

Floristic links between N. W. Africa and S. W. Asia

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(Mit 7 Textabbildungen)

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Abstract. A new species of Umbelliferae, *Cuminum maroccanum* DAVIS & HEDGE, is described from S. W. Morocco. The nearest ally of this species grows in S. W. Asia. Examples of other floristic links between N. W. Africa and S. W. Asia are considered in different families and belonging to different phytogeographical elements. Some suggestions are made as to how the present-day distributions may have come about.

Introduction

The recent discovery of a new Umbellifer in Morocco, belonging to the small genus *Cuminum*, and related to a species from S. W. Asia, has focused our attention on the occurrence of other examples with somewhat similar or analagous geographical connections. Such species are scattered in different families and belong to groups centred in different phytogeographical regions. These connections include every transition from continuous to strikingly disjunct distributions. This paper includes a description and discussion of the new *Cuminum*, followed by examples of other links between the floras of N. W. Africa and S. W. Asia, and some suggestions concerning their present-day distributions.

A new species from Morocco with S. W. Asiatic Affinities

Cuminum maroccanum DAVIS & HEDGE, sp. nov. Fig. 1.

Species insignis, affinis *C. setifolii* (BOISS.) KOS.-POL. sed laciniis foliorum brevioribus, pedunculis scabrellis, dentibus calycis brevioribus subaequalibus, fructibus maioribus setis densioribus longioribus bene differt.

Annum. Caulis erectus, simplex vel pauciramosus, angulatus, tenuissime striatus, glaber, 5—9 cm altus, internodiis 10—15 mm. Folia infima in statu fructifero ± delapsa. Folia caulina inferiora longipetiolata; petiolus

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ad 20 mm longus basi in vaginam anguste membranaceo-marginatam dilatatus, pallide viridis glaucescens basi purpureo-suffusus; lamina ad 25×25 mm, glabra, in lacinias linearibus biternatis divisa; lacinae ultimae lineares vel lineari-filiformes, c. $8-15 \times 0,5$ mm, acutae, glabrae. Folia caulina media decrescentia. Pedunculi scabrelli. Involucrum e phyllis biternatis compositum. Umbella 1-2-radiata; radii aequales c. 10-12 mm, erecto-patentes, minute scabrelli, validi. Involucellum 3-5-phyllum, phyllis linearibus, c. 5 mm, vel apice trifidis vel ternatis, patulis vel parum reflexis. Umbellulae 4-8-radiatae; pedicelli aequales, fructiferi 5-7 mm longi, erecto-patuli,

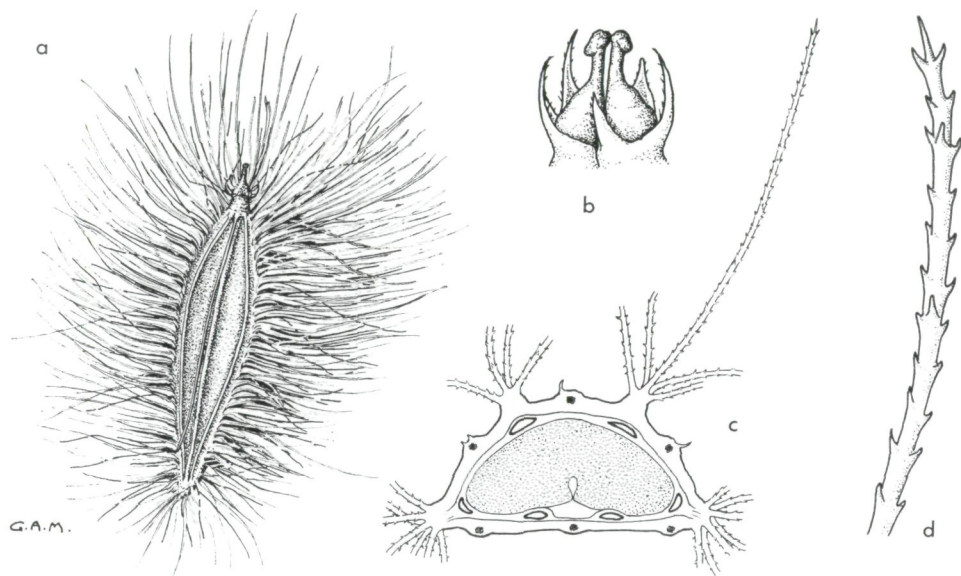


Fig. 1. Fruit of *Cuminum maroccanum*: a) mericarp $\times 5$; b) calyx lobes and stylopodia $\times 18$; c) transverse section of mericarp $\times c. 90$.

scabrelli. Petala ignota. Fructus anguste ellipticus basi et apice attenuatus a dorso subcompressus densissime rufo-setulosus, c. 7×2 mm sine pilis. Dentes calycis subaequales brevissimi. Mericarpi jugis filiformibus primariis 5, secundariis 4; juga secundaria setis multicellulis rubellis ad 7 mm dense tecta; juga primaria brevissime setulosa. Vittae commissurales 2; vittae valliculares 4, sub jugis secundariis solitaires. Stylopodium conicum in stylos attenuatum.

S. W. Morocco. WD. Oued Dra, between Goulmime and Tan-Tan, 75 m, stony slopes of valley, annual, 23 iii 1969, P. & J. DAVIS, D. 48594 (holo. E; iso. BM).

This distinct new species has its closest ally in *Cuminum setifolium* (BOISS.) Kos.-Pol. from Syria, Iran, Afghanistan and Central Asia. The two species, both small annuals, share a similar fruit structure: they have long

setose hairs on the secondary ridges of the pericarp and the vittae are solitary under these ridges. In leaf shape and division they are also similar, but as indicated in the Latin diagnosis there are several clear differences between them, such as the minutely scabrous peduncles, the short subequal calyx lobes and the larger fruits of *C. maroccanum*.

C. setifolium was originally described by BOISSIER in 1856 (Diagn. ser. 2(2): 99) as *Torilis setifolia*, and later transferred by him to *Psammogeton* (BOISSIER, Fl. Orient. 2: 1079, 1872). The transfer to *Cuminum* was first made by KOSO-POLJANSKY (Bull. Soc. Nat. Mosc. n. s. 29: 209, 1916), and later supported by WAGENITZ *) (1956) in his revision of *Psammogeton*. WAGENITZ showed clearly the similarities between '*P. setifolius*' and *Cuminum cyminum* L., and indicated clear differences between them and *Psammogeton* as typified by *P. canescens* (DC.) VATKE. In addition to *Cuminum cyminum* (the type of the genus), *C. setifolium* and *C. maroccanum*, there are two other species in the genus, *C. sudanense* WOLFF from the Sudan and *C. borsczovii* (RGL. & SCHMAL.) KOS.-POL. from C. Asia. The wild distribution of the widely cultivated and often naturalised *C. cyminum* is uncertain; Egypt, Ethiopia, S. W. and C. Asia have variously been suggested. Although the fruits of *C. cyminum* are often glabrous, forms occur throughout its range with setose fruits, but in these the setae are never as long or as dense as in our new species. In general facies and leaf characters, *C. maroccanum* is only distantly related to *C. cyminum*.

There is one feature of the new species which distinguishes it from the other five members of *Cuminum*. This is the form of the calyx lobes. In *C. maroccanum* the lobes are small and almost equal, whereas in the other species they are very prominent and clearly unequal.

By widening the circumscription of *Cuminum* to include species with very prominently setose fruits and one (our new species) with a calyx structure clearly different from that of the other species, the question is raised as to its correct position in the family. *Cuminum*, when it was a monotypic genus, was placed by BOISSIER in Flora Orientalis (1872) beside *Psammogeton* and *Chaetosciadium* BOISS. in the *Caucalineae*. DRUDE (1898) and WOLFF (1927) considered *Cuminum* anomalous there and transferred it to *Ammineae-Carinae*, near to *Apium* and far removed from *Psammogeton*. Flora Europaea 2 (1968) and Flora Kavkaza 7 (1967) are two of several Floras which have recently followed DRUDE. But if *Cuminum* is defined as having glabrous to densely setose fruits, and because of the basic similarity of the internal fruit structure of *Cuminum* s. l. to the genera of the *Dauceae*, there is little doubt that it should be removed from the *Ammineae* and transferred to the *Dauceae*. The question of the closest generic allies of *Cuminum* needs further examination, but *Psammogeton*, *Chaetosciadium* and *Ammodaucus* COSS. & DUR. are probably its nearest relatives.

*) We are grateful to Prof. G. WAGENITZ, Göttingen, for examining a specimen of our new species. He endorsed our opinion that it must belong to *Cuminum*.

Cuminum maroccanum grows in a Saharo-Sindian community accompanied by *Limonium fallax*, *Fagonia latifolia* and *Asteriscus* sp. indet. In the same coastal belt of S. W. MOROCCO, OZENDA (1958) records the following endemics: *Fagonia harpago*, *Zygophyllum waterlotti*, *Limoniastrum weygandiorum*, *L. ifniense*, and *Echiochilon chazaliei*.

Cuminum setifolium, often a very common plant throughout much of its range, is a member of the Turanian element in the Irano-Turanian region. The rather ill-defined Turanian province includes the Kizyl Kum and Kara Kum deserts, the steppes between the Aral and Caspian seas, the W. and S. W. outskirts of the Central Asiatic mountain ranges and the N. W. of Afghanistan, and numerous sandy or halophytic enclaves in Iran (ZOHARY 1963, 1966). The floristic affinities between the Turanian province and the Saharo-Sindian region are particularly close.

Other floristic connections between S. W. Asia and N. W. Africa

The examples listed below are to be treated as a preliminary, very incomplete and uneven survey. They are based on an amalgam of our personal field knowledge, information derived from the Edinburgh herbarium, taxonomic revisions and the major Floras covering S. Europe, N. Africa and S. W. and C. Asia. Only one of us (DAVIS) has collected in N. Africa, and as both of us are much better acquainted with S. W. Asian than N. W. African floras, we have tended to view these floristic connections from a S. W. Asian rather than a N. W. African viewpoint.

We have attempted to group our examples by phytogeographical elements, distinguishing Euro-Siberian, Mediterranean, Irano-Turanian (provisionally including the Mauritanian steppe of N. W. Africa), and Saharo-Sindian elements, according to the phytogeographical region in which each example is centred (cf. ZOHARY 1962, 1966). This grouping, however, is approximate, distributions being disturbed by altitude, and by the fact that some species (or species pairs: vicariads) flourish in more than one region. However, the grouping of species according to phytogeographical elements has made it easier to make some brief explanatory suggestions about the distribution of the taxa concerned. Generally the geographic distributions of individual species are given by countries; in this respect "Egypt" includes Sinai, and "Palestine" covers both Israel and Jordan. "Libya" implies both Tripolitania and Cyrenaica unless one of these is cited, when the other is automatically excluded. Crete is cited separately from the other Aegean islands.

Before we can consider the floristic connections between S. W. Asia, Europe and N. Africa, it is necessary to mention possible Cainozoic migration routes between N. Africa and the land to the N. and E. of it. A recent symposium on Tethyan biogeography (ADAMS & AGER, 1967) exposes a wide spectrum of disagreement not only about the chronology of Tethys-Mediterranean geography but even disagreement as to where the various land and sea connec-

tions were. Nevertheless, we must hazard a historical outline here before we can attempt some interpretation of plant distributions.

By Early Miocene, the sea connection between the Tethys and the Indian Ocean was broken and "Paratethys" extended from the Vienna basin to beyond the Caspian. At the end of Middle Miocene, a land connection joined S. Spain to the Rif area, south of which the Mediterranean was still joined to the Atlantic by the S. Rif Strait. Following RUGGIERI's summary (1967), towards the end of the Miocene the communication with the Atlantic completely ceased, and the Mediterranean shrank to a series of lagoons with land connections between them. With the continuation of the tectonic deformation of the Betic-Rif massif, the Straits of Gibraltar opened at the start of the Pliocene, causing the Atlantic to pour into the Mediterranean. There was thus a persistent land connection between S. Spain and N. Morocco from the end of the Middle Miocene to the beginning of the Pliocene. The land connection between S. Italy, Sicily and Tunisia may be more recent, and of shorter duration. Anatolia remained joined to the Balkans across what is now the Aegean from the Miocene to near the close of the Pliocene (CREUTZBERG 1963, GREUTER 1970). It should be pointed out that the Iberian, Balkan and Anatolian peninsulas are considerably older than Italy and Sicily, most of which did not emerge from the Mediterranean till the Pliocene.

Judging by present-day distributions, the Gibraltar land bridge has proved a more effective migration route to and from N. W. Africa than the Sicilian one (see the pioneer floristic analysis by MATHEWS, 1880). There must also have been a long-persisting migration path from S. W. Asia into N. W. Africa along the south side of the Mediterranean. The migration route favoured apparently differed in relation to the phytogeographical element concerned. In addition, there is always the possibility of direct dispersal across the Mediterranean in its narrower parts: Spain-Morocco, Italy-Sicily-Tunisia, and probably Sardinia-Tunisia and Crete-Cyrenaica. One must, of course, bear in mind the glacial-interglacial changes of the Pleistocene in the Mediterranean area, and the increasing desiccation of the Sahara in the Holocene.

1. Euro-Siberian connections

There are numerous connections between the Euro-Siberian flora N. and N. E. of the Mediterranean and climatically favourable parts of N. W. Africa (mostly in Morocco and Algeria). Plants in this category which extend to S. W. Asia (e. g. N. Turkey, Caucasia, N. Iran) include *Taxus baccata*, *Ligustrum vulgare*, *Hedera helix*, *Acer campestre*, *Daphne laureola*, *Alnus glutinosa*, *Euphorbia amygdaloides*, *Sanicula europaea*, *Primula vulgaris*; *Calluna vulgaris* only reaches the Tangier peninsula. A few European species have isolated, alpine stations in the High Atlas of Morocco, e. g. *Gentiana verna*, *G. ciliata*. *Hypericum androsaemum* shows an E.-W. disjunction; it is widespread in W. Europe and is scattered in S. Europe and Algeria, but is virtually absent from the Balkans, reappearing in Turkey, N. W. Syria, Caucasia and N. Iran. European

species absent from the Iberian peninsula include *Acer obtusatum* (Algeria, Corsica, Sicily, S. & C. Italy, Balkans) and *Euonymus latifolius* (Morocco, Algeria, C. and S. Europe — extending westwards to C. Italy and S. France — Turkey, Caucasia, N. Iran).

Most of these Euro-Siberian elements show no significant morphological differentiation in N. W. Africa. A few connections, however, involve vicariads (allied species-pairs). For example, the European *Doronicum pardalianches* is replaced in Morocco, Algeria and Tunisia by *D. atlanticum*; *Heracleum sphondylium* (with several overlapping subspecies in Europe) by subsp. *atlanticum* in Algeria. *Rhamnus (Oreoherzogia) fallax*, centred in the mountains of the

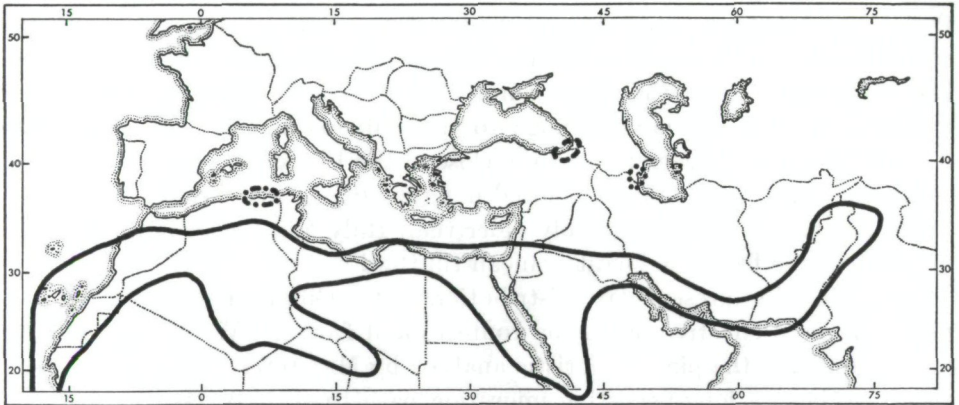


Fig. 2. Distribution of — *Salvia aegyptiaca*, - - - *Epimedium pinnatum* subsp. *colchicum*, *E. pinnatum* subsp. *pinnatum*, - . - . - *E. perralderianum*. The southern extension of *Salvia aegyptiaca* to Cape Verde Islands is not shown.

Balkans, has outlying stations in E. Anatolia and Lebanon; it is very closely related to *R. alpina* of the Alps and southern Europe (Spain to C. Italy), with scattered localities in Morocco and Algeria (cf. VENT 1962). A striking, and presumably older vicariad connection is provided by *Laurocerasus officinalis* (*Prunus laurocerasus*) and *L. lusitanica*. The first grows in Bulgaria, Yugoslavia, Turkey (N. Anatolia, Amanus), W. Caucasia and N. Iran; the second in S. W. France, Iberian peninsula, Morocco (Rif) and Macaronesia.

All the Euro-Siberian examples mentioned, however, show close connections between N. W. Africa and Europe rather than S. W. Asia. Only one example of a direct floristic connection between N. W. Africa and S. W. Asia has come to our attention: *Epimedium perralderianum* is endemic to moist montane woods in Algeria; its close ally is *E. pinnatum* subsp. *colchicum* from W. Caucasia and N. E. Anatolia; subsp. *pinnatum* grows in the Talysch (Fig. 2).

Discussion. Judging by the present distribution of the Euro-Siberian connections, the Spain-Morocco route certainly seems to have been used far more frequently than the Sicilian bridge, and was presumably most effective

during glacial periods, when the climate was cooler and wetter than it is now. The fact that most of the Euro-Siberian connections have not differentiated on the N. and S. side of the Mediterranean, suggests that they could hardly have reached N. W. Africa before the Pliocene or Pleistocene. However, the occurrence of bird-dispersed diaspores in many of the Euro-Siberian trees and shrubs of N. W. Africa makes direct dispersal across the narrow Straits a distinct possibility. Some Euro-Siberian species are now very rare or local in N. W. Africa; their area (and probably the number of species) has presumably declined in post-glacial (Holocene) times. East-West disjunctions (e. g. *Hyperic-*

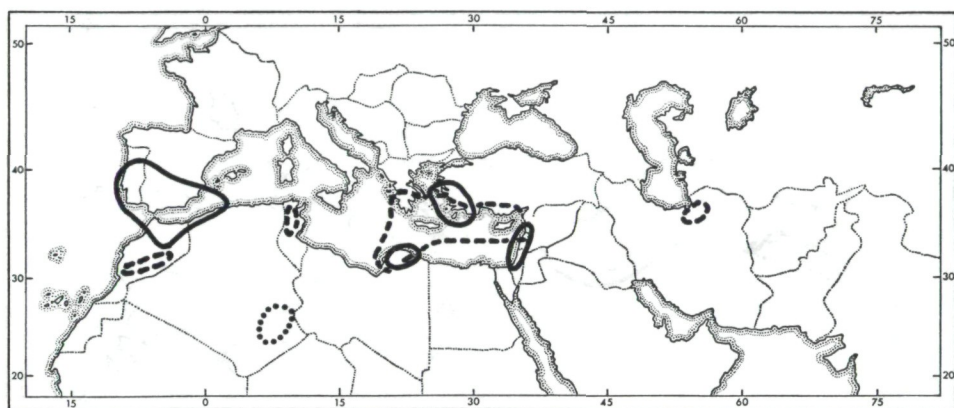


Fig. 3. Distribution of ——— *Ferula tingitana*, - - - *Cupressus sempervirens* var. *horizontalis*, *C. dupreziana*. Recent collections show that the *Cupressus* in N. Persia extends to the western end of the Elburz range.

cum androsaemum, *Euonymus europaeus*) probably represent an intermediate stage in the process of extinction in southern Europe, no doubt connected with the Alpine glaciations; *Epimedium* represents the penultimate stage in contraction. Without fossil evidence, the last stage — when the species no longer survives in N. W. Africa — could not be distinguished from failure to arrive!

2. East — West Mediterranean connections

Specific connections:

Cupressus sempervirens var. *horizontalis* (Fig. 3): Morocco (High Atlas), Tunisia, Libya (Cyrenaica), Greece, Aegean, Crete, Turkey, Cyprus, Lebanon, N. Iran. (The very closely related *C. dupreziana* grows in the mountains of C. Sahara).

Thlaspi bulbosum: Algeria, Greece, Aegean. Montane forest.

Hypericum aegyptiacum: Morocco, Algeria, Cyrenaica, Sardinia, Malta, Sicily, Greece, Crete. Usually chasmophytic. The other species in Sect. *Triadenia* (*H. russeggeri*) grow in the east Mediterranean.

Cistus laurifolius: Portugal, Spain, S. France, Morocco, Corsica, Italy, N. Greece, Turkey (Anatolia). Montane; one of the most frost-hardy species in this predominantly W. Mediterranean genus.

Fumana scoparia: Spain, Morocco to Tunisia, Libya (G. Nefoussa), Italy, Albania, Greece, Crete?, Turkey, N. W. Syria, Lebanon. (COODE & DAVIS, 1964).

Onobrychis crista-galli: Morocco, Algeria, Libya, N. Egypt, Aegean, Crete?, Turkey, Cyprus, Syria, Lebanon, Palestine.

Ferula tingitana (Fig. 3): Portugal, S. Spain, N. Morocco, Algeria, Libya

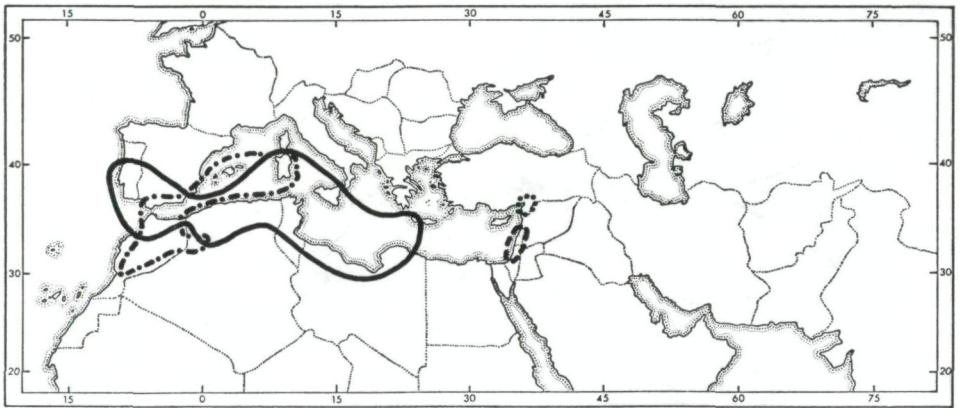


Fig. 4. Distribution of ——— *Iris planifolia*, - - - *I. palaestina*, - . - . *Buxus balearica*, *B. longifolia*.

(Cyrenaica), S. W. Turkey and E. Aegean islands, Palestine, Lebanon, W. Syria. Calcareous rocks.

Viburnum tinus: Portugal to Greece, Aegean, Morocco to Tunisia, Libya (Cyrenaica), Palestine, Lebanon. Bird-dispersed.

Viscum cruciatum: Portugal, Spain, Morocco, Palestine, Lebanon. Bird-dispersed, branch parasite.

Euphorbia dendroides: S. Europe (Spain to Greece, incl. Sicily), Algeria, Tunisia, Libya (Cyrenaica), Palestine, S. W. Turkey, Aegean (incl. Crete). (Allied to *E. obtusifolia* in W. Morocco and the Canary Islands).

Vicariads:

Cedrus libani. Subsp. *atlantica*: Morocco, Algeria. Subsp. *libani* (incl. subsp. *stenocoma*): Turkey (mainly Taurus), Lebanon. Subsp. *brevifolia*: Cyprus. Replaced in Afghanistan, W. Pakistan and W. Himalayas by *C. deodara*. Montane.

Ceratocarpus heterocarpa (*Fumariaceae*): Spain, Morocco, Algeria. *C. palaestina*: Palestine, Lebanon, W. Syria, Cyprus. Ditypic genus.

Geranium malviflorum: S. Spain, Morocco to Tunisia. *G. macrostylum*: Albania, Greece, Aegean, Turkey; and related S. W. Asian species of Sect. *Tuberosa*. Montane. (DAVIS 1970).

Erodium hymenodes: Morocco, Algeria, Tunisia. *E. pelargoniiiflorum*: Turkey (Taurus). Both saxatile species of the *Cedrus* belt.

Chronanthus (Cytisus) biflorus: Spain, Morocco, Balearics. *C. orientalis*: Turkey (W. Anatolia). Ditypic genus.

Astragalus lusitanicus subsp. *lusitanicus*: Portugal, Spain, Morocco, Algeria. Subsp. *orientalis*: Greece, Turkey, Cyprus, Lebanon.

Ebenus pinnata: Morocco to Libya (Tripolitania). Nearest relatives in Anatolia, where all 14 species are endemic out of a generic total of 20 species. The only other N. African species, *E. armitagei*, grows in Cyrenaica and adjacent N. W. Egypt, and is related to *E. cretica* from Crete.

Eryngium bourgatii: France, Spain (Pyrenees), Morocco. *E. heldreichii*: Turkey (Taurus), Lebanon and Anti-Lebanon ranges; probably not more than a subsp. of *E. bourgatii*. Montane — subalpine.

Buxus balearica: S. Spain, Balearics, Sardinia, Morocco, Algeria. *B. longifolia*: Turkey (Amanus and Anti-Taurus); probably only a subspecies of *B. balearica* (Fig. 4).

Iris planifolia (alata): Portugal, Spain, Morocco to Libya (Cyrenaica), Sardinia, Sicily, Crete. *I. palaestina*: Palestine, Lebanon. Sect. *Juno*. (Fig. 4).

Discussion. Most of the species disjunctions between the E. and W. Mediterranean can be thought of in terms of contraction of once more continuous areas (e. g. *Hypericum aegyptiacum*, *Euphorbia dendroides*, *Viburnum tinus*), mainly brought about by the accentuation of aridity in the eastern Mediterranean. The number of E.-W. vicariads is high, and some of these are taxonomically rather distinct, suggesting that, at least for these, initial separation was probably pre-Pleistocene. As with the Euro-Siberian connections, the floristic links between Spain and Morocco are much stronger than between Italy, Sicily and Tunisia. All species listed are absent from the desertic Sinaitic-Libyan gap; a few occur in Cyrenaica, which serves as a limestone Mediterranean "island" between sea and desert, and shows strong floristic connections with lowland Crete (SANDWICH & SIMPSON 1941). The sea is deep (up to 9,000 ft.) between Cyrenaica and Crete, and though there is no geological evidence for a land bridge, it seems likely these two areas (which have undoubtedly acted as refugia) may once have been somewhat closer together than they are now. Though the Sinaitic-Libyan gap is now unsuitable for the persistence of all but a few littoral Mediterranean elements, this may not necessarily have been so during the glacials (pluvials). It seems possible that *Ferula tingitana* and *Onobrychis crista-galli* may have taken the N. African route, probably from east to west, to judge by the asiatic centres of these genera.

3. Irano-Turanian — Mediterranean connections

Specific connections:

Ranunculus asiaticus (Fig. 5): Libya to N. Egypt, Crete, Rhodes, Turkey, Cyprus, Lebanon, Syria, Palestine, Iraq, S. & W. Iran. A taxonomically isolated species with local flower-colour variants.

Ranunculus isthmicus s. l. (incl. *R. orientalis* auct. non L.). Morocco, Algeria, Libya (Tripolitania), Sicily, Greece, Turkey, Cyprus, N. W. Iran. Polymorphic, with morpho-ecological races.

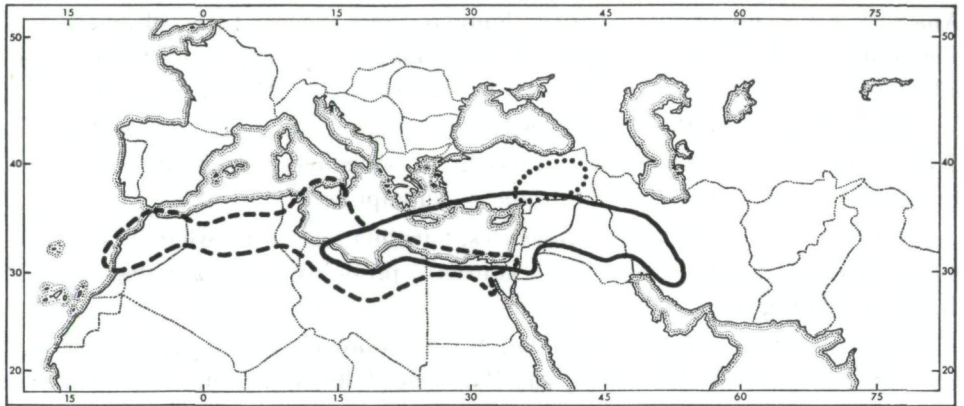


Fig. 5. Distribution of ——— *Ranunculus asiaticus*, - - - *Scorzonera undulata*, *S. suberosa*.

Pistacia atlantica agg. (incl. *P. mutica*, *P. eurycarpa*, *P. cabulica*). Canary Is., Morocco, Algeria (N. and Hoggar), Tunisia, Libya (G. Nefoussa), Aegean (but not Crete), N. E. Greece, Crimea, Cyprus, Palestine, Syria, Turkey, N. Iraq, Caucasia, Iran, Afghanistan, W. Pakistan. Dioecious tree.

Scutellaria orientalis s. l.: Spain, Morocco; Balkans, Crimea, Caucasia, Turkey, Lebanon, N. Iraq, Iran. A polymorphic species of mountains and high steppe. Allied species in S. W. Asia.

Vicariads:

Isatis djurdjurae: N. Morocco, Algeria. A member of Sect. *Samerarioides*, with its maximum concentration of species in Anatolia and Iran; *I. cappadocica* s. l. seems to be its closest ally.

Onobrychis kabylica: Morocco to Tunisia. *O. pallasii* from steppic Crimea (allied to Irano-Turanian species in S. W. Asia).

Eryngium dichotomum: S. Spain, Algeria, Tunisia, Sicily, Lampadusa, Italy. Very close to *E. caeruleum* (*biebersteinianum*) from the S. Russian steppes, Caucasia, N. E. Anatolia, N. & N. W. Iran, eastwards to Tibet. It seems quite likely that the basically Irano-Turanian *E. caeruleum* has given

rise both to *E. dichotomum* and to *E. planum* (E. Europe to C. Asia and Siberia), by persistence of the juvenile type of foliage into the adult stage.

Eryngium triquetrum: Morocco to Tunisia, Pantelleria, Sicily, Italy (Calabria); Sardinia? *E. bithynicum*: Turkey (C. Anatolia).

Lonicera arborea: S. Spain, Morocco, Algeria. *L. nummulariifolia*: Greece, Crete, Turkey, Lebanon, N. Iraq, Iran, Afghanistan, eastwards to C. Asia (Turkestan). Bird-dispersed.

Salvia blancoana: S. E. Spain, Morocco, Algeria (often in the Mauritanian steppe). *S. aucheri*: Turkey (Taurus).

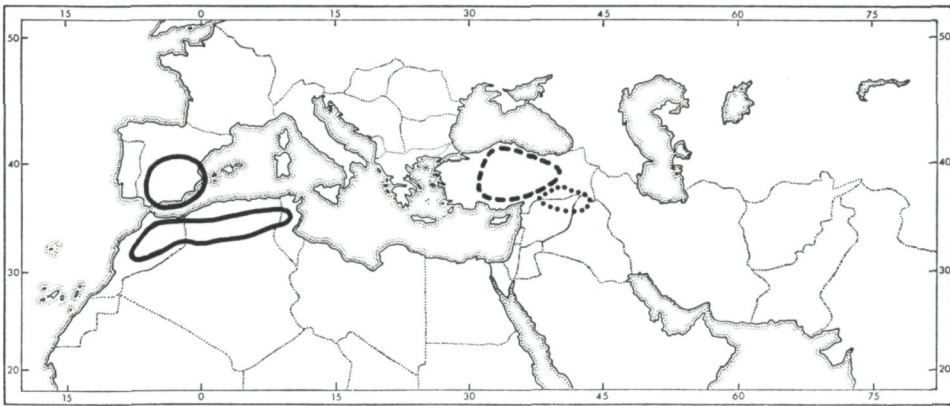


Fig. 6. Distribution of ——— *Salvia phlomoides*, - - - *S. hypargeia*, *S. montbretii*.

Salvia phlomoides: Spain, Morocco, Algeria, Tunisia. Two related species in Turkey: *S. hypargeia* (C. Anatolia) and *S. montbretii* (Turkish Mesopotamia, N. Syria & N. Iraq) (Fig. 6).

Discussion. A peculiarity about this group is that in nearly all cases the species in S. W. Asia are centred in the Irano-Turanian region, whereas in N. W. Africa the same species, or its vicariad, has penetrated into the Mediterranean belt. The species mostly belong to groups centred in S. W. or C. Asia, so that we must think of them as being of Irano-Turanian origin; as they migrated westwards, colonisation of Mediterranean communities may have facilitated differentiation. A few of the species may have spread from S. W. Asia via the N. African route (e. g. *Ranunculus asiaticus*, Fig. 5); others appear to have taken the Sicilian route (*Ranunculus isthmicus*, *Eryngium bithynicum* — *E. triquetrum*). If others travelled westwards across southern Europe, entering Morocco through Spain, they presumably did so during inter-glacials. It is possible that *Scutellaria orientalis*, *Lonicera nummulariifolia* — *L. arborea*, and *Eryngium biebersteinianum* — *E. dichotomum* reached N. W. Africa in this way but glaciation has so disturbed distribution patterns in C. Europe that we can hardly expect to trace them there. How some of the vicariads reached N. W. Africa (e. g. *Isatis*, *Onobrychis*, *Salvia* listed above) remains a mystery. It

seems remarkable that the dioecious *Pistacia atlantica* agg. extends interruptedly from W. Pakistan to the Canary Islands; it is characteristic of the Mauritanian steppe belt in N. W. Africa, though now decimated in many areas. Such a distribution must surely date from the Tertiary. It may be pointed out here that, although we have followed ZOHARY (1962, 1966) and others in including the "Mauritanian steppe province" in the Irano-Turanian region, its affiliation remains in some doubt. This N. W. African province is characterised by *Artemisia herba-alba*, *Lygeum spartum* and *Stipa tenacissima* among its leading species, but is so penetrated by Mediterranean and Saharo-Sindian elements that its Irano-Turanian affinities are often obscured.

4. Irano-Turanian connections

Specific connections:

Zizyphus lotus: Spain, Morocco to Libya, Sicily, Greece, Cyprus, Palestine, S. Turkey (?), tropical Arabia. There is some doubt as to what element this invasive shrub be referred, since it penetrates beyond the "Mauritanian steppe province" into Mediterranean and Sudano-Deccanian regions.

Rhus tripartita (*oxyacanthoides*) (Fig. 7): Canary Is., Morocco, Algeria (incl. Hoggar), Tunisia, Sicily, Libya, Egypt, N. Sudan (Nubia), Palestine, Lebanon, Syria.

Astragalus lanigerus s. l. (incl. *A. alexandrinus*, *platyrhaphis*): S. E. Spain, Morocco to Egypt, Cyprus, Palestine, Lebanon, Syria, Turkey (E. Anatolia), Iraq. The Sicilian *A. huetii* may not be specifically distinct.

Hohenackeria exscapa (*bupleurifolia*) (*Umbelliferae*): S. Spain, Morocco, Algeria, Turkey, Caucasia. The related *H. polyodon*, the only other member of the genus, grows in C. Spain and Algeria.

Achillea santolina: Morocco to Egypt, Palestine, Lebanon, Syria, Turkey, Cyprus, Iraq, Iran, Afghanistan, W. Pakistan, C. Asia (?).

Artemisia herba-alba: Spain, Morocco to Egypt, Palestine, Syrian Desert, Turkey (Mesopotamia), Iran, and perhaps eastwards to C. Asia. The complex needs revision.

Fraxinus xanthoxyloides (Fig. 7): Morocco, Algeria, E. Afghanistan, W. Pakistan to W. Himalayas.

Marrubium alysson: S. E. Spain, Morocco to Tunisia, Italy, Sardinia, Libya (Cyrenaica), Egypt, Palestine, Syria.

Haloxylon articulatum: S. E. Spain, Morocco to Egypt, south to Hoggar Mts., Palestine, Lebanon, Syria, Iraq.

Noaea mucronata: Morocco to Egypt, Arabia, Aegean, Cyprus, Palestine, Lebanon, Syria, Iraq, Turkey, Caucasia, Iran to C. Asia.

Vicariads:

Cicer atlantica: Morocco (High Atlas). Allies in S. W. and C. Asia; the nearest relative may be *C. chorassanica* from Iran and Afghanistan.

Scorzonera undulata (incl. *S. alexandrina*): Morocco to Egypt & S. Palestine, Sicily; (the closely related *S. drarii* has been described from N. Sinai). Allied to *S. suberosa* from E. and adjacent S. Anatolia. (Fig. 5).

Convolvulus caput-medusae (*C. trabutianus*). Canary Is., Morocco, Algeria. Allied to such S. W. Asiatic species as *C. fruticosus* and *C. leiocalycinus*.

Dracocephalum renatii (*mairei*): Morocco (High Atlas, alpine). Related to *D. setigerum* (E. Anatolia) and *D. kotschyi* (N. & W. Iran); all are in Sect. *Moldavica*.

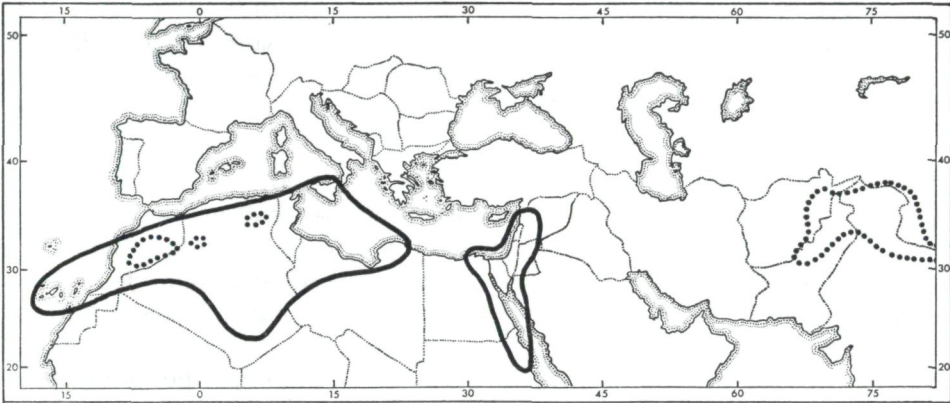


Fig. 7. Distribution of ——— *Rhus tripartita*, *Fraxinus xanthoxyloides*.

Discussion. Many of these Irano-Turanian species still occur throughout most of N. Africa, and probably took this route from S. W. Asia into N. W. Africa, many even reaching Spain. Examples include *Astragalus lanigerus*, *Haloxylon articulatum*, *Artemisia herba-alba*, *Noaea mucronata*, *Achillea santolina*. A more southern subtropical origin may underly the extensive occurrence of *Zizyphus lotus* in N. Africa. How the alpine endemics, *Cicer atlantica* and *Dracocephalum renatii* (*mairei*), reached the High Atlas is anybody's guess; but they have certainly been derived from allied stocks in S. W. Asia. These (and the distinct vicariads listed under *Convolvulus* and *Scorzonera*) may well date back to pre-Pleistocene times. It is worth pointing out that the extensive but highly disjunct distribution of *Fraxinus xanthoxyloides* extends from Morocco to the W. Himalayas, and is paralleled by the rather similar ranges of *Cedrus*, *Cupressus* and *Pistacia* listed under other phytogeographical headings. All now show an oblique E.-W. distribution, and may have reached N. W. Africa via southern Europe.

5. Saharo-Sindian connections

The Sahraro-Sindian flora is remarkable for the large number of species which extend from Morocco (or in some cases even from the Canary Islands) to Afghanistan or W. Pakistan (Sind) — a distance of over 5000 miles. These

include the following monotypic genera: *Notoceras bicornis*, *Gymnocarpus decander* (*fruticosus*), *Savignya parviflora*, *Anastatica hierochuntica*, *Neurada procumbens*, in addition to species in larger genera, such as *Cleome amblyocarpa* (*arabica*), *Plantago ovata*, *Citrullus colocynthis* and *Salvia aegyptiaca* (Fig. 2). Several of them extend southwards in N. Africa to the Hoggar and Tibesti mountains.

It would be wrong, however, to overemphasise the wide distribution of Saharo-Sindian species. Many genera well developed in this region are represented by a succession of vicarious species across much of the belt, e. g. *Fagonia*, *Tamarix*, *Farsetia*, *Zilla*, *Launaea*, *Calligonum*, *Aristida*. OZENDA (1958) draws attention to the fact that as much as 25% of the Saharo-Sindian flora of the northern Sahara (Mauritania to Tripolitania) is endemic to this territory, some areas being particularly rich in localised species. These endemic species include some monotypic genera in several different families: *Fredolia aretioides* (*Chenopodiaceae*), *Ammodaucus leucotrichus* (*Umbelliferae*), *Tourneuxia variifolia* (*Compositae*), *Warionia saharae* (*Compositae-Mutisieae*), etc. The occurrence of so many morphologically very isolated monotypic genera — of both wide and narrow distribution — is one of the most striking features of this region which, for its vast size, is poor in the total number of species.

Discussion. The Saharo-Sindian connections present no problem of dispersal. In most of this vast region, land connections have probably existed throughout the Upper Tertiary and Quaternary; topography, climate and soil are relatively uniform over large areas. The considerable number of monotypic genera characteristic of the Saharo-Sindian region suggests a distant Tertiary origin and the probable extinction of linking forms. Although the region appears to have an autochthonous core of endemic genera, Irano-Turanian, Mediterranean (more rarely) and subtropical floras all appear to have added their quota to the Saharo-Sindian region; for example, many of the dominant *Chenopodiaceae* have probably been derived from Irano-Turanian stocks in the deserts of C. Asia, while *Cleome* appears to have penetrated from the south.

Concluding Remarks

It remains to add that, in an area such as we have been dealing with, the climatic vicissitudes of the Quaternary make any speculation on paths of migration based on present-day distribution very dangerous ground. A map published by FERGUSON (1967) of fossil *Cedrus* (pollen and leaves) shows that this genus, now with an oblique E.-W. distribution in Asia and N. W. Africa, was established in C. Asia and C. & S. E. Europe in Eocene-Miocene, later migrating southwards in Europe as the Ice Age developed. In the lower Pleistocene, fossil *Cedrus* has only been found south of the Alps (including N. Spain and S. Italy) and in Morocco. QUÉZEL & MARTINEZ (1958—1959) show that *Cedrus* (together with *Quercus ilex*, *Pinus halepensis*, *Juniperus*, etc.) became abundant in the C. Saharan mountains (Hoggar, Tassili, Tibesti)

in post-pluvial (Holocene) times. This Mediterranean flora apparently migrated south-eastwards from N. W. Africa, becoming established in the C. Sahara by c. 10,000 BC. and persisting there till at least c. 2800 BC. Without this factual information on floristic history, one would have been badly misled by inferring past from present-day distribution. The suggestions made in this paper are a poor substitute for facts based on reliably identified fossil remains, but if they serve to stimulate discussion and further research they will have served their purpose.

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