



A new species of the wild dragon tree, *Dracaena* (Dracaenaceae) from Gran Canaria and its taxonomic and biogeographic implications

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The arborescent taxa of *Dracaena* which form the dragon tree group comprise five species found in Macaronesia, Morocco (*D. draco*), East Africa (*D. ombet*, *D. schizantha*), Arabia (*D. serrulata*) and the island of Socotra (*D. cinnabari*). A new species of dragon tree, *Dracaena tamaranae* A. Marrero, R.S. Almeida & M. González-Martín, is described from Gran Canaria, Canary Islands. This new species differs from *D. draco*, the only other *Dracaena* species currently known in Macaronesia, in having a growth form and inflorescence type and leaves more similar to the East African and Arabian species of *Dracaena*. In contrast, *D. draco* appears to be related to *D. cinnabari*. In this paper, we also present a study of the taxonomy, habitat and ecology of all the species of the dragon tree group. These are found in thermo-sclerophyllous plant communities of tropical–subtropical regions which are rather xerophilous and have a rainfall range of 200–500 mm. Our study indicates two independent colonization events for *Dracaena* in Macaronesia. In addition, we suggest that the dragon tree group provides an example of two major biogeographical disjunctions between East and West Africa. We postulate that this group has a Tethyan origin, a hypothesis supported by fossil and palaeoclimatic data, and thus parallels the distribution and dispersal pattern of other taxonomic groups.

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ADDITIONAL KEY WORDS:—Canary Islands – corology – ecology – Macaronesia.

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INTRODUCTION

The genus *Dracaena* comprises approximately 60 species (Mabberley, 1990)—50 species *sensu* Friis (1992)—which are mainly found in tropical and subtropical Africa. At least 23 species occur in the Guinea-Congo region in western Africa (Bos, 1984). The genus also reaches Macaronesia, Arabia, Socotra, Madagascar, southeastern Asia, northern Australia, and one species (*D. americana* Donn. Sm.) is found in the neotropics.

The dragon tree group is formed of five arborescent species (i.e. *D. cinnabari* Balf. f., *D. draco* (L.) L., *D. ombet* Kotschy & Peyr., *D. serrulata* Baker and *D. schizantha* Baker), and provides one of the best known examples of disjunct distribution between Macaronesia, Morocco and East Africa.

Until the discovery of the new species described here, *Dracaena draco* was the only species found in Macaronesia. It occurs in the Madeira archipelago, where it has been reported for the islands of Madeira and Porto Santo, although it is currently regarded as extinct in the latter. This species also thrives in the Canary Islands, where it is currently found on all the islands. However, wild populations of this species are only known in Tenerife and Gran Canaria; it is likely, therefore, that the present populations of *D. draco* in the rest of the archipelago are of cultivated origin. *Dracaena draco* also reaches the Cape Verde Islands where it is found on the islands of São Nicolau, Santo Antão and Fogo, and it is considered extinct on the islands of São Vicente and São Tiago (Byström, 1960). *Dracaena draco* has been recently discovered in southern Morocco, in the Anti-Atlas region, where it is regarded as a distinct taxon: *D. draco* subsp. *ajgal* Benabid et Cuzin (Benabid & Cuzin, 1997).

Dracaena draco has been considered as closely related to the three species found in Socotra, *D. cinnabari* and East Africa, *D. ombet* (*D. orabet sensu* Engler, 1908), and *D. schizantha* (Balfour, 1883; Christ, 1885; Baker, 1898; Sunding, 1970). It is noteworthy that there is another species in Arabia (*D. serrulata*) which is usually ignored in accounts of the genus for the Red Sea region. These four East African and Arabian species have an allopatric distribution. *Dracaena cinnabari* is endemic to Socotra island where it thrives in the northeastern mountain range of Haggier (Balfour, 1883), mainly in the highlands of Mumi (Beyhl, 1995). *Dracaena serrulata* has a scattered distribution along the southwestern edge of the Arabian Peninsula, mainly in the hills of southern Medina and the El Asir mountains in Saudi Arabia; in the foothills of the highlands of Yemen and on northern slopes of Dhofar at Oman (Collenette, 1985; Miller & Cope, 1996). *Dracaena ombet* grows along the African hills which face the Red Sea; it is found in Jebel Elba in southeastern Egypt, Mount Erkowit in Sudan, escarpments of the Eritrean mountains and in the mountains of Djibouti

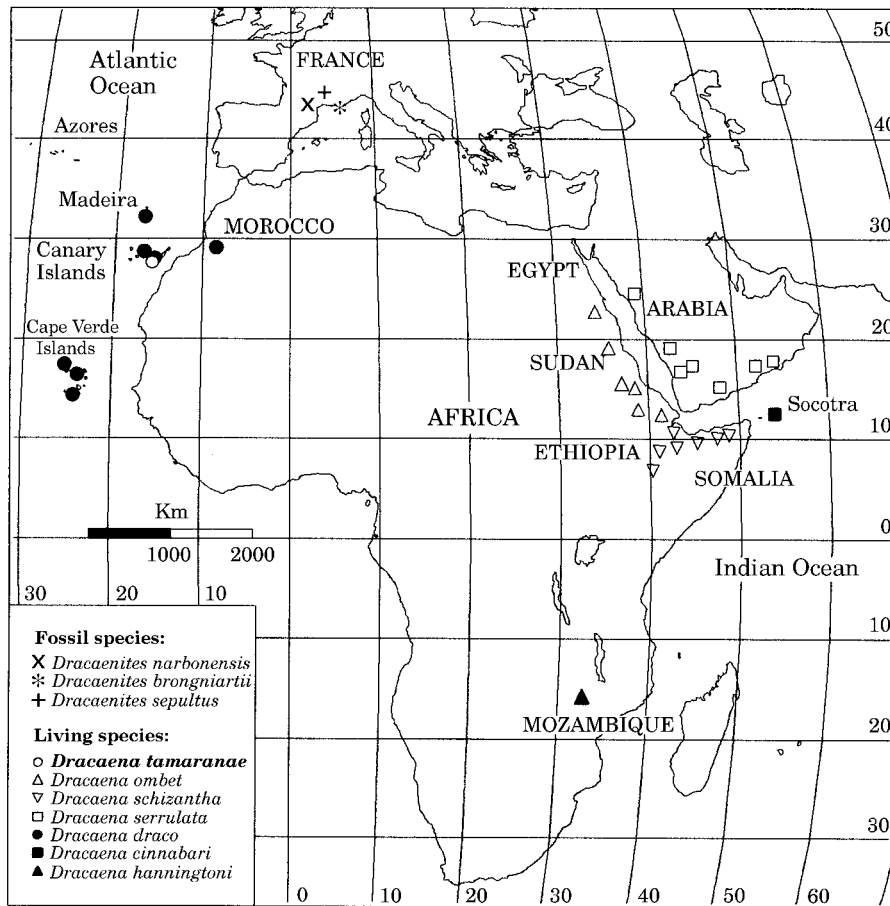


Figure 1. Distribution of the seven living species and three fossil species of the dragon tree group.

(Baker, 1897, 1898; Täckholm & Drar, 1973; Friis, 1992). Lastly, *D. schizantha* is found in north-facing escarpments of Harar in Ethiopia, in the mountains of Djibouti and in the northern mountains of Somalia to the Ahl Mountains where it almost reaches the Horn of Africa (Baker, 1877; Friis, 1992; Thulin, 1995). A further species, *D. hanningtoni* Baker, restricted to Mozambique, also appears to be related to the five species which comprise the dragon tree group (Baker, 1898) (Fig. 1).

Wild dragon trees are extremely rare in Gran Canaria, and it was only in the early 1970s that they were reported for the first time, in the western mountains of Tauro and in the Barranco de Arguineguín (Kunkel, 1972, 1973). Most recently the distribution of this species has been mapped by Rodrigo & Montelongo (1986). All these references identified the individuals as *D. draco*.

In the last 5 years one of us (R.S. Almeida) has undertaken extensive field studies relating to the distribution, phytogeography and conservation status of the wild dragon trees on Gran Canaria. As a result of these studies we were able to collect ripe fruits in 1994. Seedlings cultivated from these studies led us to the belief that the Gran Canaria individuals could not, in general, belong to *D. draco*.

There are several morphological differences between the seedlings of these two species. The seedling leaves of *D. draco* are flat whereas those of the new taxon are conduplicate. In addition, the young root of the Gran Canaria endemic is napiform. These obvious differences in juvenile characters did also extend to other traits of adults such as the shape and habit of the inflorescence or the articulation of the pedicels.

MATERIAL AND TAXONOMIC REFERENCES

To conduct this study we have used morphological studies of living material and also of herbarium specimens (Appendix). It is also based on a critical review of several morphological descriptions of the different species of the dragon tree group: Linnaeus, 1767; Webb & Berthelot, 1836–50; Hooker & Smith, 1851; Schweinfurth, 1868; Baker, 1877, 1894, 1897, 1898; Bentham & Hooker, 1880; Balfour, 1883, 1888; Engler, 1908; Brown, 1914; Andrews, 1956; Maire, 1958; Thonner, 1962; Täckholm & Drar, 1973; Beyhl, 1995; Thulin, 1995; Turland, 1995; Benabid & Cuzin, 1997.

DESCRIPTION

Dracaena tamaranae A. Marrero, R.S. Almeida & M. González-Martín, **sp. nov.**

PLANTA arborescens robusta, 6–10 m alta, ramificatione primaria trichotoma, rare tetrachotoma et ramificationibus posterioribus dichotomis vel simplicibus. CORTEX flavo-griseus, vix signis foliaribus notatus, leviter nitidus. PLANTULAE foliis equitantibus bilateralibus compressis, radicibus valde succulentis, primariis cylindrico-globosis, secundariis napiformibus. FOLIA subulata, canaliculata, leviter falciformia, 40–80 (110) × 3–4.5 cm, glauca, subtus leviter striata, margine omnino hyalina, ad basim incrassata cum pseudovagina fusco-rubinea, subamplexicauli, atque arcu manifesto et angusto, 10 (8–11) cm longo. INFLORESCENTIA paniculata complexa, glabra, tripinnata, gracilis, 80–100 cm, per totam longitudinem ramificata. PEDUNCULUS brevissimus. BRACTEAE basales foliis similes, ad apicem cito decrescentes in formam diminutam, primum ensiforme demum subulatae et lineares, acuminatae. FLORES 2–5 in fasciculis dispositi. PEDICELLI 2.25–3.25 mm longi, ad apicem articulati. BRACTEOLAE minutae, triangulares vel ovato-triangulares. PERIANTHIUM 9–15 mm, laete albo-viride; tepala oblongo-lineararia, interna paulum angustiora quam exteriora, basi connati tubo brevissimo. STAMINA quam tepala breviora, ad stigma sub anthesi adiacentia; filamenta 6.5–9 mm, connata ad 2 mm, leviter medio incrassata, non complanata; antherae 2 mm, flavo-virides. OVARIUM 3-loculare, 3.6 × 2.4 mm, ovulo in quoque loculo solitario. OVULUM stipitatum. STYLUS filiformis quam ovarium longior, 5.8 mm, stigmate capitato trilobulato. FRUCTUS glauco-virides, demum aurantiaci, globosi, 10–11.5 mm, vulgo monospermi. SEMINA globosa vel late ovoidea, leviter compressa, 6–7 mm.



Figure 2. Holotype of *Dracaena tamaranae* A. Marrero, R.S. Almeida & M. González-Martín, **sp. nov.**

Type. *Dracaena tamaranae* A. Marrero, R.S. Almeida & M. González-Martín. *Habitat* in Canaria Magna (Gran Canaria dicta) in loco dicto "barranquillo Andrés", 825 m supra mare, *loc. class. leg.:* A. Marrero, M. González-Martín & A. Quintana, die 31.vii.1997 (LPA:18525, *holotypus* in MA, Fig. 2). *Isotypi:* *ibidem* (*duplicata* in LPA, TFC, K), *idem*, R.S. Almeida, A. Marrero & A. Quintana, 20.vii.1997 (LPA: 18524 *cum duplicata* in MA, ORT, BM). (*Icon:* Fig. 3).

Additional material examined. *Dracaena tamaranae* A. Marrero, R.S. Almeida & M. González-Martín, Gran Canaria, San Bartolomé de Tirajana, los Vicentillos, leg.



Figure 3. *Icon: Dracaena tamaranae* sp. nov. A, habit. B, seedling. C, leaves. D, terminal branch with inflorescence. E, flowers. F, bracts. G, bracteoles. H, tepals. I, pistil. J, stamens. K, fruits. L, seeds.

R.S. Almeida & A. Marrero, 17.vii.1997 (LPA: 18521); *Ibidem*, Mogán, barranco de Arguineguín, Los Peñones, leg. R.S. Almeida & A. Marrero, 3.vii.1997 (LPA: 18517); *Ibidem*, los Gavilanes, R.S. Almeida, A. Marrero & M. González-Martín, 11.vii.1997 (LPA: 18518, 18519); *Ibidem*, El Palmarete, R.S. Almeida, A. Marrero & M. González-Martín, 11.vii.1997 (LPA: 18520); *Ibidem*, Barranquillo Andrés, leg. R.S. Almeida, A. Marrero & A. Quintana, 20.vii.1997 (LPA: 18522); *Ibidem*, *ex horto*, 193–194/96, A. Marrero, 26.vi.1997 (LPA: 18526, 18527) (seedling); *Ibidem*, barranco de Mogán, Los Laerones, leg. R.S. Almeida, A. Marrero & M. González-Martín, 19.viii.1997 (LPA: 18523).

HABIT arborescent, robust, 6–10 m high, primary branching trichotomous, rarely tetrachotomous and subsequent branches dichotomous or simple. BARK yellow-grey, barely marked by foliar scars, slightly glossy. SEEDLINGS: leaves equitant, bilateral and compressed, roots highly succulent with a cylindrical globose primary root and napiform secondary roots (Fig. 4A). LEAVES 40–80 (110) cm long, 3–4.5 cm wide, subulate and canaliculate, rather falcate, glaucous, rather striate below, hyaline-white entire margin, swollen at the base with a basal brown-reddish pseudo-sheath which is subamplexicaul and forms a patent and narrow arc 10 (8–11) cm long. INFLORESCENCE 80–100 cm long, panicle complex, glabrous, tripinnate, slender, branches dispersed along the main axis (Fig. 4B). PEDUNCLE very short. BRACTS basals are similar to the mature leaves, secondary bracts decrease rapidly in size, ensiform to subulate and linear, acuminate. FLOWERS 2–5 clustered. PEDICEL 2.25–3.25 mm long, articulate towards the apex. BRACTEOLES minute, triangular or ovate-triangular. PERIANTH 9.5–11 mm, bright greenish-white, tepals oblong-linear, inner tepals narrower than outer ones, joined at the base, tube very short. STAMENS shorter than tepals and adjacent to the stigma during anthesis; filaments 6.5–9 mm, joined 2 mm from the base, slightly swollen in the middle, unflattened; anthers 2 mm, yellow-greenish. OVARY trilocular 3.6 × 2.4 mm, with a single, stipitate ovule per locule. STYLE 5.8 mm, filiform, longer than the ovary; stigma capitate, trilobulate. FRUITS 10–11.5 mm globose, greenish, glaucous but orange when ripe, usually mono-spermous. SEEDS 6–7 mm globose to broadly ovoid and slightly compressed (Tables 1–4).

Dracaena tamaranae is a species restricted to the island of Gran Canaria, Canary Islands. This species is found between 400 and 900 m altitude, and along an arc in the southwestern region, from Fataga valley in the southern slopes to La Aldea valley in the west.

CONSERVATION STATUS

This species is extremely rare and is known from few localities. We propose that it merits CR status (Critically Endangered) in the IUCN (IUCN, Red List Categories, 1994). Although some populations are located within the network of Gran Canaria nature reserves (Act 12/94 Espacios Naturales de Canarias) there are still many unprotected individuals. There is a strong need to establish a rescue programme to preserve the genetic integrity of this species.

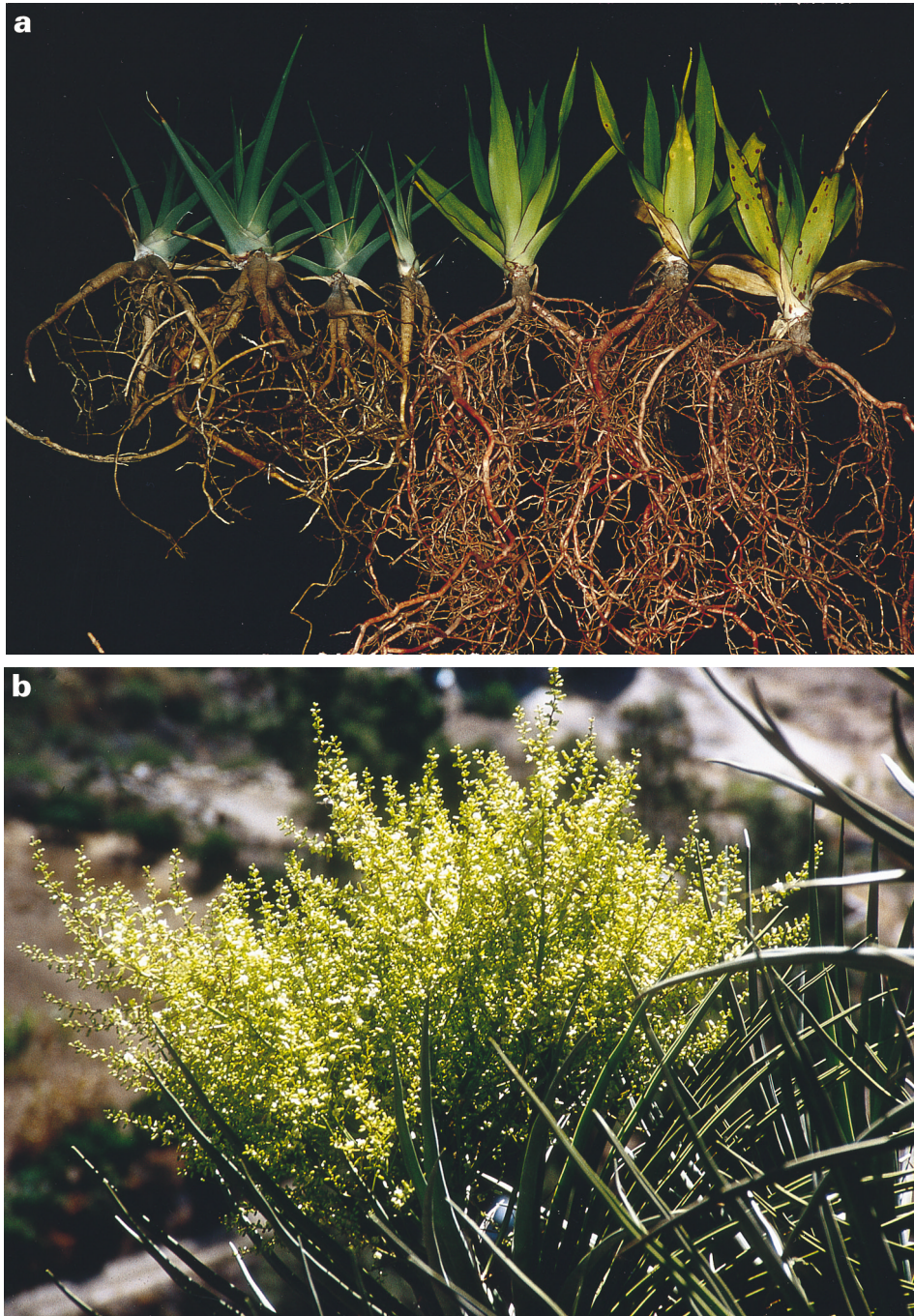


Figure 4. A, seedling of *Dracaena tamaranae* sp. nov. (left) and *D. draco* (right). B, inflorescence of *D. tamaranae* sp. nov.

TABLE 1. Qualitative data for growth form and leaves of species of the dragon tree group

Species	General appearance			Leaves				Basal portion of the leaves		
	Aspect	Branching	Shape	Colour	Margin	Blade	Venation	Length along the base	Width from the base	
<i>D. tamaranae</i>	robust developed trunk	slightly dense	subulate	glaucous greenish to greyish	entire hialine	slightly succulent, canalliculate and rigid grooved	patent	very long	narrow	
<i>D. draco</i>	very robust developed trunk	dense	ensiform	green glaucous	entire reddish	slightly succulent, flat, slightly flexible	patent	long	wide	
<i>D. draco</i> subsp. <i>ajgal</i>	very robust, very developed trunk	dense	ensiform	glaucous greenish	entire	slightly succulent, flat, hardly flexible	patent	long	wide	
<i>D. canabari</i>	very robust developed trunk	very dense	slightly subulate to linear ensiform	green glaucous	serrulate towards the base and hialine	very succulent, flat, rigid with a thick and sharp apex	not patent	very long	wide	
<i>D. ombet</i>	robust short trunk	slightly dense	ensiform linear to linear subulate	glaucous greenish yellowish	serrulate hialine	slightly succulent, slightly canalliculate, semi-rigid	not patent	short	very wide	
<i>D. schizantha</i>	robust short trunk	slightly dense	linear subulate	glaucous greenish greyish	serrulate	slightly succulent, slightly canalliculate, rigid	not patent	long	very wide	
<i>D. serrulata</i>	robust short trunk	slightly dense	ensiform linear to linear subulate	glaucous greenish	serrulate	slightly succulent, slightly canalliculate, semi-rigid	not patent	long	wide	

TABLE 2. Qualitative data for flower traits of species of the dragon tree group

Species	Inflorescence			Bracteoles	Pedicels	
	Ramification	Hairiness	Bracts		Articulation	n°/cluster
<i>D. tamaranae</i>	tripinnate along the axes	glabrous	subulate-linear, acuminate	triangular-ovate, minute	apical extreme	3–5
<i>D. draco</i>	bipinnate below the middle	glabrous	linear-subulate, acuminate	subulate ovate, acuminate	middle	4–7
<i>D. draco</i> subsp. <i>ajgal</i>	bipinnate below the middle	glabrous	linear-subulate, acuminate	subulate ovate, acuminate	middle	4–7
<i>D. cinnabari</i>	bipinnate middle	glabrous	subulate to subulate-acuminate	triangular-ovate, acuminate	middle extreme	3–7
<i>D. ombet</i>	tripinnate along the axes	glabrescens	triangular, acuminate	ovate minute	middle	–
<i>D. schizantha</i>	tripinnate along the axes	felted tomentose	subulate triangular, acuminate,	triangular, acuminate minute	middle to middle extreme	1–4
<i>D. serrulata</i>	tripinnate along the axes	tomentose or dense tomentose	subulate, triangular, acuminate	triangular, subulate acuminate	middle to middle extreme	1–5

Species	Perianth			Stamens		Fruits
	Segment	Tube	Colour	Anthers	Filament	Colour
<i>D. tamaranae</i>	oblong linear	very short	whitish green	$\frac{1}{3} \frac{1}{4}$ filament	slightly thickened, not flattened	orange
<i>D. draco</i>	subspatulate linear	short campanulate	whitish pink	$\frac{1}{2} \frac{1}{3}$ filament	thickened flattened	orange reddish
<i>D. draco</i> subsp. <i>ajgal</i>	subspatulate linear	short campanulate	whitish yellow	$\frac{1}{2} \frac{1}{3}$ filament	thickened flattened	red orange
<i>D. cinnabari</i>	oblong	basal and barely developed	pale greenish yellow	twice filament	subulate	red scarlet
<i>D. ombet</i>	linear	very short, barely developed	whitish pink	subequal filament	–	–
<i>D. schizantha</i>	lanceolate	very short, barely developed	white	$\frac{1}{2} \frac{1}{3}$ filament	subulate thickened	–
<i>D. serrulata</i>	–	–	–	–	–	orange

TAXONOMIC DISCUSSION

Dracaena tamaranae sp. nov. seems to be closely related to the three species found in the Horn of Africa and Arabia (i.e. *D. ombet*, *D. schizantha* and *D. serrulata*). All these species have glaucous leaves, minute bracteoles and are not densely branched.

TABLE 3. Quantitative data for growth form, leaves and inflorescences of species of the dragon tree group. l/w = length/width

Species	Height (m)	Leaves			
		Length (cm)	Width (cm)	l/w	Base (cm)
<i>D. tamaranae</i>	6–10	40–80 (110)	3–4.5 (5)	10–18	9.8–19.4 × 3.7–5.5
<i>D. draco</i>	8–12	40–90 (110)	2–3.5 (4)	20–25	6–10.4 × 3–4.2
<i>D. draco</i> subsp. <i>ajgal</i>	10–20	60	3	20	–
<i>D. cinnabari</i>	6–10	30–60	2.5–4.5	12–13.3	6.5–13.5 × 2.2–5
<i>D. ombet</i>	2–8	35–65	2.2–3	16–21.7	4.5–8 × 3.2–5.6
<i>D. schizantha</i>	2–9	35–70	0.7–2.5	28–50	4.5 × 2.4–3.7
<i>D. serrulata</i>	2–8	30–60	2–3.5	15–17	8–10 × 2.5–4.5

Species	Inflorescence			
	Length (cm)	Flower pedicels (mm)	Fruit pedicels (mm)	Bracteoles (mm)
<i>D. tamaranae</i>	80–100	2.25–3.25	–	1.90
<i>D. draco</i>	60–120	4.00–6.00 (10)	8.30–10.50	0.80–2.80
<i>D. draco</i> subsp. <i>ajgal</i>	–	1.00–4.00	–	–
<i>D. cinnabari</i>	30–75	3.00–7.00	6.00–8.00	1.00–4.00
<i>D. ombet</i>	20–40	3.10–4.50	semipedicel 2.50–4.50	0.50–1.50
<i>D. schizantha</i>	45	1.50–3.00	3.50–5.00	0.50–1.50
<i>D. serrulata</i>	–	–	2.50–5.00	0.50–1.50

TABLE 4. Quantitative data for flower and fruit traits of species of the dragon tree group

Species	Flowers		Stamens		Ovary length (mm)	Fruit diameter (mm)	Seed size (mm)
	Perianth (mm)	Tube (mm)	Filament (mm)	Anther (mm)			
<i>D. tamaranae</i>	9.50–11.00	0.75–1.00	6.08–8.75	1.75–2.00	3.50–3.75	10.00–11.50	6.00–7.00
<i>D. draco</i>	7.00–9.50	1.30–3.50	5.80–8.00	1.00–1.50	3.60–4.50	14.30–14.60	7.50–10.00
<i>D. draco</i> subsp. <i>ajgal</i>	7.00–8.00	1.00–2.00	–	–	–	–	7.50–10.00?
<i>D. cinnabari</i>	5.00–9.50	–	–	2.00–2.25	3.50–4.00	8.00–13.00	3.50–5.00
<i>D. ombet</i>	6.30–6.40	–	–	–	–	–	–
<i>D. schizantha</i>	3.50–6.50	–	3.20–4.75	1.00–1.50	2.75–3.00	5.00–7.00	–
<i>D. serrulata</i>	5.00	–	–	–	–	5.00–8.00	3.50–5.50

In addition, the tripinnate, slender and erect inflorescences are branched along all the axes.

These continental species have flowers and inflorescences which are smaller than those of *D. tamaranae*. Furthermore, they also have rather succulent and linear-ensiform leaves with acutely serrulated margin and no patent nerves, the trunks are usually shorter and the pedicels are articulated in the middle section. Moreover, *D. schizantha* tends to have linear leaves which are extremely narrow and greyish in colour, it has tomentose panicles which are dense and short. The basal pseudo-sheaths of the leaves of *D. ombet* are only slightly developed, and this species has

glabrescent inflorescences. Plants of *D. serrulata* are distinguished from the Gran Canaria species by their tomentose inflorescence.

There are several morphological characters which differentiate *D. tamaranae* from *D. draco* and *D. cinnabari*. These two latter species have ensiform leaves which are flat and not as glaucous, their inflorescences are bipinnate and robust. In addition, the branching of the inflorescences is basal. Other unique features of these species are pedicels articulated in the middle, smaller perianth, flattened filaments and a robust and dense growth-form. Furthermore, *D. cinnabari* has extremely rigid leaves with finely serrate margin towards the base, and nerves which are not patent. In contrast *D. draco* usually has reddish leaf-margins, inflorescence branches which tend to be reflexed or patent after fruiting, linear, acuminate inflorescence bracts and a whitish-pink perianth with a longer tube. *Dracaena hanningtoni* seems to be closely related to *D. ombet* (Baker, 1898), and it is rather different from the other species of the dragon tree group in that it has a much longer perianth, with the segments twice as long as the tube, the stamens are as long as the segments and the style is exerted. However, the general shape of the inflorescence indicates that this species seems to be closely related to the *D. draco*–*D. cinnabari* group.

We consider that *D. tamaranae* has strong morphological relationships with the East African and Arabian species. The main morphological features which support this hypothesis are the type of inflorescence and the general habit. However, we postulate that *D. draco* is closely related to the Socotra species, *D. cinnabari*. This assumption would mean that there are two biogeographical disjunctions between Macaronesia and the Red Sea region. A phylogenetic confirmation of this hypothesis would provide one of the few cases for independent colonizations of oceanic islands by congeneric species. Previous studies based on molecular data have proven this to be the case for *Lavatera* (Malvaceae) in the Canary Islands (Ray, 1995; Fuertes-Aguilar *et al.*, 1996) and for *Gossypium* (Malvaceae) in Galapagos (Wendel & Percival, 1990; Wendel & Percy, 1990). It is likely that other genera such as *Convolvulus*, *Euphorbia*, *Limonium*, *Salvia*, *Senecio* or *Viola*, with endemic species in Macaronesia, have also colonized these islands more than once.

Two species, *D. draco* and *D. tamaranae*, occur in western Africa. The former occurs both on the mainland and the Macaronesian Islands, whilst the latter is restricted to Gran Canaria. The occurrence of the insular species can only be explained through long-distance dispersal because these islands appear to be oceanic and therefore have never been joined to the continent (Araña & Carracedo, 1978; Araña & Ortiz, 1984; Carracedo, 1984). It is likely that these two species remained in a refuge in the Macaronesian Islands, and following a decrease of continental populations of dragon trees from western Africa. *D. draco* is now only found in a very restricted area of southern Morocco. It is noteworthy that these Morocco populations have been given subspecies rank as *D. draco* subsp. *ajgal*, an indication that the taxon is in early stages of speciation (Fig. 5A).

The geological events which led to the formation of the African Great Rift have had an impact in the current distribution of dragon trees in East Africa. In this region the Great Rift splits into two major fissures, one towards the Red Sea, the other towards the Aden Gulf. These geological events began in the early Miocene and resulted in the fragmentation of the original populations of dragon trees. These new sub-populations probably initiated new speciation events which yielded the three species which currently thrive in Arabia (*D. serrulata*), the African hills of the Red Sea (*D. ombet*) and the Horn of Africa (*D. schizantha*). These three species are

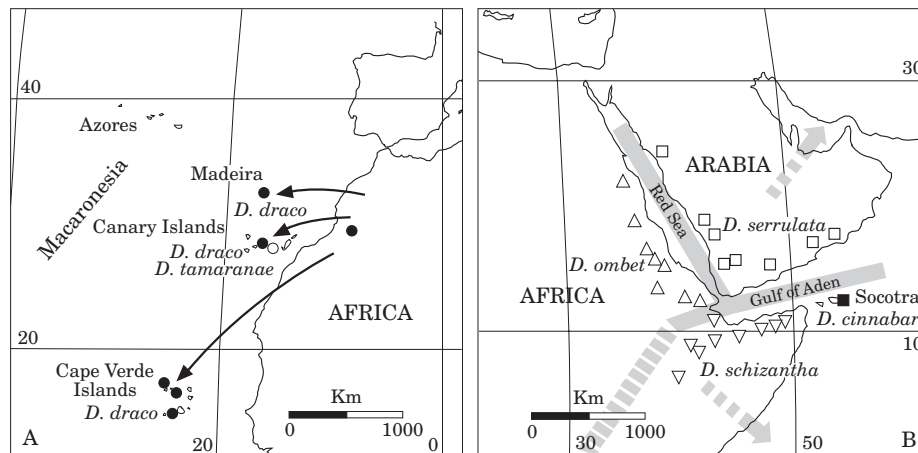


Figure 5. A, dispersal and colonization from the African mainland make the Macaronesian Islands a refuge for several species of *Dracaena*. B, African Grand Rift leads to the disruption and vicariance of *Dracaena* in the Red Sea region.

closely related, and they might form a species complex; indeed, some authors have suggested that they are conspecific with *D. ombet s.l.* (Deil, 1988; Friis, 1992; Thulin, 1995). However, Miller & Cope (1996) considered *D. serrulata* to be a distinct species. Our preliminary studies indicate that *D. schizantha* also has some morphological differences. In contrast, *D. cinnabari* is a distinct species which has several unique morphological features. It is restricted to the continental island of Socotra. This island was part of the Horn of Africa before the Middle Pliocene (Fig. 5B).

Saporta (1862, 1865, 1873a,b) described three Neogene fossil species of dragon tree (*Dracaenites brongniartii* Saporta, *D. sepultus* Saporta and *D. narbonensis* Saporta) from southern France, which he suggested were closely related to *D. draco*. However, at that time the dragon trees of East Africa and Arabia were not known to the scientific community. *Dracaenites brongniartii*, like *Dracaena draco* and *D. cinnabari*, has ensiform leaves. Plants of *D. ombet s.l.* have linear-ensiform leaves, but they are never truly ensiform. The two other fossil species have strictly linear leaves and, therefore, they may be related to those species which have subulate-linear or linear-ensiform leaves (Table 5). All the species have foliar scars in the bark, and these are particularly evident in the *D. ombet* group and *D. cinnabari*. The foliar scars have a rough margin in *D. cinnabari*. In contrast, they are tenuous in the fossil species and in *D. tamaranae*. *Dracaenites sepultus* has an extremely warty bark, a feature which is unknown in any of the living species. However, we are aware that based on these morphological features, it is difficult to establish phylogenetic links between the fossil species and the present ones. There is no reason to assume that these fossils represent the direct ancestors of the living species. Sadly there are no fossils of fruits and flowers which would help to clarify this issue.

HABITAT AND ECOLOGY

Dracaena tamaranae sp. nov. is found in the thermophile zone where it grows on inaccessible slopes and cliffs which tend to be shady and humid. The open *Juniperus*

TABLE 5. A selection of the most important morphological features of several fossil species (*Dracaenites*) from the French Tertiary

Fossil taxon	Locality	Stipe	Leaf branches			Foliar scars
			Diameter	Bark		
<i>D. narbonensis</i>	Armissan	arboreal	10 cm	slightly rough without protuberance		slightly patent
<i>D. sepultus</i>	Aix, Provence	bush	—	warty with protuberance		very tenuous
<i>D. brongniartii</i>	Aix, Provence	giant	10 cm	—		—
<i>D. minor</i>	Aix, Provence	frutescens	—	—		very patent

Fossil taxon	Leaves					
	Shape	Outward appearance	Venation	Length	Width	Base
<i>D. narbonensis</i>	linear	flat with margin entire	delicately nerved	150 cm	4 cm	gradually expanded 10–12 cm
<i>D. sepultus</i>	linear	firm	nerved	—	—	broad
<i>D. brongniartii</i>	ensiform	rigid and firm	nerved striated	—	3 cm	clearly broad 10–12 cm
<i>D. minor</i>	strictly linear	shiny and firm	very tenuous delicate compressed unequal	extremely long	—	little and sharply expanded

bushland (*Oleo-Rhamnetalia crenulatae* Santos 1983) and the *Cistus* scrubland (*Cisto-Micromerietalia* P. Pérez *et al.* 1991) form a mosaic in this area. Species which grow in this zone are: *Juniperus turbinata* Guss. subsp. *canariensis* (Guyot) Rivas Mart., Wildpret & P. Pérez, *Olea europaea* L. subsp. *cerasiformis* (Webb & Berthel.) G. Kunkel & Sunding, *Teline rosmarinifolia* Webb & Berthel., *Globularia cf. salicina* Lam., etc. (Rodrigo & Montelongo, 1986; Marrero, González-Artiles & González-Martín, 1995). Species which are characteristic of northern and northeastern humid slopes of the archipelago also occur in this area. Among these are: *Davallia canariensis* (L.) J.E. Sm., *Pericallis webbii* (Sch. Bip.) Bolle, *Sonchus acaulis* Dum. Cours., *Hypericum canariense* L., *Ranunculus cortusifolius* Willd., etc. *Dracaena tamaranae* reaches the dry canary pine forest (*Cytiso-Pinetea canariensis* Rivas Goday & Esteve *ex* Sunding 1972) at higher altitude. This species can also be found at lower altitude among elements of the *Kleinio-Euphorbietalia canariensis* (Rivas Goday & Esteve 1965) Santos 1976. The average annual rainfall of the zones where *D. tamaranae* grows is 200–350 mm.

Both in Macaronesia and Morocco, *D. draco* lives in areas which are not as xeric as those of *D. tamaranae*. For instance, on Madeira, it is mainly found as an element of thermo-sclerophyllous zones between sea-level and 200 m, and on sea-facing cliffs where some species of the laurel forest also occur (Turland, 1995). On Tenerife, *D. draco* also grows in thermo-sclerophyllous zones (*Mayteno-Juniperion canariensis* Santos & Fernández Galván *ex* Santos 1983) between 100 and 600 m. Other species found in this zone are: *Juniperus turbinata* subsp. *canariensis*, *Maytenus canariensis* (Loes.) G. Kunkel & Sunding, *Rhamnus crenulata* Aiton, *Olea europaea* subsp. *cerasiformis*, *Pistacia*

atlantica Desf., *Globularia salicina*, etc. (Santos, 1983; Rivas Martínez *et al.*, 1993). In addition, *Sideroxylon marmulano* Banks *ex* Lowe and *Apollonias barbuiana* (Cav.) Bornm., two thermophile species of the laurel forest, are also found in this zone. The annual average rainfall of this zone ranges between 200 and 400 mm. On Gran Canaria this species grows in similar areas, but it is extremely rare. On Cape Verde Islands, *Dracaena draco* is found between 700 and 1000 m where it grows together with *Euphorbia tuckeyana* Steud. *ex* Webb, *Echium* spp., *Ficus sur* Forssk. (*F. capensis* Thunb.), *F. sycomorus* L. subsp. *gnaphalocarpa* (Miq.) C.C. Berg, *Sideroxylon marmulano*, *Acacia albida* Del., etc. (Byström, 1960). The Anti-Atlas populations of *D. draco* are located between 400 and 1300 m with *Laurus azorica* (Seub.) Franco, *Davallia canariensis*, *Rhamnus alaternus* L., *Quercus rotundifolia* Lam., *Ceratonia siliqua* L., *Teline segonnei* (Maire) Reynaud, *Argania spinosa* Skeels, *Olea maroccana* Greuter & Burdet, etc. These species are part of the association *Davallio canariensis*–*Dracaenetum ajgal* Benabid & Cuzin 1997 in the order *Acacio-Arganietalia* Barbéro *et al.* 1982 (Benabid & Cuzin, 1997). Annual rainfall is around 400 mm. However, Rivas-Goday & Esteve-Chueca (1965) defined the thermo-sclerophyllous shrubs with *Dracaena draco* as the climax of the *Crassi-Euphorbietea*, *Diacanthio-Euphorbietea* (*Kleinio-Euphorbietea*).

The ecology of these species is similar to that of all the East African and Arabian species. For example, *D. ombet* is usually found in mountain escarpments together with *O. europaea* subsp. *africana* (Mill.) P.S. Green (including *O. chrysophylla* Lam.), *Euclea racemosa* Murr., *Euphorbia abyssinica* J.F. Gmel., *Acacia etbaica* Schweinf., *A. tortilis* (Forssk.) Hayne, *Ziziphus spina-christi* (L.) Desf. and *Lycium arabicum* Schweinf. (Kassas, 1956; White, 1983). *Dracaena ombet* occurs in plant communities of *Dracaeno-Euphorbietalia abyssinicae* Knapp 1968 (Deil & Müller-Hohenstein, 1984) which are situated below the evergreen scrub zone where there are thermo-sclerophyllous species such as *Maytenus senegalensis* (Lam.) Exell and *Euclea schimperi* (DC.) Dandu, and widespread species such as *Euphorbia abyssinica*, *Acacia etbaica* and *A. tortilis* (Kassas, 1956). Annual average rainfall of these zones is 200 mm.

Dracaena schizantha grows on escarpments along the northern mountains of Somalia. It is found in transition plant communities, which are situated between afro-montane forests and evergreen sclerophyllous scrubs. In these transition plant communities the following species are found: *Olea europaea* subsp. *africana* (including *O. chrysophylla* and *O. somaliensis* Baker), *Juniperus procera* Hochst. *ex* Endl., *Acokanthera schimperi* Oliver, *Pistacia aethiopica* Kokwaro, (*P. lentiscus* L. subsp. *emarginata* Engl.), *P. falcata* Mart., *Osyris lanceolata* Hochst. & Steud. *ex* DC., *Euphorbia abyssinica*, *Monothea buxifolia* DC. (*Sideroxylon gillettii* Hutch. & E.A. Bruce), *Maytenus undata* (Tunb.) Blakelock, etc. (Fici, 1991; Friis, 1992). Annual average rainfall reaches 500 mm.

Dracaena serrulata is a very rare species which is found in the xerophile zone, in an area where *Acacia*–*Commiphora* bushland is dominant. This zone is situated either below the deciduous forest of *Acacia* or forms a mosaic with bushes of *Olea europaea* subsp. *africana* and *Juniperus procera*. This dragon tree occurs in the Red Sea and Aden Gulf mountains of the Arabian Peninsula. Populations are located on sea-facing slopes and on inner regions of these mountains. In the xerophile zone are found several species of *Acacia* and *Commiphora*: *A. niotica* (L.) Willd. *ex* Del., *A. etbaica*, *A. gerrardii* Benth., *A. tortilis*, etc.; *C. habessinica* (Berg) Engl., *C. foliaceae* Sprague, *C. gileadensis* C. Chr., etc. Other species include *Maerua crassifolia* Forssk., *Ziziphus spina-christi*, *Euphorbia balsamifera* Aiton subsp. *adenensis* (Delf) Bally, *E. cuneata* Vahl, *E. triaculeata* Forssk., etc. (Miller & Cope, 1996). Average annual rainfall is approximately 200 mm.

Dracaena cinnabari is found on slopes of the highlands of northeastern Socotra. This area is mainly covered by thickets of *Rhus thyrsiflora* Balf. f., *Cephalocroton socotranus* Balf. and *Allophyllus rhoidiophyllus* Balf. f. Other species present are *Boswellia ameero* Balf. f., *B. socotrana* Balf. f., *Jatropha unicostata* Balf. f. and *Croton socotranus* Balf. f. At higher altitude, this type of thicket is intermixed with *Hypericum* shrubland. All the plant communities are under the influence of the northeastern humid monsoons (White, 1983; Beyhl, 1995; Miller & Cope, 1996). Mean average rainfall is approximately 400 mm.

Byström (1960) suggested that all the dragon tree species share similar ecological requirements. They tend to grow in areas with average temperatures of 18–20°C. They are found between 10° N in Somalia and 33° N in Madeira, and there is a clear correlation between latitude and altitude. The populations of Madeira may be found at sea-level whilst those of Somalia never occur below 1400–1800 m.

In general, all these arborescent species with an umbrella-shaped canopy are found mainly on the margins of the tropical-subtropical regions. They are part of a thermo-sclerophyllous vegetation similar to the Canarian *Oleo-Rhamnetalia crenulatae* or to the Arabian communities of *Acacia-Commiphora*. These plant communities are usually intermixed with xerophilous formations which are similar to the Canarian *Kleinio-Euphorbietalia*. They are mostly linked to steep and rocky landscapes, but there are some ecological differences between them.

Dracaena tamaranae grows in more xeric and hotter areas than *D. draco*. Populations of the latter tend to be affected by the northeastern trade winds and also grow under more humid conditions. The most xeric species of warm environments are *D. serrulata* and *D. ombet*. In contrast, *D. cinnabari* is the most mesophilic species. It grows along a belt of the highlands of Socotra which has the highest levels of rainfall. This habitat has similar features to those found in the region where *D. draco* is located in Macaronesia and Morocco.

BIOGEOGRAPHIC RELATIONSHIPS

Balfour (1883) and Christ (1885) have previously suggested close taxonomic relationships between the members of the dragon tree group. Other authors use this group as one of the best examples of biogeographic disjunction between Macaronesia and East Africa (Meusel, 1965; Sunding, 1970, 1979; Bramwell, 1986). Hooker (1878) was the first to propose that the dragon tree, together with other species of the Macaronesian laurel forest, are relicts of an old vegetation which once existed in northwest Africa. Axelrod (1975) is in agreement with this idea, and proposed that subtropical elements, such as *Dracaena* and *Sideroxylon*, found refuge in East and West Africa, as a consequence of the desertification of the Sahara in the late Oligocene.

Dracaena and the Rand Flora

The flora which existed in the southwestern region of South Africa during the Palaeocene was defined by Lebrun as the Rand Flora (cf. Quézel, 1978; Quézel & Barbéro, 1993). According to Quézel (1978, 1983) some of the elements which

currently thrive in northern Africa might be considered part of this ancient flora. These elements include species of the following genera: *Aristida*, *Amphinomia*, *Andrachne*, *Gaillonnia*, *Periploca*, *Tribulus*, *Trichodesma*, *Zygophyllum*, *Asthenaterum*, *Oropetium*, *Enneapogon*, *Cocculus*, *Neurada*, *Ifloga*, *Oligomeris*, etc. Some of the xerophilous taxa which currently exist in Macaronesia, the Red Sea region and the Saharan highlands have been assigned to this flora (Quézel, 1978, 1983). These xerophilous taxa include *Euphorbia balsamifera*, and several species of genera such as: *Euphorbia* of the cactiform types, *Acacia*, *Ceropegia*, *Commelina*, *Dracaena*, *Kalanchoe*, *Kleinia*, *Mesembryanthemum*, *Pentzia*, *Wahlenbergia*, etc.

Quézel (1978, 1983) reviewed the most important biogeographical components of the North African region, and he considered *D. draco* as one of the elements of the Rand Flora. However, Quézel (1978) proposed that the East African *D. ombet* is linked to another floristic group associated with "tropical elements of mountain massifs next to coast". In addition, most recently Bramwell (1986, 1990) included all the species of the dragon tree group among the elements of the Rand Flora.

Quézel (1978) suggested that many of the elements of the Rand Flora reached the Sahara region using the East Africa mountains as a dispersal route during the Oligo-Miocene, and this is the reason why there are several present disjunctions between northern and southern Africa. During this process there was an intermixing with northern elements. It is well known that there have been many climatic fluctuations in northern Africa since the late Oligocene, and these major climatic changes had a drastic effect on the vegetation of this region (Aubréville, 1970, 1976; Axelrod, 1973; Quézel & Barbéro, 1993), and, therefore, the fact that the flora of this region has several components should be borne in mind. Some of these components originated on the shores of the African Tethys which had a tropical flora similar to that found today in the Congo-Guinea region. Other North African elements are related to the laurasian subtropical flora, whereas some groups come from the dry tropical flora of the Sahara (Axelrod, 1975; Aubréville, 1976). There is no doubt that some of the North African species are linked to the Rand Flora; however, we believe that the most primitive species of the dragon tree group may have been derived from any of these flora. Fossil evidence could provide new insights into this issue.

The fossil data

None of the Tertiary Sahara fossils found so far belong to any of the Rand Flora groups (Maley, 1980). However, there are at least six species of *Dracaena* (*Dracaenites*) from remains of the French Eocene and Neogene (Saporta, 1862, 1865, 1873a,b, 1888, 1889). Three of them are considered as members of the dragon tree group (i.e. *D. brongniartii*, *D. narbonensis* and *D. sepultus*). One of the other three fossil species, *D. resurgens* Saporta, has been proposed to be closely related to the shrubby *D. angustifolia* Roxb. (Saporta, 1889), a species of the xerophytic group (Engler, 1908; Mies, 1995). It seems feasible from the morphology of the two remaining fossil species (*D. minor* Saporta and *D. pusillus* Saporta) that they may be also associated with the xerophytic group. However, these two fossil species are dwarf and have very long, narrow leaves.

Two additional extinct *Dracaena* species have been identified based on pollen from the Neogene (Van Campo & Sivak, 1976). Pollen of the first species, *D. saportae* Van

Campo & Sivak comes from Bohemia whilst the second one, *D. guinetii* Van Campo & Sivak, was found in Tunes. These two species seem to be related to those which are currently found in the Guinea–Congo region. *Dracaena saportae* appears to be related to *Dracaena ovata* Ker Gawl. whilst *D. guinetii* is associated with *D. humilis* Baker (Van Campo & Sivak, 1976).

From these palaeobotanical data it is obvious that the only fossils which seem referable to the dragon tree group come from the Eocene–Neogene European Tethyan area. These fossils have been found together with other elements of the subtropical laurasian forest which existed in southern Europe during the Tertiary. These are related to some of the taxa which currently thrive in the Macaronesian laurel forest (Saporta, 1862, 1865, 1873b, 1889; Depape, 1922; Andreánszky, 1968; Takhtajan, 1969; Sunding, 1970, 1979; Bramwell, 1972, 1976; Axelrod, 1975). The only fossil available from the African Tethyan is clearly related to *Dracaena* taxa which currently grow in tropical Africa. We are aware that the *Dracaena* fossil data do represent a limited sample of all the taxa which existed in the past. However, palaeobotanical data suggest that at least seven *Dracaena* species existed in European Tethyan and also indicate that the genus *Dracaena* had an important centre of diversity in this region.

Panbiogeographic interpretation

A biogeographic interpretation of the patterns of distribution of the dragon tree group can be made using the panbiogeographic approach (Croizat, 1958, 1968). According to this methodology, and using both data from living and fossil species, we can establish a route which links Macaronesia with East Africa and Arabia through the European Tethyan (Fig. 6). It is worth mentioning that Croizat (1968) previously found a similar route for *Sedum* sect. *Afrosedum* and sect. *Epetium* (Crassulaceae), which runs from Macaronesia–northwest Africa to Mesopotamia, Ethiopia and Kenya. A similar situation might be found with *Aeonium* (Crassulaceae: Sempervivoideae) which occurs in Macaronesia, northwestern Africa and in the Red Sea region. This genus does not have any species or fossil data from the Mediterranean region, and it has been proposed as one of the Rand Flora elements by Bramwell (1986). However, an inclusive study of *Aeonium* and *Sempervivum* (Sempervivoideae) supports that both genera have a Tethyan subtropical origin (Meusel, 1965). This is in agreement with recent molecular data which suggest that the tribe Sempervivoideae is nested within the tribe Sedoideae and *Sedum* (Hart, 1991; van Ham, 1995; Mes, 1995; Stevens, 1995). Bearing in mind the hypothesis of an holarctic origin for *Sedum* (Croizat, 1968; Hart & Eggli, 1995), it seems likely that *Aeonium* would also have an origin in this region. This hypothesis had already been proposed by Fici (1991) who considered that this genus migrated towards southern latitudes during the Quaternary cool periods. Other examples which seem to follow similar routes are *Lavandula* and *Coris monspeliensis* L. (Fici, 1991). The data presented in this paper indicate that *Dracaena* and *Aeonium* may have similar dispersal routes (cf. Meusel, 1965). These two genera seem to have an origin in a thermo-sclerophyllous flora which existed in the Tethyan, and they do not seem to be associated with the South African eremitic-xerophile Rand Flora.

Our study gives support to the hypothesis that the current species of the dragon tree group are a depleted and relict representation of the Mio-Pliocene Saharan

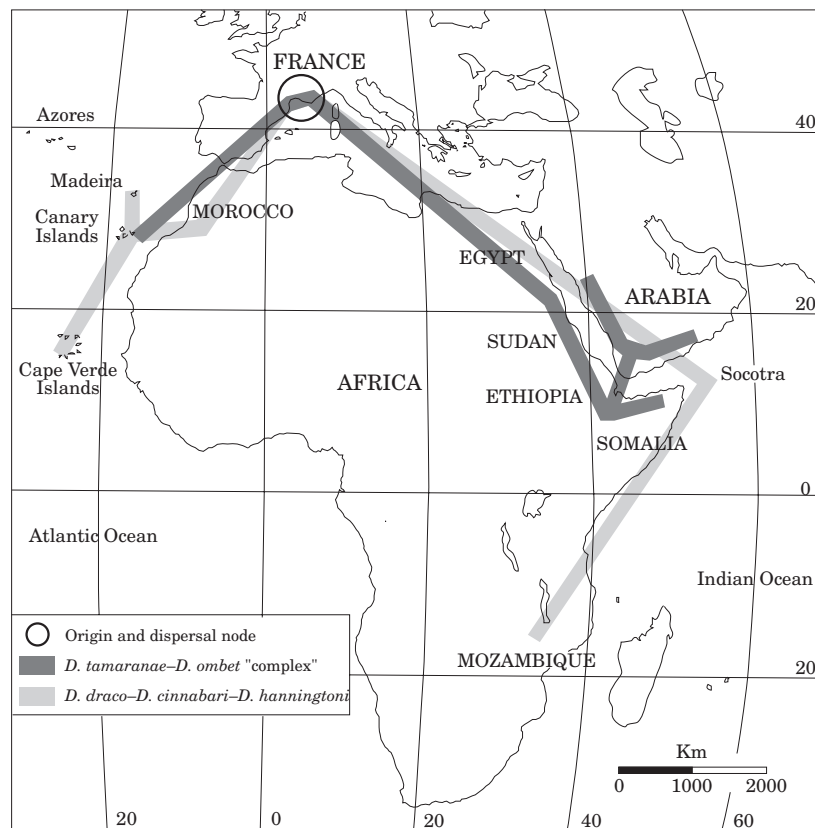


Figure 6. The two routes which link the distribution of the living and fossil species of the dragon tree group.

xerophile-sclerophyllous flora. These species would have their origin in the most thermic elements of the Oligo-Miocene laurasian subtropical flora. They existed in the edges of the forests and it is likely that they occurred on sunny and exposed areas of rocky slopes, cliffs and escarpments. Following the major climatic changes of the Miocene, they might have migrated southward where they established new populations in northern Africa. Further climatic changes might have led to the gradual disjunction of these populations towards the eastern and western margins of Africa and towards the Saharan islands mountains.

Aubréville (1976) cites *Bombax* as a good example of a laurasian group which could have migrated towards Africa in the Tertiary. This genus with eight species is currently restricted to tropical regions of Asia (Indo-Malaysia) and Africa. There is strong palaeobotanical evidence for the existence of *Bombax* in the Sahara region (*Bombacoxylon*) and Europe (Aubréville, 1970, 1976; Saporta, 1862, 1873b). This seems to indicate that the current African species come from an original Saharan pool which previously had a Tethyan European laurasian origin (Aubréville, 1976).

Many of the biogeographical studies of Macaronesia and North Africa have suggested that most of the xerophilous elements of these regions originated from the Rand Flora (Quézel, 1978, 1983; Maley, 1980; Bramwell, 1986, 1990; Quézel

& Barbéro, 1993). This view has meant that there has been a trend to postulate strong biogeographic relationships between North Africa–Macaronesia and an ancient flora which originated in southern Africa in the Palaeocene. This idea has led workers to underestimate the contribution of the thermo-sclerophyllous Tethyan flora. It might well be that *Dracaena* provides an example of this underestimation, which could also apply to other plant groups.

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APPENDIX

Plant material: Herbarium specimens

Dracaena draco (L.) L., Tenerife, Buenavista del Norte, Ravelo, leg. A. Marrero, R.S. Almeida & M. González-Martín, 31.vii.1997 (LPA: 18504); *Idem*, Tenerife, Adeje, barranco del Infierno, leg. R.S. Almeida & A. Marrero, 11.viii.1997 (LPA: 18505); *Idem*, Gran Canaria, Santa Brígida, barranco Alonso, Pino Santo (sub-spontaneous), leg. A. Marrero & R.S. Almeida, 4.viii.1997 (LPA: 18503) (inflorescence, basal bracts, leaves); *Idem*, Gran Canaria, Jardín Botánico Viera y Clavijo (*ex horto*), leg. A. Marrero, 22.vii.1997 (LPA: 18506, 18507) (inflorescence, basal bracts, leaves); *Idem*, (*ex horto*), from Cape Verde, leg. A. Marrero, 4.vii.1997 (LPA: 18510, 18511, 18512) (seedling, inflorescence, infructescence, basal bracts, leaves); *Idem*, Gran Canaria, El Batán–Guiniguada (*ex horto*), leg. A. Marrero, 25.vii.1997 (LPA: 18508) (inflorescence, basal bracts, leaves). *D. cinnabari* Balf. f., Socotra, Feb.–March, 1880, comm. Prof. Bayley Balfour, Aug. 1880 (K TYPUS) (2 sheets, inflorescence, basal bracts, leaves, + Ic. Prof. Balfour 5/93); *Idem*. (BM TYPUS Dupl. inflorescence, basal bracts, leaves); *Idem*, Socotra, Dr. Balfour, April, 1880 (K) (infructescence); *Idem*, Ins. Socotra (Hort. Kew.), coll. Wikeham Perry, s/n, 19.ix.1878 (K) (leaves); *Idem*, Socotra, Jebel Shihali, Hagghiher Mts., 3500 ft., leg. A.R. Smith & J. Lavranos, 448, 20.iv.1967 (K) (inflorescence); *Idem*, Socotra, Taukak village, above Hasen, 450–480 m, leg. M. Thulin & N. Gifri, 8603, 19.i.1994 (K) (infructescence, basal bracts); *Idem*, Gran Canaria, Jardín Botánico Viera y Clavijo (*ex horto*), leg. A. Marrero, 1.ix.1997 (LPA: 18513, 18514) (leaves). *D. ombet* Kotschy et Peyr., Mount Erkowit, near Suakin, Schweinfurth, 250, 16.ix.1868 (K) (inflorescence, leaves + Hooker's Ic. Pl. t. 2539); *Idem*, Gran Canaria, Jardín Botánico Viera y Clavijo (*ex horto*), leg. A. Marrero, 22.viii.1997 (LPA: 18515); *Idem*, 1.ix.1997 (LPA: 1'8516) (leaves); *D. cf. ombet*, Djibouti, Wadi Dounyar, S of Ali Sabreh, crest of limestone ridge, 2400 ft., I.S. Collenette, 8644, 20.iv.1993 (K) (inflorescence, leaves). *D. serrulata* Baker, found on the hills near Dobaibah, elevation about 4000 ft., coll. W. Lunt., 206, 26.ii.1894 (K TYPUS) (leaves); *Idem*, Jebel Minmar, Khawlaan as Sham, c. 2500 m, J.R.I. Wood, Y/75/624, 29.viii.1975 (BM) (2 sheets, infructescence, leaves); *Idem*, on the south side of Jebel Minmar (Sādah-Sagayn), c. 2600 m, J.R.I. Wood, 624,

29.viii.1975 (K) (infructescence); *Idem*, Saudi Arabia, the Asir, about 10 km south of Abha, I.S. Collenette, 628, 6.iv.1978 (K) (leaves); *Idem*, Saudi Arabia, South Hijaz, Jebel Aba Hassan, a sandstone massif about 50 km south of the escarpment between Abha-Najran, 5500 ft., I.S. Collenette, 1291, 6.iv.1979 (K) (inflorescence); *Idem*, Saudi Arabia, S-SW of Madinah, 80 km, 5000 ft. (c. 4600 m), I.S. Collenette, 3789, 15.viii.1982 (K) (infructescence); *Idem*, Oman, N of Jabel Qaars, road to Sarfay & Dhofar, R.M. Lawton, 2398, 28.viii.1982 (K) (2 sheets, infructescence, basal bracts, leaves); *Idem*, *Duplic.* (BM) (infructescence, basal bracts); *Idem*, Oman, Dhofar, Jebel Semhan above Mirbat, 1350 m, A.G. Miller & J.A. Nyberg, M-9167, 7.ix.1989 (K) (infructescence, leaves). *D. schizantha* Baker, Somali-Land, Meid, Ahl-n. Serrusgeb, 800–1800 m, J.M. Hildebrandt, 1742, April 1875 (BM *TYPUS*) (inflorescence); *Idem*, (K *Duplic.*) (inflorescence); *Idem*, Ethiopia, Harar Prov., Steep slopes below Dangago, 15 km SE of Diredawa, along the road to Harar, 1700 m, W. Burger, 1516–1516a, 24.ii.1962 (K) (3 sheets, inflorescence, leaves); *Idem*, Ethiopia, Harar Prov., Steep slopes below Dangago, 15 km SE of Diredawa, along the road to Harar, W. Burger, 3714, 4.iii.1965 (K) (2 sheets, inflorescence, leaves); *Idem*, Somalia, Valley sides, site A/5 Limestone Mountains, 1340 m, J.B. Billett & R.M. Watson, 23462, 16 & 18.vi.1981 (K) (2 sheets, infructescence, leaves); *Idem*, NE Somalia, environs de Galgala, C. Barbier, 962, 5.xii.1983 (K) (infructescence, basal bracts); *Idem*, Royal Botanical Gardens, Kew, (*ex horto*), leg. P. Wilkin, A. Marrero & R.S. Almeida, 21.x.1997 (LPA: 18509) (leaves). *D. hanningtoni* Baker, E Trop. Africa, German East Africa, Unyamwezi, Msalala, coll. & com. rev. J. Hannington (K *TYPUS*) (inflorescence).