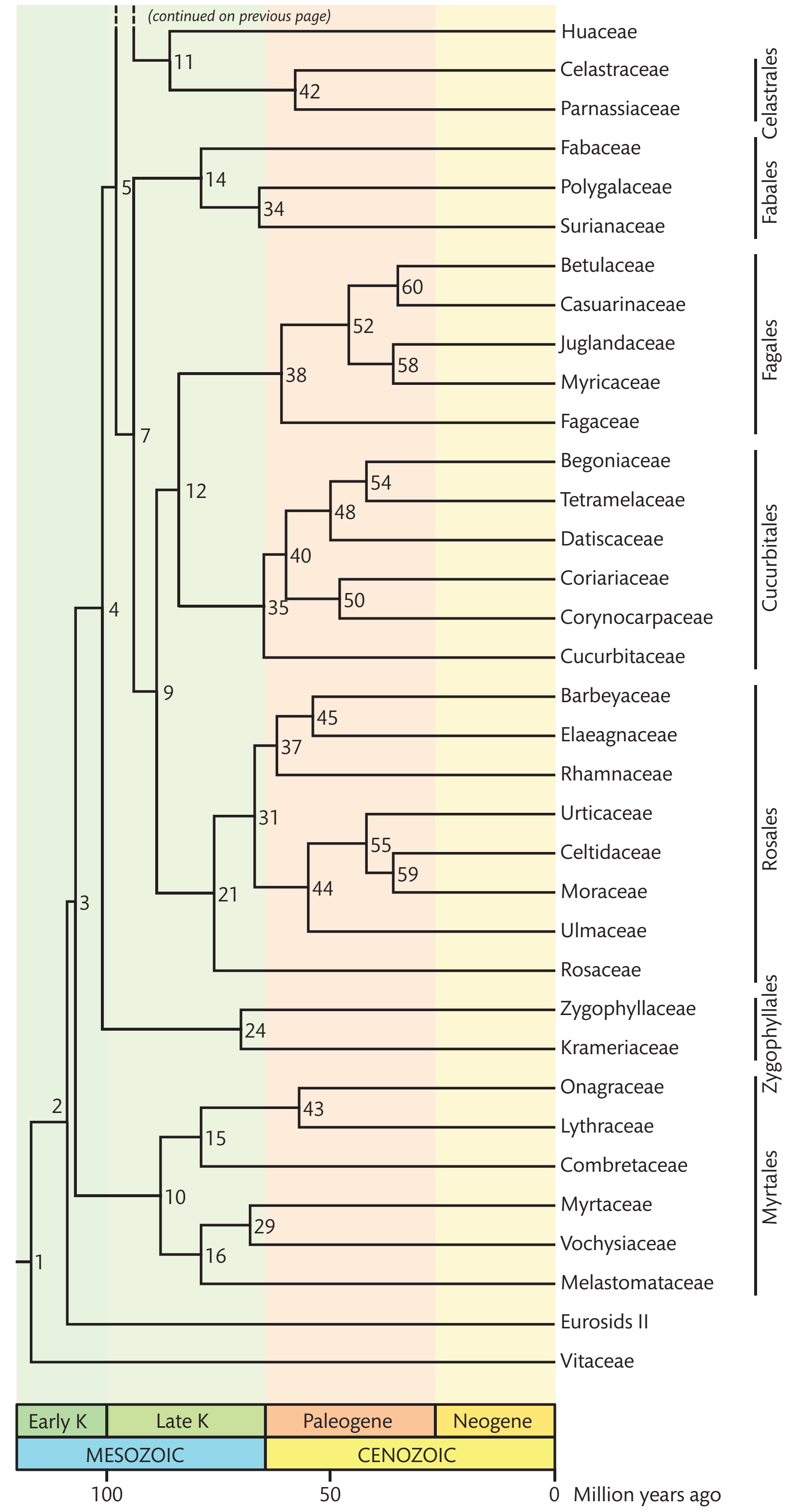

Fig. 2 A timetree of Eurosid I. Divergence times are shown in Table 1. *Abbreviation*: K (Cretaceous).

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

Timetree		Estimates			
Node	Time	Ref. (*9*)(a)		Ref. (*9*)(b)	Ref. (*9*)(c)
		Time	CI	Time	Time
1	117	117	121–113	115	108
2	109	109	113–105	106	100
3	107	107	110–104	104	100
4	101	101	104–98	99	95
5	98	98	101–95	96	94
6	94	94	97–91	93	89
7	94	94	96–92	90	89
8	91	91	94–88	89	88
9	89	89	91–87	88	88
10	88	88	92–84	82	78
11	86	86	89–83	87	85
12	84	84	–	84	84
13	81	81	84–78	77	77
14	79	79	82–76	78	74
15	79	79	83–75	78	75
16	79	79	84–74	77	74
17	78	78	81–75	74	76
18	77	77	80–74	72	75
19	77	77	80–74	76	72
20	76	76	79–73	70	73
21	76	76	79–73	76	76
22	74	74	77–71	69	72
23	73	73	76–70	71	72
24	70	70	74–66	69	64
25	69	69	72–66	65	68
26	69	69	72–66	71	71
27	68	68	71–65	67	70
28	68	68	71–65	66	69
29	68	68	73–63	68	67
30	67	67	71–63	65	68
31	67	67	70–64	65	67
32	66	66	69–63	63	66
33	66	66	70–62	65	64
34	66	66	69–63	68	67
35	65	65	67–63	66	66
36	62	62	65–59	65	67
37	62	62	65–59	62	64
38	61	61	65–57	60	61
39	60	60	63–57	60	63
40	60	60	63–57	62	64
41	58	58	61–55	57	59
42	58	58	61–55	62	58
43	57	57	61–53	67	63
44	55	55	59–51	56	57
45	54	54	58–50	55	58
46	53	53	56–50	55	57
47	51	51	54–48	55	56
48	50	50	53–47	54	57
49	49	49	53–45	53	54
50	48	48	51–45	49	52
51	46	46	49–43	58	60
52	46	46	50–42	47	47
53	45	45	48–42	54	54
54	42	42	45–39	49	51
55	42	42	45–39	48	49
56	41	41	44–38	49	50
57	36	36	40–32	39	38
58	36	36	40–32	37	38
59	36	36	39–33	43	46
60	35	35	38–32	35	36
61	29	29	32–26	36	35
62	29	29	32–26	40	40
63	26	26	28–24	40	36

Note: Node times in the timetree are based on branch lengths computed using (a) ACCTRAN optimization in maximum parsimony in ref. (*9*). Other estimates from ref. (*9*) are obtained using (b) DELTRAN optimization in maximum parsimony and (c) maximum likelihood method. Node 12 was used as calibration point in the study of Wikström *et al.* (*9*) and was assigned a fixed age of 84 Ma. Many nodes in the Eurosid I tree are weakly supported in ref. (*5*).

family) comprise about 300 species of herbs, shrubs, and trees found in most parts of the world. Some are cultivated for their fruits (*Balanites*, desert date), timber (*Guaiacum*, lignum-vitae, one of the strongest woods known), and medicines (*10*). Depending on the analysis, Huaceae is placed as the closest relative of Celastrales (*5, 19*), Malpighiales (*18*), or Oxalidales (*6, 21*) whereas Zygophyllaceae is the closest relative to the remainder of Eurosid I (*5*), to the nitrogen-fixing clade (*19*), to Fabales (*20*), or embedded in the nitrogen-fixing clade, closely related to Cucurbitales (*18*). None of these hypotheses is strongly supported except the placement of Huaceae as the closest relative to Oxalidales in one study (*21*).

Based on the timetree (Fig. 2), Vitaceae and rosids diverged from Saxifragales, their closest relative, 121–111 Ma and split rapidly after, 117–108 Ma, followed by the first diversification in the remainder of rosids 109–100 Ma. These estimates concord with the age obtained by another study for the first divergence in rosids, 108 Ma (*22*), and are broadly consistent with results obtained by Moore *et al.* (*15*) using plastid genome-scale data. The oldest remains of Vitaceae in the fossil record are from the Late Paleocene (57.9 Ma). The molecular estimate of 117–108 Ma mentioned earlier is for the split between Vitaceae and the rest of rosids, indicating a long period of time between this event and the first divergence within extant Vitaceae.

Nitrogen fixation in root nodules through a symbiotic relation with bacteria is found in only 10 families of angiosperms. Only two groups of bacteria are known to be part of this mutualism, the genus *Frankia* (Frankiaceae) and three genera from Family Rhizobiaceae (*4*). Species of these plant families with nodular nitrogen-fixing capabilities are found in all four orders forming the nitrogen-fixing group. The plant species associated with *Frankia*, an actinomycete, are also called actinorhizal, whereas those associated with members of Rhizobiaceae are sometimes called rhizobial.

Although monophyly (inclusive group) of the four orders of the nitrogen-fixing clade is strongly supported in most studies (e.g., *5, 6*), relationships between them remain unclear, with just about every possible topology uncovered (*5, 6, 11, 14, 18–20, 23*). Some studies even found Zygophyllaceae to be included in this group, either as the closest relative to Cucurbitales (*18*) or Fabales (*20*). Only one study based on complete plastid DNA sequence data, but with sparse sampling (32 species), has found strong support for relationships within this group, with Cucurbitales as the first diverging lineage followed by Fagales, and Rosales as the closest relative to Fabales (*14*). Similar results were found in two other plastid genome analyses in which Cucurbitales are the closest relatives to Rosales + Fabales (Fagales was not included in these studies) (*15, 16*). The timetree shown (Fig. 2) portrays different relationships within this group, with Fabales as the first diverging lineage followed by Rosales, and Cucurbitales as the closest relative to Fagales. Nevertheless, the unresolved deep relationships within the nitrogen-fixing group underline the putative rapid diversification of these lineages, which would have taken place between 88 and 94 Ma, based on the timetree.

The close relationship of these families led to the suggestion that the underlying genetic basis for nodular nitrogen-fixing ability appeared only once in angiosperms (*17*). Subsequent phylogenetic studies showed that the actinorhizal symbiosis would have evolved several times (*24*) and that the same seems to be the case for the rhizobial symbiosis in Fabaceae (*25*). The various morphological features of the hosts and modes of infection, among other features, support this multiple evolution scenario. Later, Soltis *et al.* (*4*) showed that the nitrogen-fixing symbiosis appeared at least six times (Elaeagnaceae, some members of Rhamnaceae, some members of Rosaceae, Fagales, Coriariaceae, Datiscaceae) with two subsequent losses of the *Frankia* type (Ticodendraceae and most Betulaceae). It is difficult to estimate from the timetree when these independent gains of nitrogen-fixing ability appeared in the evolutionary history of this group, but can be extrapolated to be at the earliest in the Paleocene or Early Eocene.

Fabales comprises four families, of which the largest, Fabaceae (or Leguminosae; bean family), is also the third largest family of angiosperms, comprising more than 19,000 species (*26*). Fabales also includes Polygalaceae (milkwort family), a family of about 1000 species of nearly cosmopolitan distribution, and two smaller families, Surianaceae (bay cedar family) of pantropical distribution and Quillajaceae (soap bark family) restricted to southern South America. Relationships between these four families are still unclear (*5, 18, 27*). Only Fabaceae have members with nitrogen fixation capabilities within Fabales, a symbiosis with species of Rhizobiaceae. The fossil record of Fabaceae is extensive (*28*), whereas it is relatively poor for Polygalaceae and practically nonexistent for the other families. The oldest fossil remains for the order are from Fabaceae, which indicate the order was present at least from the Early Paleocene (59.9 Ma; *29*). This estimate contrasts with the timetree in which the first diversification in Fabales took place some 74 to 79 Ma. Other studies found molecular estimates more in line with the fossil record (*27, 30*).

Fagales consists of seven relatively small families of shrubs and trees among which the largest is Fagaceae (oak family) with about 700 species (*31*). Many members of this order are dominant components of temperate and sometimes tropical montane forests such as species of *Nothofagus* (southern beech; Nothofagaceae) in the Southern Hemisphere and species of *Betula* (birch), *Alnus* (alder), *Carpinus* (hornebeam), and *Corylus* (hazel) from Betulaceae, *Fagus* (beech) and *Quercus* (oak) from Fagaceae, and *Juglans* (walnut) and *Carya* (hickory) from Juglandaceae in the Northern Hemisphere. In Fagales, species of alder (*Alnus*) of Family Betulaceae, all genera of Casuarinaceae and most species of Myricaceae have nodular nitrogen-fixing symbioses with the bacteria *Frankia*. Relationships within this order are in general well supported (*32, 33*). Nothofagaceae (not included in the timetree) is the first diverging family followed by Fagaceae. The rest of the order is divided into two groups: one comprising Juglandaceae and Myricaceae and the other consisting of Casuarinaceae, Ticodendraceae (not included in the timetree), and Betulaceae (*32, 33*). Fagales boast what is possibly one of the most extensive fossil records among angiosperms, dating back to the middle Cenomanian (96.2 Ma; *29*). One of the most important features of their fossil record is pollen remains from the Normapolles complex, important and diverse components of many late Cretaceous and early Tertiary floras, in which all members have affinities with Fagales (discussed in *34*).

Of the estimated 1600 species found in Cucurbitales, more than 95% are found in only two of the seven families of the Order: Begoniaceae (begonia family; 920 species) and Cucurbitaceae (cucumber family; 640 species). The grouping of these seven families is the result of DNA-based phylogenetic studies, and no obvious morphological character seems to be common to all members of this order (*4*). Relationships between families are also not well defined. In the timetree, Cucurbitaceae is the earliest diverging lineage followed by Coriariaceae + Corynocarpaceae and the rest of the order; none of these relationships is supported (*5, 9*). The positions of Cucurbitaceae and Coriariaceae + Corynocarpaceae are interchanged in other studies (*6, 19*). The first diversification within Cucurbitales took place at the onset of the Paleocene (65–66 Ma), an estimate in line with inferences made from the fossil record; the earliest remains for this group are from the early Paleocene (59.9 Ma; *29*). Unclear relationships within the order prevent any reliable assumptions regarding the divergence times between families in this timetree.

As in Cucurbitales, species diversity in Rosales is concentrated in a few families. More than 90% of the 7725 species found in the order are in four families, Urticaceae (nettle family; 2625 species), Rosaceae (rose family; 2520 species), Moraceae (fig family; 1100 species), and Rhamnaceae (buckthorn family; 925 species). Although not as species-rich, some of the other five families in the order have nonetheless important economic value such as Cannabaceae (hop family), Elaeagnaceae (oleaster family), and Ulmaceae (elm family). Families currently assigned to Rosales consistently form a distinct and generally well-supported group (*5, 6, 11, 18–20*). In these analyses, Rosaceae is always the earliest diverging group, whereas the other families form two groups, Rhamnaceae + Barbeyaceae + Elaeagnaceae + Dirachmaceae and Ulmaceae + Urticaceae + Moraceae + Cannabaceae (also referred to as the "urticalean rosids"; *23*); only the latter is well supported in most analyses (*5, 6, 19, 23*). Based on the timetree, the diversification of Rosales started 76 Ma. The molecular estimate for the first divergence in the urticalean rosids (57–55 Ma) is about 10 Ma years younger than the estimate inferred from the fossil record of the group, in the Maastrichtian, 68 Ma (*29*). The oldest relics assigned to Family Rosaceae are from the Eocene, 44 Ma (*29*), which corresponds to the estimate from the timetree (46–47 Ma, not shown; *9*).

A group of three orders—Celastrales, Oxalidales, and Malpighiales—sometimes referred to as the "COM clade" generally has been only weakly supported in earlier analyses (*5, 18–20*), although more recent studies give them stronger support (*6, 11*). Likewise, relationships between Celastrales, Oxalidales, and Malpighiales were unclear in earlier studies (*5, 18–20*), but more recent phylogenetic investigations indicate that Malpighiales are more closely related to Celastrales with either weak (*6*) or strong support (*21*).

Celastrales comprise three families of which Celastraceae (spindle tree family) is by far the largest with about 1200 species of shrubs, trees, and climbers found mainly in tropical and subtropical regions, with also a few species growing in temperate areas. Members of Celastraceae have many uses such as medicines, insecticides, and edible fruits and seeds (*10*). Parnassiaceae consist of about 70 species grouped in two genera of perennial (*Parnassia*) and annual (*Lepuropetalon*; the smallest terrestrial angiosperm *4*) herbs found predominantly in China, but also in other parts of the Northern Hemisphere (*10*). The third family, Lepidobotryaceae, comprises only two monotypic genera; one found in tropical Africa (*Lepidobotrys*) and the other in tropical South America (*Ruptiliocarpon*) (*10*). The latest study of Celastrales based on seven DNA regions shows that Lepidobotryaceae is the earliest diverging lineage in the order and that Parnassiaceae and Celastraceae are each other's closest relative, although Celastraceae is not resolved as an inclusive group (*21*). The close relationship of Parnassiaceae and Celastraceae is supported by features of the floral structure (*35*). Celastraceae and Parnassiaceae diverged in the late Paleocene (62–58 Ma), an estimate much older than the one inferred from Oligocene pollen remains, 28.8 Ma (*29*). Lepidobotryaceae is not included in the timetree.

The six families forming Oxalidales were not traditionally placed together, but rather scattered within various rosid orders until molecular studies first revealed their close relationships. The largest family of the Order Oxalidaceae (starfruit family), which comprises about 900 species of trees, shrubs, climbers, and herbs widespread across most of the globe (*10*), forms the earliest diverging lineage in the order (*5, 6, 11, 19*), sometimes together with Connaraceae—the zebrawood family (*18, 21*)—a family of 190 species of pantropical trees, shrubs, and climbers (*10*). Brunelliaceae, comprising 60 species of evergreen trees from the Neotropics, is the closest relative of the remainder of the order, which consists of Eleaocarpaceae (600 species of mostly trees and shrubs) and Cephalotaceae (one carnivorous species from Australia) + Cunoniaceae (300 species of Southern Hemisphere evergreen trees and shrubs) (*18*). Only three of the six families are included in the timetree: Oxalidaceae is the closest relative of Elaeocarpaceae + Cunoniaceae, relationships supported by most analyses including only representatives of these three families (*5, 6, 19*). Oxalidales split from their closest relative, Malpighiales, in the timetree, 91–88 Ma, followed by the divergence of Oxalidaceae from Elaeocarpaceae + Cunoniaceae 77–72 Ma. Elaeocarpaceae and Cunoniaceae diverged in the early Paleocene, 66–64 Ma, an estimate somewhat in line with inferences made from the fossil record of Cunoniaceae (*29*).

Malpighiales is a large and diverse order and comprises several species-rich families as well as many smaller ones. The largest family is undoubtedly Euphorbiaceae (spurge family), with about 6300 species that are diverse morphologically, cosmopolitan in distribution, and of great economic importance as crops (e.g., *Manihot esculenta*; cassava, tapioca; natural rubber, *Hevea brasiliensis*), medicines, and ornamentals (*10*). Other important families include Clusiaceae (mangosteen family; economically important for their fruits, timber, and drugs among others), the pantropical Chrysobalanaceae (cocoa plum family; about 750 species of trees and shrubs used as timber, seed oil, and fruits), Ochnaceae (tree, shrubs, and herbs, used as ornamentals as well as medicines and timber), Passifloraceae (passion flower family; 700 species of trees, shrubs, herbs, and climbers used as ornamentals and cultivated for their edible fruits), and Phyllanthaceae (2000 species, cosmopolitan, mainly in the tropics, cultivated for timber and their edible fruits). Although many family groups within the Malpighiales are well supported (e.g., Clusiaceae, Hypericaceae, Podostemaceae), relationships between these groups remain unresolved (*5, 6, 18, 19, 36, 37*). The poor resolution of early diverging lineages in molecular phylogenetic analyses is thought to be the result of an explosive radiation in the early history of the order, which would have taken place 112–94 Ma, in the mid-Cretaceous (*36*). The timetree also shows that the great majority of the first divergences in the order took place at the end of the Cretaceous, ~80–66 Ma (*9*), estimates supported by the fossil record (*29*). Because many malpighiales are found in the understorey of tropical rain forests, these age estimates for the early diverging lineages of this order have been taken as support for the origin of tropical rain forests before the end of the Cretaceous (*36*).

The exact position of Myrtales within rosids remains unclear. Although not formerly included in Eurosid I, they are treated here because they are shown to be the closest relatives to this group in the timetree of Wikström *et al.* (*9*). Molecular phylogenetic analyses have placed them in various positions: as the closest relatives to all rosids except Vitaceae (*6*); as the closest relative to all rosids except Geraniales and Vitaceae (*11*); as the closest relative to Eurosid II (*14, 18, 19*); and unresolved in Eurosid II (*15, 16, 20*). Because none of these relationships was strongly supported, additional data will be necessary to determine with certainty the position of Myrtales within rosids.

Based on the classification of the Angiosperm Phylogeny Group (*8*), Myrtales comprise 13 families, but two of these, Heteropyxidaceae and Psiloxylaceae, have been since included in Myrtaceae (*38*). The most important families in terms of numbers of species are also those with the most important economic value. Myrtaceae (eucalyptus family) is by far the largest in the order with the 5800 species assigned to this family accounting for almost three quarters of all the species found in Myrtales. Myrtaceae consist of trees and shrubs of pantropical distribution with one genus found in the Mediterranean region (*Myrtus*, myrtle). They are used as timber (*Eucalyptus*) and cultivated as ornamentals (e.g., *Callistemon*, bottlebrush), fruits (e.g., *Psidium*; guava), and spices (e.g., *Syzygium*, clove) (*10*). The three largest families after Myrtaceae comprise more than 1700 species whereas the other seven families in the order contain only 39 species. Onagraceae (evening primrose family) is a cosmopolitan family of 656 species, mostly herbs, used as ornamentals and medicines. Lythraceae (pomegranate family) comprises 600 species of trees, shrubs, and aquatics, widespread but mainly found in the tropics and cultivated as ornamentals and timber and for their fruits. The ~500 species of trees, shrubs, and lianas that form Combretaceae are found mainly in the tropics (*10*).

Myrtales has been the subject of extensive DNA-based phylogenetic analyses (*39–41*). Combretaceae is either found as the closest relative to Onagraceae + Lythraceae (*40*) or as the first diverging lineage in the order (*39*); Combretaceae was not included in the study of Rutschmann *et al.* (*41*). The rest of the order is divided into two groups: Myrtaceae + Vochysiaceae and Melastomataceae as the closest relative to a group formed by the other five families, both with strong support (*39–41*). Within the five-family group, Crypteroniaceae is the earliest diverging lineage followed by Azateaceae, Penaeaceae, and Oliniaceae + Rhychocalycaceae (*39, 41*). Conti *et al.* (*40*) obtained slightly different results for this group in which Rhynchocalyceae are the closest relative to Oliniaceae + Penaeaceae.

The timetree presented here indicates that the first divergence in Myrtales took place 88–78 Ma, estimates that concord with inferences made from the fossil record of the group, for which the earliest remains are from the early Coniacian, 88.2 Ma; (*29*), whereas two other studies using molecular dating placed the first divergence in the order much earlier, >110 Ma (*39, 41*). By the end of the Paleocene, most families in the order were differentiated, although many did not start to diversify until later (*9, 39, 41*). The disjunct distribution of the large family Myrtaceae in the Southern Hemisphere has been explained by a combination of the breakup of Gondwana in the early Cretaceous and subsequent long-distance dispersals between South America and Australasia and Africa and the Mediterranean basin (*39, 42*). The diversification of this family in the late Cretaceous supports this proposition (*39, 41*). On the other hand, because Vochysiaceae is a younger family, the presence of some of its members in Africa has been hypothesized to be the result of long-distance dispersal from South America, not the result of the breakup of Gondwana (*39*).

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