

# A revision of the genus *Mandragora* (Solanaceae)

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**SYNOPSIS.** The Old World genus *Mandragora* L. (Solanaceae) is revised for the first time across its entire geographical range. The introduction reviews the extensive mythological and medicinal as well as the taxonomic history of the genus. On morphological and phenological grounds three geographically widely disjunct species can be distinguished: the Mediterranean *M. officinarum* L., the narrowly local Turkmenian endemic *M. turcomanica* Mizg. and the Sino-Himalayan *M. caulescens* C.B. Clarke. The generic monophyly of *Mandragora* L. as traditionally circumscribed is supported by cladistic analysis of morphological data. The ecological and historical phytogeography of the genus is discussed and alternative biogeographical scenarios are evaluated. Finally, a concise taxonomic treatment of the taxa is provided, based on the evidence of the preceding analyses.

## INTRODUCTION

The nightshade family (Solanaceae) is a cosmopolitan but predominantly tropical group and is especially well represented in the Neotropics. The family is of considerable economic importance. Food plants include potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L. (= *Lycopersicon esculentum* Mill.)), pepper (*Capsicum annuum* L.) and aubergine (*Solanum melongena* L.). Another species of great commercial value is tobacco (*Nicotiana tabacum* L.). The family also contains ornamental plants such as garden petunias (species of *Petunia* Juss.) and the Chinese lantern (*Physalis alkekengi* L.). Many members of the family are poisonous, but several such as deadly nightshade (*Atropa belladonna* L.), henbane (*Hyoscyamus niger* L.) and thorn-apple (*Datura stramonium* L.) provide drugs traditionally used in medicine. The subjects of this study, the mandrakes (*Mandragora* L.), belong to this latter group of pharmaceutically interesting Solanaceae.

The long history of mythology and medicinal use of the mandrake combined with the variable morphology and phenology have led to considerable confusion in the classification of *Mandragora*. The nomenclatural situation is, considering the small size of the genus, amazingly chaotic. In particular the Mediterranean *Mandragora* is burdened with synonyms, and some authors (Mill, in litt.) have expressed doubts about the placement of the Himalayan mandrake in *Mandragora* at all. This study represents the first taxonomic revision of the genus over its entire range. We address the following main questions in this study. Firstly, which of the described *Mandragora* taxa are justifiable if the whole range of the morphological variation is considered? Secondly, is the genus as currently delimited (including the Himalayan mandrake, *M. caulescens*) monophyletic? Finally, does the phylogeny, combined with the distribution patterns of the taxa, support a particular historical biogeographical scenario and do the ecological requirements of the defined taxa impinge upon this?

## Mythological and medicinal history

The origin of the myth surrounding the mandrake root is hard to trace. It is clear, however, that the mandrake was a focus of superstition and belief in magic and demons for many centuries. The sometimes vaguely humanoid shape of the root and its potent, psychotropically active alkaloids are probably responsible for the long history of myths. However, the properties ascribed to the plant as a whole, and especially to its root, are highly ambiguous and the first references in Ancient Egypt and in the Bible remain controversial. Ornaments on the casket and throne from the tomb of Tutankhamun seem to depict mandrakes (Hepper, 1990; Roland, 1991). *Mandragora* is not known to be native in Egypt but may have been cultivated there. The Biblical 'Dudaim' is often said to be identical with *Mandragora* (Moldenke & Moldenke, 1952; Feinbrun-Dothan, 1978; Fleisher & Fleisher, 1994). Dudaim is mentioned in the Song of Solomon (7: 13) and in another passage from the Old Testament (Genesis 30: 14–18), according to which it was used in relation to fertility. The 'Moly' of Homer in his *Odyssey* is presumed to be the mandrake, as is the 'Baraa' of Flavius Josephus' *Jewish Wars*, where it is described as shining in the dark (*sic*) and is attributed exorcistic powers. Pliny in his *Natural History* and Dioscorides in *De Materia Medica* wrote that the mandrake was known as 'Circaeon' after Circe, the mythical sorceress who turned men into sexually supercharged swine (Marzell, 1975; Roland 1991; Fleisher & Fleisher, 1994). The Ancient Greeks and Romans considered the mandrake so potent and valuable as a narcotic and restorative plant that the collectors of its roots had to obey rigid ceremonial rules which were described by Theophrastus and Pliny (Randolph, 1905).

In Medieval Europe the plant was known as 'Alraune' in Germany and 'Main de gloire' in France. Carved to emphasize the anthropomorphic male or female character of the root, it was popular as an aphrodisiac, charm against sterility and love talisman alike. But the plant was soon connected with witchcraft; for example, Joan of Arc, who was tortured and burnt at the stake in 1431 as a heretic, was also accused of the witches' crime of possessing a mandrake (Thompson, 1934). It was believed that the plant grew under gallows and that the root owed its human shape to urine or sperm of unjustly hanged men. The gathering of the root was considered to be highly dangerous and dogs had to perform the supposedly lethal procedure of pulling out the plants, whereupon the roots would shriek so 'that living mortals hearing them run mad': Shakespeare, *Romeo and Juliet* Act IV (Randolph, 1905; Moldenke & Moldenke, 1952; Marzell, 1975; Roland, 1991; Talalaj et al., 1992; Fleisher & Fleisher, 1994). Perhaps the most interesting aspect of the mythology of the mandrake is convergent myths in the eastern area of the genus in the disjunct region of Central Asia, the Himalayas and China where *Mandragora* has a similarly long history of application and traditional use. For instance in Sikkim, the roots of *Mandragora caulescens*, called 'Lakshmana', were used in magical rites and in folk medicine (Mehra, 1979); and in Central Asia the mandrake, called 'Khaoma-soma', was considered a holy plant (Khlopina, 1979).

The mythology of the mandrake and its use in traditional medicine are hard to keep apart. In a wide range of applications it was used as an aphrodisiac, hypnotic, emetic and purgative, sedative and narcotic, for example as a pain-killer at childbirth as well as to relieve crucifixion agony (Duke, 1985; Talalaj et al., 1992); in fact, according to Heiser (1969), it has been questioned that Christ died on the Cross at all, suggesting that the vinegar supplied to him had contained the drug, inducing merely a deathlike trance. The secondary metabolites of major pharmaceutical importance are chiefly

tropane alkaloids and their esters. Staub (1962), Hegnauer (1973), Romeike (1978), Evans (1979) and Jackson & Berry (1979) list alkaloids of *Mandragora* and other Solanaceae. Tropane alkaloids occur mainly in the Solanaceae, but they are not entirely restricted to this family; other tropane alkaloids of importance include cocaine, found in the family Erythroxylaceae. However, esters with tropic or related acids of alkamines derived from tropane do seem to be restricted to the Solanaceae (Romeike, 1978).

The most important alkaloid components of *Mandragora* are: atropine, apoatropine, belladonnine, cuscohygrine, hyoscyamine, hyoscyamine-N-oxide, norhyoscyamine, scopolamine, 3 $\alpha$ -tigloyloxytropine, 3 $\alpha$ ,6 $\beta$ -ditigloyloxytropine, and 6 $\beta$ -hydroxyhyoscyamine. The root, stem, leaves, fruits and seeds of *Mandragora* all contain a different alkaloid profile. However, the root is considered to be the site of synthesis of the tropane alkaloids (Romeike, 1978) and is the most poisonous part of *Mandragora*, due to the high concentration therein. The total content of alkaloids in the root is around 0.4% (Kessler, 1951; Maugini, 1959; Duke, 1985), hyoscyamine being the most important constituent (Duke, 1985). In contrast, the berries are said to be sweet and edible in moderation (Viney, 1994). The synthetic pathways leading to the alkaloids in different taxa of the Solanaceae have been proposed to be homologous to each other (Tétényi, 1987) and to be a linear or spiralling phyletic sequence. Tropane alkaloids are effective as analgesics, anaesthetics, antispasmodics, and are used to increase the circulation, reduce secretions and dilate pupils. Scopolamine is a hypnotic (Duke, 1985) and achieved a notorious reputation as a 'truth-drug' in police and secret service investigations (Heiser, 1969). 'Quishen', a Chinese herbal medicine consisting of dried roots of *M. caulescens*, is used in Yunnan and Xizang as a ginseng substitute for all kinds of physical weaknesses (Xiao & He, 1983). In allopathic western medicine, however, the mandrake has largely lost its importance as valued source of alkaloids, although the plant itself is still surrounded by myth.

## Taxonomic history

### *The classification of Mandragora*

MEDITERRANEAN PLANTS. As mentioned above, considering the small size of the genus, there has been a fair amount of confusion in respect to the classification of *Mandragora*. The long taxonomic history, especially of the Mediterranean *Mandragora* species, led to a large number of often imprecisely defined species and subspecies or varieties. As a consequence, there is a plethora of names, and their somewhat indiscriminate use renders the meaning and reliability of identifications of specimens in herbaria, as well as in the literature, highly problematic. Here we present the taxonomic history of the Mediterranean part of the genus in periods, with examples of major taxonomic works and their treatment of the genus, in order to outline the main taxonomic trends through the centuries.

*Pre-Linnaean*: The Ancients distinguished two species that they called the female or black mandrake (*Mandragoras femina*), and the male or white mandrake (*Mandragoras mas*). These plants were described by both Dioscorides and Pliny (cf. Randolph, 1905 for translations), and this division was widely adopted, for instance by Parkinson (1629) and by Jean Bauhin et al. (1651) as late as the seventeenth century. The male mandrake corresponds to a spring flowering entity; the female mandrake represents an autumn flowering one. Caspar Bauhin (1623) and Tournefort (1719), on the other hand, each recognized three 'species'. Both authors listed *Mandragora fructu rotundo* and *M. flore subcaeruleo, purpurascente*.

Bauhin's third species was *M. fructu pyri* while Tournefort's was *M. flore subcaeruleo, foliis minoribus, fructu globoso*.

**Linnaeus:** In his *Hortus cliffortianus*, Linnaeus (1738) considered these variants as mere forms of a single species. In the first edition of *Species plantarum* (1753), he accordingly recognized only one species that he named *Mandragora officinarum*. Later, however, he changed his mind with respect to the distinctness of this taxon and placed it within his genus *Atropa*, calling it *Atropa mandragora* (Linnaeus, 1759, 1762).

**Post-Linnaean:** Linnaeus's idea of a single species did not last very long. The nineteenth and the first half of the twentieth centuries were characterized by an increasingly elaborate division of the genus (Table 1). Heldreich (1886) additionally described an infertile hybrid between two vernal entities: *Mandragora vernalis* Bertol. and *M. haussknechtii* Heldr., called *M. × hybrida* Haussk. & Heldr.

**Post-1950:** In recent decades, however, there has been a trend towards reversing this ever greater subdivision of the genus. In fact, since the 1950s there have been a number of proposals to re-adopt the two traditional, pre-Linnaean taxa only (Tercinet, 1950; Hawkes, 1972b; Jackson & Berry, 1979). This viewpoint was adopted in *Flora Europaea* (Hawkes, 1972a), using the names *Mandragora officinarum* L. for a vernal entity and *M. autumnalis* Bertol. for an autumnal one. However, *M. officinarum* L. might be considered an ambiguous name since it was formerly used for an autumnal entity as well (Greuter & Rechinger, 1967; see Table 1). Hawkes (1972b) rejected this reservation on the grounds of the priority, the wide use and the generic type status of the Linnaean epithet *officinarum*. Knapp in Jarvis et al. (1993) finally lectotypified *M. officinarum* L. with a specimen in the Bursar herbarium, to which no phenological data are attached.

**SINO-HIMALAYAN PLANTS.** In contrast to the Mediterranean plants, the classification of the disjunct Central and East Asian part of the genus was never as contentious and did not arouse much comment, in part reflecting its far younger taxonomic history. *Mandragora caulescens* was described by C.B. Clarke (1883) in Hooker's *The flora of British India* (Hooker fil. and Thomson labelled the specimens '*Scopolia humilis*' but this name was never published). *Anisodus caulescens* (C.B. Clarke) Diels and *A. mariae* Pascher, as well as *Mairella yunnanensis* H. Lév., were placed in synonymy with *Mandragora caulescens* in the *Flora of China* (Zhang et al., 1994). Grubov (1970) described a new species from Xizang, China which he named *Mandragora tibetica*, and Kuang Ko-zen & Lu An-ming (1978) described a new species found in Qinghai and Xizang which they named *Mandragora chinghaiensis*. In the *Flora of China* (Zhang et al., 1994) the latter two taxa were provisionally put into synonymy with *M. caulescens* until a more detailed revision could

establish their distinctiveness. *Mandragora shebbeari* C.E.C. Fischer, described from a single specimen from Xizang (Fischer, 1934), was transferred to the monotypic solanaceous genus *Przewalskia* by Grubov (1970). One attempt to subdivide *Mandragora caulescens* was made by Grierson & Long (1978) who split it into four subspecies (subsp. *caulescens*, subsp. *flavida* Grierson & Long, subsp. *purpurascens* Grierson & Long and subsp. *brevicalyx* Grierson & Long) differentiated on the basis of corolla colour and various morphometric characters, especially of flower parts.

**TURKMENIAN PLANTS.** Finally, *Mandragora turcomanica* Mizg. was described in 1942 from a small area (the Shevlan 'pocket', Mizgireva, 1955) near Kara Kala in the southwestern Kopet Dag in Turkmenistan. Only a few collections of this restricted endemic exist, and these are all to be found in herbaria of the former Soviet Union. Its status as a distinct taxon has never really been questioned, but only because so few specimens exist for comparison. Mizgireva (1955) worked for 12 years on the detailed anatomy and morphology of this species and her revision remains the best source for data on characters and their variation.

### *The position of Mandragora within the Solanaceae*

More than 200 years after the original outline by Jussieu (1789), the higher level classification of Solanaceae is far from being settled, and the placement of *Mandragora* in the various proposed classifications is just as controversial. In the following review, the most widely followed classifications of the Solanaceae are presented together with the positions of *Mandragora* and the other genera used in our cladistic analysis: *Anisodus* Link, *Atropa* L., *Lycium* L. and *Nicotiana* L.

In his artificial sexual system, Linnaeus (1753) placed *Mandragora* within his group Pentandria Monogyna, together with *Atropa*, *Lycium* and *Nicotiana*. Jussieu (1789) defined the 'order' Solaneae with *Mandragora* in group II (fructus baccatus) alongside *Atropa* and *Lycium*. *Nicotiana* on the other hand was placed in group I (fructus capsularis). In the nineteenth century, classifications became more elaborate and tribes and subtribes were established in order to approximate a more 'natural' classification. In Table 2, the three most widely adopted classifications of the Solanaceae in this period (Dunal, 1852; Bentham, 1876; Wettstein, 1895) are presented together with the more recent one of Baehni (1946).

The last few decades have seen the analysis of new types of data, such as DNA sequences (Olmstead & Sweere, 1994) and secondary plant metabolites (Tétényi, 1987), as well as application of cladistic methodology to morphological data (Hoare & Knapp, 1997). This has led to new hypotheses concerning relationships within the Solanaceae, as well as the placement of *Mandragora*. However, opinion still differs widely on whether *Mandragora* should be placed within the tribe Hyoscyameae (Hoare & Knapp, 1997; = *Atropeae sensu* Tétényi, 1987) or in an isolated, basal monogeneric tribe Mandragoreae (Olmstead & Sweere, 1994; Hunziker, 1995; Olmstead et al., in press).

## MATERIALS AND METHODS

### Material examined

This revision is based exclusively on herbarium specimens. The material examined includes the *Mandragora* specimens in the herbaria of The Natural History Museum of London (BM) and Kew (K) together with specimens borrowed from the following herbaria:

**Table 1** Post-Linnaean classifications of the increasingly subdivided Mediterranean taxa of *Mandragora*.

Classification type	Vernal species	Autumnal species
1 VERNAL, 1 AUTUMNAL TAXON Sprengel (1825)	<i>M. vernalis</i> Bertol.	<i>M. autumnalis</i> Bertol.
1 VERNAL, 2 AUTUMNAL TAXA Bertoloni (1835), Dunal (1852)	<i>M. vernalis</i> Bertol.	<i>M. officinarum</i> L. <i>M. microcarpa</i> Bertol.
2 VERNAL, 2 AUTUMNAL TAXA Heldreich (1886)	<i>M. vernalis</i> Bertol. <i>M. haussknechtii</i> Heldr.	<i>M. autumnalis</i> Spreng. <i>M. microcarpa</i> Bertol.
3 VERNAL, 2 AUTUMNAL TAXA Vierhapper (1915)	<i>M. mas</i> Garsault <i>M. hispanica</i> Vierh. <i>M. haussknechtii</i> Heldr.	<i>M. autumnalis</i> Bertol. <i>M. foemina</i> Garsault

**Table 2** Tribal classification of the Solanaceae and the position of *Mandragora* and the outgroup genera *Anisodus*, *Atropa*, *Lycium* and *Nicotiana*.

Author	Classification	Genera of this study
Dunal (1852)	Nolaneae	Nolanineae Grabowskieae Triguereae Solanaceae
	Solaneae	
		Solanineae Atropineae Lycineae
		Datureae Hyoscyameae Nicotianeae Retzieae Fabiaceae Metternichieae Cestreae
		<i>Mandragora</i> <i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Nicotiana</i>
Bentham (1876)	Solaneae	Lyciinae
	Atropeae	
	Hyoscyameae Cestrineae Salpiglossidae	
		Hyoscyaminae Solaninae Mandragorinae
	Daturae Cestreae	Cestrinae Goetzeinae Nicotianinae
	Salpiglossidae	
		<i>Mandragora</i> <i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Nicotiana</i>
Wettstein (1895)	Nicandreae	Lyciinae
	Solaneae	
	Daturae Cestreae	Cestrinae Goetzeinae Nicotianinae
	Salpiglossidae	
		<i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Mandragora</i> <i>Nicotiana</i>
Baehni (1946)	Solaneae	Solaninae Sarachineae Margaranthinae Physalidinae Iochrominae Goetzeinae Discopodiinae Atropinae
	Atropeae	Markeinae Hyoscyaminae Parabouchetiinae
	Anthocercideae Nicotianeae	Nicotianinae Daturinae Nicandrinae
	Salpiglossidae	
		<i>Mandragora</i> <i>Atropa</i> <i>Lycium</i> <i>Anisodus (Scopolia)</i> <i>Nicotiana</i>

Berkeley (UC, JEPS), Edinburgh (E), Kunming (KUN), Palermo (PAL) and Reading (RNG). The collections of the Muséum National d'Histoire Naturelle in Paris (P) were examined on site during a research visit. Regrettably it was not possible to obtain any specimens, including the types, of *Mandragora turcomanica* and *M. tibetica* from St. Petersburg (LE) or *M. chinghaiensis* from Xining (HNWP).

Material with the same collection number or specimens collected at the same locality and at the same date were unified and treated as one sample. Unlocalized material or specimens with illegible, doubtful or very imprecise collection locality and collector data were excluded, cultivated material being the exception. Only collections with precise locality data are listed in the taxonomic account of the species. A complete listing of the specimens examined can be found in the Exsiccatae.

### Taxonomic concepts

The adopted taxonomic methodology in this study of herbarium material is necessarily largely pattern-oriented. If process-based terms like 'population' or 'hybrid' are used, these properties are only informally applied, i.e. inferred rather than rigidly defined, let alone experimentally circumscribed.

The adopted species concept is operational, i.e. the ability to distinguish between sets of specimens serves as the criterion for the delimitation of the terminal taxa (species). Cladistic analysis results in an estimate of these relationship between the species and the delimitation of higher level taxa, i.e. monophyletic groups and their hierarchical relationships. The requirement for a species description is thus at least one distinguishing qualitative, or discontinuous quantitative, diagnostic character state (monothetic species) or a unique set of character states (polythetic species) (cf. Nelson &

Platnick, 1981; Nixon & Wheeler, 1990). Morphological and phenological variation plus ecological and geographical information are the data that were collected from herbarium specimens and their labels respectively.

## Morphometrics

### Specimen sampling

The inherent weakness of the traditional herbarium record of a taxon for taxonomic studies is well known (Du Rietz, 1930; Anderson & Turrill, 1935; Anderson, 1941). For species that are well represented in herbaria, one can obtain a more or less accurate record of the general range of variation. Seldom or never, however, is it possible to calculate frequencies of the different variants and the resolution of the classification is limited by the lack of a random sample.

Plant variation also occurs on different hierarchical levels (cf. Bateman, 1989), which can become confused and overlap. In *Mandragora* the confounding of within-group and between-group variation is most pronounced in the Sino-Himalayan complex, due to the secondary growth of the plants during the late flowering and the fruiting period (ontogenetic variation, see Fig. 9, also Hoare & Knapp, 1997: fig. 5d). Combining all samples to a pooled matrix easily leads to a confusion of the two sources of variation which can seriously compromise interpretation of many applications of morphometric analyses (Gibson et al., 1984). Avoiding within-group variation, for example by calculating the mean or only considering the largest or smallest example of a particular character is not a solution, but merely reduces the total amount of variation encountered in a taxon, leading ultimately to a simplistic taxon delimitation. In the taxonomic process, characters and their variability necessarily have priority over all other considerations since taxa are attributed to characters—not the other way around (characters all attributed to individuals). It follows that the basal unit of investigation, the specimen, must be evaluated in respect to its variability. Therefore, maximal as well as minimal values of the flowering part measurements of each specimen were assessed, rather than solely mean or maximal values.

### Character sampling

A genus with a long taxonomic history is unlikely to yield any 'new' gross morphological characters which distinguish species. This is especially true when working with inadequate herbarium material (i.e. incomplete with much missing data and/or very old and often in poor condition). The emphasis in this study was thus much more on evaluating the traditional and obvious characters in respect to their ability consistently to delimit proposed taxa. The analysis was therefore carried out using the following data.

**GEOGRAPHY.** The entire distributional range of *Mandragora* was divided into 20 geographic areas. These are (1) Cultivated specimens, typically from botanic gardens north of the Alps, (2) North Africa, (3) Iberia, (4) northern Italy and Dalmatia, (5) peninsular Italy with Sardinia and Sicily, (6) mainland Greece, (7) Aegean islands, (8) Asia Minor, (9) Cyprus, (10) Levant, (11) Kopet Dag, (12) Nepal, (13) Sikkim, (14) Bhutan, (15) Arunchal Pradesh (Assam), (16) north Myanmar (Burma), (17) Yunnan, (18) Sichuan, (19) Qinghai and (20) Xizang.

**PHENOLOGY.** Flowering and fruiting dates were recorded, resulting in the cumulative reproductive period.

**MORPHOLOGY.** Corolla length, calyx length, fruit size, fruiting calyx length, leaf length, leaf length/width ratio. The corolla colour

of herbarium material is not reliably determinable and was thus only recorded if it was stated on the labels. The shape of the berry (globose or ovoid) was excluded as a character since it is not accessible through pressed herbarium material and is only rarely stated on the labels. Berry shape in the Solanaceae is quite variable and this variation is occasionally a developmental sequence (Bohs, 1994).

### Data analysis

Univariate and multivariate analyses were applied as a descriptive, explorative tool to study the joint relationships of the morphological, phenological and geographical variables of the specimens at hand. As mentioned above, since the examined specimens are not a random sample, the result of inferential data analysis with significance testing would be invalid. A cluster analysis or a cladistic analysis of the data at population level, on the other hand, was rejected on the grounds that these methods assume hierarchical relationships, an assumption that is not justified. Phenotypic characters may be distributed clinally or in a reticulate manner, but are unlikely to be strictly hierarchical (Crisp & Weston, 1993). If hierarchical structure exists, it would suggest that the populations have already undergone speciation and have to be treated as terminal taxa in the phylogenetic analysis. The explorative data analysis was performed on SYSTAT for the Macintosh Version 5.2 (Wilkinson, 1992).

**UNIVARIATE ANALYSES.** Phenological data are circular (Fisher, 1993). The reproductive period was thus analysed in a polar coordinate system. In order to dampen peak values, which might merely reflect a particularly high collecting effort, the collection proportion of each month was converted to its logarithm.

**MULTIVARIATE ANALYSES.** Ordination techniques reduce a data matrix of distances (similarities) among the samples to one or a few dimensions. These types of techniques seem to be most appropriate under a nonhierarchical model of infraspecific variation. Principal component analysis (PCA) is the method most commonly applied in multivariate systematics studies (James & McCulloch, 1990). It aims to show the eventual existence of distinguishable groups with discontinuous variation without *a priori* postulates of groups such as populations. Since data sets with missing data cannot be processed using PCA, only the most commonly represented characters of the herbarium specimens (see above and Table 3) were analysed. Fortunately, these are also the characters that are most commonly applied to differentiate between the traditionally recognized Mediterranean taxa. In contrast to many other analyses of specimen-based data, within-collection variation was accounted for by recording and analysing both minimal and maximal values of the flowering part lengths. Only fully developed and open flowers were considered and measured. The length/width ratio of the leaves was not included in the PCA analysis on the grounds that ratios are often not linearly related to the length measurements (Miles & Ricklefs, 1984). All the variables have been standardized (normalized) by the standard

**Table 3** Variables used in the principal component analysis of the Mediterranean complex.

Length measurements	Variable 1	Corolla length max.	mm
	Variable 2	Corolla length min.	mm
	Variable 3	Calyx length max.	mm
	Variable 4	Calyx length min.	mm
	Variable 5	Leaf length max.	cm
Phenology	Variable 6	Flowering time	month

deviation to obtain a variance of one and a mean of zero by performing the analysis on a correlation matrix.

Due to a lack of available specimens from Asia of the taxa *Mandragora caulescens* subsp. *brevicalyx*, *M. chinghaiensis*, *M. tibetica* and *M. turcomanica*, the discussion of variability among these taxa (and its implications on their delimitation) has to remain qualitative.

## Cladistics

Cladistic analysis is a parsimony-based search for hierarchical arrangements or patterns of terminal units (in most cases species). The premises are accordingly that there is a hierarchical structure of the taxa and therefore of the characters used to define them, and that the level of homoplasy in the chosen characters is low enough not to infer convergent groups. As a strictly numerical procedure, there is no need for additional models or assumptions relating to biological processes, such as reproduction or descent (Davis & Nixon, 1992). The resulting cladogram therefore represents a synapomorphy scheme, merely suggesting closeness of relationship due to recency of shared common ancestry. It might be congruent with the actual phylogenetic tree, featuring the ancestors and descendants; however, there are many possible phylogenetic trees compatible with one cladogram (Eldredge, 1979). The cladogram was rooted by means of outgroup comparison.

A phylogeny of the tribe Hyoscyameae based mainly on morphological characters was recently published by Hoare & Knapp (1997) suggesting that *Mandragora*, as traditionally defined, is monophyletic. To test the monophyly of *Mandragora* as a whole, we included in this analysis material of species representing two other genera of the Hyoscyameae, *Anisodus luridus* Link and *Atropa belladonna* (see Table 4). The three recognized terminal taxa of *Mandragora* represent the ingroup (*M. caulescens*, *M. officinarum*,

**Table 4** Taxa used in the cladistic analysis.

<i>Nicotiana glauca</i> Graham
<i>Lycium chinense</i> Mill.
<i>Anisodus luridus</i> Link
<i>Atropa belladonna</i> L.
<i>Mandragora officinarum</i> L.
<i>M. turcomanica</i> Mizg.
<i>M. caulescens</i> C.B. Clarke

**Table 5** Character set used in the cladistic analysis.

<b>Habit</b>
1. Woody plant (shrub or tree) 0; herb 1
<b>Root</b>
2. Tap-root: enlarged tap-root absent 0; present 1
<b>Stem</b>
3. Axis: condensed 0; first condensed, later elongated 1; elongated 2
<b>Leaves</b>
4. At anthesis: leaves clustered in a rosette 0; leaves alternate 1
<b>Inflorescence</b>
5. Type: numerous flowers in panicle 0; 1(–3) axillary flowers 1
<b>Corolla</b>
6. Shape: tubular-infundibuliform 0; campanulate-urceolate 1
<b>Fruit</b>
7. Type: berry 0; capsule 16
<b>Fruiting calyx</b>
8. Not enlarged in fruit 0; markedly enlarged in fruit 1
9. Without prominent ribs 0; with prominent ribs 1
<b>Seeds</b>
10. Embryo: not curved 0; curved circularly or in a spiral 1
11. Testal cells deep 0; shallow 1

**Table 6** Data matrix used in the HENNIG86 analysis

Taxon	Character		
		1	1
		12345	67890
<i>Nicotiana glauca</i>		00200	01000
<i>Lycium chinense</i>		00200	00001
<i>Anisodus luridus</i>		11201	11111
<i>Atropa belladonna</i>		10201	10001
<i>Mandragora officinarum</i>		11011	10001
<i>M. turcomanica</i>		11011	10101
<i>M. caulescens</i>		11111	10111

*M. turcomanica*). The outgroup, *Nicotiana glauca* Graham, was chosen based upon previous cladistic analyses of chloroplast DNA data sets (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press). *Lycium chinense* Mill. was included as an additional taxon (but not defined as an outgroup, see Tables 2 and 4).

Although acknowledging that there is no such thing as an *a priori* 'perfect cladistic character' (Thiele, 1993), the suggestion of Chappill (1989) and Stevens (1991) not to include purely morphometric, quantitative data in the cladistic analysis was followed. This limitation is feasible in view of the minimal size of the ingroup and the already established analysis of an extensive character set including quantitative character states (Hoare & Knapp, 1997). The characters used in the present work (Table 5) and their states are largely self-explanatory. The data matrix used in the analysis is presented in Table 6.

Cladistic analyses were undertaken with HENNIG86 (Farris, 1988) using the *ie* option (implicit enumeration) with all characters unordered, thus avoiding any character state change assumptions. The generated cladogram statistics include length (L), the number of character state changes on the tree, the ensemble consistency index (CI) which provides a measure of character fit on the cladogram (amount of homoplasy), and the ensemble retention index (RI) which expresses the fraction of similarities on the cladogram interpreted as synapomorphy (Farris, 1989). Both of these indices have an optimal value of 1.

## RESULTS AND DISCUSSION

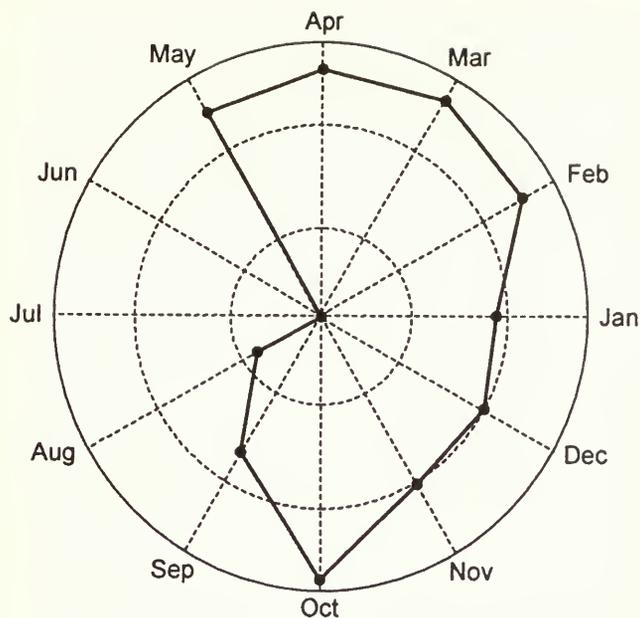
### Species delimitation using morphometric analyses

For the Mediterranean taxa a number of specific hypotheses were tested using the above described statistical analyses.

#### *Univariate analysis of reproductive period.—Are there two distinct vernal and autumnal taxa?*

By adopting the two species *Mandragora vernalis* and *M. autumnalis*, Sprengel (1825) argued against Linnaeus's unified *Mandragora officinarum* concept. Even in later, more elaborate classifications the division into these two major groups remained important (Table 1) since it was obvious that two groups with widely differing flowering periods would hardly be able to interbreed due to the seasonal isolation. So, is there evidence in the compiled Mediterranean data set that there are two phenologically distinct species? Figure 1 shows the distribution of the collecting dates (in flower or in fruit) as an indicator of the reproductive period.

It is evident that there is actually only one, very extensive period of reproductive activity from autumn to spring. In fact only during the hottest summer months does the cycle break. If conditions are



**Fig. 1** Relative distribution of the vegetative period of the Mediterranean complex (*Mandragora officinarum*) in the course of the year (logarithmized monthly fractions: for analysis see text).

favourable, the same individual can flower twice a year, in autumn and then again in spring, as can be seen from annotated herbarium material, especially from cultivated material in botanical gardens. The key factor is probably sufficient rainfall; for instance, sudden and widespread flowering after exceptionally heavy autumn rains was recorded from Tunisia (label data from Tomkinson 72). A more detailed discussion pertaining to the influence of the climate and the summer dormancy is given in the section on ecological biogeography below.

*Multivariate analysis of morphometric characters.* – Are there distinct clusters within the Mediterranean mandrakes that are recognizable from gross morphology?

The different eigenvector values of the PCA (Table 8) indicate the relative contribution of the variables. The first three axes (see Table 7) explain 92.2% of the variation if length measurements are considered only (Fig. 2a), and 87.1% of the variation if the analysis was run including the phenological variable of flowering time (Fig. 2b). In both cases it is obvious that no clear-cut clusters can be distinguished. Cryptic species may exist within the Mediterranean region but are likely to be revealed only if extensive, field-based studies over the entire range, as well as transplant experiments, are undertaken (Clausen et al., 1940). The information currently available does not justify recognition of more than a single species of Mediterranean mandrake.

Other characters traditionally applied in keys but not analysed quantitatively here include the following:

*Corolla colour:* Hawkes (1972b) considered the elaborate splitting of the vernal and autumnal groups as unjustified and recognized only the white-flowered vernal plants from northern Italy and Dalmatia as distinct from the remaining Mediterranean group. Restricted to only a small part of the total Mediterranean range, the white-flowered plant has often been considered as the most distinctive group (Heldreich, 1886; Vierhapper, 1915). The diagnostic value of this character which has been extensively used in past and current

**Table 7** Principal components (PC) of the Mediterranean complex. A: Length measurements only. B: Length measurements and flowering period combined.

Component	Eigenvalue	% of variance explained
A PC 1	3.248	64.97
PC 2	0.977	19.54
PC 3	0.383	7.66
B PC 1	3.328	55.47
PC 2	1.410	23.50
PC 3	0.490	8.17

**Table 8** Eigenvectors of the three most important axes (component loadings).

Variable	PC 1	PC 2	PC 3
A 1 Corolla length max.	0.885	0.023	0.131
2 Corolla length min.	0.875	0.011	0.435
3 Calyx length max.	0.898	0.114	-0.391
4 Calyx length min.	0.924	0.065	-0.147
5 Leaf length max.	-0.197	0.979	0.047
B 1 Corolla length max.	0.882	0.067	-0.160
2 Corolla length min.	0.851	0.189	0.042
3 Calyx length max.	0.897	0.123	0.066
4 Calyx length min.	0.905	0.156	0.175
5 Leaf length max.	-0.181	0.865	-0.453
6 Flowering time	-0.413	0.763	0.471

keys is minimal, however, if one considers that flowers are very variable in colour even within individuals (Jury et al. 12238 from Morocco, Jury & Jury 13111 from Spain).

*Fruiting calyx length:* The relative length of the accrescent fruiting calyx to the berry (longer: *M. autumnalis* or shorter: *M. officinarum*) has also been proposed as a diagnostic character (Hawkes, 1972b). Again, it seems that within-group variation is just as high, considering for instance a specimen housed in P of a cultivated plant which features two berries that are clearly shorter than the calyx, but three others which are longer.

*Leaf shape:* This is perhaps the most variable character of all. One can get at least an idea of the variability if the length to width ratios of mature leaves are compared. The variability within an individual ranges from 1.7:1–4:1 (in Reverchon s.n.) to 4.6:1–10.5:1 (in Welwitsch 159). The total variability within the whole set of examined specimens was found to be between 1.5:1–10.5:1.

Any distinction between *Mandragora officinarum* and *M. autumnalis* or any other splitting of the Mediterranean *Mandragora* on morphological or phenological grounds would be intentionally giving formal status to divergent ends of clines. Thus overlapping intermediates would be difficult if not impossible to assign to either of the taxa in any other way than arbitrarily. Extensive overlap and putative hybrids must be considered if aiming at expressing the whole range of variability. This confirms Meikle's (1985) doubts concerning the validity of the different proposed Mediterranean species. Although certain plants of particular populations are quite different in appearance from some plants of other populations, when the total pattern of variation over the entire range is considered, no diagnosable taxa within the Mediterranean complex of *Mandragora* are discernable. Further morphological support for the unification of the Mediterranean *Mandragora* comes from the anatomy of the tap roots which has been shown to be identical in vernal and autumnal taxa and in their chemical composition which is also similar (Jackson & Berry, 1979).

For *Mandragora turcomanica*, a statistically valid morphometric analysis is not feasible with the available literature data only. The

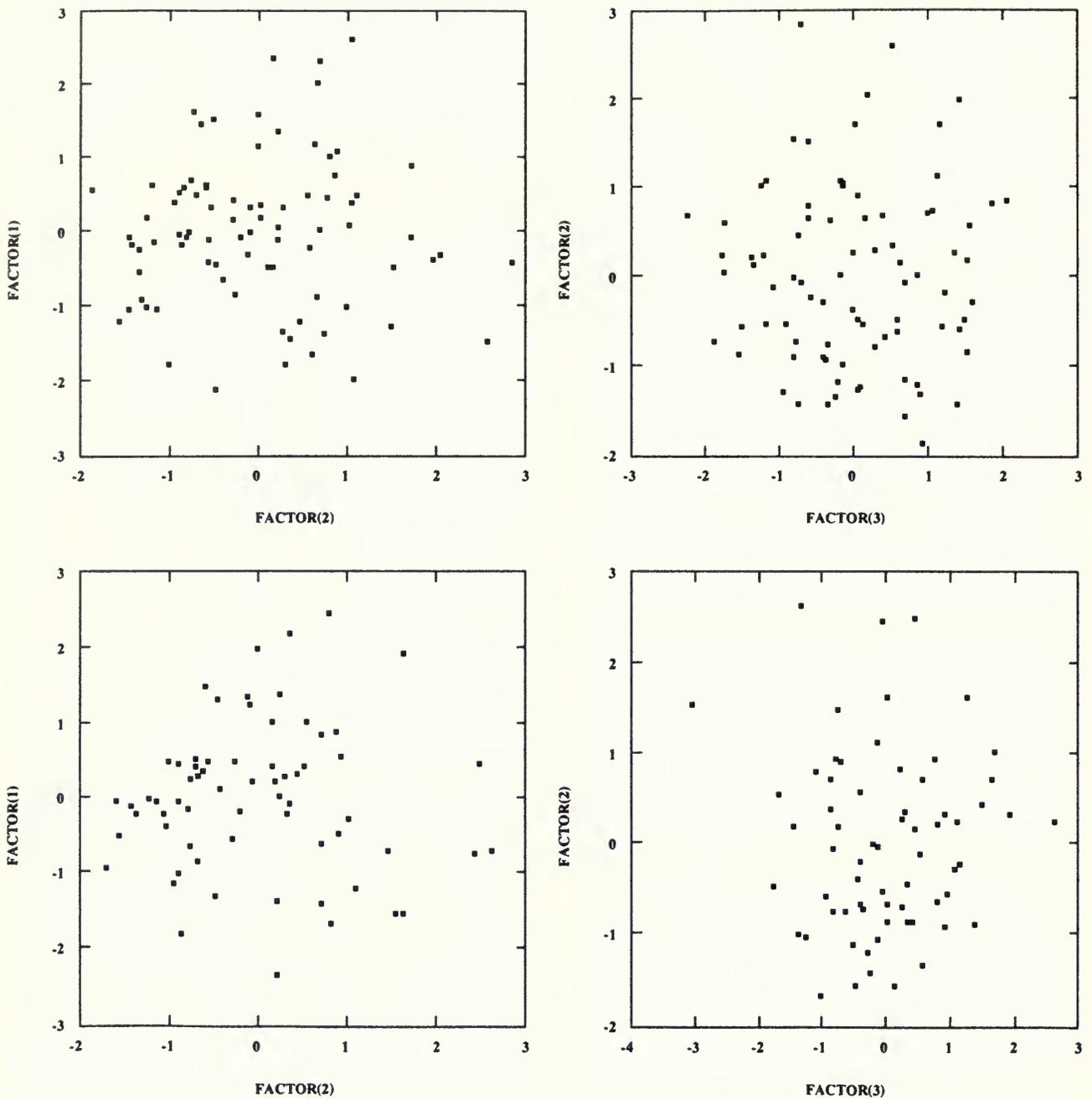


Fig. 2 Principal component analysis of the Mediterranean complex (*Mandragora officinarum*). Top pair: a. Bottom pair b. Left: PC 1,2. Right: PC 2,3.

range of the Turkmenian plants is so small that variability at population level is considered equivalent with the variability over the whole range. Mizgireva (1955) meticulously documented teratogenic forms of flowers and fruits of *M. turcomanica*, but did not cite field collected vouchers for these forms. She also documented huge variability in the shape and size of tap roots, and described the growth of the plant in detail, from seed germination to fruiting. *Mandragora turcomanica* is accepted as a distinct species on the grounds of the evidence given in Mizgireva (1942, 1955, 1978) and Lincevskij (1955). The whole plant is much larger than *M. officinarum*. The lower leaves ( $\pm 90 \times 60$  cm) are especially large resulting in a rosette with a diameter of 150–180 cm. *Mandragora turcomanica* blooms in both the autumn and the spring (Mizgireva,

1955, see taxonomic treatment), with different individuals in the population exhibiting one or the other flowering time. Geographically the species is isolated, occurring only in a narrowly restricted range, and within that range it is only found in localized regions (Mizgireva, 1955). It is also widely disjunct, being some 1500 km from the closest Mediterranean *Mandragora* population in the Near East and about 2500 km from the nearest Himalayan population in western Nepal.

In common with the Mediterranean mandrake, the Himalayan plants make up a complex with considerable variation in size, shape and colour of the flowers and leaves. The following questions are addressed:



speculative as disregarding the flower as a mere artefact of preparation. The synonymy presented in the taxonomic treatment here, especially in respect to the undercollected plants from central and northeastern Xizang, is therefore provisional and subject to confirmation once more material of both flowering and fruiting plants becomes available. Only then will it be possible to judge whether or not there exist distinct taxa not included within the range of variation of *M. caulescens*.

*Mandragora* is a genus with pronounced variability, both within and between individuals and therefore necessarily within the proposed polymorphic species. Furthermore, discordant variation in the applied gross morphological characters impedes a workable subdivision based on a whole set of differential characters, rather than just one (apparently non-existent) diagnostic character.

## Phylogeny

The cladistic analysis resulted in a single most parsimonious cladogram of length = 16, CI = 75 and RI = 73 (Fig. 3). The genus *Mandragora* defined in the traditional sense is monophyletic in our analysis: the species share synapomorphies in characters 3 (a condensed axis), 4 (leaves clustered in a rosette) and 9 (fruiting calyx with prominent ribs). If the inaperturate pollen known from *M. caulescens* and *M. officinarum* (see Hoare & Knapp, 1997 for details) is also found in *M. turcomanica*, this too would be a synapomorphy of the genus.

*Mandragora officinarum* and *M. turcomanica* are more closely related to each other than to *M. caulescens*. They share reversals in characters 3 (a condensed axis) and 9 (a fruiting calyx without prominent ribs), but no unambiguous synapomorphies. The peculiar life-cycle, i.e. the mode of development of the leaves and flowers, is evidence for a shared common ancestry of the Mediterranean-Turkmenian clade. Mizgireva (1955) also suggested this in her revision of the Turkmenian species. In order to determine more clearly the relationships among the three species of *Mandragora*, a different, probably field-based set of characters is necessary. Here, however, we are concerned more with the delimitation of terminal taxa, especially among the Mediterranean plants, and whether or not the genus as currently defined is monophyletic.

A comparison between alternative hypotheses concerning the position of *Mandragora* based on morphological, chemical and

molecular (chloroplast DNA) characters is given in Figure 4. The most pronounced discrepancy concerning the position of *Mandragora* is that the molecular data set (Fig. 4a) deviates from the morphological (Fig. 4c) and chemical ones (Fig. 4b) by attributing this genus a very independent position due to extremely divergent and autapomorphic cpDNA sequences. This is reflected in the proposal of a monogeneric tribe Mandragoreae (Olmstead et al., in press). Morphological and chemical evidence, on the other hand, suggests a placement within the tribe Hyoscyameae (Hoare & Knapp, 1997; = Atropeae *sensu* Tétényi, 1987). The present study is far too limited in its scope to allow any conclusions concerning higher level classification within the Solanaceae. However, it is clear that our limited data set supports the inclusion of *Mandragora* within the Hyoscyameae (synapomorphies in characters 1, 5 and 6) but, as mentioned above, a much larger and more field-based data set will be needed to address this problem. *Mandragora* is an anomalous genus in the family, both morphologically and in terms of molecules, but this should not prevent us from eventually identifying its true affinities and relatives given adequate data.

## Biogeography

The biogeography of an exclusively Laurasian genus within the Solanaceae is of interest because the family is largely Gondwanan in distribution. It is useful to approach biogeography from two different angles. Ecological biogeography considers a short temporal scale in evaluating ecological factors relevant for present-day distributions of taxa. Historical biogeography, on the other hand, is concerned with the change of distributions and the potential causes thereof on a long temporal scale. We attempt here to summarize some of the most important data with respect to the geographical distribution of *Mandragora*, both now and in the past, and pinpoint major gaps in knowledge.

### Ecological biogeography

The present approximate distribution of the genus is given in Figure 5. Apart from the herbarium material examined, the sources presented in Table 9 were used. Most comprehensive are the distribution data in Heldreich (1886) and Vierhapper (1915). *Mandragora* does not appear to penetrate into the Arabian Peninsula, being absent

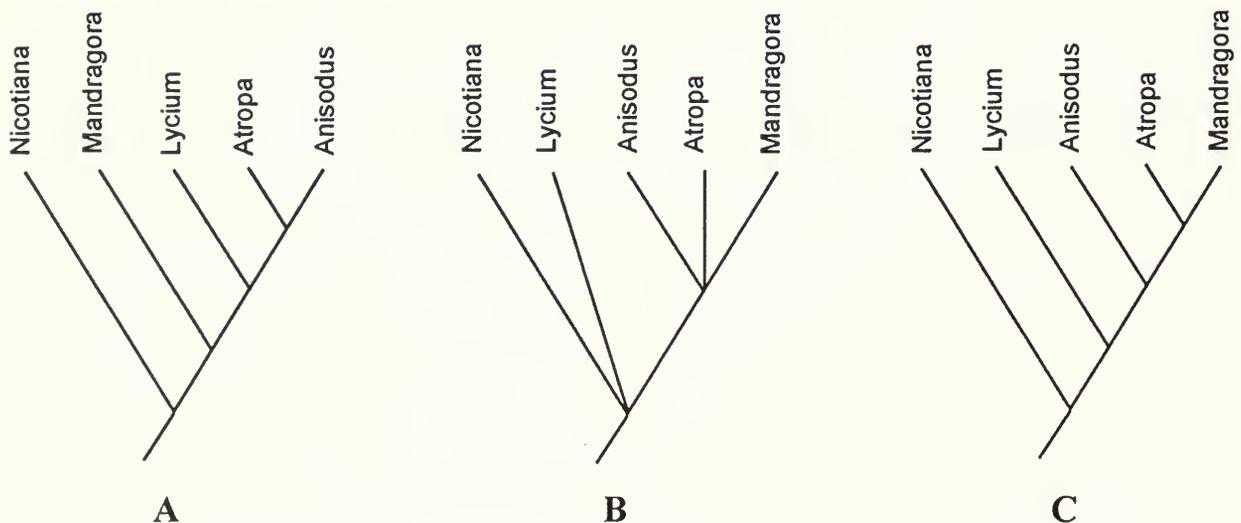


Fig. 4 Differing hypotheses of the relationships of *Mandragora* within the Solanaceae. a: Olmstead et al., in press, b: Tétényi, 1987, c: Hoare & Knapp, 1997.

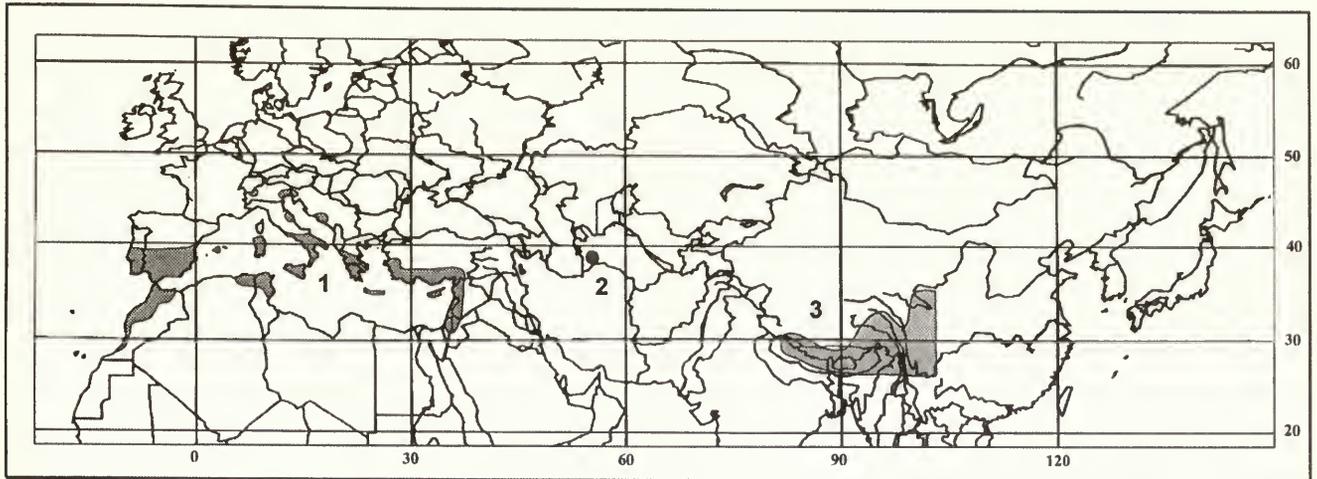


Fig. 5 Distribution of the genus *Mandragora*. 1) *M. officinarum*, 2) *M. turcomanica*, and 3) *M. caulescens*.

even in the most northern parts of Saudi Arabia (Migahid, 1989) as well as from Mesopotamia (Rechinger, 1964; Mouterde, 1979). The genus was naturalized in Malta in the nineteenth century but is now presumably extinct there (Borg, 1927; Maugini, 1959). *Mandragora* does not appear in works covering France and Corsica (Fournier, 1990), Albania (Demiri, 1983), Egypt (Täckholm, 1974; Boulos, 1995) or Libya (Siddiqi, 1978) and is presumed absent from these areas. Likewise, the genus is absent from the Macaronesian archipelagos of the Canaries, Madeira and the Azores (not recorded either by Hansen & Sunding, 1993; or Press & Short, 1994).

*Mandragora turcomanica* is found only in the Kopet Dag range of southern Turkmenistan. It has not yet been reported from the Iranian part of these mountains (Rechinger, 1972). In eastern Asia, *Mandragora* (*M. caulescens*) occurs in the central and eastern Himalaya

and southwestern China, but there are no records from the western extensions of these mountain ranges (Karakorum, Pamir, Hindu Kush and Tien Shan).

Apart from historical factors, dealt with below, the principal factor determining the geographical distribution of taxa on a large scale is typically climate. Although one might disagree on the relative importance of means and extreme values of various climatic variables, the prime importance of climate in general has long been accepted (Cain, 1944).

A convenient way of depicting and comparing different climates is by means of standardized diagrams. The purpose of the so-called ecological climate-diagrams is to portray the climate of a locality in a readily comparable way and visually to present the most important climatic factors affecting the growth of plants (Walter et al., 1975). By choosing a scale at which 10°C correspond to 20 mm precipitation, a relatively wet (dark) and relatively dry (light) season can be identified on the diagrams (Fig. 6). These climate diagrams make it evident that the range of *Mandragora* comprises not only quantitatively different climates but qualitatively different climate types. The amount and especially the main season of rainfall is particularly significant.

The Mediterranean climate is characterized by mild, rainy winters and hot, dry summers. Although the total amount of rainfall for other locations for *Mandragora officinarum* may differ somewhat from that presented here (Iraklio, on the northern coast of Crete, Fig. 6), the general aspect of a winter rainfall regime remains the same all over the Mediterranean basin, even extending towards Afghanistan and the Hindu Kush. The typical vegetation consists of adapted sclerophyllous vegetation, analogous to that found in the same climate type in California, Chile, the Cape region of South Africa and southwestern Australia.

The Kopet Dag is a Transcasian mountain range surrounded by the Irano-Turanian desert. The climate there represents a continental, dry version of the Mediterranean type with much lower rainfall (Fig. 6: Kasil-Arvat) and an extended summer arid period. During this dry summer, *Mandragora turcomanica* exhibits a long period of xerothermic dormancy (Kurbanov, 1994). Mizgireva (1955) suggested that *M. turcomanica* is much more cold-tolerant than its mediterranean congeners. The typical vegetation in the Kopet Dag consists of broadleaved deciduous forest in the moister microhabitats and open shrubland in drier areas.

The eastern part of the *Mandragora* range in the Sino-Himalayan

Table 9 Sources used for determining the overall distribution of the genus *Mandragora*.

Geographical area	Reference
Tunisia	Bouquet (1952), Pottier-Alapetite (1981)
Algeria	Quezel & Santa (1963)
Morocco	Jahandiez & Maire (1934)
Portugal	Amaral Franco (1984)
Spain (incl. Balearic Is.)	Lázaro é Ibiza (1907), Bonafè Barceló (1980), Valdés et al. (1987)
Italy (incl. Sicily, Sardinia)	Maugini (1959), Pignatti (1982), Cellinese et al. (1994)
Former Yugoslavia	Hayek & Markgraf (1931)
Greece (incl. Aegean Is.)	Halácsy (1902), Hayek & Markgraf (1931)
Turkey	Baytop (1978)
Cyprus	Meikle (1985), Viney (1994)
Syria	Post (1933), Feinbrun-Dothan (1978), Mouterde (1979)
Lebanon	Post (1933), Feinbrun-Dothan (1978), Mouterde (1979)
Israel	Post (1933), Feinbrun-Dothan (1978)
Jordan	Post (1933), Feinbrun-Dothan (1978)
Turkmenistan	Pojarkova (1955), Kurbanov (1994)
Nepal	Grierson & Long (1978)
India (Sikkim, Arunachal Pradesh)	Hara (1966), Grierson & Long (1978), Deb (1979)
Bhutan	Hara (1971), Grierson & Long (1978)
Myanmar	Grierson & Long (1978)
China	Grierson & Long (1978), Zhang et al. (1994), Zhang & Lu (1994)

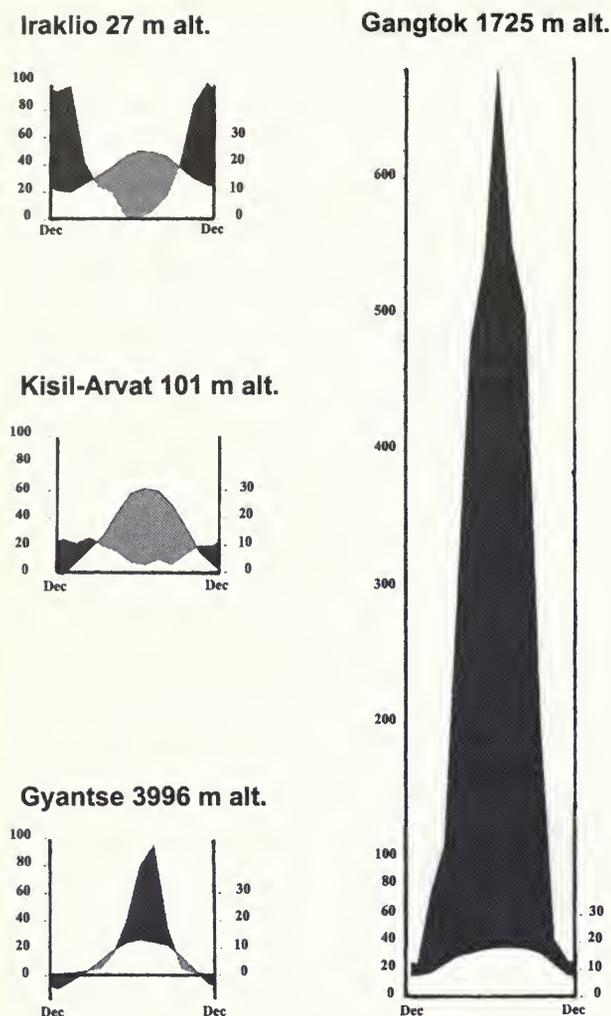


Fig. 6 Climate diagrams of four representative weather stations in three different climate regimes. Given are the rainfall and temperature curves, resulting in wet (dark shading) and dry (light shading) seasons. Based on Walter et al. 1975.

region is characterized by a completely different rainfall regime altogether. The influence of the monsoon renders not the winter but the summer the season of the highest rainfall. The amount of precipitation during the monsoon period, however, does vary enormously. The Himalayan chain functions as a rain screen resulting in high rainfall on the southern slope of the mountain range (Fig. 6: Gangtok) as well as in the southwestern Chinese mountains of Yunnan and Sichuan, and much lower rainfall in the inner regions of Xizang (Fig. 6: Gyantse). Even at high altitudes, winters are very mild in the high rainfall areas (see climate-diagram of Gangtok, about 1700 m above sea level) and snow is scarce. Generally speaking, the eastern Himalaya and southeastern Xizang, Sichuan and Yunnan enjoy a much more humid and milder climate than the western Himalaya and central Xizang. The locality data of the examined specimens suggest that the distributional boundary of the Himalayan mandrake towards the central Xizang highland lies within the 200–400 mm annual precipitation strip north of the main ranges. Due to the immense altitudinal gradient, the vegetation is strikingly zonal and ranges from subtropical forests to alpine scrub and meadows. The upper forest limit lies between about 3600 and 4200 m, the upper tree limit between 4200 and 4500 m. The belt in

between is characterized mainly by a succession of various *Rhododendron* species. This is the typical habitat of *Mandragora caulescens*. The permanent snow line lies at about 4800 m in the south and 5800 m in the north towards central Xizang (Walter, 1962).

Other factors affecting plant distribution, albeit on a smaller and less important scale, include soil type and competition. *Mandragora officinarum* especially grows in ruderal habitats, on clayey and nitrogen-rich soils. So far, it is not clear whether *M. caulescens* occurs on acidic (granitic) or base-rich (limestone) soils in the subalpine and alpine zone of the Himalaya. It cannot be ruled out that there might be two different, vicariant ecological groups as is often the case in the Alps, for example in *Rhododendron* (Walter, 1966). The type of climate and soil typically only indirectly determine the occurrence of a species in a certain locality, in that they affect the fitness of that species in relation to others (Walter, 1977). Both *Mandragora officinarum* and *M. turcomanica* seem more or less restricted to low-competition localities, representing typical *r*-species (good colonizers but poor competitors).

### Historical biogeography

The atemporal cladogram of a group together with historical evidence, namely paleoclimatic and paleogeographical data allow for the formulation of historical scenarios. A scenario is a model of the basic features (including space and time) of the evolutionary history of a group which can serve to stimulate directions of further investigation. However, the essentially speculative character of such a model renders it more like a tool than a serious scientific statement (Eldredge, 1979) and *ad hoc* assumptions are inevitable (Humphries & Parenti, 1986). In attempting to construct scenarios for the historical biogeography of any group, plate movement, eustasy (worldwide changes of sea level) and climate changes are considered the major factors to be considered (Hallam, 1981). In the case of the Solanaceae, virtually no fossil record is available (PaleoNet Listserv, <http://www.ucmp.berkeley.edu/Paleonet/>), thus historical hypotheses concerning *Mandragora* are inevitably founded on extant taxa only.

The Mediterranean region presents a very complex tectonic jigsaw puzzle, hard to resolve adequately (Hallam, 1981). It seems clear, however, that during most of the Tertiary, summer was the rainy season and only before the Pleistocene was there a shift towards the current pattern of rainfall in winter. The plants had to adapt and reduce activity during the dry summer months (Walter, 1977). The northern Mediterranean localities for *Mandragora* in northern Italy and on the Dalmatian coast are very patchy, resulting in a highly fragmented range there, and the precise status of these populations is uncertain. We have been unable to discover any modern collections from these regions (Cellinese et al., 1994) and some, or all, of the populations may no longer exist. Vierhapper (1915) maintained that these plants are Tertiary relics, the scattered remnants of a formerly larger, continuous range, that have been unable to adapt to the changing climate and still exhibit the vernal phenology type. Relict status based on Tertiary processes, however, is normally attributed to groups of far wider disjunct ranges than is the case here. Hawkes (1972a) based his definition of *M. officinarum* L. on these northern Italian and Dalmatian populations only, using corolla colour and phenology. On the evidence of our multivariate analyses, Hawkes's position is untenable, since the plants fall within the range of variation exhibited by the rest of the Mediterranean plants. It could be argued that the different corolla colour (white) of the northern Italian and Dalmatian plants, coupled with their discrete distribution is sufficient to recognize them at least at subspecific rank. We have already pointed out that the corolla colour is only an

apparent distinction, with similar colours occurring in populations outside northern Italy and Dalmatia. The somewhat isolated distribution alone is insufficient reason to recognize the Italian and Dalmatian plants as a separate taxon.

The close relationship between the Mediterranean and the Turkmenian mandrake as suggested by the cladistic analysis is reflected in a linked history of the regions particularly during the Tertiary. It can be proposed that in this period, after the Tethys Sea receded and the middle Asian mountains became exposed during their simultaneous uplift, a vicariance event of the Mediterranean and Turkmenian ancestors took place. Both extant species show a comparable adaptation to the aridization and change from a summer to a winter rainfall regime. In other words, *Mandragora turcomanica* can be seen as an example of a plant that has been evolving in isolation in Turkmenistan since the Tertiary from ancient Tethyan stock (Kurbanov, 1994). It is of some interest to note that there is a highly congruent pattern within *Atropa* where the disjunct distribution of the Turkmenian *Atropa komarovii* Blin. & Schal., consists of a very narrow range south of the river Sumbar only a few miles away from the *Mandragora turcomanica* population north of the river (Kurbanov, 1994).

The Sino-Himalayan area is of particular interest because of its position at the transition between the Palearctic and the Oriental floristic realms. The period of the collision of the Indian subcontinent with Asia is contentious but probably occurred in the Paleogene approximately 50 million years ago (Scotese et al., 1988) with the penetration of the Eurasian border continuing during the early Neogene (c. 20 millions years ago) (Dercourt et al., 1986). The connection between Tethys and the Mediterranean, on the other hand, probably did not close until the mid-Miocene (c. 15 million years ago) (Hallam, 1994). Climate changes during the Paleogene were severe. Temperatures increased up to the early Eocene (c. 55 million years ago) followed by a global cooling which marks the passage from a warm domain of the Mesozoic and early Palaeogene to the cool domain thereafter (Hallam, 1994). According to Rudman et al. (1989) much of the uplift in the Xizang plateau region occurred only in the last 5 to 10 million years (Plio-Pleistocene uplift). It must be assumed that the glaciation of the high altitude regions of the Sino-Himalayan area during the Pleistocene (Ice-Ages) was more or less complete, posing the question whether refugia further south and at lower altitudes might have served as speciation centres.

Schuster (1976) argued that the Indian plate served as a vehicle for the dissemination of Gondwanan taxa into Laurasia. But at the same time he expected that due to the migration through several climatic zones the Indian plate probably arrived with a rather depleted and altered flora and therefore only remnants of the original Gondwanan flora are recognizable in India today. If angiosperms were indeed on the Indian plate in early Cretaceous time, they could probably not be assigned to presently recognizable families. On the basis of a proposed late Triassic (c. 210 million years ago) start of the Indian plate migration, serious doubt is cast on the possibility that early Solanaceae could have been 'on board'. The main objection is that the plate drift simply occurred too early, before modern groups were in existence. However, other data (Smith et al., 1994) suggest that India did not break free from Gondwana until the late Jurassic to early Cretaceous (130–140 million years) or even near the Cretaceous-Tertiary boundary only 60–65 million years ago (Hallam, 1994). Lu & Zhang (1986) proposed southwestern China as a later, secondary speciation centre of the whole tribe Hyoscyameae on the grounds of its high species-richness.

A different biogeographical scenario proposes a migration from Gondwana to the Mediterranean basin. Migration routes that are

closed today were wide open in the Mesozoic. Indeed, massive and relatively unimpeded migrations from Gondwana to Laurasia might have been feasible until the late Cretaceous (Schuster, 1976). Contrary to the first scenario, the mandrake ancestors would therefore have spread eastwards from the Protomediterranean to the developing eastern Asian mountain ranges where the massive uplift possibly resulted in a vicariance event. The Mediterranean populations on the other hand would have had to adapt to the increasing aridization in the western part of the continent during the late Tertiary (Weinert, 1972) and thus slowly changed their mode of development from a summer flowering to a autumn-winter-spring flowering rhythm. Proskuryakova & Belyanina (1985) claim that the slow succession of the development phases, particularly of the germination, the long growth and flowering period and the large size of the plant speak for the great age of the Mediterranean group. They draw the conclusion that the Mediterranean section must be older, representing a Tertiary relic, than the apparently highly adapted Himalayan mandrake. The Himalayan mandrake, in fact, might have arisen from now-extinct ancestors as late as the Quaternary glaciations.

To conclude, the massive timespan covered in the Tertiary, the many fluctuations in climate and transgressions of the seas and the current very inaccurate timing of even the major events render definitive statements or falsifications concerning the above scenarios and the history of *Mandragora* hardly possible. In this context the distinction between a cladogram (what is more closely related?) and the actual phylogenetic tree (what is the ancestor?) must be stressed. The cladogram (Fig. 3) suggesting a more recent common ancestry of *Mandragora officinarum* and *M. turcomanica* is congruent with only one of the many possible trees equally resulting in this particular cladogram, which therefore represents a far less informative (more general) mode of expression. Thus, it does not allow for statements concerning the ancestor and does not imply that *Mandragora caulescens* is the older taxon. Nevertheless, it can be proposed that the major events affecting speciation and present distribution of *Mandragora* in the Mediterranean-Turkmenian area were probably the receding of the Tethys and the aridization of the climate in the Tertiary. In the Sino-Himalayan area, on the other hand, the collision of the Indian plate and the subsequent uplift of the Himalayan range, as well as the later glaciation periods during the Quaternary, are probably most important.

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## TAXONOMIC TREATMENT

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*Mandragora* L., *Sp. pl.* 1: 181 (1753). Type species: *M. officinarum* L.

Perennial herbs. Stout tap-root, often branched, sometimes vaguely anthropomorphic. Stem very short or with secondary growth during flowering and fruiting, sometimes branched. Leaves simple, normally entire, occasionally toothed. Inflorescence of typically solitary axillary, pedicellate flowers. Floral envelope actinomorphic. Calyx 5(6)-lobed, persistent, enlarged in fruit. Corolla 5(6)-lobed. Stamens 5(6), included, inserted in lower half of corolla-tube; filaments filiform, pubescent at base; anthers dorsifixed, dehiscent longitudinally. Ovary 2-locular; ovules numerous; style elongate; stigma capitate or somewhat bilobed. Fruit a fleshy, many seeded berry, globose or ovoid, borne beneath the leaves on nodding pedicel or lying on the ground. Seeds compressed; embryo curved.

FLORAL FORMULA.  $K(5) C(5) A5 \underline{G}(2)$

DIVERSITY AND DISTRIBUTION. Three disjunct species: Mediterranean region, central Asia, Sino-Himalayan region.

**PHENOLOGY AND HABITAT.** All three *Mandragora* species are geophytes with a conspicuous tap-root which is the perennating organ of these herbs, linking the annual vegetative periods. The Turkmenian mandrake with its prolonged dry season dormancy has been referred to as an ephemeroïd (Proskuryakova & Belyanina, 1985), its rhythm of development more closely related to the Mediterranean than to the Himalayan climatic cycle. Propagation is usually by seeds or vegetatively by underground buds on the tap-root. The species grow in open woodland, olive groves, grassland, fallow land, waysides, railway embankments, ruins, in rock crevices, grassy and stony mountain slopes and screes. The altitudinal range is 0–1200 and 3000–4900 m.

**ETHNOBOTANY.** Once important medicinal plants with a long tradition in mythology and superstition. All parts of the plant contain potent narcotic alkaloids.

**ETYMOLOGY.** Origin uncertain, possibly from the Greek  $\mu\alpha\nu\text{-}\delta\rho\alpha\gamma\omicron\rho\alpha\sigma$ , original meaning controversial; alternatively from the Sanskrit *mandros*, meaning sleep and *agora*, meaning object or substance (Thompson, 1934).

### Key to the species of *Mandragora*

- 1 Young leaves arranged in a cluster on top of a stem with scales, later along the secondarily elongated, sometimes branched stem; corolla yellow to dark purple; style not exceeding stamens. Sino-Himalayan. Alt. 3000–4900 m ..... 3. *M. caulescens*
- Leaves permanently arranged in a rosette, the stem not elongating; corolla white to pale blue or violet; style exceeding stamens ..... 2
- 2 Mature lower leaves in a large rosette of 150–180 cm; berries 40–60 mm in diameter. Turkmenian. Alt. 500–700 m ..... 2. *M. turcomanica*
- Mature lower leaves in a rosette of less than 100 cm; berries less than 40 mm in diameter. Mediterranean. Alt. 0–1200 m ... 1. *M. officinarum*

1. *Mandragora officinarum* L., *Sp. pl.* 1: 181 (1753). Type: Herb. Burser IX: 26 (UPS-lectotype, designated by Knapp in Jarvis et al. (1993), microfiche-BM!).

Figs 7, 8.

- ≡ *Atropa mandragora* L., *Syst. nat.* 10th ed.: 933 (1759), nom. illeg. (Art. 52.1).
- ≡ *Mandragora foemina* Garsault, *Fig. pl. méd.* 3: 221, t. 363 p.p. (1764).
- ≡ *Mandragora mas* Garsault, *Fig. pl. méd.* 3: 221, t. 363 p.p. (1764).
- ≡ *Mandragora acaulis* Gaertn., *Fruct. sem. pl.* 2: 236, t. 131 (1791).
- ≡ *Atropa humilis* Salisb., *Prodr. stirp. Chap. Allerton*: 132 (1796).
- ≡ *Atropa acaulis* Stokes, *Bot. mat. med.* 1: 396 (1812).
- ≡ *Mandragora autumnalis* Bertol., *Elench. plant. viv.*: 6 (1820).
- ≡ *Mandragora vernalis* Bertol., *Virid. Bonon. veg.*: 6 (1824).
- ≡ *Mandragora praecox* Sweet, *Brit. fl. gard.* 2: t. 198 (1827).
- ≡ *Mandragora neglecta* G. Don ex Loudon, *Hort. brit.*: 71 (1830).
- ≡ *Mandragora microcarpa* Bertol., *Comm. Mandrag.*: 12, t. 3 (1835).
- ≡ *Mandragora haussknechtii* Heldr. in *Mitt. Geogr. Ges. Jena.* 4: 77, app. (1886).
- ≡ *Mandragora* × *hybrida* Hausskn. & Heldr. in *Mitt. Geogr. Ges. Jena.* 4: 77 (1886).
- ≡ *Mandragora hispanica* Vierh. in *Österr. Bot. Z.* 65: 132–133 (1915).

**ILLUSTRATIONS.** Wettstein (1895: fig. 12M-O); Feinbrun-Dothan

(1978: fig. 278); Pignatti (1982: figs on p. 518); Hoare & Knapp (1997: fig. 5c).

Plant virtually stemless. Root stout, often branched, very long. Leaves arranged in a rosette, leaf shape and size very variable, but usually elliptic to obovate, max. 45 cm long, length/width ratio 1.5–10, variously pubescent. Flowers borne in leaf axils. Pedicels very variable in length, max. 15 cm. Calyx 6–28 mm long, lobed  $\frac{1}{2}$ – $\frac{2}{3}$  of the way to the base, lobes 3–15 mm, acuminate, only slightly accrescent in fruit. Corolla 12–65 mm long, campanulate, greenish white to pale blue or violet, lobed  $\frac{1}{2}$  to nearly to the base, the lobes 6–60 mm. Stamens adnate to lower half of corolla; filaments 7–15 mm long; anthers 2.5–4.0 mm long, yellow to brown, sometimes pale blue. Style 8–20 mm long, exceeding stamens; stigma capitate. Fruit 5–40 mm in diameter, globose to ellipsoid, glossy yellow to orange when ripe, juicy, edible. Seeds 2.5–6.0 mm long, reniform, the surface reticulate, yellow to light brown.

**HABITAT.** Open woodland, olive groves, fallow land, waysides, railway embankments, ruins, crevices. Altitudinal range 0–1200 m.

**VERNACULAR NAME.** Mediterranean mandrake.

**PHENOLOGY.** Flowering September to April. Fruiting November to June.

**CONSERVATION STATUS.** Populations are scattered throughout the species range. Northern Italian populations are vulnerable (Cellinese et al., 1994) as they are apparently known only from old herbarium records and the present occurrence and abundance of these populations are unclear.

**DISTRIBUTION.** Circum-Mediterranean. (Tunisia, Algeria, Morocco, Portugal, Spain, Italy, former Yugoslavia, Greece, Cyprus, Turkey, Syria, Lebanon, Israel, Jordan).

**SELECTED SPECIMENS EXAMINED.** **TUNISIA.** Cap Bon, roadsides and orchards, 0–150 m, 6 October 1969, Tomkinson, M.J. 72, 72A (BM). Nabel, 60 m, 14 October 1907, Gandoger, M. 84 (K).

**MOROCCO.** Guercif, 144 km E. of Fes near 'La Kazbah', 38 km before the town of Guercif, 34°16'N, 3°45'W, 510 m, disturbed gravelly area by road, 3 November 1994, Jury, S.L. et al. 15434 (RNG); Gharb, c. 4 km NNE of Souk-El-Arbaa-du-Rharb on road to Ksar-El-Kebir, by bridge and salt works, 34°43'N, 6°00'W, 30 m, pasture between fields at side of salt pans, 7 November 1994, Jury, S.L. et al. 15701 (RNG); Zerhoun, c. 3 km NW of Moulay Idriss and 33 km from Meknes along road to Sidi Kacem and Tanger, 34°04'N, 5°33'W, 390 m, ruins of Roman city of Volubilis, 1 November 1994, Jury, S.L. et al. 15398 (RNG); Prerif Central, N. of Fes, on the road to Ouezzane, 34°22'N, 5°09'W, 210 m, roadside ruderal community, 24 October 1993, Jury, S.L. et al. 12634 (RNG); Haut Ouerrha, c. 50 km N. of Fes on the road between Fes-el-Bali and Ourtzarh, 34°33'N, 5°02'W, 120 m, in olive plantation on steep N-facing slope with *Zizyphus lotus*, 24 October 1993, Jury, S.L. et al. 12653 (RNG); Temara, 10 km S. of Rabat, 0–30 m, sandy roadside, 14–20 October 1981, Lewalle, J. 10054 (BM, RNG); 5 km W. of Oued, Beht on Rabat-Meknes road, 33°52'N, 5°58'W, 400 m, 27 September 1991, Gardner, M.F. et al. 4885 (E, RNG); Loukkos, SW of Chefchaouen, on road to Ksar-el-Kebir, 35°1'N, 5°45'W, 120 m, in cultivated fields of wheat, 21 October 1993, Jury, S.L. et al. 12542 (RNG); Loukkos, c. 1 km E. of Larache on road to Asilah, c. 200 m from Oued Loukkos, 35°12'N, 6°08'W, 5 m, at side of road by saltpans, 28 October 1994, Jury, S.L. et al. 15237 (RNG); Tanga, just N. of airport, road to Cap Spartel, 35°45'N, 5°55'W, 35 m, fallow area at side of ploughed field with *Urginea maritima*, 16 October 1993, Jury, S.L. et al. 12217 (RNG); Tanga, E. on road to Sebta (Ceuta), Oued Dliane, 35°50'N, 5°39'W, 5 m, nitrophilous areas on fallow cultivated land on heavy clay alluvial plain, 17 October 1993, Jury, S.L. et al. 12238 (RNG); Allal-Tazi, close to the river Sedou, 1 November 1965, Taton, A. 1630 (BM).

**SPAIN.** Balears, Palma, between S. Sardina and S. Bernardo, 22 September 1913, Bianor & Sabasien 1877 (BM, E, P, RNG); Province Cadíz,



Fig. 7 *Mandragora officinarum*. a) Flowering, cultivated at RBG Kew, b) Fruiting, cultivated at RBG Kew.



**b**



**a**

Fig. 8 *Mandragora officinarum*. a) Flowering, *Heldreich* s.n. (E), b) Fruiting, *Reverchon* s.n. (E).

Chiclana, on clayey soil by the river, 10 January 1855, *Bourgeau, E.* 2304 (E, K, P); Torredonjimeno, 600 m, 10 December 1986, *Espinosa, A.* 870252 (K); alrededores de Córdoba, Cuesta del Espino, 2 December 1967, *Galiano, E.F. & Valdes, B.* 820 (E, RNG); Province Málaga, C 341 from Campillos to Ronda, 36°52'N, 5°00'W, 525 m, disturbed ground near new road cutting, 27 October 1990, *Gardner, M.F. & Knees, S.G.* 4769 (RNG); Province Cadiz, 23 km from Jerez de la Frontera, 36°32'N, 5°59'W, 130 m, ruderal area by road with abundant *Silybum marianum* below ruined castle of El Pedroso, 22 December 1993, *Jury, S.L. & Jury, L.C.* 13111 (BM, RNG); Province Jaén, Torredonjimeno, between Porcuna and Torredonjimeno, near Pilar de Moya, 500 m, roadside on chalky soil, 3 November 1979, *Ladero, M.* et al. 10605 (RNG); Málaga, near Churiana, 3 December 1957, *Partridge, F.* 2 (BM); Campamento, 9 November 1911, *Wolley-Dod, A.H.* 22 (BM).

**ITALY.** Sicily, Province Palermo, Madonie, near Polizzi, 950 m, rocky limestone slopes, 18 August 1964, *Davis, P.H.* 40134 (E); Sicily, Trapani, 200 m, steep slopes, 25 August 1964, *Davis, P.H.* 40182 (RNG); Sicily, Province Siracusa, Augusta, October–November 1911, *Vaccari, A.* 2326 (BM, K).

**FORMER YUGOSLAVIA.** Hercegovinae, Dolnja Glavska, 6 May 1908, *Reiser, C.* s.n. (K); Silieski, near Ragusa, 500 m, 29 April 1909, *Maly, K.* s.n. (K).

**GREECE.** Near Corinth, 30 m, waste grounds and waysides, April 1931, *Atchley, S.C.* 819 (K); Crete, Frangokastello, 29 March 1973, *Barclay, C.* 3004 (K); Crete, Canea, 1 December 1943, *Bickerich, G.* 15324 (BM, K); Crete, Kolokithia, December 1977, *Bowen, H.J.M.* 694 (RNG); Crete, Agios Nikolaos, December 1983, *Bowen, H.J.M.* 3088 (RNG); Peloponnese, 5 km from Pilos on the road from Kalamata, 250 m, in cultivated fields near stream, 12 November 1973, *Brickell, C. & Mathew, B.* 8088 (K); Crete, Canea, frequent in hills and ditches throughout Crete up to 300 m, 1 January 1940, *Davis, P.H.* 1100 (E, K); Cyclades, Amorgos, 10 April 1940, *Davis, P.H.* 1438 (K); Dodecanese, Kos, Asfendion, 300–600 m, rocky slopes, 27 March 1965, *Davis, P.H.* 40478 (K); Crete, near Candia, Hagios-Deka, December 1913, *Duffour, C.* 1501 (P); Cyclades, Kea, 30 April 1961, *Gathorne-Hardy, E.* 14 (E); Dodecanese, Tilos, near chapel of Ayios Nicolaos c. 180 m above Livadia, 26 April 1962, *Gathorne-Hardy, E.* 139 (E); Crete, near Sitia, 150–200 m, on clayey soil, 30 October 1966, *Greuter, W.* 7821 (E); Near Corinth, Examillia, 8 February 1931, *Guiol, F.* 1731 (BM); Crete, Canea, on wasteland, 10 March 1883, *Reverchon, E.* 117 (BM, E, K, P, PAL); Dodecanese, Kos, by track near Asclepeion, 23 March 1985, *Townsend, C.C.* 85/11 (K); Dodecanese, Rhodes, 9 February 1914, *Vaccari, A.* 1141 (K); Crete, Nomos Lasithiou, Monastiraki, roadside, 5 April 1980, *Walree, A.M.* 22226 (BM).

**CYPRUS.** Kyrenia, fallow olive grove, 13 February 1949, *Casey, E.C.* 221 (K).

**TURKEY.** Province Mugla, Kemer-Kestep, 50 m, edge of fields, 29 March 1956, *Davis, P.H. & Polunin, O.* 25469 (BM, E, K); Side, 22 February 1966, *Baytop, A.* et al. 8504 (E).

**SYRIA.** Baniyas, 300 m, foot of hill, beneath tree, 11 March 1945, *Norris, F.H.* s.n. (BM).

**ISRAEL.** Jerusalem, fields, 800 m, 20 February 1908, *Meyers, F.* 4377 (E); Mount Carmel, upper Nahal Neshet, 2 km S. of Neshet, 32°45'N, 35°31'E, 280 m, terra rossa on hard limestone, 6 April 1989, *Danin, A. & Knees, S.G.* 1709 (RNG); Mount Gerizim, near Nablus, fields, 700 m, 22 December 1910, *Meyers, F.S. & Dinsmore, J.E.* 6377 (E); District Haifa, near Waldheim (Alloney Aba), open places in *Quercus ithaburensis* forest, 28 March 1942, *Davis, P.H.* 4166 (E, K).

The confusion surrounding specific epithets for the taxon we are here calling *Mandragora officinarum* is incredible. This morass has arisen for two basic reasons, firstly orthographic errors, and secondly, the confusion over the phenological status of type specimens. Orthographic errors made by early authors persist through floristic works, adding and compounding any ambiguities that may have arisen. A name often used in synonymy (or as a valid name) of *M. officinarum* is *Mandragora officinalis* Mill., said to be validly published in 1768 (see Jackson & Berry, 1979: 508, footnote). However, in the eighth edition of *The gardener's dictionary* (Miller, 1768), where Miller used Linnaean epithets for the first time, Miller actually used the epithet *officinarum* ('MANDRAGORA (*officinarum*)'), not *officinalis*. In the ninth edition (Miller & Martyn,

1807), the taxon was classified as *Atropa mandragora*, following *Systema naturae* (Linnaeus, 1759) and the second edition of *Species plantarum* (Linnaeus, 1762). *Mandragora officinalis* was cited in synonymy, with reference made to the illustrations produced to compliment the earlier editions (Miller, 1760). These illustrations bear no specific epithets, thus the 1807 reference to the epithet *officinalis* is almost certainly an orthographic error for the 1768 use of Linnaeus's epithet *officinarum*, which was not cited in synonymy in the ninth edition (Miller & Martyn, 1807). Thus the name *Mandragora officinalis* Mill. has persisted in the literature, but has no real nomenclatural standing.

Similarly, Bertoloni (1820) attributed the epithet *officinalis* (see below) to Willdenow, explicitly citing 'W. En.'. Willdenow (1809), in his *Enumeratio plantarum*, attributed the epithet *officinalis* to DeCandolle (in Lamarck & DeCandolle, 1805), where it is again attributed, in error, to Miller's *Gardener's dictionary*. Thus it is apparent that the numerous occurrences of the epithet *officinalis*, attributed to many authors, are traceable to a single orthographic error from Miller's 1767 edition of the *Gardener's dictionary*. Even if the epithet *officinalis* had nomenclatural standing, it would be invalid under Article 52.1 (see above), as it is homotypic with *Mandragora officinarum* L.: in DeCandolle (in Lamarck & DeCandolle, 1805) and Willdenow (1809), *Atropa mandragora* L. is cited in synonymy.

Assumptions as to the phenological status of type specimens has also led to confusion about the correct application of epithets (e.g. Jackson & Berry, 1979). Bertoloni (1820, 1824, 1835) contributed greatly to the confusion surrounding names for the Mediterranean mandrake. In a list of plants cultivated in the Botanic Gardens at Bologna (Bertoloni, 1820), he included two species of mandrakes: *Mandragora autumnalis*, which he coined as a new name, and *M. officinalis*, which he attributed to Willdenow. In a later work (Bertoloni, 1824) he designated two different taxa: *M. vernalis* and *M. officinarum*, explicitly citing Linnaeus as the source of the latter epithet. He put *M. officinalis* in synonymy with *M. vernalis* and put *M. autumnalis* in synonymy with *M. officinarum*. In *Commentarius de Mandragoris* (Bertoloni, 1835), he revised the genus and recognized three species: *M. vernalis*, *M. officinarum* and *M. microcarpa*. In synonymy he left out both of the previously used epithets, *autumnalis* and *officinalis*, which he may have considered to be superfluous.

The lectotype of *Mandragora officinarum*, selected from amongst the elements used by Linnaeus in his description, bears no phenological information at all. The specimen in Burser's herbarium is labelled 'Misnia, Lusatia', indicating it came from Germany. It is probable therefore that it is from a botanical garden, and since plants of *Mandragora* in northern European gardens usually bloom in spring, it has been assumed that this one did as well. This is not founded in fact, thus rendering much of the debate as to which name is the vernal or autumnal taxon irrelevant.

2. *Mandragora turcomanica* Mizg. in *Trudy Turkmen. Fil. Akad. Nauk SSSR. Ashkabad* 2: 165 (1942). Type: Turkmenistan, western Kopet Dag, Kara Kala region, southern foot of Mt Syunt, Schevlan valley, on scree slopes, 26 November 1938, *O.G. Mizgireva, M. Nastacalicz & G. Nastacalicz* s.n. (ASH-holotype; LE-isotype(?)).

ILLUSTRATIONS. Mizgireva (1942: figs 1, 2; 1955: figs 2–7, 9, 14, 15, 18, 19, 24); Belyanina (1982: figs 1, 2).

Plant virtually stemless. Leaves arranged in a rosette: lower leaves c. 90 × 60 cm, length/width ratio c. 1.3–1.5, broadly elliptical or ovate,

usually with large, irregular teeth in upper half, upper leaves smaller, oblong-ovate or broadly lanceolate, usually without large teeth, on both sides sparsely hairy, the hairs mostly arranged along veins. Flowers borne 1(–3) in leaf axils, occasionally the pedicels up to 2–6-flowered. Pedicels 2–3 cm long, 7–18 cm in fruit. Calyx 15–20 mm long, lobes 10–15 mm, acuminate, accrescent in fruit. Corolla 20–25 mm long, campanulate, violet or purple, with three narrow white stripes at base, the lobes c. 15 mm. Stamens c. 10 mm long, attached to lower half of corolla; filaments 6–7 mm, densely pubescent at the base and in the lower ½; anthers c. 4 mm long, pale blue. Style exceeding stamens; stigma capitate, slightly bilobed, green. Fruit 40–60 mm in diameter, glossy yellow to orange when ripe, pulpy, juicy, smelling of melons, edible. Seeds 4–5 × 6–7 mm, reniform, yellow to light brown.

**HABITAT.** Shrubland in ravines and on stony mountain slopes, especially among *Paliurus spina-christi* Mill. (Rhamnaceae). Altitudinal range 500–700 m.

**VERNACULAR NAME.** Turkmenian mandrake.

**PHENOLOGY.** Flowering October to March. Fruiting until June. Summer dormancy until autumn rains begin. Xerothermic ephemeroïd.

**CONSERVATION STATUS.** Only small populations in a restricted area within the Syunt-Khassardagh Reserve, and in the valleys of Chokhadgh, Shevlan, Altybai, Ekechinar, Sarymsakli and Dagdanli are known (Kurbanov, 1994). According to Mizgireva (1978) the population in the Syunt-Khassardagh reserve consists of fewer than a thousand plants.

**DISTRIBUTION.** Southwestern Kopet Dag. (Turkmenistan, ?Iran).

**SELECTED SPECIMENS EXAMINED.** No specimens were available for examination: the data here are drawn exclusively from the literature.

In the original article in which this species was described (Mizgireva, 1942) the type is cited as being in Ashkabad (ASH). Subsequently, in the *Flora of the USSR* (Lincevskij, 1955), the type was said to be in Leningrad (now St. Petersburg, LE) and this citation has been followed in other floristic works (Schönbeck-Temesy, 1972). Since we have been unable to obtain specimens from either herbarium, it is uncertain whether or not the holotype remains in ASH or has been transferred to LE, thus we have cited its location as in the original publication.

Mizgireva's (1955) detailed study of this species documented the flowering times (Mizgireva, 1955: fig. 16) of individual plants and clearly shows that some individuals flower in autumn (October and November) while others flower in spring (February and early March). This is the same situation as that in *Mandragora officinarum*, and is markedly different from that found in much of the rest of the flora of Kopet Dag (Mizgireva, 1978). Mizgireva (1955) stated that the differences between her species, *M. turcomanica*, and the Mediterranean mandrakes (separated by her into *M. officinarum* and *M. autumnalis*) were largely size of plant, colour of anthers and relative sizes of calyx and corolla. It is clear from her work that these characteristics are consistent throughout the range of wild and greenhouse grown material she examined, but since she cites no specimens, nor have we been able to examine any of the known specimens of *M. turcomanica*, an in-depth analysis of these characters relative to the range of variation found in *M. officinarum* awaits future study.

3. ***Mandragora caulescens*** C.B. Clarke, *Fl. Brit. Ind.* 4: 242 (1883). Type: India, Sikkim, Lachen, *Hooker* s.n. (K!-lectotype, designated here by R. Mill).

Fig. 9.

= *Anisodus mariae* Pascher in *Feddes Repert. Spec. Nov.* 7: 227 (1909).

= *Mairella yunnanensis* H. Lév., *Cat. pl. Yun-Nan*: 199 (1916).

≡ *Anisodus caulescens* (C.B. Clarke) Diels in *Feddes Repert. Spec. Nov. Beih.* 12: 480 (1922).

= *Mandragora tibetica* Grubov in *Rast. Tsentral. Azii.* 5: 108–109 (1970).

= *Mandragora caulescens* subsp. *brevicalyx* Grierson & D.G. Long in *Notes Roy. Bot. Gard. Edinburgh* 36: 144 (1978).

= *Mandragora caulescens* subsp. *flavida* Grierson & D.G. Long in *Notes Roy. Bot. Gard. Edinburgh* 36: 143 (1978).

= *Mandragora caulescens* subsp. *purpurascens* Grierson & D.G. Long in *Notes Roy. Bot. Gard. Edinburgh* 36: 143 (1978).

= *Mandragora chinghaiensis* Kuang & A.M. Lu, *Fl. reip. pop. Sin.* 67: 159 (1978).

**ILLUSTRATIONS.** Grubov (1970: pl. IV, fig. 2; pl. V, fig. 2); Kuang & Lu (1978: fig. 36, 1–6). Hoare & Knapp (1997: fig. 5d).

Root stout, often branched. Stem present, max. 60 cm long. Leaves arranged in a cluster on top of the young stem above scale leaves, later along the secondary growth of the stem, max. 30 cm long, length/width ratio 1.9–5.5, oblanceolate or spathulate, glabrous to densely pubescent beneath, especially along the veins. Flowers borne in leaf axils, often nodding, pleasantly scented. Pedicels 5–10 cm long. Calyx 5–30 mm long, often nearly as long as corolla, lobed c. ¼ of the way to the base, accrescent in fruit. Corolla 5–30 mm long, campanulate to cup-shaped, yellow to purple, the venation usually darker, lobed about ¼ of the way to the base, the lobes 2–10 mm. Stamens adnate in lower half of corolla; filaments 3–10 mm; anthers 1–5 mm long, white to yellow. Style 3–6 mm long, not exceeding the stamens; stigma capitate, somewhat bilobed. Ovary 2.5–5 mm in diameter, globose. Fruit 10–25 mm in diameter, globose, pale greenish white or greenish yellow. Seeds 1.5–3.0 mm long, numerous, reniform, the surface pitted, yellow to light brown.

**HABITAT.** Grassy and stony slopes, open moorland, pastures and screes. Subalpine and alpine zone, especially among *Rhododendron* shrubs. Altitudinal range 3000–4900 m.

**VERNACULAR NAMES.** Himalayan mandrake. China: qie shen.

**PHENOLOGY.** Flowering April to September. Fruiting August to October.

**CONSERVATION STATUS.** Locally common. Not threatened.

**DISTRIBUTION.** Sino-Himalayan. (Nepal, India, Bhutan, Myanmar, China).

**SELECTED SPECIMENS EXAMINED.** **NEPAL.** Topke Gola, 27°39'N, 87°35'E, 3810 m, in short grassland, 3 July 1971, *Beer*, L.W. 8264 (BM); Tarakot, 28°53'N, 82°59'E, 3900 m, 25 May 1969, *Dobremez*, J.F. 175 (BM); Jangla Banyang, wet place, 3800 m, 5 June 1973, *Einarsson*, L. et al. 430 (BM); Ganesh Himalaya, Shior Khola, 4270 m, bouldery alpine meadow, *Gardner*, P.C. 479 (BM); Topke Gola-Tasagon, 3600–4350 m, 17 August 1977, *Ohashi*, H. et al. 775165 (BM); Langtang Valley, 28°14'N, 85°32'E, 4420 m, among rocks in turf, June 1949, *Polunin*, O. 631 (BM); 5 miles E. of Timure, oak wood, 4110 m, 3 July 1949, *Polunin*, O. 780 (BM); pass NW of Jumla, 6 miles Pansae Dara, 3050 m, growing in loose soil recently free of snow, 30 April 1952, *Polunin*, O. et al. 878 (BM); Dozam Schola, near Simikot, 3510 m, grass slopes, 2 June 1952, *Polunin*, O. et al. 4250 (BM); near Jumla, 3810 m, open grassy slopes, 14 July 1952, *Polunin*, O. et al.



4668 (BM); Arun-Tamur watershed, Topke Gola, 3960 m, 11 May 1956, *Stainton, J.D.A.* 254 (BM); Balangra Pass, W. of Tibrikot, 29°06'N, 82°41'E, 3810 m, 28 May 1963, *Stainton, J.D.A.* 4263 (BM); Rolwaling, 27°55'N, 86°23'E, 3810 m, beneath small shrubs, 25 June 1964, *Stainton, J.D.A.* 4676 (BM); Khunde-Khumjung, 3820 m, 6 June 1952, *Zimmermann, A.* 688 (BM).

**INDIA. Sikkim:** Changu, 3960 m, in crevices of rocks, 28 June 1913, *Cooper, R.E.* 80 (E); Gnatong, 3960 m, peaty marsh, 31 August 1913, *Cooper, R.E.* 759 (E); Jongri, 4000–4200 m, 22 May 1960, *Hara, H.* et al. 443 (BM, K); Tungu, 3660–3960 m, 23 July 1849, *Hooker, J.D.* s.n. (K); Jongri, 4420 m, campsites towards Yakhut amongst *Juniperus* scrubs, 29 May 1990, *Kirkpatrick, G.* 53 (E); District Darjeeling, Phalut, 3350–3660 m, 30 May 1902, *Lace, J.H.* 2266 (E); West District, Bikbari, Choktsering Chhu valley; 27°30'53"N, 88°08'28"E, 3950 m, amongst scrub, 12 July 1992, *Long, D.G.* et al. 266 (E); Chulong, 4570 m, 12 September 1912, *Rhomoo, L.* 210 (E); Gamothang, 3960 m, 12 August 1913, *Rhomoo, L.* 1059 (E); Giagong, 3960 m, 6 September 1911, *Ribu & Rhomoo* 5492 (BM, E, K); Phalut, 3350–3660 m, 27 May 1911, *Smith, W.W.* 4593 (E); Jongri, 4000 m, in shelter of dwarf *Rhododendron* and *Juniperus*, 23 June 1983, *Starling, B.N.* et al. 92 (K); Tangshing campsite, 4000 m, open grazed areas among *Rhododendron* and around campsite, 24 June 1983, *Starling, B.N.* et al. 106 (K); summit of Sandakphu, 3660 m, small dense tufts amongst grass, 18 May 1881, *Watt, G.* 5373 (E, K). **Arunachal Pradesh (Assam):** Orka La, Bhutan frontier, 3960 m, on stony slopes, scattered, 7 June 1938, *Kingdon Ward, F.* 13840 (BM).

**BHUTAN.** Paco Chu, 4110 m, loose sandy crevice, 15 May 1966, *Bowes Lyon, S.* 3156 (BM); Phajudin Timpu, 3960 m, 5 August 1914, *Cooper, R.E.* 3232 (BM, E); Tare-La area, 3660 m, 19 May 1938, *Gould, B.J.* 109 (K); Laum Thang, 3900 m, in alpine herbage with moderate humidity, 18 May 1967, *Hara, H.* et al. 11973 (BM); Western Bhutan, 3510 m, among boulders above tree line, 17 June 1933, *Ludlow, F. & Sherriff, G.* 107 (BM); Byasu La, 4110 m, growing among stones on open hillside, 18 May 1937, *Ludlow, F. & Sherriff, G.* 3073 (BM); Cheli La, 3810 m in open moorland, 4 May 1949, *Ludlow, F.* et al. 16139 (BM); Pangotang, 3960 m, open hillside above fir zone, 27 May 1949, *Ludlow, F.* et al. 18986 (BM); Kantanang, Tsampa, 4110 m, among shrubs on steep hillside, 3 June 1949, *Ludlow, F.* et al. 19040 (BM); Shingbe, Me La, 3350 m, growing amongst other herbs and small shrubs, 16 May 1949, *Ludlow, F.* et al. 20645 (BM, E).

**MYANMAR (Burma).** Chenochi Pass, 3600 m, 3 July 1920, *Farrer, J.R.* 1694 (E).

**CHINA. Yunnan:** Diqing Prefecture, E. slope of Bai Ma Shan, 28°19'N, 99°05'E, 3895 m, among stones in *Abies* forest, 9 June 1993, *Alden, B.* et al. 1021 (E); Diqing Prefecture, Zhongdian County, above Napa Hai, N. of Zhongdian, 27°55'N, 99°34'E, 4000 m, forested ridge, snow-bed vegetation and dwarf *Rhododendron* scrub, 12 June 1993, *Alden, B.* et al. 1185 (E); western flank of the Lichiang range, 27°20'N, 3050–3350 m, open alpine pasture, June 1910, *Forrest, G.* 5999 (E, K); Lichiang range, 27°25'N, 3660–3960 m, July 1913, *Forrest, G.* 10474 (BM, E, K); western slopes of Likiang snow range, Yangtze watershed, 30 May–6 June 1922, *Rock, J.F.* 4211 (BM); Mo-ting shan, NE of Atuntze, eastern slopes of Yangtze-Mekong divide, 3660 m, along trail, June 1932, *Rock, J.F.* 22771 (E); slopes of Mt Gyi-na lo-ko, the second peak of the Yu-lung shan, 3660 m, in alpine meadows, April–May 1932, *Rock, J.F.* 25005 (BM, E); Chungtien, Chiren, 2200 m, grass slope, 17 May 1937, *Yü, T.T.* 11327 (KUN); Mekong-Salween divide, Chingpoh, 3800 m, alpine pasture lands, 14 June 1938, *Yü, T.T.* 19078 (E); Upper Kiukiang valley, Clulung Lungtsahmuru, 3700 m, mountain slope, open and grassy place, 9 August 1938, *Yü, T.T.* 19843 (E, KUN). **Sichuan:** Tien-chuan-hsien, 3500 m, 14 June 1936, *Chu, K.L.* 2791 (BM); mountains E. of Yungning, 27°48'N, 101° E, 3660 m, open stony pasture, June 1922, *Forrest, G.* 21407 (BM, E, K); mountains around Muli, 28°12'N, 101° E, 3660 m, July 1930, *Forrest, G.* 28416 (BM, E); Liukuliangdse, 27°48'N, 3700–4200 m, 18 May 1914, *Handel-Mazetti, H. von* 2349 (K); Minya Konka snow range, S. of Tatsienlu, 4450 m, in meadows, July 1929, *Rock, J.F.* 17530 (E); Mu-li-ka-bu, 3600 m, mountain slope, grassy place, 18 May 1937, *Yü, T.T.* 5496 (KUN). **Qinghai:** Dari (Darlag) Xian, just N. of Manzhang, along the Manzhang He, between Dari and Banma, 33°17'51"N, 100°25'55"E, 4000 m, on moist rodent disturbed slope, 12 August 1993, *Ho, T.N.* et al. 1172 (E); Chindu Xian, Xiwu Xiang, E. of pass on road between Xiwu and the Szechwan border, 33°09'14"N, 97°32'35"E, 4250 m, damp slope with extensive pika warrens, 11 September 1996, *Ho, T.N.* et al. 3063 (BM). **Xizang:** Dotha, 3960 m, 20 June 1945,

*Bor & Kirat Ram* 20511 (K); Mt. Demula, Yiwei County, 4100 m, 23 August 1973, *Chinese Tibet Expedition 1973* 1214 (KUN); District Chengtang, Dingjie County, Ladang to Xingeng, 3800–4000 m, 9 June 1975, *Chinese Tibet Expedition 1975* 5679 (KUN); Londre Pass, Tsarong, Mekong-Salween divide, 28°14'N, 98°40'E, 3960 m, July 1921, *Forrest, G.* 19630 (UC/JEPS, P, K); Tha Chu valley, 3660 m, in clumps, alpine region, in stony pastures and on grassy slopes, 11 July 1950, *Kingdon Ward, F.* 19613 (BM); N. of Sanga Choling, 28°41'N, 93°02'E, 4110 m, on open grassy bank, 14 May 1936, *Ludlow, F. & Sherriff, G.* 1590 (BM); hills S. of Lhasa, 4420 m, ground left bare by melting snow, 6 June 1942, *Ludlow, F. & Sherriff, G.* 8676 (BM); hills S. of Lhasa, 4720 m, herb growing under boulders, 21 August 1942, *Ludlow, F. & Sherriff, G.* 9014 (BM); Pome, above Showa Dzong, 29°55'N, 95°25'E, 3350 m, open hillsides midst grass, 11 June 1947, *Ludlow, F.* et al. 13149 (BM, E); Sobhe La, near Tongyuk Dzong, Pome, 30°07'N, 94°54'E, 3510 m, 21 May 1947, *Ludlow, F.* et al. 13750 (BM, E); Province Kongbo, Nyima La, 29°38'N, 94°52'E, 3350 m, on dry ground under trees, 21 May 1947, *Ludlow, F.* et al. 15051 (BM, E); Lo La, Pachakshiri, 28°49'N, 93°59'E, 3810 m, in openings of *Rhododendron* forest, mostly above *Abies* zone, 15 May 1938, *Ludlow, F.* et al. 3776 (BM); Province Kongbo, south side of Lusha Chu, 29°20'N, 94°35'E, 3810 m, in *Lonicera* and *Berberis* scrub, 13 June 1938, *Ludlow, F.* et al. 4591 A (BM, E); valley above Tse, Tsangpo valley, 29°23'N, 94°22'E, 3350 m, in grassy banks under *Rhododendron*, *Ludlow, F.* et al. 4591 (BM).

The status and identity of the previously proposed subspecies of *Mandragora caulescens* (Grierson & Long, 1978) are discussed in the section on the species delimitation (p. 25). It is clear from our studies that *M. caulescens* is extremely variable and that a detailed field-based study over the entire species range is necessary.

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- Baker, E.W. 149, *M. officinarum* (BM)
- Ball, J. s.n., *M. officinarum* (E)
- Barclay, C. 3004, *M. officinarum* (K)
- Bauer, K. & Spitzenberger, F. 53, *M. officinarum* (BM)
- Baytop, A., Tanker, N. & Sezik, E. 8504, *M. officinarum* (E)
- Beer, L.W. 8264, *M. caulescens* (BM)
- Bianor & Sabasien 1877, *M. officinarum* (BM, E, P, RNG)
- Bickerich, G. 15324, *M. officinarum* (BM, K)
- Biro, L. s.n., *M. officinarum* (K)
- Bor & Kirat Ram 20481, *M. caulescens* (K); 20511, *M. caulescens* (K)
- Bommüller, J. s.n., *M. officinarum* (K)
- Bourgeau, E. s.n., *M. officinarum* (K, P), 2304, *M. officinarum* (E, K, P)
- Bowen, H.J.M. 694, *M. officinarum* (RNG); 3088, *M. officinarum* (RNG)
- Bowes Lyon, S. 3156, *M. caulescens* (BM); 3239, *M. caulescens* (BM)
- Brickell, C. & Mathew, B. 8088, *M. officinarum* (K)
- Carr, J.W. s.n., *M. officinarum* (RNG)
- Casey, E.C. 221, *M. officinarum* (K)
- Chaboisseau, C. 575, *M. officinarum* (BM)
- Chatterjee, D. 75, *M. caulescens* (BM)
- Chinese Tibet Expedition 1973 1214, *M. caulescens* (KUN)
- Chinese Tibet Expedition 1975 5679, *M. caulescens* (KUN)
- Chu, K.L. 2791, *M. caulescens* (BM)
- Clarke, C.B. 34977, *M. caulescens* (K); 34983 A, *M. caulescens* (BM); 35704, *M. caulescens* (K)
- Clarke, E.D. s.n., *M. officinarum* (BM)
- Coincy, M.A. de s.n., *M. officinarum* (P)
- Cooper, R.E. 80, *M. caulescens* (E); 759, *M. caulescens* (E); 3232, *M. caulescens* (BM, E)
- Danin, A. & Knees, S.G. 1709, *M. officinarum* (RNG)
- Davis, P.H. 1100, *M. officinarum* (E, K); 1438, *M. officinarum* (K); 2108, *M. officinarum* (E, K); 4166, *M. officinarum* (E, K); 40134, *M. officinarum* (E); 40182, *M. officinarum* (RNG); 40478, *M. officinarum* (K)
- Davis, P.H. & Polunin, O. 25469, *M. officinarum* (BM, E, K)
- Delavay, J.M. s.n., *M. caulescens* (P); 263, *M. caulescens* (P); 1026, *M. caulescens* (P)
- Dhwoj, L. 513, *M. caulescens* (BM, E)
- Dinsmore, J.E. B 377, *M. officinarum* (E)
- Dobremez, J.F. 175, *M. caulescens* (BM)
- Duffour, C. 1501, *M. officinarum* (P)
- Economides, S. 1055, *M. officinarum* (K)
- Einarsson, L., Skärby, L. & Wetterhall, B. 430, *M. caulescens* (BM)
- Espinosa, A. 870252, *M. officinarum* (K)
- Ex Herb. Postian. apud Colleg. Syriens. Protest. 952, *M. officinarum* (BM)
- Farrer, J.R. 1694, *M. caulescens* (E)
- Fay, J.M. 815, *M. officinarum* (K); 864, *M. officinarum* (K)
- Forbes s.n., *M. officinarum* (UCJEPS)
- Forrest, G. 569, *M. caulescens* (E); 5999, *M. caulescens* (E, K); 10474, *M. caulescens* (BM, E, K); 19630, *M. caulescens* (UCJEPS, P, K); 21407, *M. caulescens* (BM, E, K); 26951, *M. caulescens* (P); 28416, *M. caulescens* (BM, E)
- Galiano, E.F. & Valdes, B. 820, *M. officinarum* (E, RNG)
- Gammie, G.A. s.n., *M. caulescens* (BM, E)
- Gandoger, M. s.n., *M. officinarum* (K); 84, *M. officinarum* (K); 8400, *M. officinarum* (K)
- Gardner, M.F., Jury, S.L. & Rejdali, M. 4885, *M. officinarum* (E, RNG)
- Gardner, M.F. & Knees, S.G. 4769, *M. officinarum* (RNG)
- Gardner, P.C. 479, *M. caulescens* (BM)
- Garnett, C.S. 33/5, *M. officinarum* (BM); 158/7, *M. officinarum* (BM)
- Gathorne-Hardy, E. 14, *M. officinarum* (E); 139, *M. officinarum* (E); 194, *M. officinarum* (E)
- Girgenti s.n., *M. officinarum* (BM)
- Gould, B.J. 109, *M. caulescens* (K)
- Greuter, W. 7821, *M. officinarum* (E)
- Guiol, F. 1731, *M. officinarum* (BM)
- Haig, E. s.n., *M. officinarum* (BM)
- Handel-Mazetti, H. von 2349, *M. caulescens* (K)

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## EXSICCATAE

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Arranged by collector, with collection numbers (s.n.: collections without collection number), species and herbaria.

- Al-Eisawi, D. & Al-Jallad, W. 2221, *M. officinarum* (BM)
- Alden, B., Alexander, J.C.M., Long, D.G., McBeath, R.J.D., Noltie, H.J. & Watson, M.F. 1021, *M. caulescens* (E); 1185, *M. caulescens* (E)
- Atchley, S.C. s.n., *M. officinarum* (BM); 315, *M. officinarum* (K); 819, *M. officinarum* (K)

- Hara, H., Kanai, H., Murata, G. Ohashi, H., Tanaka, O. & Yamazaki, T. 11973, *M. caulescens* (BM)
- Hara, H., Kanai, H., Murata, G., Togashi, M. & Tuyama, T. 443, *M. caulescens* (BM, K)
- Hardy, E. s.n., *M. officinarum* (BM)
- Hart, H.C. s.n., *M. officinarum* (BM)
- Hay, J.H. 1707, *M. officinarum* (K); H. 2484, *M. officinarum* (K)
- Helbaek, H. 74, *M. officinarum* (K)
- Heldreich, T. von s.n., *M. officinarum* (BM, E, K, P); 257 [1860], *M. officinarum* (BM); 257 [1857], *M. officinarum* (P); 257 [1859], *M. officinarum* (K); 2817 [1853], *M. officinarum* (P); 2817 [1860], *M. officinarum* (K, P)
- Higgins, E.K. s.n., *M. officinarum* (BM)
- Ho, T.N., Bartholomew, B. & Gilbert, M. 1172, *M. caulescens* (E)
- Ho, T.N., Bartholomew, B., Watson, M. & Gilbert, M. 3063, *M. caulescens* (BM)
- Hooker, J.D. s.n., *M. caulescens* (E, K-lectotype, P)
- Huguenin s.n., *M. officinarum* (BM)
- Jury, S.L., Achhal, A. & Mouks, H. & Upson, T.M. 12634, *M. officinarum* (RNG); 12653, *M. officinarum* (RNG)
- Jury, S.L., Aitlafkih, M., Hedderson, T. & Kahouadji, A. 15237, *M. officinarum* (RNG)
- Jury, S.L., Aitlafkih, M., Hedderson, T. & Rutherford, R. W. 15398, *M. officinarum* (RNG); 15434, *M. officinarum* (RNG); 15701, *M. officinarum* (RNG)
- Jury, S.L. & Jury, L.C. 13111, *M. officinarum* (BM, RNG)
- Jury, S.L., Rejdali, M., Taleb, A. & Upson, T.M. 12542, *M. officinarum* (RNG)
- Jury, S.L., Taleb, A. & Upson, T.M. 12217, *M. officinarum* (RNG); 12238, *M. officinarum* (RNG)
- Jussieu, A. de s.n., *M. officinarum* (P)
- King, G. s.n., *M. caulescens* (E); 4368, *M. caulescens* (P)
- Kingdon Ward, F. 13840, *M. caulescens* (BM); 19613, *M. caulescens* (BM)
- Kirkpatrick, G. 53, *M. caulescens* (E)
- Lacaiita, C.C. s.n., *M. officinarum* (BM); s.n., *M. caulescens* (BM)
- Lace, J.H. 2266, *M. caulescens* (E)
- Ladero, M., Lopez Guadalupe, M., Molero, J. & Perez Raya, F. 10605, *M. officinarum* (RNG)
- Lange, J. s.n., *M. officinarum* (K, P)
- Laukkonen, P. 55, *M. officinarum* (K)
- Le Testu, G. s.n., *M. officinarum* (BM)
- Lewalle, J. 10054, *M. officinarum* (BM, RNG)
- Lojacono-Pojero, M. s.n., *M. officinarum* (BM)
- Long, D.G., McBeath, R.J.D., Noltie, H.J. & Watson, M.F. 266, *M. caulescens* (E)
- Lowne, B.T. s.n., *M. officinarum* (BM)
- Ludlow, F. & Sheriff, G. 107, *M. caulescens* (BM); 1590, *M. caulescens* (BM); 3073, *M. caulescens* (BM); 8676, *M. caulescens* (BM); 9014, *M. caulescens* (BM)
- Ludlow, F., Sherriff, G. & Elliot, H.H. 13149, *M. caulescens* (BM, E); 13750, *M. caulescens* (BM, E); 15051, *M. caulescens* (BM, E)
- Ludlow, F., Sherriff, G. & Hicks, J.H. 16139, *M. caulescens* (BM); 18986, *M. caulescens* (BM); 19040, *M. caulescens* (BM); 20645, *M. caulescens* (BM, E)
- Ludlow, F., Sherriff, G. & Taylor, G. 3776, *M. caulescens* (BM); 4591 A, *M. caulescens* (BM, E); 4591, *M. caulescens* (BM)
- Maly, K. s.n., *M. officinarum* (K)
- Manberg, T. s.n., *M. caulescens* (K)
- Mavzomoustakis, G.A. 8, *M. officinarum* (BM)
- Mc Laren's collectors AC 67, *M. caulescens* (E, P)
- Meyers, F. 4377, *M. officinarum* (E)
- Meyers, F.S. & Dinsmore, J.E. 6377, *M. officinarum* (E); B 6377, *M. officinarum* (K)
- Mill, J.S. s.n., *M. officinarum* (K)
- Moreau, W.M. 62, *M. officinarum* (K)
- Norris, F.H. s.n., *M. officinarum* (BM)
- Ohashi, H., Kanai, H., Ohba, H. & Tateishi, Y. 775165, *M. caulescens* (BM)
- Olivier & Bruguère s.n., *M. officinarum* (P)
- Orphanides, T.G. 75, *M. officinarum* (BM, E, K, P)
- Paine, J.A. s.n., *M. officinarum* (K)
- Pantling, R. s.n., *M. caulescens* (K); 46387, *M. caulescens* (K)
- Partridge, F. 2, *M. officinarum* (BM)
- Pastor, J. & Valdes, B. s.n., *M. officinarum* (RNG)
- Perraudière, H. de la s.n., *M. officinarum* (P)
- Petter, F. s.n., *M. officinarum* (BM)
- Pichler s.n., *M. officinarum* (BM, E, K)
- Pignant s.n., *M. officinarum* (K)
- Pitard, C.-J. 1757, *M. officinarum* (K)
- Polunin, O. 631, *M. caulescens* (BM); 780, *M. caulescens* (BM); 6616, *M. officinarum* (K)
- Polunin, O., Sykes, W.R. & Williams, L.H.J. 878, *M. caulescens* (BM, P); 4250, *M. caulescens* (BM); 4668, *M. caulescens* (BM); 4696, *M. caulescens* (BM)
- Pratt, A.E. 755, *M. caulescens* (BM, K, P)
- Probyn, F.M. 49, *M. officinarum* (K)
- Raulin, V. s.n., *M. officinarum* (P); 302, *M. officinarum* (P)
- Rehinger, K.H. 90, *M. officinarum* (BM); 3630, *M. officinarum* (BM, K)
- Reiser, C. s.n., *M. officinarum* (K)
- Reverchon, E. s.n., *M. officinarum* (BM, E, P, K); 117, *M. officinarum* (BM, E, K, P, PAL); 469 [1888], *M. officinarum* (BM, P); 469 [1890], *M. officinarum* (P)
- Rhomoo, L. 210, *M. caulescens* (E); 1059, *M. caulescens* (E)
- Ribu & Rhomoo 5492, *M. caulescens* (BM, E, K)
- Rock, J.F. 3597, *M. caulescens* (E); 3985, *M. caulescens* (P); 4211, *M. caulescens* (BM); 17530, *M. caulescens* (E); 22771, *M. caulescens* (E); 24750, *M. caulescens* (BM, E); 25005, *M. caulescens* (BM, E)
- Ross, H. s.n., *M. officinarum* (BM)
- Ross, H. 266, *M. officinarum* (E, K, P)
- Schneider, C. 3501, *M. caulescens* (E, K)
- Sintenis & Rigo 8, *M. officinarum* (K, PAL); 8a, *M. officinarum* (K)
- Smith, W.W. 4593, *M. caulescens* (E)
- Soulié, J.-A. 849, *M. caulescens* (P); 1252, *M. caulescens* (P); 2102, *M. caulescens* (P)
- Stainton, J.D.A. 254, *M. caulescens* (BM); 4263, *M. caulescens* (BM); 4676, *M. caulescens* (BM)
- Starling, B.N., Upward, E.M., Brickell, C.D. & Mathew, B. 92, *M. caulescens* (K); 106, *M. caulescens* (K)
- Syngrassides, A. 1464, *M. officinarum* (K)
- Taleb, A. 38, *M. officinarum* (RNG)
- Taton, A. 1630, *M. officinarum* (BM)
- Thomas, P. s.n., *M. officinarum* (K)
- Tilman, H.W. 23, *M. caulescens* (K)
- Todaro, A. s.n., *M. officinarum* (P)
- Todd, E. s.n., *M. officinarum* (BM)
- Tomkinson, M.J. 72, 72A, *M. officinarum* (BM)
- Townsend, C.C. 85/11, *M. officinarum* (K)
- Tozer, H.F. s.n., *M. officinarum* (K)
- Treffewy, A.W. 11, *M. officinarum* (K); 20, *M. officinarum* (K)
- Vaccari, A. 1141, *M. officinarum* (K); 2326, *M. officinarum* (BM, K)
- Virantonio s.n., *M. officinarum* (BM)
- Walree, A.M. 22226, *M. officinarum* (BM)
- Walsh, E. 113, *M. caulescens* (K)
- Watt, G. 5373, *M. caulescens* (E, K); 5436, *M. caulescens* (E, K)
- Welwitsch, F.M.J. s.n., *M. officinarum* (P); 159, *M. officinarum* (BM); 337, *M. officinarum* (P)
- White, M.F. s.n., *M. officinarum* (BM)
- Williams, L.H.J. 700, *M. caulescens* (BM)
- Wilson, E.H. 4192, *M. caulescens* (BM, K, P); 4194, *M. caulescens* (BM, K, P); 4195, *M. caulescens* (K)
- Wolley-Dod, A.H. 22, *M. officinarum* (BM)
- Yü, T.T. 5496, *M. caulescens* (KUN); 11327, *M. caulescens* (KUN); 19078, *M. caulescens* (E); 19843, *M. caulescens* (E, KUN)
- Zimmermann, A. 688, *M. caulescens* (BM)

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Accepted names are given in roman, synonyms in *italics*. An asterisk denotes a figure.

*Anisodus caulescens* (C.B. Clarke) Diels 34

*A. luridus* Link 22

*A. mariae* Pascher 34

*Atropa acaulis* Stokes 30

*A. belladonna* L. 30

*A. humilis* Salisb. 30

*A. mandragora* L. 30

*Lycium chinense* Mill. 22

*Mairella yunnanensis* H. Lévl. 34

*Mandragora acaulis* Gaertn. 30

*M. autumnalis* Bertol. 30

*M. caulescens* C.B. Clarke 34, 35\*

*M. caulescens* subsp. *brevicalyx* Grierson & D.G. Long 34

*M. caulescens* C.B. Clarke subsp. *caulescens* 34

*M. caulescens* subsp. *flavida* Grierson & D.G. Long 34

*M. caulescens* subsp. *purpurascens* Grierson & D.G. Long 34

*M. chinghaiensis* Kuang & A.M. Lu 34

*M. foemina* Garsault 30

*M. haussknechtii* Heldr. 30

*M. hispanica* F. Vierh. 30

*M. × hybrida* Hausskn. & Heldr. 30

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*M. microcarpa* Bertol. 30

*M. neglecta* G. Don ex Loudon 30

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*M. praecox* Sweet 30

*M. shebbearei* C.E.C. Fisch. 19

*M. tibetica* Grubov 34

*M. turcomanica* Mizg. 33

*M. vernalis* Bertol. 30

*Nicotiana glauca* Graham 22

*Przewalskia* Grubov 19