

RESEARCH ANALYSIS

Evolutionary considerations of the presence of both morphophysiological and physiological seed dormancy in the highly advanced euasterids II order *Dipsacales*

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Abstract

Although the underdeveloped embryo, and thus morphological (MD) or morphophysiological (MPD) seed dormancy, is basal in angiosperms, it also occurs in advanced groups. A synthesis of the literature, combining phylogeny and the kind of seed dormancy in the highly evolutionarily advanced order *Dipsacales*, shows that MPD (or MD) occurs throughout all clades except the most advanced one, *Valerina*. Seeds of taxa in the *Valerina* clade have fully developed embryos and physiological dormancy (PD) or are non-dormant (ND); thus, PD and ND are derived conditions in *Dipsacales*. Assuming that types of seed dormancy have not changed since the Early Tertiary, the fossil record suggests that MPD (or MD) was present in extant genera of *Dipsacales* by the Palaeocene, but PD (or ND) not until the Miocene. Molecular dating indicates that the ages of dipsacalean lineages with MPD and PD are older than those indicated by the fossil evidence.

Keywords: *Dipsacales*, evolution of seed dormancy, fossil fruits and seeds, morphophysiological dormancy, phylogeny, physiological dormancy, underdeveloped embryo

Introduction

In both gymnosperms and angiosperms, it is agreed generally that the underdeveloped embryo in mature seeds, and thus morphological (MD) or morphophysiological (MPD) seed dormancy (*sensu* Baskin and Baskin, 2004), is the basal (ancestral) condition, whereas seeds with a fully developed embryo and physiological dormancy (PD) or non-dormancy (ND) are the evolutionarily advanced condition (Martin, 1946; Grushvitsky, 1967; Baskin and Baskin, 1998; Nikolaeva, 1999; Forbis *et al.*, 2002). However, MD and MPD are not restricted to primitive groups of seed plants and, in fact, occur within advanced clades of both gymnosperms (i.e. non-*Pinaceae* conifers, *sensu* Chaw *et al.*, 2000) and angiosperms [i.e. euasterids, *sensu* Angiosperm Phylogeny Group (APG) II, 2003] (Baskin and Baskin, 1998, 2003). Thus, although mature seeds of many primitive families of angiosperms have underdeveloped embryos, and seeds of many advanced families have fully developed embryos, the underdeveloped embryo does occur in quite a few advanced taxa (Baskin and Baskin, 1998; Forbis *et al.*, 2002).

The *Dipsacales* is an example of a highly advanced order of angiosperms that contains taxa whose seeds have MPD (or MD), as well as those whose seeds have PD (or are ND) (Baskin and Baskin, 1998; Hidayati, 2000; see below). Further, the phylogeny of this group has been well studied, it has a reasonably good fossil record and information is available on seed dormancy of representative taxa

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throughout this monophyletic clade, i.e. from the most primitive to the most advanced members (see below). The purpose of this study was to test the hypothesis that, within the *Dipsacales*, seeds of less-advanced taxa have MPD (or MD), whereas seeds of more-advanced taxa have PD or are ND. Further, if this is the case, then taxa of nearest living relatives whose seeds have MPD (or MD) should appear in the fossil record before taxa of nearest living relatives whose seeds have PD (or ND). To determine if there is support for this conjecture, a literature survey was conducted of the fossil record of *Dipsacales* in the Northern Hemisphere, where the group originated and diversified (see below).

Taxonomy and phylogeny of *Dipsacales*

The Angiosperm Phylogeny Group (APG, 1998) placed *Dipsacales*, along with *Aquifoliales*, *Apiales* and *Asterales*, in the evolutionarily advanced euasterids II clade. The following six families were included in *Dipsacales*: *Caprifoliaceae*, *Diervillaceae*, *Dipsacaceae*, *Linnaeaceae*, *Morinaceae* and *Valerianaceae*. However, Judd *et al.* (1994) and Donoghue *et al.* (2001a, 2003) recognized only two major lineages in this order, namely *Adoxaceae* and *Caprifoliaceae*. *Adoxaceae* included *Adoxa* and relatives, *Sambucus* and *Viburnum*, and *Caprifoliaceae* included *Diervilleae*, *Caprifolieae*, *Heptacodium*, *Morinaceae*, *Linnaeae*, *Dipsacaceae*, *Triplostegia* and *Valerianaceae*. The traditional families *Dipsacaceae* and *Valerianaceae* along with *Morina* (*Morinaceae*) and *Triplostegia* (*Triplostegiaceae sensu* Takhtajan, 1997) were included in the most advanced clade, *Valerina*. The most evolutionarily advanced member of this clade is *Valerianaceae* (Fig. 1). APG II (2003) recognized this broader circumscription, but they also stated that the families *Diervillaceae*, *Dipsacaceae*, *Linnaeaceae*, *Morinaceae* and *Valerianaceae* '... are acceptable monophyletic alternatives...'. Although macrofossil evidence for *Dipsacales* from the Cretaceous is equivocal, molecular data 'strongly imply' that this group had originated by the mid-Cretaceous, and the *Adoxaceae* and *Caprifoliaceae* (its two major lineages) had diverged by the beginning of the Tertiary (Bremer *et al.*, 2004; Bell and Donoghue, 2005) (Fig. 1).

Seed dormancy in *Dipsacales*

We have added information available to us on seed dormancy class (*sensu* Baskin and Baskin, 2004) in *Dipsacales* to the phylogenetic diagram in Fig. 1. The six genera studied by Hidayati and co-workers, i.e. *Lonicera* (Hidayati *et al.*, 2000a), *Sambucus* (Hidayati *et al.*, 2000b; Hidayati and Walck, unpublished),

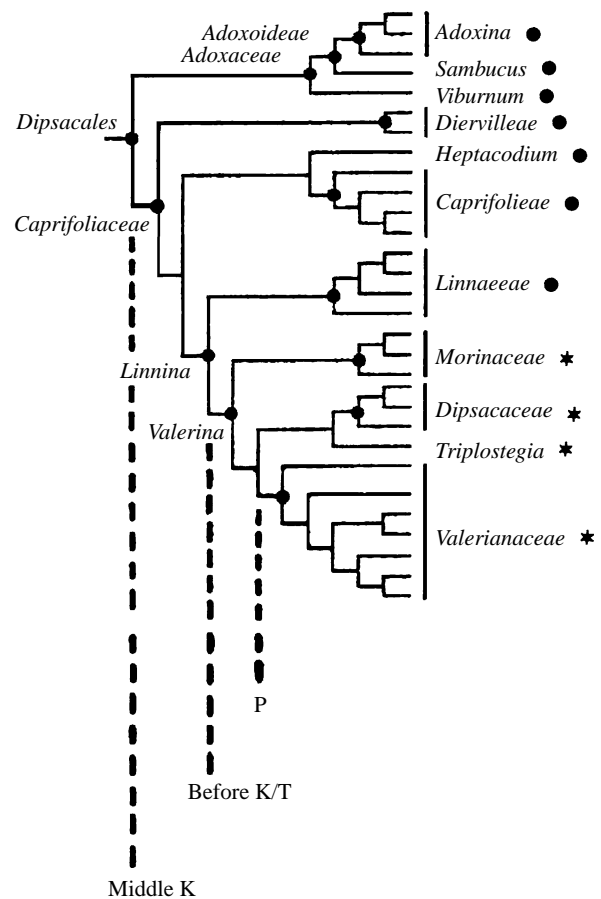


Figure 1. Phylogeny of *Dipsacales* showing the evolutionary position of morphophysiological seed dormancy (dot) and of physiological dormancy (star). K, Cretaceous; K/T, Cretaceous/Tertiary boundary; P, Palaeocene. [Phylogenetic diagram (reproduced with permission from the *American Journal of Botany*) and divergence times are from Bell and Donoghue, 2005].

Diervilla (Hidayati *et al.*, 2000c), *Symphoricarpos* (Hidayati, 2000; Hidayati *et al.*, 2001; see also Flemion, 1934; Flemion and Parker, 1942; Pelton, 1953), *Viburnum* (Hidayati *et al.*, 2005; see also Giersbach, 1937; Knowles and Zalik, 1958) and *Triosteum* (Hidayati *et al.*, unpublished data; see also Martin, 1946), have underdeveloped embryos and thus MPD (or MD, see below). In *Adoxa*, *Weigela* and *Linnaea*, the embryo is underdeveloped and physiologically dormant, and thus the seeds have MPD (Sprague, 1927; McLean, 1967; Hara, 1983; Nikolaeva *et al.*, 1985; Nikolaeva, 1989; Watson and Dallwitz, 1992 onwards; Hidayati, 2000). Embryos of *Heptacodium* (Bian *et al.*, 2004; Baskin *et al.*, unpublished) and *Kolkwitzia* (*Linnaeae*) (Mei *et al.*, 1996) are underdeveloped and thus seeds have MPD or MD. The embryo length/seed length ratio in seeds of two plants of *Heptacodium jasminoides* growing in

cultivation on the University of Kentucky campus was only 0.096 ± 0.003 (SE), $n = 15$ (Baskin and Baskin, unpublished).

In contrast, the water-permeable seeds of the closely related traditional families *Dipsacaceae* and *Valerianaceae* (*Valerina* clade *sensu* Donoghue *et al.*, 2001a, 2003) (Fig. 1) have fully developed embryos and thus either PD or ND (Baskin and Baskin, 1998). Since *Morina* (*Morinaceae sensu* APG, 1998), also in the *Valerina* clade (Fig. 1), has a fully developed embryo (Hutchinson, 1959; Takhtajan, 1997) and a water-permeable seed coat (Baskin *et al.*, 2000), its seeds also have PD or ND. Figure 12 in Peng *et al.* (1995) is an 'LS of mature seed' of *Triplostegia glandulifera* from Taiwan, and it shows that the embryo is underdeveloped (c. 1.0 mm long), being only a small fraction of the length of the seed or endosperm. However, seeds of this species collected in Taiwan in 2004 and in 2005 had fully developed embryos. Seeds collected in both 2004 and 2005 imbibed water, but none of them had germinated after 4 weeks of incubation at 5, 15/6, 20/10 or 25/15 °C in light. Further, seeds germinated best at 5 °C, but the first ones did so only after 22 weeks of incubation at this temperature (Baskin *et al.*, unpublished). Thus, we conclude that the seeds have PD.

In describing seeds of *Dipsacaceae*, Takhtajan (1997, p. 401; see also Ferguson, 1965) says 'Seeds with thin testa, large straight embryo and rather scanty, fleshy, oily endosperm'; and for *Valerianaceae* (p. 400), 'Seeds with large, straight, oily embryo and without endosperm'. Donoghue *et al.* (2001a) suggest that reduction in endosperm may be a reproductive synapomorphy in the *Morinaceae-Valerianaceae-Triplostegia-Dipsacaceae* clade. Evidently, then, based on molecular dating (but not on fossil evidence, see below) within the *Dipsacales*, the beginning of endosperm reduction and the acquisition of a fully developed embryo, and thus seeds with PD or ND, originated in the Late Cretaceous, i.e. before the Cretaceous/Tertiary (K/T) boundary (Fig. 1). No endosperm is present in *Valerianaceae* (Takhtajan, 1997; Donoghue *et al.*, 2001a), the most evolutionarily advanced member of the *Valerina* clade (Fig. 1).

However, within the genera of *Dipsacales* with MPD, class of seed dormancy is consistent within a genus, whereas level of dormancy (*sensu* Baskin and Baskin, 2004) may or may not be consistent. In *Sambucus*, the very closely related eastern North American *S. pubens* (= *S. racemosa* ssp. *pubens* var. *pubens*) and the Eurasian *S. racemosa* (= *S. racemosa* ssp. *racemosa*) (Eriksson and Donoghue, 1997) have different levels of MPD, whereas the not-so-closely related eastern North American *S. canadensis* and *S. pubens* (Eriksson and Donoghue, 1997) have the same level of MPD (Hidayati *et al.*, 2000b). Moreover, levels of MPD

in the north-western North American *S. callicarpa* (= *S. racemosa* ssp. *pubens* var. *arborescens*) and *S. racemosa* are similar (Hidayati and Walck, unpublished). Most species of *Viburnum*, for which the level of seed dormancy has been elucidated, have deep, simple, epicotyl MPD (Giersbach, 1937; Zolobova, 1970; Hidayati *et al.*, 2005). However, *V. tinus* has non-deep, simple, epicotyl dormancy (compare Nikolaeva, 2001 with Karlsson *et al.*, 2005), and apparently *V. nudum* and *V. scabrellum* have either MD or non-deep simple MPD (Giersbach, 1937). According to Giersbach, 'These [latter] two species failed to exhibit the epicotyl dormancy shown by the other forms [i.e. several other *Viburnum* species] studied...'. The East Asian species *V. odoratissimum* also does not have epicotyl dormancy (Chien *et al.*, 2002; Baskin *et al.*, unpublished). In the four species of *Lonicera* studied by Hidayati *et al.* (2000a), seeds of *L. fragrantissima* had deep simple MPD, and those of *L. japonica*, *L. maackii* and *L. morrowii* had non-deep simple MPD. On the other hand, the three species of *Symphoricarpos* for which dormancy type has been determined have non-deep complex MPD (Hidayati, 2000; Hidayati *et al.*, 2001).

Likewise, in non-dipsacalean genera with MPD, the level of dormancy among species may differ, e.g. *Aristolochia* (Adams *et al.*, 2005), *Erythronium* (Baskin *et al.*, 1995; Kondo *et al.*, 2002), *Osmorhiza* (Baskin *et al.*, 1995; Walck *et al.*, 2002; Wen *et al.*, 2002), or not, e.g. *Jeffersonia* and *Panax* (Baskin and Baskin, 1998). Finally, within the *Liliaceae s. str.* clade, the level of MPD varies between genera and tribes, and between species within a genus (Kondo *et al.*, 2006). Thus, at least within a genus, MPD is more likely to remain stable over geological time (see below under 'Fossil record...') than is the level of MPD.

Fossil record and evolutionary interpretations

The purpose of this section of the paper is briefly to review the literature on the fossil record of *Dipsacales* in the Northern Hemisphere, where most of the lineages occur in temperate regions (Bell and Donoghue, 2005). Unless there are reports to the contrary, we have accepted the generic assignment to the fossil material reported by the author, with the caveat that some of the identifications may be incorrect [e.g. see Hickey, 1973; Wolfe, 1973; Dilcher, 1974; Hickey and Wolfe, 1975; Taylor, 1990; Collinson *et al.*, 1993; Manchester and Donoghue, 1995; Manchester and Hably, 1997; Manchester, 2002 [i.e. fossil leaves and fruits of the plant previously referred to as *Viburnum antiquum* were determined to be those of *Davidia antiqua* (Cornales)]; Bell and Donoghue, 2005]. Such a review, along with information on the kinds of dormancy in seeds of extant genera of *Dipsacales* with a fossil record, will allow us to gain

some insight about seed dormancy in this group far back into geological time.

There is a fairly extensive Tertiary fossil record for extant genera in both major lineages of *Dipsacales* (*sensu* Donoghue *et al.*, 2001a, 2003), i.e. *Adoxaceae* (*Sambucus*, *Viburnum*) and *Caprifoliaceae* [*Lonicera*, *Symphoricarpos*, *Heptacodium*, *Diervilla*, *Weigela*, *Dipelta*, *Scabiosa*, *Valeriana*, *Dipsacus*, *Patrinia* and possibly *Triosteum* (see Song *et al.*, 2004)]. However, there are only a few reports for genera in the traditional families *Dipsacaceae* (*Scabiosa*, *Dipsacus*) and *Valerianaceae* (*Valeriana*, *Patrinia*) and (apparently) none for *Morina* (but see Song *et al.*, 2004) or *Triplostegia*, all of which are relegated to the (advanced) *Valerina* clade of *Caprifoliaceae* by Donoghue and co-workers (Donoghue *et al.*, 2001a, 2003; Bell and Donoghue, 2005; also see Zhang *et al.*, 2003) (Fig. 1).

The fossil record of extant genera of *Dipsacales* extends to at least the Early Tertiary (Muller, 1981, 1984; Magallón *et al.*, 1999) (Fig. 2), and perhaps even further back in geological time (e.g. Song *et al.*, 2004; also see below). In North America, *Sambucus* has been reported from the latest Eocene–earliest Oligocene (Evanoff *et al.*, 2001; Manchester, 2001) [originally dated Oligocene (see Manchester and Donoghue, 1995; Graham, 1999)] (MacGinitie, 1953; Manchester, 2001),

Oligocene (Axelrod, 1987), Miocene (Wolfe, 1981; Matthews and Ovenden, 1990) and Pliocene (Matthews and Ovenden, 1990); *Viburnum* from the Palaeocene (Wing *et al.*, 1995), Palaeocene–Eocene (McIver and Basinger, 1999), Eocene (Wolfe, 1968; McIntyre, 1991; Kalkreuth *et al.*, 1993; Axelrod, 1998a), latest Eocene–earliest Oligocene (Leopold and Clay-Poole, 2001), Oligocene (Lakhanpal, 1958) and Miocene (Liu and Leopold, 1994); *Lonicera* from the Eocene (Rouse, 1977; McIntyre, 1991; McIver and Basinger, 1999), Miocene (Chaney and Axelrod, 1959; Wolfe and Tanai, 1980; Leopold and Denton, 1987; Matthews and Ovenden, 1990) and Pliocene (Matthews and Ovenden, 1990); *Symphoricarpos* from the Oligocene (Becker, 1961; Axelrod, 1987, 1998b) and Miocene (Chaney and Axelrod, 1959; Leopold and Denton, 1987; Matthews and Ovenden, 1990; Axelrod, 1991); *Diervilla* from the Palaeocene (Kalkreuth *et al.*, 1993), Palaeocene–Eocene (McIver and Basinger, 1999), Eocene (McIntyre, 1991; McIver and Basinger, 1999), Oligocene (Piel, 1971; Rouse, 1977) and Miocene [Wolfe, 1969; Liu and Leopold, 1994 (as *Diervilla/Weigela*)] *Weigela* from the latest Eocene–earliest Oligocene (Wingate and Nichols, 2001), Miocene and Pliocene (Matthews and Ovenden, 1990); and *Valeriana* from the Pliocene (Nelson and

Genus	Epochs of the Tertiary period					Recent	Family/clade
	P	E	O	M	Pl		
<i>Sambucus</i>		●	●	●	●	●	} <i>Adoxaceae</i>
<i>Viburnum</i>	●	●	●	●	●	●	
<i>Diervilla</i>	●	●	●	●		●	
<i>Weigela</i>		●	●	●	●	●	
<i>Heptacodium</i>				●		●	} <i>Caprifoliaceae</i>
<i>Lonicera</i>	●	●	●	●	●	●	
<i>Symphoricarpos</i>			●	●		●	
<i>Dipelta</i>		●				●	
<i>Diplodipelta</i>		●	●	● (extinct)			
<i>Scabiosa</i>				●	●	●	
<i>Dipsacus</i> type				●		●	
<i>Patrinia</i>				●	●	●	
<i>Valeriana</i>				●	●	●	
						●	

Figure 2. Tertiary (65.5 to 1.8 Ma) fossil record of *Dipsacales* in the Northern Hemisphere (from numerous sources, see text). P, Palaeocene; E, Eocene; O, Oligocene; M, Miocene; and Pl, Pliocene. Recent indicates that genera are extant today. Seeds of members of the *Valerina* clade have physiological dormancy (or they are non-dormant), and those of all the other taxa (i.e. other *Caprifoliaceae* and all *Adoxaceae*) have morphophysiological seed dormancy (or morphological seed dormancy).

Carter, 1985). Based on fossil fruit material, Manchester and Donoghue (1995) and Manchester (2001) described the extinct genus *Diplodipelta* from the Eocene, Oligocene and Miocene of western North America, and Axelrod (1998b) reported it from the Oligocene of Idaho. Manchester and Donoghue (1995) concluded that *Diplodipelta* is the sister group to the extant genus *Dipelta*, native to China (Mabberley, 1997), but with a fossil record in Europe.

Macrofossils (seeds, fruits) of *Sambucus*, *Viburnum*, *Abelia* and *Dipelta* and pollen of *Sambucus*, *Viburnum*, *Lonicera* and *Abelia* have been reported from the lower Tertiary of England (Chandler, 1964) and *Abelia*-like fruits from the Palaeogene of Scotland, North America (Crane, 1987) and Europe (see Manchester and Hably, 1997). However, Manchester and Donoghue (1995) and Manchester and Hably (1997) rejected the fossil record of *Abelia*. Manchester and Hably (1997) stated that '... a reliable fossil record for *Abelia* remains to be demonstrated...'. Thus, this extant genus is not included in Fig. 2 (but see Song *et al.*, 2004). Fossil seeds of *Viburnum* have been reported from the Miocene of Germany (Ferguson *et al.*, 1998); of *Weigela* from the Miocene and Pliocene of Poland, the Miocene of Denmark and western Siberia; and of *Patrinia* from the Tertiary of western Siberia, the Pliocene of Baskiria and the Miocene of Poland (summary in Manchester and Donoghue, 1995). Fruits of *Scabiosa* (*Dipsacaceae*) have been reported from the Pliocene of Poland and pollen from the Miocene of Hungary (Collinson *et al.*, 1993). In Europe, *Sambucus* has a Tertiary fossil seed record extending from the middle Eocene to the uppermost Pliocene (van der Burgh, 1987, 1994; Collinson, 1988; Mai, 1995; Gastaldo *et al.*, 1998; van der Burgh and Zetter, 1998; Wilde and Frakenhäuser, 1998). *Dipsacus*-type pollen, presumably from Europe, extends to the Miocene (Muller, 1984).

For East Asia, where the *Dipsacales* probably originated (Donoghue *et al.*, 2003), Tanai (1992) reported Tertiary fossil records for *Sambucus*, *Viburnum*, *Diervilla* and *Weigela*. On the Korean Peninsula, *Viburnum* is reported from the Cretaceous, Oligocene and Miocene (Kong, 2000). For Japan, the fossil record for *Viburnum* extends continuously from the lower Eocene to the Upper Pliocene, whereas that of *Lonicera* includes only the Miocene and Pliocene (Sato, 1963; Tanai, 1961, 1970, 1972, 1976; Endo, 1968; Ozaki, 1980, 1981). In Japan, *Weigela* is reported from the Pliocene by Iwauchi (1994), and fruits of *Heptacodium* and *Patrinia* from the Miocene by Ozaki (1980). For China, *Viburnum* has been reported from the Late Cretaceous, Palaeocene, Eocene, Miocene and Pliocene; *Lonicera* from the Palaeogene, Miocene and Pliocene; *Diervilla* from the Miocene; and *Abelia* from the Palaeocene–Eocene [(Hsü, 1983; Guo, 1990; Tao, 1992; Li *et al.*, 1995), but see comment above by Manchester and Donoghue (1995) and Manchester and Hably (1997) regarding *Abelia*].

Thus, assuming that the kinds of seed dormancy in these fossil taxa of *Dipsacales* were the same as those in modern species of the genera, the fossil record indicates that MPD has been present in this lineage from the time it originated, at least as far back as the Late Cretaceous or Early Tertiary [and even earlier according to molecular dating (Fig. 1)]. If, indeed, for example: (1) the Late Oligocene *Sambucus longifolia* is an 'allied species' of the extant *S. racemosa* complex (Axelrod, 1987); (2) the extant *Viburnum odoratissimum* is represented by pollen from the Middle and Upper Eocene, *V. tinus* by pollen from the Pliocene (Muller, 1981), *V. lentago* by pollen from the latest Eocene–earliest Oligocene (Leopold and Clay-Poole, 2001), *V. otukai* from the Miocene is 'closely similar' to extant *V. betulifolium* [which has epicotyl dormancy (Baskin *et al.*, unpublished)] (Tanai, 1961) and *V. basiobliquum* of the Oligocene is similar to extant *V. dentatum* (Tanai, 1970); (3) the extant *Weigela floribunda* is represented by pollen from the Oligocene (Wingate and Nicholas, 2001); (4) *Heptacodium jasminoides* is a 'living equivalent' of the extinct *H. hokianum* from the Miocene (Ozaki, 1980, 1981); and (5) *Symphoricarpos albus* is a 'living equivalent' of the Miocene–Pliocene species *S. salmonensis* (Smiley, 1963; Axelrod, 1964, 1998b), then our supposition that MPD has been present in these five genera for millions of years would be strongly supported. Seeds of *Sambucus*, *Viburnum*, *Weigela*, *Heptacodium* and *Symphoricarpos* have MPD (Fig. 1). On the other hand, the fossil record indicates that PD did not originate in the *Dipsacales* until the Miocene [but much earlier according to molecular dating (Fig. 1)]. In any case, apparently PD is restricted to the most advanced dipsacalean clade, *Valerina*, and it occurs in seeds of all members of this monophyletic group (Fig. 1).

Indeed, it does appear that class of seed dormancy within a lineage can remain stable over long periods of geological time, perhaps from the origin of a genus [e.g. in *Rhus* tribe *Rhoeae* that exhibits physical dormancy and in members of the tribe *Spondideae* that exhibit PD, of the family *Anacardiaceae* (Baskin *et al.*, 2000)]. Further, evidence for long-term stasis of MPD within lineages comes from comparisons of seed dormancy in eastern Asian/Eurasian–North American disjunct species within several genera, e.g. *Aristolochia* subgenus *Siphisia* (Adams *et al.*, 2005), *Erythronium* (Baskin *et al.*, 1995; Kondo *et al.*, 2002), *Osmorhiza* (Baskin *et al.*, 1995; Walck *et al.*, 2002; Wen *et al.*, 2002), *Jeffersonia*, *Panax* (Baskin and Baskin, 1998), *Paeonia* (Barton, 1933; Martin, 1946; Barton and Chandler, 1957; Schlising, 1976; Sang *et al.*, 1997; Jing and Zheng, 1999) and the *Dipsacales* *Weigela*/*Diervilla* clade (Nikolaeva *et al.*, 1985; Hidayati *et al.*, 2000c) and *Sambucus* (Hidayati *et al.*, 2000b). In all of these genera, MPD has been retained in the disjuncts since their separation in the Tertiary (see Sang *et al.*, 1997; Wen, 1999; Xiang *et al.*, 2000; Donoghue *et al.*, 2001b). Interestingly, *Osmorhiza*

(*Apiaceae*, *Apiales*) and *Panax* (*Araliaceae*, *Araliales*) also are in the highly evolutionarily advanced euasterids II clade (APG II, 2003).

Molecular phylogenetic studies have placed *Dipsacales* and nine other orders in the asterid clade, a strongly supported monophyletic group (APG II, 2003). The asterids are divided further into two monophyletic clades, euasterids I and euasterids II. *Dipsacales*, along with the *Asterales*, *Apiales* and *Aquifoliales*, are included in the euasterids II clade. The order *Aquifoliales* is sister to the rest of euasterids II (APG II, 2003). Underdeveloped embryos (thus mostly likely MPD, but possibly also MD) occur in all four orders in the euasterids II clade. Further, they occur in all five families of *Aquifoliales* and in all ten families of *Apiales* (Baskin and Baskin, unpublished), and we have found no reports of fully developed embryos in these two orders (Martin, 1946; Hutchinson, 1959; Watson and Dallwitz, 1992 onwards; Takhtajan, 1997; Compilation Committee, 2000). Thus, it is not surprising that the fossil record of *Aquifoliaceae* (*Aquifoliales*) and *Araliaceae* (*Apiales*), including extant genera, also extends back to the Cretaceous (Collinson *et al.*, 1993).

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