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The origin of the early differentiation of Ivies (*Hedera* L.) and the radiation of the Asian Palmate group (Araliaceae)

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ABSTRACT

The Asian Palmate group is one of the four major clades of the family Araliaceae that is formed by 18 genera, including ivies (*Hedera* L.). The Mediterranean diversity centre and temperate affinity of ivies contrast with the inferred Asian centre of diversity of the primarily tropical and subtropical Asian Palmate group. We herein investigated the sister-group relationships of *Hedera* to reconstruct the evolutionary context for its origin and early diversification. Seven nuclear and plastid DNA regions were analyzed in 61 Araliaceae samples including all the 18 Asian Palmate genera. Maximum Parsimony, Maximum Likelihood and Bayesian Inference were run together with a battery of topology testing analyses constraining the expected *Hedera's* sister-group relationships. Additionally, Bayesian polytomy resolvability and divergence time analyses were also conducted. Genome incongruence and hard nuclear and plastid basal polytomies are detected for the Asian Palmate group where the lineage of *Hedera* is placed. Topology testing analyses do not allow rejecting any of the tentative sisters of *Hedera*. An early radiation with inter-lineage hybridization and genome doubling is suggested for the Asian Palmate group where all the seven temperate genera, including *Hedera*, seem to have played an important role. The radiation took placed during the Upper Cretaceous in Asia under a general cooling and the eastern Asian mountain uplift that produced new temperate environments and promoted lineage connections. This allows us to hypothesize that the origin of the *Hedera* lineage may fit in a temperate niche conservatism scenario where the combination of the radiation with lineage admixtures prevents us form discovering its sister-group.

1. Introduction

The family Araliaceae in its modern circumscription constitutes a monophyletic lineage largely congruent with the conventional delimitation of the family (Mitchell et al., 2012; Plunkett et al., 2004). Only two tribes traditionally considered within Araliaceae (*Mackinlayeae*, Harms, 1898; Mackinlayaceae, Doweld, 2001; and *Myodocarpeae*, Calestani, 1905; Viguier, 1906; Myodocarpaceae, Doweld, 2001) appear out of the core as two independent lineages (Chandler and Plunkett, 2004; Plunkett and Lowry, 2001; Plunkett et al., 2004). As a result, 41 genera are now considered in the Araliaceae (Mitchell et al., 2012; Plunkett et al., 2004). Phylogenetic reconstructions of the Araliaceae reveal three main clades (Asian Palmate, *Aralia–Panax* and *Polyscias–Pseudopanax*) placed in a basal polytomy together with a group of poorly resolved minor lineages (Plunkett et al., 2004; Wen et al., 2001). A recent study has revealed a new fourth main clade also placed in the basal polytomy (Greater *Raukaua* clade, Mitchell et al., 2012). None of these four main clades has any congruence with the tribes traditionally recognized based on morphology (Plunkett et al., 2004; Wen et al., 2001). However, a geographical pattern is detected with two of the four main clades centered in Southeast Asia (Asian Palmate and *Aralia–Panax* groups) and the remaining two in the Pacific and Indian Ocean basin (Greater *Raukaua* and *Polyscias–Pseudopanax* group, Mitchell et al., 2012; Plunkett et al., 2004; Wen et al., 2001). The basal polytomy and short internal branches retrieved in the phylogenies of the Araliaceae have been interpreted as a result of a period of fast proliferation of lineages linked to the break-up of Gondwana (Plunkett et al., 2004; Yi et al., 2004). The first divergence time estimates of the family partially confirmed this hypothesis since the Araliaceae crown age coincides with the end of the break-up of Gondwana (*c.* 84 mya; Mitchell et al., 2012).

Eighteen morphologically diverse genera have been traditionally included in the Asian Palmate group (Plunkett et al., 2004; Wen et al., 2001; Fig. 1). However, the total number of genus-level

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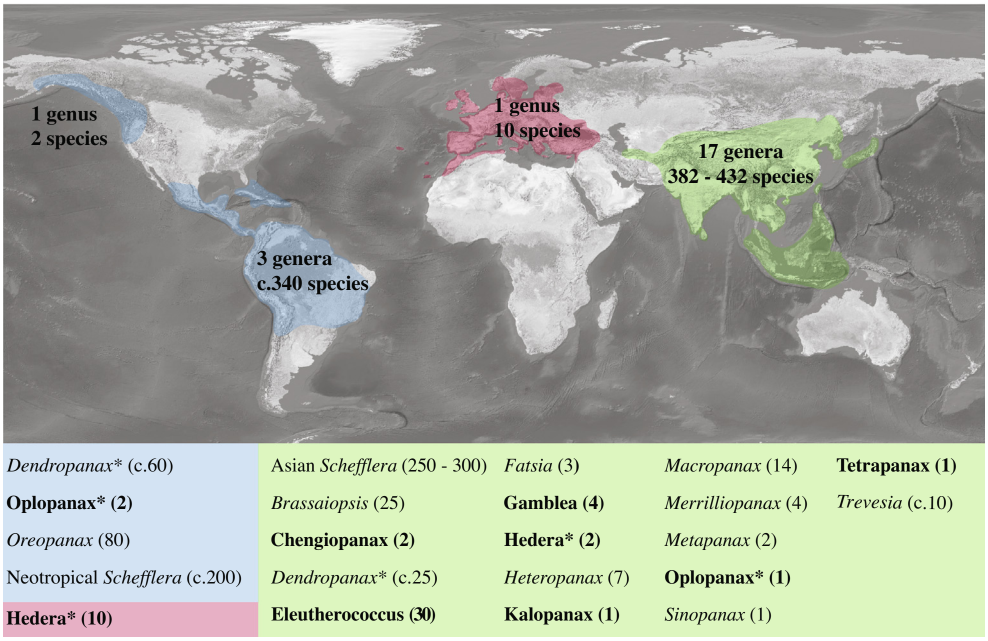

*Dendropanax** (c.60)	Asian *Schefflera* (250 - 300)	*Fatsia* (3)	*Macropanax* (14)	**Tetrapanax (1)**
Oplopanax* (2)	*Brassaiopsis* (25)	**Gamblea (4)**	*Merrilliopanax* (4)	*Trevesia* (c.10)
Oreopanax (80)	**Chengiopanax (2)**	**Hedera* (2)**	*Metapanax* (2)	
Neotropical *Schefflera* (c.200)	*Dendropanax** (c.25)	*Heteropanax* (7)	**Oplopanax* (1)**	
Hedera* (10)	**Eleutherococcus (30)**	**Kalopanax (1)**	*Sinopanax* (1)	

Fig. 1. Worldwide distribution of the Asian Palmate genera. The number of species per genus and geographical area is provided in parenthesis. Temperate genera are highlighted in bold. Asterisks indicate genera with inter-continental disjunction.

lineages is 20. This is due to the split of the: (1) Old World species of *Dendropanax* (*Dendropanax* subgen. *Textoria*, Li and Wen, 2013) into two separate clades (the *Dendropanax hainanensis* clade *vs.* the remaining *Dendropanax* subgen. *Textoria*; Li and Wen, 2013) and (2) Scheffleras included in the Asian Palmante group into the Neotropical and the Asian *Schefflera* subgroups (Fiaschi and Plunkett, 2011; Plunkett et al., 2004, 2005). Aside from the palmate-like leaves, there is only one morphological character (unarticulated pedicels) that is shared by all the 18 genera of the group except for *Macropanax* and *Metapanax* (Plunkett et al., 2004). In addition to this scant morphological affinity and the above-described geographical congruence it is interesting to notice that most of the members of the Asian Palmate group are polyploids (Yi et al., 2004). In fact, 14 of the 18 Asian Palmate genera with chromosome counted to date are tetraploids, three of which also have diploid species placed in terminal positions (Yi et al., 2004). Interestingly, members of the remaining three main clades of the family are diploids (*Aralia–Panax*, greater *Raukaua* and *Polyscias–Pseudopanax* groups). Considering all this, Yi et al. (2004) proposed either (1) a single polyploidization event at the origin of the Asian Palmate group followed by at least three independent reversals to the diploid condition or (2) a diploid origin followed by multiple independent polyploidyzations affecting all main lineages within the group. However, the basal polytomy also retrieved for the Asian Palmate group prevented the authors from setting up the most likely scenario.

The genus *Hedera* has 12 extant species (Valcárcel and Vargas, 2010) with a range that extends from Macaronesia to Japan throughout North Africa, Europe, and continental Asia. Its phylogenetic placement is indisputably within the Asian Palmate group, although the closest relatives remain unknown (Lowry et al., 2001; Plunkett and Lowry, 2001; Plunkett et al., 2004; Valcárcel et al., 2003; Valcárcel, 2008; Wen et al., 2001; Yi et al., 2004). Disclosing the sister-group of *Hedera* is challenging since ivies barely share any geographical, ecological or morphological affinity with the remaining members of the Asian Palmate group. Indeed, 13 of the 18 Asian Palmate genera are restricted to Asia while the distribution of *Hedera* extends to Europe (Fig. 1). The remaining four Asian Palmate genera with an extra-Asian range occur in the New World (*Dendropanax, Oplopanax, Oreopanax, Schefflera;* Fig. 1). Besides, *Hedera,* together with six other genera of the group (*Chengiopanax*, *Eleutherococcus*, *Gamblea*, *Kalopanax*, *Oplopanax*, and *Tetrapanax;* Fig. 1) display a north temperate distribution. This latitudinal range contrasts with the strict tropical/subtropical affinity of the remaining 11 genera. Finally, while the diversity centre of the whole Asian Palmate group and some of its genera (*Dendropanax* subgen. *Textoria, Trevesia, Brassaiopsis*) have been located in tropical/subtropical Southeast Asia (Fig. 1; Li and Wen, 2013; Mitchell and Wen, 2005; Mitchell et al., 2012; Plunkett et al., 2004; Wen et al., 2001, 2007), the primary center suggested for ivies has been placed in the Mediterranean basin (Ackerfield and Wen, 2003; Green et al., 2011; Valcárcel et al., 2003; Valcárcel and Vargas, 2013; Vargas et al., 1999). Unfortunately, phylogenetic studies have systematically failed to infer *Hedera* sister-group, and thus to reconstruct its origin and early divergence. Four different lineages of the Asian Palmate group are consistently suggested as putative sister-groups although with marginal support: (i) *Trevesia-Brassaiopsis* group (Lowry et al., 2001; Plunkett and Lowry, 2001; Plunkett et al., 2004; Valcárcel et al., 2003; Wen et al., 2001; Yi et al., 2004), (ii) *Dendropanax* (Li and Wen, 2013; Valcárcel, 2008), (iii) *Kalopanax* (Chandler and Plunkett, 2004), and (iv) *Merrillionapax* (Mitchell and Wen, 2004; Mitchell et al., 2012; Plunkett et al., 2004). The sister-group relationship between *Hedera* and the *Trevesia-Brassaiopsis* group is supported by morphology. Traditional taxonomy of the family Araliaceae has related *Hedera* within a reduced group of genera with single styles that includes *Brassaiopsis* (Seeman, 1868). Additionally, both genera share smooth fruits (Frodin and Govaerts, 2003), similar multicellular foliar trichomes (Ackerfield, 2001; Lum and Maze, 1989; McAllister and Rutherford, 1990; Valcárcel and Vargas, 2010; Wen et al., 2003) and lobed leaves (Mitchell and Wen, 2005; Valcárcel and Vargas, 2010). Morphology does also support the association between *Hedera* and *Dendropanax* since they both have single styles (Seeman, 1868), 3–5 carpels (Li and Wen, 2013; Valcárcel, 2008) and entire to (2)3–5(7) lobed leaves (Li and Wen, 2013; Valcárcel, 2008). Limited morphological affinity does also support

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