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REGULAR PAPER

# The oldest *Mahonia* (Berberidaceae) fossil from East Asia and its biogeographic implications

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**Abstract** Interpretation of the biogeography of the genus *Mahonia* (Berberidaceae) is limited by the lack of fossil records in East Asia. Compressed fossil foliage, described here as *Mahonia mioasiatica* sp. nov., were collected from the Upper Miocene Xiaolongtan Formation in Wenshan, Yunnan, southwest China. These specimens represent the oldest reliable fossil record of *Mahonia* in East Asia. This new fossil species shows a general similarity to Group Orientales and is most similar to the extant eastern Asian *Mahonia conferta*. Considering other fossil evidence of *Mahonia*, we propose a migration route of this genus to Asia over the North Atlantic Land Bridge rather than the Bering Land Bridge. Our results also suggest that North America, Europe and East Asia have been successive centers of diversity for the genus, as a consequence of diversification in Group Orientales potentially related to historical climate change.

**Keywords** Berberidaceae · Biogeography · East Asia · Miocene · Mahonia · Southwestern China

## Introduction

The floristic similarities between East Asia and North America have long been recognized (Boufford and Spongberg 1983; Wen 1999) and the disjunct distribution of the floras has been the focus of a great deal of research (Qian and Ricklefs 2004; Wen 1999; Wen et al. 2010; Xiang et al. 1998). Studies on the origins and dispersal routes of this intercontinental flora are important for understanding modern biogeographical patterns.

The genus *Mahonia* Nuttall (Berberidaceae, Ranunculales) is a member of the basal eudicots (The Angiosperm Phylogeny Group 2009, Ying et al. 2001), a group with many taxa with East Asia-North America disjunct distributions. They are shrubs or small trees with evergreen, coriaceous (sclerophyllous), compound leaves (Ahrendt 1961; LoConte 1993). In total, there are ca. 60 living species mainly distributed in East Asia, the western part of North America and Central America. The modern center of diversity of *Mahonia* lies in southern China where ca. 30 species are native (Ying et al. 2001). In the United States there are ca. 20 species found mainly in the southwest (Whetstone et al. 1997). Some North American species, such as *M. aquilifolium,* are widespread, invasive plants in Europe (Auge and Brandl 1997).

Ahrendt (1961) divided *Mahonia* into two groups based on inflorescence bracts. Based on a molecular phylogenetic study of ITS data, Kim et al. (2004) distinguished three clades of extant *Mahonia*: one corresponding to Ahrendt's Group Orientales, and two comprising the members of Group Occidentales (Fig. 1).

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**Electronic supplementary material** The online version of this article (doi:10.1007/s10265-015-0775-y) contains supplementary material, which is available to authorized users.

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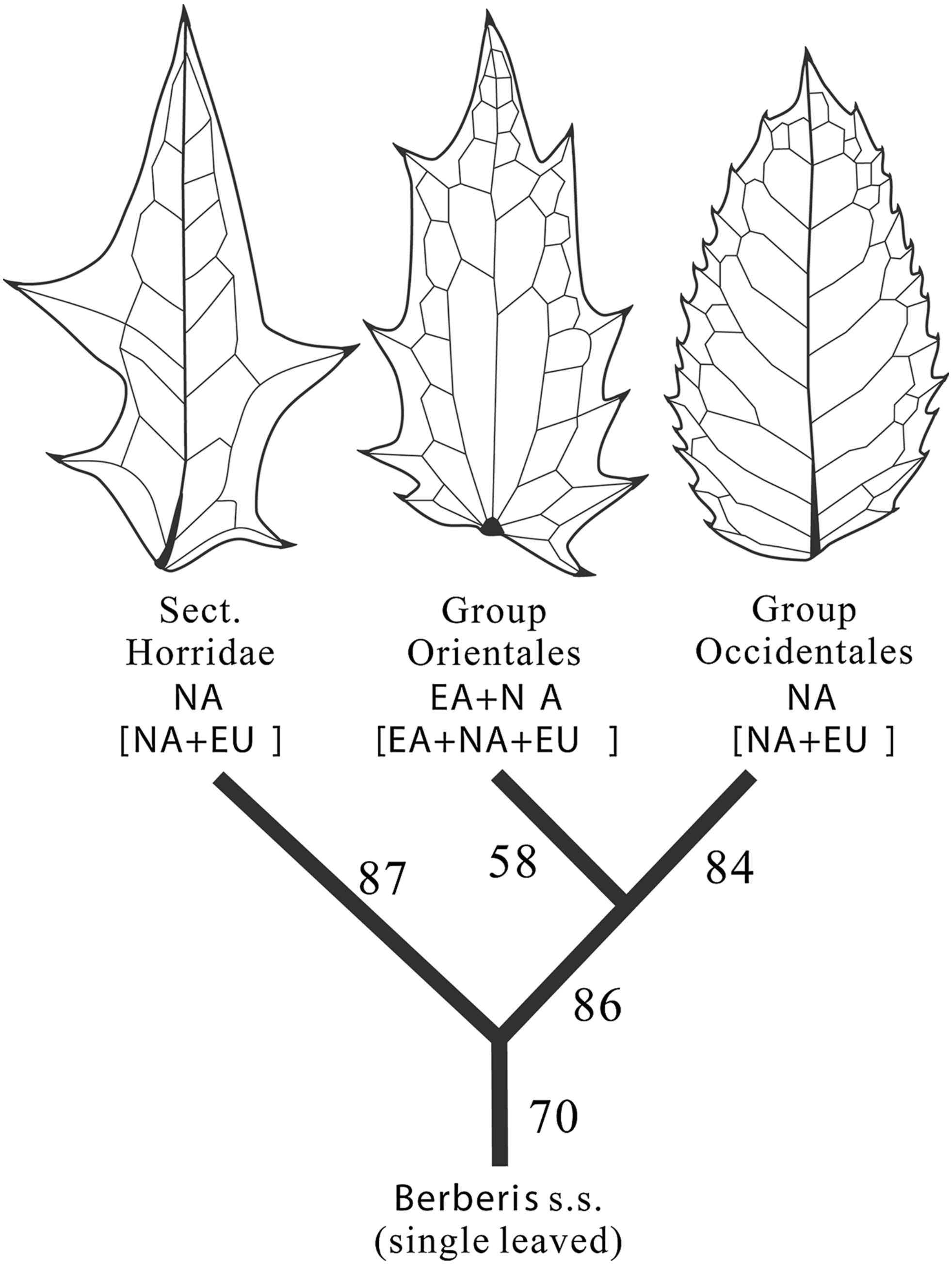

**Fig. 1** Phylogeographic relationships in Berberidaceae based on Kim et al. (2004); numbers are bootstrap values. Leaf architecture of different clade: Group Occidentales Section Horridae (*M. haematocarpa*); Group Orientales (*M. lomariifolia*); Group Occidentales (*M. aquifolium*) are according to Ahrendt (1961). *NA* North America including Mexico, *EU* Europe and Asia Minor, *EA* East Asia. Areas in *square brackets* indicate the fossil distribution of the major groups of *Mahonia*. Figure Modified from Güner and Denk 2012

Group Orientales has leaflets with palmate venation and is mainly distributed in south China, extending to the western Himalayas. A few species occur in southern India, Vietnam, Taiwan, Sumatra, and the Philippines, and a single species is native to western North America. Group Occidentales has leaflets with pinnate venation and is widespread in western North America from British Columbia to western South America. Sect. Horridae in Group Occidentales has leaf margins with coarse dentation and is present in deserts of the southwest United States and Mexico (Ahrendt 1961; Fang et al. 2011; Whetstone et al. 1997; Ying et al. 2001).

*Mahonia* species can easily be recognized by the distinctive architecture of their imparipinnately compound leaves and spiny leaflets. These are also good characters for identification of *Mahonia* in the fossil record without the need for associated flowers or fruits (Manchester 1999). The oldest fossils of this genus are from the late Eocene Florissant flora in Colorado (MacGinitie 1953; Manchester 2001) and the late Eocene deposits of the John Day Formation in Oregon (Manchester 2000). Many fossil leaves of *Mahonia* have been reported from the Oligocene to Pleistocene deposits of North America (Arnold 1936; Axelrod 1964, 1985, 1987, 1998; Becker 1959, 1962, 1969, 1972; Hollick 1929; Meyer and Manchester 1997; Ramírez and Cevallos-Ferriz 2000) and Europe (Güner and Denk 2012; Givulescu 1979; Kolakovsky 1964; Kräusel 1938; Kvaček and Bůžek 1994; Mai and Walther 1988; Martinetto et al. 1997; Mihajlovic 1996; Saporta 1866; Stephyrtza 1971). However, until now, no reliable fossil records of *Mahonia* had been identified from East Asia, even though the genus is widely distributed and highly diversified in the modern East Asian flora (Manchester 1999). This lack of Asian fossils has limited the interpretation of the biogeography of this genus (Güner and Denk 2012).

Recently, we found fossils of *Mahonia* leaflets from the Upper Miocene of Wenshan, southwestern China. This constitutes the first reliable fossil record of the genus to be described from East Asia. In this article, we establish a new species of *Mahonia* and compare it with extant and other fossil species. Furthermore, we discuss the biogeographical implications of this finding and propose potential migration routes of *Mahonia* during the Cenozoic, shedding new lights on the East Asian-North American disjunct distribution.

## Materials and methods

### Geological setting

Fossil leaves were collected from Wenshan, southeastern Yunnan Province, China (23°20N; 104°17E, 1,271 m a.s.l.) (Fig. 2). Paleogene Breccia unconformably underlies the fossiliferous outcrop, which belongs to the Xiaolongtan Formation. This Formation has been assigned to late Miocene based on combined evidence from regional stratigraphy (Ming 2007; Bureau of Geology and Mineral Resources Yunnan Province 1990), palynology (Wang 1996), vertebrate paleontology (Dong and Deng 2001), and plant megafossils (Guo and Zhou 1992; Tao et al. 2000; Xia et al. 2009). A detailed stratigraphy of this locality can be found in Meng et al. (2014).

The fossil leaves were found in sediments made of a creamy yellow fine calcareous mudstone and the environment of deposition was interpreted to be a deep lake. The fossils are well preserved, suggesting that the leaves were deposited close to the place they were shed.

### Morphological observations

The fossils were compared to leaves of extant species of *Mahonia* housed in the herbarium at the Kunming Institute of Botany, CAS (KUN) and the herbarium of the Xishuangbanna Tropical Botanical Garden, CAS (HITBC), as well as online data sources including the Herbaria of Kew Royal Botanic Gardens (http://apps.kew.org), and the French National Museum of Natural History (http://coldb.mnhn.fr). Twelve extant species of *Mahonia* and one species of *Ilex* (*Ilex cornuta*) were collected from the Kunming Botanical Garden (KIB) and the Xishuangbanna Tropical Botanical Garden (XTBG). Leaf clearings were prepared according to the method described in Li (1987). All fossil and cleared-leaf specimens were photographed with a Nikon D700 digital camera. Details of fossil specimens were observed and photographed with a stereo microscope (Leica S8APO) and line-drawings of the fossil specimens were created using CorelDraw X6 software. Leaflet width, length and angle were measured in the software ImageJ 1.45s (Wayne Rasband, National Institutes of Health, USA). Leaf architecture terminology follows Ellis et al. (2009).

Palaeolatitude and palaeolongitude were converted from the modern latitude and longitude of fossil sites using "Point Tracker for Windows" software, and plotted on five palaeogeographical maps of Lambert Equal-Area Azimuthal Projection (North Pole) using ArcGIS 10.0 software (Fig. 6).

## Results

### Systematic palaeobotany

Family: Berberidaceae Jussieu

Genus: *Mahonia* Nuttall

Species: *Mahonia mioasiatica* J. Huang et Z. K. Zhou sp. nov.

**Holotype:** DMS-0383 (A, B) (Fig. 3a–b).

**Paratypes:** DMS-0386, DMS-1279, DMS-1281 (Fig. 3c–e).

**Repository:** Holotype and paratypes are housed at the Paleoecology Laboratory, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

**Type locality:** Dashidong Village, Wenshan City, Yunnan Province, China.

**Stratigraphy:** Upper Miocene Xiaolongtan Formation.

**Etymology:** The new species is named for the oldest occurrence of *Mahonia* in the Miocene strata in East Asia.

**Diagnosis:** Leaflet sessile, c. 2.1–4.2 cm long, ratio of width to length = 1:1 to 1:2.5, base asymmetric truncate, apex acute-cuspidate, venation palmate, festooned

**Fig. 2** Map of Yunnan Province, China. The *leaf symbol* represent the fossil site near Wenshan

semicraspedodromous, 2–3 (–4) spinose teeth on each side of lamina, the first pair of teeth below the leaf apex comparatively large.

**Description:** Isolated leaflets; leaflets sessile; lamina of lateral leaflets 3.3–6.5 cm long, 2.2–3.3 cm wide (Fig. 3d); basal leaflets smaller, c. 2.3 cm long; lamina ovate to oblong, leaf base asymmetric, truncate (Fig. 3a, b), apex cuspidate; margin dentate, spinose, teeth with long basal side and short apical side, number of teeth on each side 2–3 (–4), teeth triangular with spinose apex 0.2–1.6 cm long (Fig. 3b,e); venation palmate, festooned semicraspedodromous, secondary veins forming loops followed by additional loops, the first and the second loops on each side of the primary vein reaching the middle of the lamina, veins departing from primary or secondary loops and ending in teeth (Fig. 3b); tertiary venation random reticulate or regular polygonal reticulate. Free-ending venations (FEVs) absent (Fig. 4e).

**Remarks:** This species is similar to several modern Asian species of Ahrendt's (1961) *Mahonia* Group *Orientales* (=Sect. Longibracteatae). Leaflets of species in Group Orientales are quite variable; basal leaflets are often smaller and roundish in shape. One leaf with a smaller and roundish shape (DMS-1281) was found in the same strata (Fig. 3d).

## Discussion

### Determination

Leaflets of *Mahonia* are easily segregated from the laminae of most other angiosperm species by their distinctive spinose tooth shape. Additionally, the secondary venation pattern in the fossil leaflets is similar to the venation in modern *Mahonia*. The secondary venation is festooned semicraspedodromous (secondaries form more than one set of loops and the branches from the most exmedial loops terminating to the teeth) (Figs. 3a, 4a–b).

However, some species of *Ilex* (Aquifoliaceae), such as *Ilex cornuta*, have similar leaf outline and marginal teeth as *Mahonia* (Fig. 5l). For example, fossil *Mahonia bilinica* was originally misidentified as *Ilex bilinica* (Güner and Denk 2012; Kräusel 1938; Kvaček and Bůžek 1994). Leaves of *Mahonia* can be distinguished from those of *Ilex* by an obvious asymmetric base (Fig. 3a, b) and palmate-festooned semicraspedodromous venation (Fig. 3b). Most importantly, the veinlets of *Mahonia* and *I. cornuta* are very different. The venation of *I. cornuta* has curved veinlets with multiple ranks of branching (FEVs dendritic branching) (Fig. 4f, g), while the venation pattern in

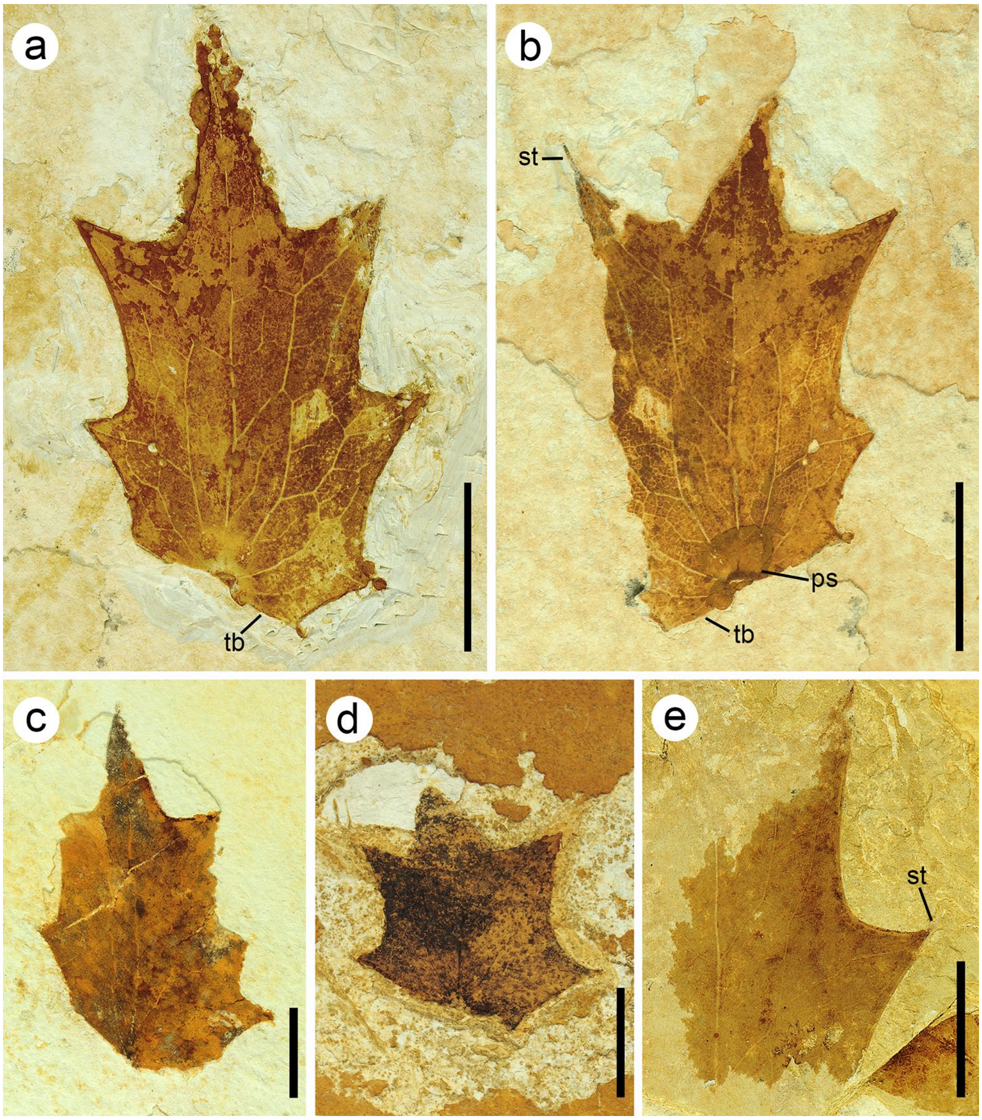

**Fig. 3** *Mahonia mioasiatica* J. Huang *et* Z. K. Zhou sp. nov. from Wenshan, Yunnan, China. **a** *M. mioasiatica* (DMS-0383A)(Holotype) leaflet with obliquely truncate(tb). **b** DMS-0383B (Counterpart of DMS-0383A) *tb* truncate base, *ps* palmate secondary venation (indicate by grey color lines), *st* spinose tooth. **c** DMS-1279. **d** DMS-1281, probably a basal leaflet. **e** DMS-0386 *st* spinose tooth. *Scale bar* 1 cm

*Mahonia* is random reticulate, regular polygonal reticulate with single branching or nearly devoid of veinlets (FEVs absent or unbranched) (Fig. 4c, d). The veinlets of DMS-0383B show the same architecture as extant *Mahonia* (Fig. 4e).

## Morphological comparison with extant *Mahonia*

Botanists disagree on the relationship between *Mahonia* and 'true *Berberis*'. *Berberis*, with simple leaves is easily distinguished from *Mahonia* which has compound leaves. Nevertheless, some taxonomists have combined them in a single genus (Kim et al. 2004; McCain and Hennen 1982; Morean 1982; Whetstone et al. 1997), but for this study we consider *Mahonia* as an individual genus.

Both morphology and molecular studies have provided a clear classification at the sectional level for the genus (Ahrendt 1961; Kim et al. 2004), three major types are divided: Group Orientales, Group Occidentales and Section Horridae in Group Occidentales (Fig. 1). This grouping has a high consistency with leaflet morphology, so identification at this level is feasible. The characteristic of leaflet morphology is consistent with this grouping: (1) the "Orientales Type" leaflet refers to Group Orientales, which have palmate, festooned semicraspedodromous secondary venation, spread out like a fan (palmate); (2) the "Occidentales

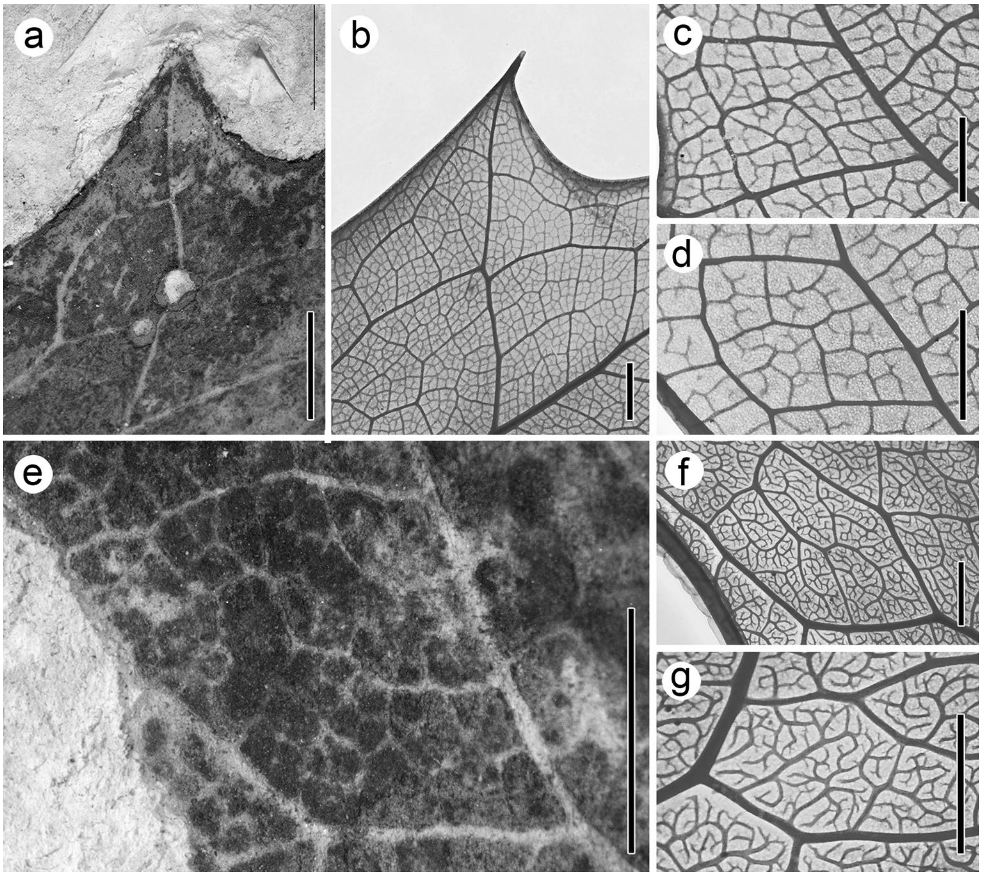

**Fig. 4** Venation comparison between fossil, extant *Mahonia* and *Ilex*. **a** Tooth of *M. mioasiatica* (DMS-0383A). **b** Tooth of *M. conferta*. **c** *M. duclouxiana*, FEVs absent or unbranched. **d** *M. napaulensis*, FEVs absent or unbranched. **e** *M. mioasiatica* (DMS-0383B), FEVs absent or unbranched. **f** *I. cornuta* (Aquifoliaceae), FEVs dendritic branching. *Scale bar* 2 mm

Type" refers to Group Occidentales, which have numerous pinnate secondary veins (pinnate); (3) the "Horridae Type" refers to Section Horridae in Group Occidentales, which has coarse dentition and the venation pattern is intermediate between Orientales and Occidentales, the secondary venation is chiefly pinnate but the basalmost pair is greater in gauge, descend steeply from the primary vein and enters the tooth finally (pinnate-palmate complex).

Species of the Group Orientales have a distinctive type of secondary venation compared to the other two clades: it has a palmate-festooned semicraspedodromous venation where secondary veins form series of loops followed by additional lateral loops (Fig. 1). Based on this character, *M. mioasiatica* (Fig. 5a) is confidently placed as a member of Group Orientales.

Although the sectional classification is well established, the lower level classification is still unclear/debated. Ahrendt classified Group Orientales species into nine subsections and several unclassified species, but this classification was not supported by Junsheng Ying (Personal communication). Subsequently, Ying treated 33 species as synonyms when revising the Flora of China (Wu et al. 2010; Ying et al. 2001). Leaf morphology in Group Orientales is also highly variable based on our observations. Leaflets in different positions in the compound leaf have different shapes (Fig. 7e). Usually the basal leaflets are smaller and bear fewer teeth, but those teeth are relatively larger. The shape and number of teeth on the leaflets differ according to the plant's growth stages or habitat. The variation in some species makes it difficult to classify them solely on their leaf morphology, even if the higher level venation is visible.

Therefore, determining the nearest living relative of *M. mioasiatica* according to the general leaf morphology is difficult. So, a comparison based on the leaflets closest to the base was performed (Table 1). The base of *M. mioasiatica* is truncate, thereby species with obvious acute or obtuse base such as *Mahonia breviracema*, *Mahonia eurybracteata*, *Mahonia fortunei*, *Mahonia gracilipes*, *M. microphylla*, *Mahonia nitens*, *Mahonia polyodonta* and *Mahonia taronensis* can be excluded (Fig. 5 h–k); There are large and relatively few teeth (2–4 teeth on each side)

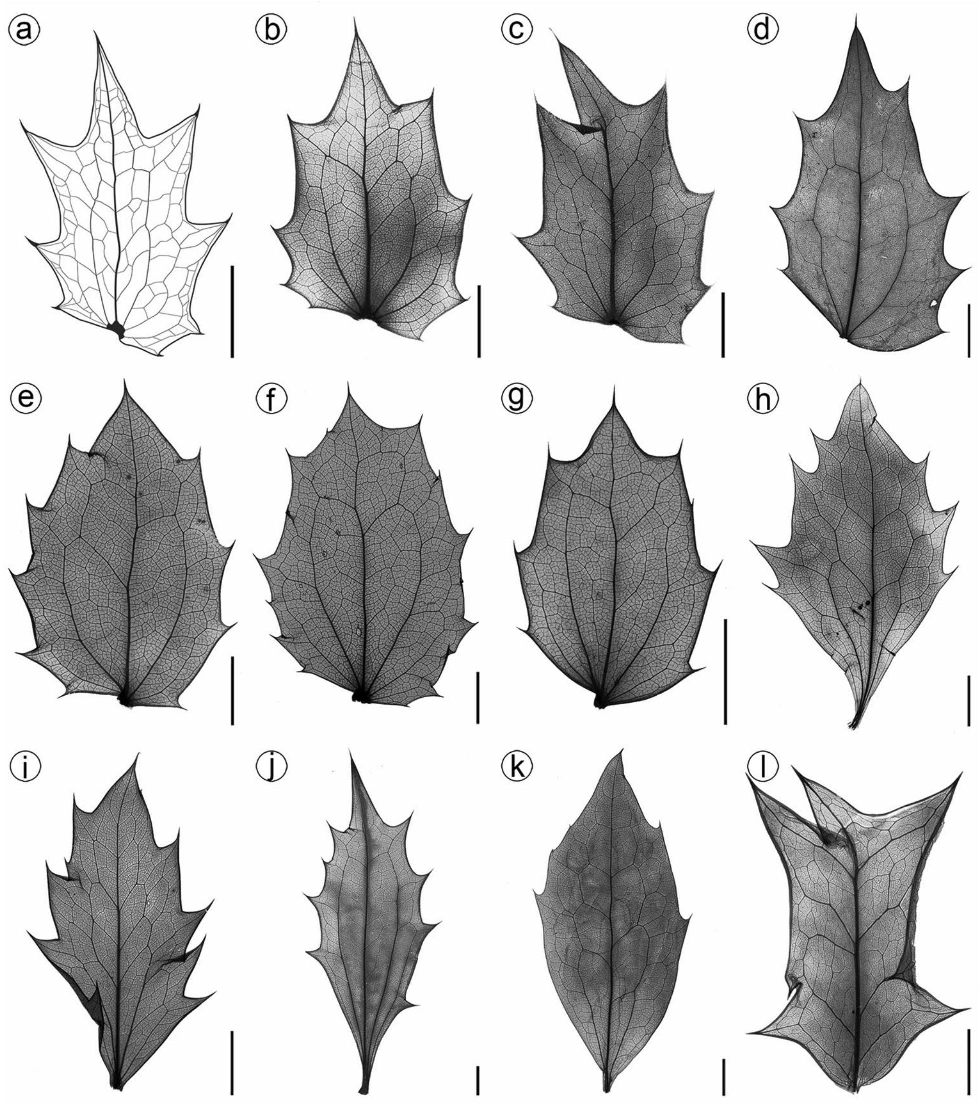

**Fig. 5** Leaflet architecture of *Mahonia mioasiatica*, several representative extant species in Group Orientales and *Ilex cornuta*. Left sides of the leaflets are all adaxial (closer to the rachis) and right sides are all abaxial. **a** *M. mioasiatica* based on DMS-0383A. **b** *M. conferta*. **c** *M. oiwakensis*. **d** *M. bealei*. **e** *M. napaulensis*. **f** *M. duclouxiana*. **g** *M. hancockiana*. **h** *M. breviracema*. **i** *M. fortunei*. **j** *M. nitens*. **k** *M. gracilipes*. **l** *Ilex cornuta* (Aquifoliaceae). *Scale bar* 1 cm

in *M. mioasiatica*. The leaf teeth of *Mahonia bracteolata*, *Mahonia napaulensis* and *Mahonia duclouxiana* are shorter and more numerous [(2)3–6 teeth each side] than in our fossil (Fig. 5e–g); Besides, both sides of leaflet base in the fossil are straight and differ from the curved *Mahonia bealei*, *Mahonia hancockiana*, *M. hypoleuca*, and *Mahonia japonica*, which are markedly curved. For the same reason, *Mahonia conferta* possesses the most similarities with *M. mioasiatica* rather than the *Mahonia oiwakensis* (Fig. 5c) and *Mahonia bodinieri* with slightly curved base.

After comparing the characteristics of basal leaflets with several possible and representative species of *Mahonia* (Table 1), the newly discovered fossil with oblong shape, truncate and straight base, small amount of teeth, is most similar to *M. conferta* of Group Orientales (Fig. 5b). The difference between them is that the leaflet of *M. mioasiatica* is smaller in size, but the first pair of teeth below the leaf apex comparatively larger than *M. conferta* (Fig. 5a, b). *M. conferta*, the nearest living relatives (NLR) is now scatteredly distributed in southeast Yunnan, south Sichuan, south Chongqing and northwest Jiangxi (Fang et al. 2011).

## Morphological comparison with fossil *Mahonia*

The leaf architecture of *M. mioasiatica* suggests that it belongs to Group Orientales. Güner and Denk (2012)

**Table 1** Morphological comparison between Mahonia mioasiatica and basal leaflet of several extant species

| Taxa | Leaflet shape | Leaflet base | Adaxial side base of leaflet | Abaxial side base of leaflet | Number of teeth each side |
|---|---|---|---|---|---|
| *Mahonia mioasiatica* J. Huang *et* Z. K. Zhou | Oblong | Truncate | Straight | Straight | 2–4 |
| *Mahonia bealei* (Fortune) Pynaert | Oblong | Obtuse | Straight | Curved | 2–4 |
| *Mahonia bodinieri* Gagnep. | Obovate–oblong | Obtuse | Curved | Curved | 3–5 |
| *Mahonia bracteolata* Takeda | Ovate to lanceolate | Obtuse | Straight or slightly curved | Curved | 3–6 |
| *Mahonia breviracema* Y.S. Wang *et* P.G. Xiao | Ovate | Acute | Slightly curved | Slightly curved | 3–4 |
| *Mahonia conferta* Takeda | Oblong | Truncate | Straight | Straight | 2–4 |
| *Mahonia duclouxiana* Gagnep. | Oblong | Truncate | Straight | Straight | 3–5 |
| *Mahonia eurybracteata* Fedde | Ovate to lanceolate | Acute | Slightly curved | Curved | 3–6 |
| *Mahonia fortunei* (Lindl.) Fedde | Obovate to oblong | Acute | Straight | Straight | 3–5 |
| *Mahonia gracilipes* (Oliv.) Fedde | Oblong | Acute | Curved | Curved | 2–4 |
| *Mahonia hancockiana* Takeda | Oblong–lanceolate | Obtuse | Curved | Curved | 2–4 |
| *Mahonia japonica* (Thunb.) DC. | Oblong | Obtuse | Straight | Curved | 2–5 |
| *Mahonia napaulensis* DC. | Elliptic to ovate | Truncate | Straight | Straight | 2–5 |
| *Mahonia nervosa* (Pursh) Nutt. | Ovate | Obtuse to truncate | Straight | Curved | 4–9 |
| *Mahonia nitens* C.K. Schneid. | Narrowly oblong | Acute | Slightly curved | Slightly curved | 3–4 |
| *Mahonia oiwakensis* Hayata | Oblong–elliptic | Truncate | Slightly curved | Slightly curved | 2–4 |
| *Mahonia paucijuga* C.Y. Wu ex S.Y. Bao | Ovate to oblong | Acute | Curved | Curved | 5–8 |
| *Mahonia polyodonta* Fedde | Oblong | Obtuse | Slightly curved | Curved | 3–8 |
| *Mahonia shenii* Chun | Obovate to oblong | Acute | Curved | Curved | 0–2 |
| *Mahonia taronensis Hand.–Mazz.* | Ovate to lanceolate | Acute | Slightly curved | Curved | 3–5 |

This statistics is based on leaflets closest to the base and may not be representative of the other leaflets

reviewed *Mahonia* fossils from Europe and North America and hypothesized their group affinity. We used their classification as a basis for choosing taxa for a morphological comparison between the fossil species and species belonging to the 'palmate-venation' group of Group Orientales. Due to the transitivity between Group Orientales and Section Horridae in Group Occidentales, fossils with this unfixed leaf type is positioned in the "Horridae-Orientales Intermediate Type".

The leaflet shape of Group Orientales fossils can be grouped into four main types based on shape, height: width ratio and number of teeth (Table 2): (1) The Nervosa leaf type has an ovate leaflet with many small teeth similar to extant *M. nervosa* (Pursh) Nuttall, e.g. the fossil species *M. heterophylla*, *M. trainii* Arnold and *M. somaensis* Güner *et* Denk; (2) The Simplex leaf type is oblong and has an L:W ratio <2, with a small number of coarse teeth, similar to the fossil *M. simplex* (Newberry) Arnold, e.g. *M. grimmii* Güner *et* Denk, *M. martinezii* Ramirez *et* Cevallos-Ferriz;

**Table 2** Morphological comparison between different types of fossil leaflet belong to Group Orientales of *Mahonia*

| Type | Leaflet shape | Height: Width | Teeth each side | Size of teeth | Representative fossil species |
|---|---|---|---|---|---|
| Nervosa type | Ovate | 4 > H:W > 3 | 7–13 | Small | *M. heterophylla, M. trainii, M. somaensis* |
| Simplex type | Oblong | <2 | 2–4 | Coarse | *M. simplex, M. grimmii, M. martinezii* |
| Fortunei type | Oblong to lanceolate | >2 | 3–5 | Basal leaflet coarse | *M. virginiae* |
| Malheuren type | Linear | >4 | 5–9 | Small | *M. malheurensis, M. subdenticulata* |

(3) The Fortunei leaf type has an oblong to lanceolate leaflet and length:width (L:W) ratio >2, with relatively numerous teeth similar to extant *M. fortunei*, e.g. *M. virginiae* Macovei *et* Givulescu; (4)The Malheuren leaf type has linear leaflets and a L:W ratio >4, e.g. *M. malheurensis* Arnold, *M. subdenticulata* (Lesquereux) MacGinitie. The newly discovered fossil *M. mioasiatica* has a Simplex type leaflet based on these characteristics.

*Mahonia simplex* has the Simplex leaf type with a small number of teeth. This species was widespread in North America from the early Oligocene to the middle Miocene (Axelrod 1964, 1985, 1998; Becker 1969; Lakhanpal 1963; Meyer and Manchester 1997; Renney 1972). The shape and number of teeth of *M. mioasiatica* and *M. simplex* are very similar, however they differ in the shape of the base of the leaflet. In *M. simplex,* the base is rounded (base angle <180°), but in *M. mioasiatica* the base is truncate (base angle = 180°).

*M. simplex* was merged with *M. grimmii* by Güner and Denk (2012). However, there are two important differences between these species. The leaf shape of *M. grimmii* is narrower and ovate, whereas the leaf shape of *M. simplex* is relatively wide and oblong. Additionally, the asymmetrical base of the leaflet in *M. simplex* (40°–60° between the midvein) is larger than in *M. grimmii* (75°–85° between the midvein). Even though we can observed the shape shifting of the leaflets in one species of *Mahonia*, but considering the incompleteness of fossil species, where only part of the whole plant may be preserved, we suggest that *M. simplex* should remained a distinct species from *M. grimmii*.

*Mahonia martinezii* is another fossil species from Oligocene deposits in Mexico (Ramı́rez and Cevallos-Ferriz 2000). This species possesses a similar leaflet shape, but the secondary vein runs straight into the tip of the tooth, whereas the secondary vein is curved in *M. simplex* and *M. mioasiatica*.

Some fossils of Sect. Horridae, such as *M. marginata* (Lesquereux) Arnold (Orientales–Horridae Intermediate type) and *M. obliqua* MacGinitie (Horridae type) from the upper Eocene Florissant Beds (MacGinitie 1953), as well as *M. creedensis* Axelrod (Horridae type) from the Oligocene Creede Flora (Axelrod 1987) and *M. bilinica* Kvaček and Bůžek from Europe (Kräusel 1938) have morphological similarities to *M. mioasiatica*. However, these taxa have stronger secondary veins pinnate and much coarser dentition (especially on the long apex of the leaflet) than in Group Orientales.

## Fossil history of Genus *Mahonia*

The oldest known fossils of this genus date from the Eocene (Chadronian, 37.8–33.9 Ma) in the Florissant flora, Colorado, western North America (MacGinitie 1953; Manchester 2001), where there are three known *Mahonia* species: *M. marginata* (Horridae-Orientales Intermediate Type), *M. obliqua* (Horridae Type) and *M. subdenticulata* (Orientales Type). In the upper Eocene to lower Oligocene John Day Formation in Oregon, there are two species of pinnate-venation Occidentales Type (Manchester 2000; Meyer and Manchester 1997) (Fig. 6a). This indicates that three lineages and an intermediate type had already differentiated by the late Eocene. Thus, North America was probably the center of origin of *Mahonia*. Additionally, the diversity present in the fossil record of the Eocene suggests that the genus diverged from close relatives earlier.

Fossils of Group Occidentales also appeared during the Oligocene. Therefore all three clades were present and were diverse in the Oligocene (Becker 1959, 1962, 1969, 1972; Hollick 1929; Lakhanpal 1963; Meyer and Manchester 1997; Myers et al. 2002) and expanded their distribution. The Orientales dispersed south to Central America (Ramı́rez and Cevallos-Ferriz 2000) (Fig. 6b). During this Epoch, three clades co-existed in North America and left abundant fossil records, making it a paleo-biodiversity center of the genus. Meanwhile, only one clade was present in Europe, as suggested by the presence in the Czech Republic and Germany of a single species belonging to the Sect. *Horridae* (Hably et al. 2000; Köhler 1998; Weyland 1941). Since no fossils of *Mahonia* had previously been found in East Asia, this suggested that *Mahonia* probably dispersed to Europe before dispersal to East Asia.

From the Oligocene to the Miocene, fossil records show the dispersal and differentiation of *Mahonia* in Europe (Geissert et al. 1990; Hably et al. 2000; Kovar-Eder et al. 2006; Kräusel 1938; Kvaček and Bůžek 1994; Kvaček et al. 2011; Macovei and Givulescu 2006; Mihajlovic 1996; Saporta 1866; Stephyrtza 1971; Takhtajan 1974) (Fig. 6b). The species of Group Occidentales may have dispersed

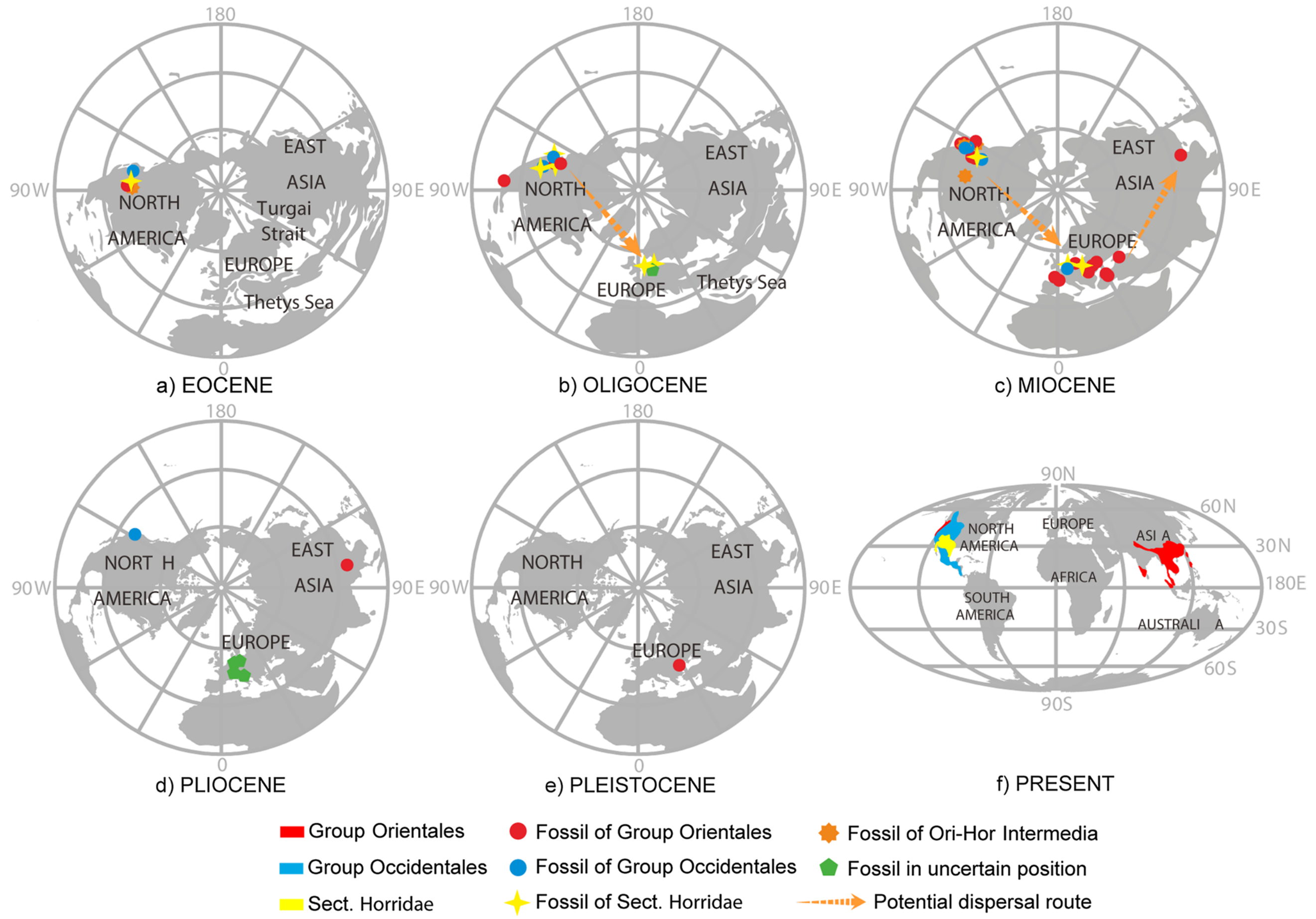

**Fig. 6** Fossil history maps and potential dispersal routes of *Mahonia* during the Cenozoic. The maps cover 6 time intervals, i.e. Eocene (ca. 40 Ma), Oligocene (ca. 30 Ma), Miocene (ca. 20 Ma) based on Blakey (2010), Pliocene (ca. 3 Ma) and Pleistocene (ca. 1 Ma) based on current world map. For detailed fossil records of genus *Mahonia*, see supplementary material available online

from North America through the NALB at that time. Europe became a second biodiversity center of *Mahonia* with a similar number of species recorded in Europe and in North America (Güner and Denk 2012). *Mahonia* dispersed through western Asia (Turkey) in early Miocene (Güner and Denk 2012) as the Turgai Strait receded, and *Mahonia* became adapted to different environments and finally reached East Asia, which will be discussed in the following section (Fig. 6c).

In the Pliocene and Pleistocene, most *Mahonia* fossils from Europe are seeds of *M. staphyleaeformis* (Mai and Walther 1988; Martinetto 2001; Martinetto et al. 1997) (Fig. 6d). Güner and Denk (2012) considered this species as a member of Group Occidentales, so its habitat may have been a summer-dry Mediterranean climate. However, Martinetto and Vassio (2010) indicate that the palaeovegetation of this fossil flora is similar to the broadleaved evergreen forest currently present in south China. The Romanian Pliocene fossil that belongs to Group Orientales was the latest known occurrence of *Mahonia* in Europe (Givulescu 1979) (Fig. 6e). During this period, *Mahonia* diversified in East Asia. The *Mahonia* fossil from the Pliocene Tuantian flora is considered to be similar to the modern species *M. fortunei* (Wu 2009). The extirpation of *Mahonia* in Europe was probably caused by climate change after the Pliocene (Kovar-Eder 2003), forming the modern disjunct pattern of the genus (Fig. 6f).

## Biogeographic implications

In the Cenozoic, plants could disperse from North America to East Asia via three possible pathways: Bering Land Bridge (BLB), North Atlantic Land Bridge (NALB) and Long Dispersal (LD).

Long dispersal, such as accidental dispersal across oceans among birds, is an unpopular hypothesis among biogeographers because it happens highly randomly in nature. It is almost impossible to falsify and usually can not be linked to specific abiotic events (McGlone 2005; Milne 2006). Before the bridge sundered 5.4–5.5 Ma ago,

**Table 3** Morphological and ecological comparison between clades of *Mahonia* species (Güner and Denk 2012; Whetstone et al. 1997; Ying et al. 2001)

| Clade | Secondary veins | Distribution | Climate | Habitat/vegetation type |
|---|---|---|---|---|
| Group Occidentales | Pinnate | NW. to C. North America | Desert, steppe, summer-dry, | Rocky area, grassland, chaparral, scrubland, open woodland |
| Group Occidentales Section Horridae | Chiefly pinnate, basalmost pair palmate | SW. North America | Desert, steppe, summer-dry | Desert, rocky area, grassland, chaparral, scrubland, open woodland |
| Group Orientales (Asia taxa) | Palmate | Himalayas, E., SE. Asia and S. India | Winter-dry, fully humid | Broadleaved evergreen forest, mixed broadleaved evergreen and deciduous forest, tropical rainforest |
| Group Orientales (*M. nervosa*) | Palmate | W. North America | Summer-dry | Rocky area, open woods, redwood forest, temperate rainforest |

the BLB was a possible dispersal route, (Milne and Abbott 2002). It seems to have acted as an important corridor for many temperate disjunct lineages. However, the NALB, available until 15 Ma ago, was a much more likely route for thermophilic elements of the flora (Milne and Abbott 2002; Wen et al. 2010), such as the subtropical *Mahonia*.

Donoghue et al. (2001) once defined ‘Atlantic track’ as a pattern that applies to groups with transatlantic disjunct distribution that have representatives in America, west Eurasia and China, but excluding Japan. In Japan, Tanai and Suzuki (1963) reported the only fossil record of *Mahonia*, ‘*Mahonia lanceolata*’, the figures of the specimens is vague, teeth are tiny and can hardly be seen, and it’s also hard to make sure it’s belongs to *Mahonia* according to author’s description. Therefore, we consider this fossil record as an uncertain one. Today, there is no native species in Japan, as *M. japonica* (Thunb.) DC. is distributed in south China and Taiwan. It was introduced from Taiwan and described after its cultivation in Japan. Therefore, the lack of fossil evidence along the BLB (no fossil record in Alaska, Far-East Russia and Japan), and the lack of extant species in Japan make the ‘Atlantic track’ more plausible than the BLB.

The representative of Group Orientales, *M. simplex*, was widely spread in North America during the Oligocene and Miocene (Axelrod 1964, 1985, 1998; Becker 1969, 1972; Lakhanpal 1963; Renney 1972). In West Asia (Turkey), the early Miocene species *M. grimmii* shared a similar leaf morphology with *M. simplex* (Güner and Denk 2012). In the western part of East Asia, easternmost of the Himalayas, the Miocene *M. mioasiatica* is also a typical Simplex Type fossil. Their morphological similarities suggest a close relationship. Moreover, the ages of these records support the dispersal direction from North America to West Asia and then to East Asia. Because the modern distribution of *Mahonia* extends to the western Himalayas, a Himalayas pathway seem plausible to explain the route from Europe to Asia based on the West Asia fossil (Güner and Denk 2012) and East Asia fossil (this study) (Fig. 6).

The adaption of *Mahonia* species to different environments may explain the disjunction pattern of the genus today. Billings (1970) and Wu (1983) distinguish two subtypes of Eastern Asia (EA) and North America (NA) flora disjunction: (1) EA–east(e)NA disjunctive distribution; (2) EA–west(w)NA disjunctive distribution. These two disjunction sub-types are mainly based on the climatic difference between eastern North America and western North America today.

In Köppen’s Climate Classification (Köppen 1936, McKnight and Hess 2000), the climate of East Asia and eastern North America is mainly warm temperate (Cfa/Cfb) and are found on the eastern side of continents between the 30° and 50° latitude. Summers are hot and are often the wettest season of the year. On the contrary, the climate in west coast of North America is mainly characterized by dry-summer or Mediterranean climates (Csa/Csb) and are usually occurs on the western side of continents between the 30° and 50° latitudes. Summers are hot, dry and winters are often the wettest season.

In the first disjunctive type, EA–eNA, where subtropical broadleaved evergreen forests or temperate deciduous forests are mainly found. The vast majority of EA–NA disjunct taxa, such as *Liquidambar* and *Lindera* (Wu 1983), are growing under this type of climate. This disjunction pattern can be explained by the retreat of the previously widespread Cenozoic evergreen broadleaved forest in the Northern Hemisphere (Mai 1995; Manchester et al. 2009; Milne and Abbott 2002). In the second disjunction type, EA–wNA, the vegetation is mainly made of subtropical evergreen sclerophyllous forest. These forests include some taxa, such as *Calocedrus, Tsuga*, *Mahonia*, which are well suited to this climate. More than 120 genera have the EA–NA disjunction (Wu 1983), but only a few taxa belong to

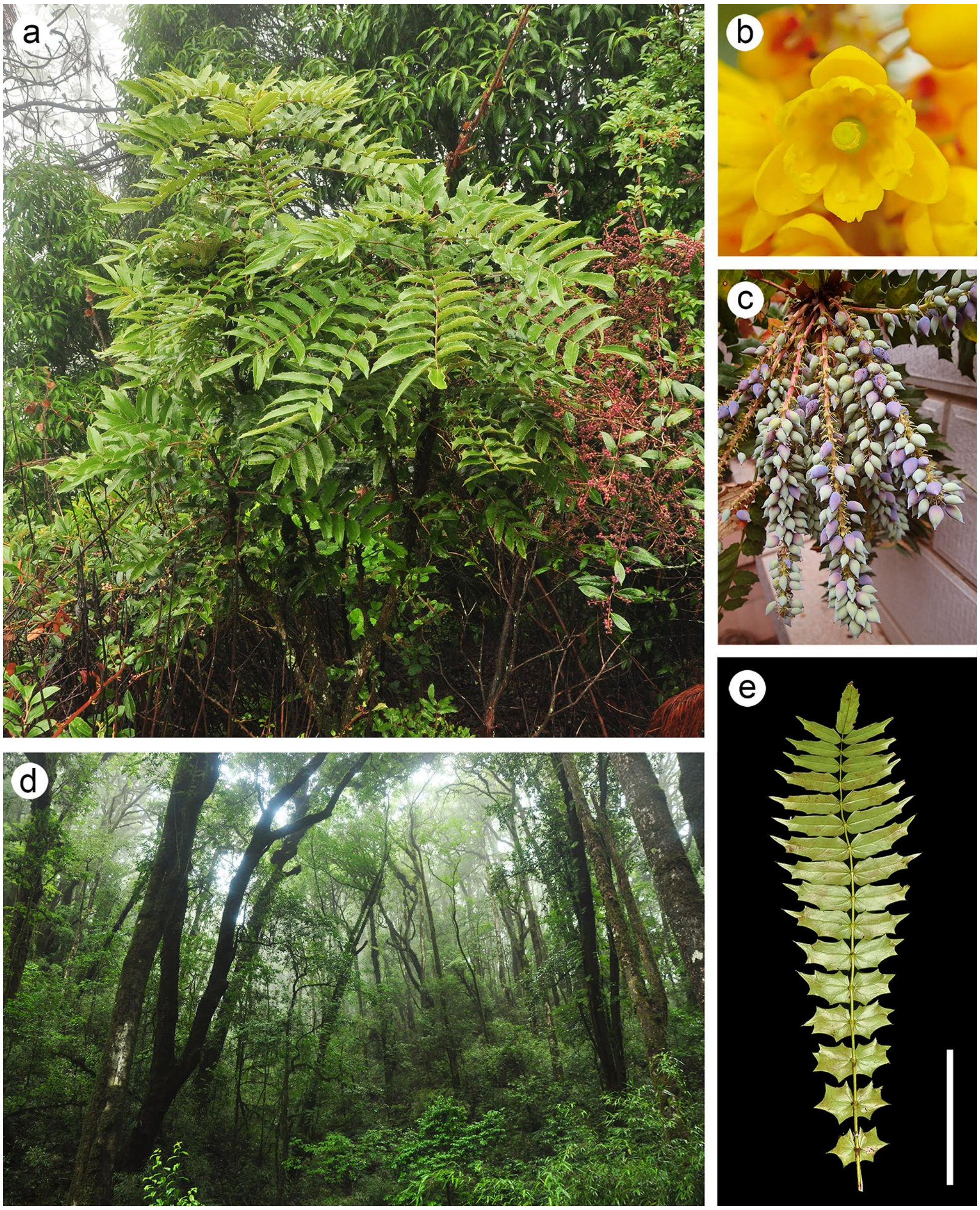

**Fig. 7** Extant *Mahonia*, their habitat and biology. **a** *M. duclouxiana* tree in the forest window in Mt. Ailaoshan, Yunnan, China, individuals of this community are dwarf shrubs when under the shady forest. **b** Flower of M. duclouxiana, the trimerous perianth indicate its basal position in the angiosperm phylogeny tree. **c** *Purple colored* berries of *M. conferta*. **d** Mid-Montane Humid Evergreen Broad-Leaved Forest in Mt. Ailaoshan, Yunnan. **e** Leaflets variation in *M. conferta*, leaflets increasing in length but decreasing in width from base to apex, and, shift from short with coarse tooth to long with drip-tip. *Scale bar* 10 cm in **e**

EA–wNA disjunction. This might be due to the large climatic differences between west coast of North America and East Asia. This phytogeographic pattern can be explained by a peculiar remnant of Cenozoic forest retreat or by the migration through Bering Landbridge (Shi et al. 2012).

In the *Mahonia* genus, the ecology of species belonging to Group Occidentales is different from Orientales Group (Table 3). While the New World taxa are commonly adapted to the summer-dry climates (West coast type) and open landscapes, the Old World taxa prefer winter-dry climates (East coast type) and shady forest habitats (Fig. 7a, d).

The only Orientales species distributed in western North America is *M. nervosa*. It was placed in Group Orientales as a sister to all other East Asian species based on molecular evidence (Kim et al. 2004) and suggests that *M. nervosa* has been isolated from the other East Asian Orientales species for a long time. Therefore, *M. nervosa is* hypothesized to be descendant of the earliest diverging Group Orientales species in North America. The habitat of *M. nervosa* is usually redwood forest or temperate rainforest—similar to its Orientales relatives on the other side of the Pacific Ocean, and different from the neighboring living Occidentales species.

In the Wenshan flora, co-occurring taxa, such as *Ailanthus* (Su et al. 2013), *Bauhinia* (Meng et al. 2014), *Berchemia, Castanopsis*, *Cinnamomum*, *Engelhardtia*, *Eurya, Exbucklandia*, *Machilus*, *Photinia* and *Quercus*, also suggest a warm and wet subtropical climate. Subtropical evergreen broadleaved forest is thought to have been widespread in the Northern Hemisphere during the early Cenozoic (Mai 1995; Manchester et al. 2009; Milne and Abbott 2002) and this habitat was suitable for *Mahonia* species from Group Orientales (Fig. 7a, d). These species might have been dispersed over half of the Northern hemisphere and reached the southern part of East Asia that had a favorable forest environment. Since molecular dating estimates support the hypothesis that the Miocene is an important period in the differentiation of extant lineages (Wen et al. 2010), *Mahonia* probably underwent an additional period of diversification in East Asia to form the current biodiversity center.

## Conclusion

We describe a new fossil species of *Mahonia* from eastern Asia. Today, the genus has a transpacific disjunct distribution with a biodiversity center in Asia. The fossil is the oldest record of *Mahonia* in East Asia and it provides evidence that *Mahonia* appeared in East Asian forests by the late Miocene. *Mahonia mioasiatica* sp. nov. bears a close morphological resemblance to the extant species *M. conferta* from Group Orientales.

Our hypothesis is that migration of the genus between North America and eastern Asia would likely have taken place over the North Atlantic Land Bridge rather than the Bering Land Bridge or long distance dispersal. Over geologic time the geographic area with the highest *Mahonia* species diversity shifted from western North America to Europe and then to southwestern East Asia. Species in Group Orientales are the most widely dispersed lineage, possibly owing to their adaption to forest environments. The discovery of more fossil records and a comprehensive fossil and molecular study are needed to further corroborate and substantiate this hypothesis.

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