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Research paper

From mesic to arid: Leaf epidermal features suggest preadaptation in Miocene dragon trees (*Dracaena*)

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ABSTRACT

Among the most prominent examples for the disjunct distribution of xeromorphic-sclerophyllous plants in Macaronesia and eastern Africa–Arabia, referred to as the Rand flora biogeographic pattern, is the "dragon tree group" within *Dracaena* (Asparagaceae). However, little is known about the evolutionary origin of this iconic group of semi-desertic trees. Here, we use exceptionally well-preserved fossils from western Anatolia to demonstrate range and ecological shifts of the lineage probably leading to some of the modern dragon trees. Compression fossils of apical leaf rosettes and detached leaves of *Dracaena tayfunii* spec. nov. were compared to modern *Dracaena* using the architecture of leaf-bearing branches, leaf morphology, and highly diagnostic leaf epidermal features observed with light and electron scanning microscopy. The palaeoecology of *Dracaena* was inferred using the depositional setting and associated plant taxa. The ca. 16 million-year-old (Ma) *Dracaena* from western Anatolia shows a character combination restricted today to the Macaronesian dragon tree, *Dracaena draco*: (1) Leaves are arranged in terminal rosettes; (2) leaves are ensiform, oblong, with a conspicuously dilated base (pseudo-sheath); and (3) leaf epidermis is strongly papillate with sunken stomata overarched by papillae of four neighbouring epidermal cells. Depositional setting, taphonomy, and the fossil plant association indicate that the Miocene *Dracaena* either grew in seasonally dry swamps within a complex fluvial–lacustrine environment or on adjacent slopes under a humid, warm climate. Hence, semi-desertic modern dragon trees allied to *D. draco* displaying distinct xeromorphism may have originated from a western Eurasian mesic lineage that had evolved xeromorphic characteristics by the Miocene. The morphology of this mesic ancestor later enabled the lineage to colonize and survive in the semi-desertic environments where it is found today. The new fossil species of *Dracaena* represents a classic example of pre-adaptation and niche shift.

1. Introduction

The genus *Dracaena* (Asparagaceae according to APG III, 2009) comprises about 120 species distributed across the wet to dry forest spectrum in the Old World tropics and ranges as far east as New Guinea, with outliers in Hawaii, the Canary Islands, Cape Verde Islands and Madeira, the Caribbean and Central America (Govaerts, 2012). Highest levels of species diversity occur in tropical Africa and Southeast Asia. *Dracaena* species occur in a variety of habitats including tropical monsoon, semi-evergreen, and evergreen rain forests, as well as specialized habitats such as escarpments, littoral forest edges, and as facultative rheophytes in riverbeds with strongly fluctuating water levels (Engler, 1908, 1910a,b; Bos, 1998).

Only a handful of tree species are typical of Mediterranean and semi-desertic habitats under warm and dry or seasonally dry subtropical and tropical climates (Engler, 1908; Marrero et al., 1998; Brown and Mies, 2012). They are commonly referred to as "dragon tree group" (Marrero et al., 1998) and are considered to be closely related on morphological grounds (Baker, 1898; Klimko and Wiland-Szymańska, 2008; Wilkin et al., 2012). Molecular data to test this assumption are currently not available. Taxa comprised within this group show a distinct west–east disjunction. *Dracaena draco* (L.) L., *D. draco* subsp. *ajgal* Benabid et Cuzin, and *Dracaena tamaranae* Marrero Rodriguez et al. thrive in Macaronesia and western Morocco; *Dracaena cinnabari* Balfour f. (Socotra), *Dracaena ombet* Heuglin ex Kotschy et Peyritsch, *D. ombet* subsp. *schizantha* (Baker) Bos (northeastern tropical Africa), and *Dracaena serrulata* Baker (western and southern Arabian Peninsula) occur along the eastern margin of Africa (Fig. 1). According to Bramwell (1985), also *Dracaena ellenbeckiana* Engler from Ethiopia and Uganda might belong to this group of ecologically and morphologically related trees. Recently, Wilkin et al. (2012) stated more precisely which morphological characters define the dragon tree group: (i.) closely packed leaves at branch apices, (ii.) differentiated leaf sheaths, (iii.) leaves lacking costae, (iv.) flowers with free tepals, and (v.) free stamens with thickened filaments. In addition, Wilkin et al. (2012) suggested a closer relationship with a number of species of Thailand that share the above-mentioned characteristics with the traditionally defined dragon tree group but are not xeromorphic species (cf. Klimko and Wiland-Szymańska, 2008; this study).

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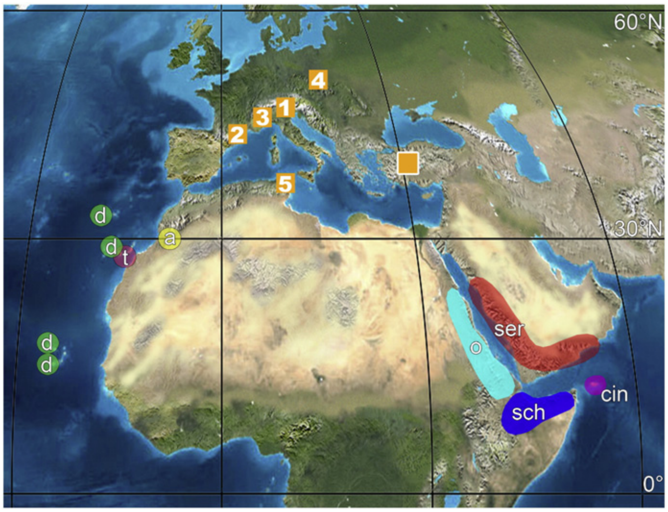

Fig. 1. Map of western Eurasia and Africa north of the equator showing the modern range of xeromorphic members of the dragon tree group and fossil records linked with *Dracaena*. Rectangles denote fossil occurrences. Macrofossils, apical portions of branches and foliage: 1 = River Chiavone, middle Oligocene; 2 = Aix en Provence, middle Oligocene; 3 = Armissan, early Miocene; Dispersed pollen: 4 = South Bohemia, early/middle Miocene; 5 = North-eastern Tunisia, Neogene. Blank square. *Dracaena tayfunii*. See Table 1 for references. Rounded outlines denote ranges of modern members of the dragon tree group. d = *Dracaena draco*; a = *D. draco* subsp. *ajgal*; t = *Dracaena tamaranae*; o = *Dracaena ombet*; sch = *D. ombet* subsp. *schizantha*; ser = *Dracaena serrulata*; cin = *Dracaena cinnabari*.

The fossil record of *Dracaena* is poor (Table 1). Oldest macrofossils ascribed to the genus are leaf imprints from middle Oligocene sediments of Italy (Massalongo, 1858) and France (Saporta, 1861, 1862, 1873a,b), and dispersed pollen has been reported from the Miocene of Tunisia and Bohemia (Van Campo and Sivak, 1976). Because macrofossils were exclusively based on impression fossils, the generic assignment or inferred generic affinity has subsequently been questioned (e.g. Horwood, 1912).

The dragon tree group is among the most cited examples of so-called 'Rand flora' elements (Axelrod, 1975; Bramwell, 1985; Marrero et al. 1998). The dry regions of northern Africa including Macaronesia and the Arabian Peninsula harbour plant species displaying taxonomic affinity with the xeric flora of southern Africa. Based on this biogeographic pattern, the Rand flora hypothesis was formulated at the end of the 19th century (Christ, 1885, 1892 as "*flore ancienne africaine*", "*flore marginale*"), assuming that a number of xeromorphic-sclerophyllous plant taxa distributed in eastern Africa, the Sahel, the Sahara, and the Maghreb are related and derived from taxa occurring in southern Africa or that an archaic xeric pan-African flora had provided the stock for the modern disjunct elements of the Rand flora (reviewed in Quezel, 1978; Maley, 1980; Le Houérou, 1995). Le Houérou (1995) lists 34 families and 222 extant genera found in South Africa that meet the requirements of Rand flora elements. Among these, the families Asteraceae and Poaceae are represented with over 50 and over 25 genera, respectively. In addition, Asparagales (including *Dracaena*) and Aizoaceae are represented by 10 or more genera, of which many are succulents. Today, Rand flora elements are mainly restricted to areas along the margin of the African continent not covered by deserts or equatorial monsoon forest and rainforest and to mountain ranges of the Sahara (Le Brun, 1971; Le Houérou, 1995).

The origin of the dry-adapted Rand flora has traditionally been linked to early Cenozoic arid vegetation stretching across southern Africa (Christ, 1892; Axelrod and Raven, 1978; Maley, 1980; see also Jacobs, 2004; Jacobs et al., 2010). Subsequent area disruptions during the Neogene that would have caused the modern Rand flora pattern have commonly been discussed within the context of a sclerophyllous palaeovegetation thriving in habitats similar to those of the modern species (Bramwell, 1985, p. 3, "*a historically more widespread semi-arid flora*"). Axelrod (1975), and others, suggested that, for example, the modern members of the dragon tree group within *Dracaena* were derived "*from the mesic Tertiary rainforests and savannahs of Africa proper*" (Axelrod, 1975, p. 322). The replacement of a savannah-woodland belt in the Sahara region by desert in the late Miocene (Axelrod and Raven, 1978; Schuster et al., 2006) would have caused the modern disjunct distribution of many Rand flora elements. Reviewing the fossil record, Marrero et al. (1998) suggested that the dragon tree group originated along the northern shores of the Tethys as part of a thermo-sclerophyllous flora. Radiation from humid-temperate habitats accompanied by ecological shifts as an additional explanation has not previously been considered to contribute to the Rand flora pattern. Such a change is known from the Mediterranean region, where the present summer-dry climate and Mediterranean woody vegetation evolved only during the late Cenozoic, partly from a humid warm-temperate stock (Suc, 1984; Mai, 1995).

In this paper, we report *Dracaena* fossils displaying diagnostic characteristics of the dragon tree group from early middle Miocene (ca. 16 Ma) sediments of western Anatolia. Based on the taphonomic setting, the floristic composition of the fossil plant assemblage, and the sedimentological context, the palaeovegetation and palaeoenvironment were reconstructed. The new species raises interesting questions about the evolutionary origin, the palaeobiogeography, and the palaeoecology of this group of plants in particular, and of the Rand flora in general.

2. Material and methods

The fossils were collected in the spring of 2010 and 2012 from four different sites in the Soma coal basin, Soma-Manisa, western Anatolia: Deniş 1, 640 m a.s.l., 39°15′07.73″N, 27°43′58.56″E; Dedetaşı, 840 m a.s.l., 39°17′04.85″N, 27°44′47.72″E, Deniş 1 + 2, 39°14′36″N, 27°44′10″E, and Eynez, 39°05′35″N, 27°32′56″E. Plant macrofossils originate from marls deposited above the lower coal seam of the Soma Formation. The slowly subsiding, fault-controlled karst-based intermontane Soma coal basin was the result of early Cenozoic collision of the Eurasian and Anatolian plates (Inci, 2002). Fluvial–lacustrine deposits from the freshwater carbonate-dominated Middle Coal succession indicate a varied landscape including lowlands with swamp forests, patches of ephemeral wetlands, lakes and an anastomosing river system, followed by well-drained slopes and mountains (Inci, 2002; Fig. 2B). Volcanic ashes on top of the lower coal seam of the Soma Formation represent the base of the Middle Coal succession and have been radiometrically dated as 17.3 ± 0.4 Ma (late Burdigalian; Takahashi and Jux, 1991); the marlstone unit containing the plant fossils reported here is just above this layer. The composition of small mammals in the lower coal seam also indicates a Burdigalian age (European Mammal Faunal Zone 3, MN3; Kaya et al., 2007). Therefore, the conservative age estimate used for the present study is ca. 16 Ma for the age of the plant-bearing sediments above the lower coal seam.

While only a single remain of *Dracaena* was recovered during the field campaign in 2010 from site Deniş 1 + 2, numerous fossils of *Dracaena* were recovered in spring 2012. Compression fossils and impression fossils without preserved cuticle were photographed and measured. Many detached leaf fossils (compressions) had intact cuticle, which was removed from the slabs and stored in plastic bags in water–glycerin mixture. Cuticles were prepared in the lab using Schulze's solution (HNO_3 and $KClO_3$) and KOH (5%), and rinsed with distilled water. For light microscopy investigation the rinsed cuticles were mounted on a slide in glycerin and covered with a coverslip. Standard procedures were followed for scanning electron microscopy (SEM) investigations. Pieces of cuticle were fixed to a stub and coated with gold and the outer and inner leaf surfaces were observed using a Hitachi S-4300 SEM at 3 kV and 5 mA with a working distance of 35 mm.