

A phylogenetic conspectus of the tribe Hyoscyameae (Solanaceae)

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CONTENTS

Introduction	11
History of classification	13
Chemistry and economic botany	14
Chemistry	14
Economic botany	14
Methods	15
Choice of taxa	15
Characters	15
Tree construction	16
Results and discussion	16
Tree topology	16
Character analysis	20
Biogeography	24
Generic conspectus	25
Artificial key to the genera of the Hyoscyameae	25
<i>Anisodus</i> Link	25
<i>Atropa</i> L.	26
<i>Atropanthe</i> Pascher	26
<i>Hyoscyamus</i> L.	26
<i>Mandragora</i> L.	26
<i>Physochlaina</i> G. Don	27
<i>Przewalskia</i> Maxim.	27
<i>Scopolia</i> Jacq.	27
References	28
Appendix I	29

SYNOPSIS. A cladistic analysis of the tribe Hyoscyameae (including *Atropa* and *Mandragora*) shows that *Atropa* and *Mandragora* are clearly part of the same monophyletic group as the traditional members of the tribe: *Hyoscyamus*, *Physochlaina*, *Anisodus*, *Atropanthe*, *Scopolia*, and *Przewalskia*. The group can further be divided into two main clades, one containing *Hyoscyamus* and *Physochlaina* and the other containing the rest of the genera. Characters used in the analysis are discussed and illustrated, and a conspectus of the genera with descriptions and lists of component species is provided. Introductory material includes a review of the nomenclatural history and the economic botany of the Hyoscyameae.

INTRODUCTION

The Solanaceae are an economically important, cosmopolitan family with over 2500 species. Members of the family are important to agriculture, with potatoes, tomatoes, peppers, and a host of minor fruit crops cultivated worldwide. Many species are also valuable to medicine, being used in both traditional and pharmaceutical treatments. The family is traditionally divided into two subfamilies. The Cestroideae, including petunias, the cestrum, and their relatives, usually have non-compressed, often prismatic seeds and tropane alkaloids. The Solanoideae, which contains the majority of the species in the family, including *Solanum* and its relatives, have compressed seeds and steroidal alkaloids. This traditional classifica-

tion has recently been challenged by cladistic analyses using chloroplast and nuclear DNA data sets, and the family can now be divided into approximately seven monophyletic groups (see Olmstead et al., in press).

The family is predominantly tropical in distribution, but the group variously defined as the tribe Hyoscyameae or subtribe Hyoscyaminae (see p. 13) is exclusively Eurasian and Middle Eastern, with no members in even the subtropics of the northern hemisphere (see Fig. 1). The six genera of the traditionally defined Hyoscyaminae (*Anisodus*, *Atropanthe*, *Hyoscyamus*, *Physochlaina*, *Przewalskia*, and *Scopolia*) and the genera of the Atropinae (*Atropa* and *Mandragora*) have often been considered related in the past (see p. 13) but are usually considered separately. As part of on-going studies into the generic phylogeny of the Solanaceae (Persson et al. 1994;

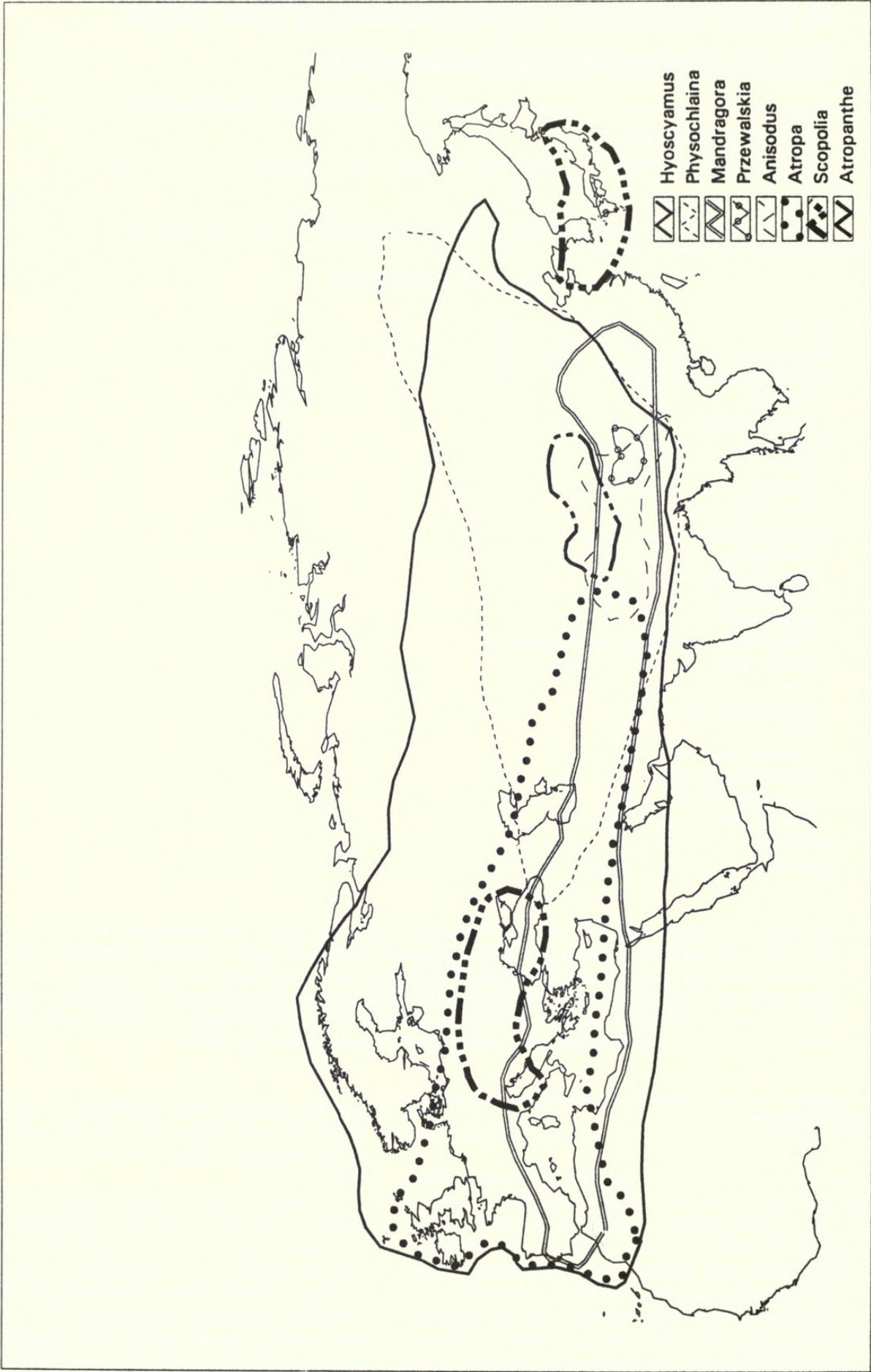


Fig. 1 Distribution of the genera of the Hyoscyameae.

Knapp et al., in press) we decided to examine the phylogenetic relationships of these eight genera using primarily morphological characters. We have attempted a preliminary generic delimitation, but several potential problems are highlighted in the analysis.

HISTORY OF CLASSIFICATION

The concept of the family Solanaceae was first used by A.L. de Jussieu in his *Genera plantarum* (1789) where he included 15 genera in the Solanaceae, all of which are still in current usage, including *Atropa*, *Hyoscyamus*, and *Mandragora*. He divided the family into three groups, the first with capsular fruits, the second having berries, and the third a group of miscellaneous taxa of less certain affinity with the rest of the family.

Following de Jussieu's work and continuing to the present, much effort has been put into the production of a classification system of the family which best reflects the relationships of the genera. G. Don (1838) was the first to recognize tribes within the family. He proposed seven tribes, largely on the basis of the corolla aestivation, characters of the stamens, fruit type, and embryo curvature. These features have been important in most subsequent classifications. Endlicher (1839) produced an alternative classification which was the first to recognize the tribe Hyoscyameae, composed of *Hyoscyamus*, *Anisodus*, and *Scopolia*. The characters by which he defined this group were a curved embryo, semi-circular cotyledons, and a bilocular capsule with circumscissile dehiscence. Endlicher placed *Atropa* and *Mandragora* in the heterogeneous tribe Solaneae, composed of genera with baccate fruits.

Miers (1849) proposed profound changes to the Solanaceae, with the erection of a new family Atropaceae. He considered this group to be intermediate between the Solanaceae and the Scrophulariaceae on the basis of corolla aestivation and symmetry of floral parts. Thus, the Atropaceae were characterized by having nearly isomeric flowers with imbricate or a peculiar aestivation. Within the Atropaceae Miers described 10 tribes, including Hyoscyameae (including the genera *Hyoscyamus*, *Scopolia*, *Physoclaena*, *Cacabus*, and *Thinogeton*) and Atropeae (including the genera *Atropa*, *Nicandra*, *Cliocarpus*, *Anisodus*, *Mandragora*, and *Lycium*). Miers stated that the Hyoscyameae formed a 'very natural tribe', but then contradicted himself by casting some doubt over the affinity of the last four genera with *Hyoscyamus*. Miers' hesitation over definition of the Hyoscyameae was clearly due to his uncertainty over the exact nature of corolla aestivation in all but *Hyoscyamus*. The Atropeae he distinguished by their supposedly baccate fruits, and the absence of an epigynous gland. Later (Miers, 1850), he reclassified *Anisodus* in the Hyoscyameae after seeing its circumscissile fruit and clearly imbricate corolla aestivation.

In 1852 Dunal published the account of Solanaceae for de Candolle's *Prodromus*. This treatment is the last published revision of all the known genera and species in the Solanaceae. It included 60 genera which were placed into two tribes, the Nolaneae and Solaneae. The latter group was subdivided into nine subtribes, including the Hyoscyaminae, defined using the same characters as Endlicher (1839) had used. Dunal recognized only *Hyoscyamus* and *Scopolia* in the Hyoscyaminae. Within *Scopolia* however, he included species now placed in *Physoclaena*, *Hyoscyamus*, *Anisodus*, and *Scopolia* s.s. which he defined as sections. His rationale for lumping these taxa under *Scopolia* was that they all differed from *Hyoscyamus* in the shape of their corolla and calyx. *Atropa* and *Mandragora* were placed in the large and heterogeneous subtribe Solaneae. Within that subtribe the division Atropineae contained many of the genera of the family, including those as diverse as *Jaborosa* and

Discopodium. This group was diagnosed by its 5-parted calyx, campanulate corolla with valvate-plicate aestivation, and its baccate fruit.

In the second half of the nineteenth century two further treatments of Solanaceae appeared, those of Bentham (1876) and Wettstein (1895). These were produced at a time when many new species were being discovered as a result of botanical explorations to new regions of the world. Also at this time, Darwin had published his *Origin of species* (1859) and the theory of evolution by natural selection was beginning to have an impact on taxonomy. *Die natürlichen Pflanzenfamilien*, in which Wettstein's system was published, was the first major work to incorporate these ideas, although this had little direct impact on the classification of the Solanaceae. Both Bentham and Wettstein recognized a group centred on *Hyoscyamus*. Their classifications are summarized in Table 1.

Table 1 Classification of the Hyoscyameae according to Bentham (1876) and Wettstein (1895).

Bentham (1876)		Wettstein (1895)
Solaneae		Nicandreae
Atropeae:	Including –	Solaneae:
	<i>Lycium</i> L.	Lyciinae – incl. <i>Atropa</i> L.
	<i>Atropa</i> L.	Hyoscyaminae – <i>Scopolia</i> Jacq.
	<i>Mandragora</i> Juss.	<i>Physoclaena</i> Don.
Hyoscyameae:	<i>Datura</i> L.	<i>Przewalskia</i> Maxim.
	<i>Scopolia</i> Jacq.	<i>Hyoscyamus</i> L.
	<i>Physoclaena</i> Don.	Solaninae
<i>Hyoscyamus</i> L.		Mandragorinae – incl.
Cestrineae		<i>Mandragora</i> Juss.
Salpiglossidae		Datureae
		Cestreae
		Salpiglossideae

Working extensively on the aestivation of the corolla and calyx, Baehni (1946) suggested pathways for the evolution of morphology in the family and proposed a new classification of the Solanaceae. He recognized five tribes, of which the Atropeae included the subtribe Hyoscyaminae. The genera which made up this subtribe were: *Hyoscyamus*, *Scopolia*, *Physoclaena*, *Tunaria*, *Vestia*, *Przewalskia*, *Petunia*, and *Nierembergia*. *Atropa* and *Mandragora* were placed in the subtribe Atropinae.

The most recent conspectus of the family (D'Arcy, 1979, revised and slightly modified in D'Arcy, 1991) is based on that of Wettstein with some modifications. In this system, 96 genera are included within the Solanaceae, representing about 2300 species. The hyoscyamoid group is recognized at the rank of tribe, and is composed of six genera: *Scopolia*, *Anisodus*, *Atropanthe*, *Przewalskia*, *Physoclaena*, and *Hyoscyamus*. This classification of the tribe Hyoscyameae follows that of Lu & Zhang (1986) who studied the Chinese members of the tribe. They listed the chief characters of the tribe as follows: embryo curved, ovary two-chambered with numerous ovules, connective between two anther cells inconspicuous, filaments inserted at the base or near the base of anthers, corolla lobes often imbricate in bud, calyx greatly enlarged after flowering and including the fruit, capsule with circumscissile dehiscence, and plants containing tropane alkaloid compounds. *Atropa* and *Mandragora* are both placed in the still large and heterogeneous tribe Solaneae, along with 33 other genera.

However, some work has cast doubt over this delimitation of the tribes. Tétényi (1987) examined the biosynthesis of alkaloids and steroids in the Solanaceae, and concluded that the family should be divided into four groups. He recognized the subfamilies Anthocercidoideae, Cestroideae, Solanoideae, and Atropoideae, based

largely on differences in the complexity of alkaloid biosynthetic pathways. Further evidence was taken from geographical and morphological data. On this basis, Tétényi placed the Hyoscyamineae, as defined by Lu & Zhang (1986), together with *Atropa* and *Mandragora* to form the subfamily Atropoideae. The subfamily was defined by its distinctive alkaloid-tropane ester synthesis relationship, where tropane esters are dominant forms (see Tétényi, 1987), imbricate corolla lobes, and Eurasian distribution.

Only Lu & Zhang (1986) have attempted to produce a phylogeny for the whole of the Hyoscyameae. This treatment has been used as the basis for the recent *Flora of China* account (Zhang et al., 1994). They did not include *Atropa* and *Mandragora* in their concept of the tribe because these genera possess baccate fruits. In their classification, *Scopolia* and *Anisodus* were considered the most primitive members of the group, with *Atropanthe* and *Przewalskia* being most closely related to them. These relationships were proposed on the basis of whether the genera showed relatively advanced or primitive characters. The primitive features were considered to be solitary flowers, an actinomorphic corolla, stamens inserted at the base of the corolla tube, and inaperturate pollen grains. However, there are a number of reasons to question their results. The first of these is doubt over the pollen descriptions given (see our results below). Secondly, they give no explanation as to how they reached their decisions regarding the evolution of characters, which could be interpreted differently. Finally, Lu & Zhang state themselves that their phylogenetic hypothesis should only be regarded as a basis for further study of the group.

Most recently, the Solanaceae have been the subject of molecular studies (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press). These chloroplast DNA based phylogenies do not include all the species or even all the genera of the family, but give ideas as to the potential monophyletic groupings of taxa. In cpDNA phylogenies based on the genes *rbcL* and *ndhF* (Olmstead & Sweere, 1994), *Atropa* is grouped with *Nolana* and *Lycium*. With restriction sites on the entire chloroplast genome, *Atropa* and *Hyoscyamus* together are sister to *Lycium* (Olmstead & Palmer, 1992). The most recent and as yet unpublished results of Olmstead et al. (in press) indicate that *Hyoscyamus*, *Physochlaina*, *Anisodus*, and *Atropa* (the only genera of the tribe used in the analysis) form a clear, well-defined monophyletic clade. These analyses do not contain enough taxa to draw clear conclusions as to the relationships of the genera, but they do clearly place the Hyoscyameae as defined here and by Tétényi (1987) together. However, *Mandragora* is extremely isolated in the cpDNA analysis and possesses many molecular autapomorphies (Olmstead et al., in press).

CHEMISTRY AND ECONOMIC BOTANY

Chemistry

The presence of abundant tropane alkaloids is characteristic of members of the Hyoscyameae. Tropane alkaloids are characterized by their five-member, nitrogen-containing rings and are found in several families in addition to the Solanaceae, most notably the Erythroxylaceae (Hegnauer, 1973; Romeike, 1978; Evans, 1979; Lounasmaa, 1988). The range and variety of tropane alkaloids in the Solanaceae arises from the esterification of various acids, such as acetic, propionic, and tiglic (see Evans, 1979) with hydroxytropanes derived from amino acids such as ornithine, tryptophan, and phenylalanine. Hyoscyamine-type alkaloids, derived from phenylalanine, are also found in the Australian genera related to *Anthocercis*, the Chilean endemic *Latua* (Schultes & Hofmann, 1980), *Acnistus*, and *Salpichroa*, but are

in the highest concentrations in members of the Hyoscyameae (Romeike, 1978; Evans, 1979). The biosynthetic pathways leading to the hyoscyamine-type alkaloids are the most complex in the family, and are homologous in all the genera studied (Tétényi, 1987). The most abundant accumulated end-products in members of the Hyoscyameae are atropine, hyoscyamine, hyoscyne (=scopolamine), and tropine, but many other minor tropanes are also found. For complete lists of component alkaloids and a detailed discussion of tropane biosynthesis, see Evans (1979), Romeike (1978), and Tétényi (1987). Studies into the chemistry of these tropane alkaloids have not only provided data useful for classification, but also have provided insight into the effectiveness of these plants in traditional medicine (Qicheng, 1980; Xiao, 1981; Xiao & He, 1982).

Economic botany

The use of the Hyoscyameae in medicine has a long history. They have been recorded in the herbals of the ancient Greeks and in the ancient Chinese, Tibetan, and Indian pharmacopoeias (Deb, 1979; Bettolo, 1981, and see references below).

Hyoscyamus niger (henbane) has a long history of use over most of its range. The oldest of the Chinese herbals, *Shen Nung Pents'ao Jing* (thought to have been written some 2000–3000 years ago) describes the virtues of the seeds of henbane, lang-tang-tze, for curing toothache and for increasing vitality (Xiao & He, 1983). Later Chinese herbals document the use of lang-tang in a variety of illnesses and state that a tonic made from the plant allowed the patient to communicate directly with devils and spirits (Rätsch, 1992). Doctors of the Assyrian empire also used henbane for the cure of toothaches (Press et al., 1989). Dioscorides used henbane to induce sleep and relieve pain, and wrote of its properties in his *De materia medica* in A.D.77 (Stockwell, 1988). The herbals of the Middle Ages also contain numerous references to narcotic and dangerous properties of henbane (Arber, 1912). One of the best known of the English herbalists, John Gerard (1597), wrote scathingly of the fraudulent use of the smoke of henbane seeds to draw worms from the teeth. There is no doubt that the drug eased the pain of toothache, but the worms so miraculously removed by medical practitioners were nothing more than the tiny coiled embryos released from the seeds by the heat (Grieve, 1992). Culpeper, an astrological botanist (see Arber, 1912) writing in the first half of the seventeenth century, recommended an infusion of the leaves for the treatment of gout, swellings, and pains of the joints. He also believed the oil of the seed to be good for deafness and worms in the ears (Culpeper, 1826), thereby perpetuating the worm myth! Several species of *Hyoscyamus* are used in North Africa for both criminal and medicinal purposes (Boulos, 1983).

The *Coloured atlas of Tibetan medicine* (1704, see Xiao & He, 1983), a commentary on the much earlier complete manual of Tibetan medicine *Rygud bzhi* of 820, describes the use of the roots of *Przewalskia tangutica* to relieve pain and reduce swellings. The *Atlas* included illustrations of the plants used, and that of *P. tangutica* is botanically extremely accurate. The roots of *Physochlaina physaloides* are used in Mongolia as a tonic and a cure for asthma, those of *P. praealta* in Tibet as an analgesic (Xiao & He, 1983) and in India as a drug to dilate the pupils and to cure boils (Sharma & Singh, 1975). Roots of *Physochlaina infundibularis* were locally regarded as a sort of ginseng in the Chinese provinces of Shanxi and Henan. Several species of *Anisodus* have a long history of use in Tibetan medicine, as analgesics, anaesthetics, and antispasmodics, but dosages are very small and great care is needed as overdoses are known to cause delirium (Xiao & He, 1983).

In addition to their value as herbal remedies, some of these plants

gained reputations for their supposed magical properties, and became associated with numerous myths. Most notable are those surrounding the mandrake, *Mandragora officinarum* (Bouquet, 1936; Moldenke & Moldenke, 1952). The roots of this plant, which sometimes bear a resemblance to the human form, were believed to be the abode of evil spirits. The mandrake was said to scream when pulled from the ground, causing the death of the person uprooting it or anyone who heard the screams. To escape such a fate, people were said to use dogs to pull the plants up, and would drown the cries by blowing loudly on horns. Mandrakes were said to sprout from the sperm of hanged men, and so were to be found growing at the foot of gallows. Gerard (1597) ridiculed these myths as the hoaxes of charlatans, saying '...they are all and everie part of them false and most untrue for I myselfe and my servants also have digged up, planted and replanted very many..'. A mandrake is clearly identifiable on the thirteenth century Mappa Mundi in Hereford, a map showing the extent of the then-known world and many of its creatures. Numerous images of mandrakes adorn Egyptian tombs and tomb art and it may have been an important drug at that time. In the Old Testament mandrakes are mentioned in two places (in Genesis and in the Song of Solomon) in relation to the procreation of children, and the roots are carried in Eastern Europe as a charm against sterility (Mehra, 1979).

Mandragora was also associated with witchcraft, as were henbane and deadly nightshade, *Atropa belladonna*. The magical powers of these plants were believed to enable witches to fly (Stockwell, 1988). The celebrated sixteenth century Spanish physician A.F. de Laguna was probably the first to correlate the use of solanaceous drugs with witchcraft. The ointments used by supposed witches were composed of henbane, nightshade, and mandrake and caused hallucinations and delusions. He believed that witches were drug users and that the use of hallucinogenic drugs also increased suggestibility. Thus the confessions wrung from these people represented the delusional speech of deranged minds and were false (Schleiffer, 1979). Accounts of hallucinations experienced while using henbane and mandrake almost always involve flying sensations and some have suggested that the urge to move is a hallmark of the intoxication (Schleiffer, 1979).

The Hyoscyameae have continued to be employed in medicine right up to the present day. They make an important contribution to both modern and traditional medicine. In traditional medicine the use of these plants is found in Tibet, China, and in the Himalayan countries. They are used to treat swellings, bruises, asthma, to relieve pain, for the treatment of travel sickness, as antidotes to nerve gases, and as anaesthetics and sedatives. Extracts of species of *Physochlaina* and *Mandragora caulescens* are also used to make a tonic in Tibet, southern China, and Mongolia, which is administered to replenish weakness and to 'warm the stomach'. Most of the Chinese species in the group are used in medicine in some way (Xiao & He, 1983; Zhang et al., 1994). *Hyoscyamus* is in the official British Pharmacopoeia (see Grieve, 1992) and has great importance in both the Ayurvedic and Unani medicinal systems of India (Dash & Kashyap, 1980; Thakur et al., 1989). The uses of this group of plants reflect the properties of their constituent alkaloids. The tropane alkaloids have been shown to be effective as analgesics, anaesthetics, antispasmodics, and to increase the circulation.

Today, five species are used commercially as a source of alkaloids in modern Western medicines. Hyoscyine, or scopolomine, most important as a sedative, is extracted from *Scopolia carniolica*. Scopolomine is the infamous 'truth serum' – used unscrupulously to extract information from uncooperative persons. *Atropa belladonna* is the source of atropine, an antispasmodic used to treat asthma, colic, and eye diseases. *Hyoscyamus niger*, *H. albus*, and *H. muticus*

are grown for the extraction of hyoscyine, atropine, and hyoscyamine.

This brief account highlights the importance of this group of plants for man. However, their beneficial effects are dependent on their wise use. All of these plants are potentially toxic and can cause death. Deadly nightshade, *Atropa belladonna*, is one of the most poisonous species of the group. This is clearly reflected in both the common and generic names of the plant: in Greek mythology Atropos was the Fate who held the shears to cut the thread of human life.

METHODS

Choice of taxa

Specimens studied were those at The Natural History Museum, London (BM) and the Royal Botanic Gardens, Kew (K). Living plants of some taxa were also examined. Individuals of *Anisodus luridus*, *Mandragora officinarum*, *Physochlaina orientalis*, *Atropa belladonna*, *Hyoscyamus albus*, *H. niger*, and *Scopolia carniolica* are all grown at Kew, and all but *Anisodus* and *Physochlaina* are grown at the Chelsea Physic Garden, London. *Scopolia carniolica* is also grown in the Harris Garden, Reading. Further details of the specimens studied are given in Appendix I and a complete database of all specimens studied is held at the University of Reading. Genera with more than one species were sampled, with species encompassing the range of variation used in the analysis. Taxa used in the analyses were: *Lycium chinense* Mill., *Datura inoxia* Mill., *Nicandra physalodes* Gaertn., *Anisodus luridus* Link, *Atropa belladonna* L., *Atropanthe sinensis* (Hemsl.) Pascher, *Hyoscyamus muticus* L., *Hyoscyamus niger* L., *Hyoscyamus senecionis* Willd., *Mandragora officinarum* L., *Mandragora caulescens* C.B. Clarke, *Physochlaina physaloides* (L.) G. Don, *Physochlaina praealta* (Dcne.) Miers, *Przewalskia tangutica* Maxim., and *Scopolia carniolica* Jacq.

Characters

The taxa were scored for variation in morphological and palynological characters. The morphological characters used were taken from the flowers, leaves, fruits, and seeds. A list of all the characters is given in Table 2, together with the coding used. Most of the characters are binary and self-explanatory. The data matrix used in the analyses is presented in Table 3.

The features of the spermoderm were determined by examining seeds prepared by enzyme etching (Lester & Durrands, 1984). Two seeds of each species were treated with a 1% solution of Driselase for 24 or 48 hours. The longer time was found to be necessary for the seeds of *Anisodus luridus*, *Atropa belladonna*, *Atropanthe sinensis*, *Mandragora officinarum*, *M. caulescens*, and *Przewalskia tangutica*. The seeds were rinsed with distilled water and allowed to dry before being examined with SEM. Seed measurements were made from 20 seeds when possible, and the average value recorded.

Table 2 Character set used in the cladistic analysis.

Inflorescence

0. Inflorescence type: raceme 0; solitary flowers 1; cyme 2
1. Flowers: pedicellate 0; sessile 1

Calyx

2. Calyx: tubular 0; campanulate–urceolate 1; cup-shaped 2
3. Calyx: actinomorphic 0; zygomorphic 1
4. Calyx: quite deeply lobed 0; very deeply lobed 1; shallowly lobed 2
5. Apices of calyx lobes: acuminate 0; rounded 1
6. Length of calyx: short (< 1 cm) 0; medium (1–3 cm) 1; long (> 3 cm) 2

Corolla

7. Corolla: flared 0; campanulate-urceolate 1; cup-shaped 2
8. Corolla: actinomorphic 0; zygomorphic 1
9. Corolla: uniform in colour 0; tube darker than the limb 1
10. Corolla lobes: quite deep 0; shallow 1; very deep 2
11. Apices of corolla lobes: rounded 0; acuminate 1
12. Length of corolla: short (< 2 cm) 0; medium (2 cm < x < 5 cm) 1; long (> 5 cm) 2
13. Width of corolla tube: narrow (< 1 cm) 0; broad (> 1 cm) 1

Stamens

14. Filament insertion on the corolla tube: near middle 0; basal (< 1/3 of way up) 1; apical (> 1/2 way up) 2
15. Stamens: exserted from corolla tube 0; included 1
16. Stamens: regular 0; declinate 1

Stigma

17. Stigma: included in corolla tube 0; exserted 1

Fruiting calyx

18. Fruiting calyx: cup-shaped 0; ovoid 1; flared-urceolate 2; tubular 3
19. Fruiting calyx: little enlarged 0; inflated 1
20. Fruiting calyx: without prominent ribs 0; with prominent ribs 1
21. Fruiting calyx: membranous 0; subcoriaceous 1; coriaceous to woody 2

Fruit

22. Fruit: berry 0; capsule 1
23. Fruit: globose 0; cylindrical 1

Leaves

24. Leaves: ovate 0; cordate 1; lanceolate 2
25. Leaf margins: entire 0; variously incised 1
26. Leaves: arranged along the stem 0; a basal rosette 1

Seeds

27. Seeds: compressed 0; not compressed 1
28. Seeds: rectangular-subreniform 0; reniform 1; sublenticular 2
29. Seed size: medium (2.5–5 mm) 0; small (< 2.5 mm) 1; large (> 5 mm) 2
30. Seed colour: light brown or mustard yellow 0; dark brown 1
31. Spermoderm cells: deep 0; shallow 1
32. Walls of spermoderm cells: sinuate 0; straight 1

Trichomes

33. Glandular hairs: absent 0; with uniseriate glands only 1; with uni- and multi-seriate glands 2
34. Eglandular hairs: all simple 0; dendritic hairs present 1

Pollen

35. Number of apertures: three 0; none 1; more than three 2
36. Length of apertures: long, almost meeting at the poles 0; short 1
37. Tectum: present 0; absent 1
38. Supratectal ornamentation: absent 0; isolated elements-scabrate 1; scabrate with gemmae 2; reticulate or striate 3

Chemistry

39. 3-tigloyloxytropene: absent 0; present 1
40. Belladonnine: absent 0; present 1
41. Tropine: absent 0; present 1

Table 3 Data matrix used in the cladistic analysis.

Character Number	0123456789	1111111111	2222222222	3333333333	44
	0123456789	0123456789	0123456789	0123456789	01
<i>Lycium</i>	0000000000	0000000000	0000000000	0000000000	00
<i>Anisodus</i>	1021001100	0011110011	1210000110	1000121020	01
<i>Atropa</i>	0020101100	0011111100	0000000121	1101000031	11
<i>Atropanth</i>	1020001100	0011111111	0110000100	0110000030	01
<i>H. muticus</i>	2111201011	0010000121	0211010001	0101100011	01
<i>H. niger</i>	2111001011	0010000121	0210010001	0102000011	01
<i>H. senecionis</i>	2010001010	2011000121	0211010001	0102000011	01
<i>M. caulescens</i>	102011200	2011010000	0000201110	111001?111	10
<i>M. officinarum</i>	1020101000	2011100000	0000101112	000001?101	10
<i>P. physaloides</i>	0000000000	0000000111	0110100001	0002020011	01
<i>P. praealta</i>	0010000000	1110100121	0111100001	1002000031	01
<i>Przewalskia</i>	1000011000	0010210111	1210201100	1001000001	01
<i>Scopolia</i>	1021200000	1101110011	0110000110	01100?1011	01

Pollen for this study was taken from herbarium specimens at The Natural History Museum (see Appendix I), except in the case of *Scopolia carnioleica*, in which pollen from live plants was studied. Pollen grains were prepared using the procedure of Erdtmann (1960). Acetolysed pollen grains were studied under the SEM and the light microscope. All chemical characters were taken from the literature, largely from Tétényi (1987) and Romeike (1978).

Tree construction

Cladistic analyses were undertaken with HENNIG86 (Farris, 1988) using the *ie** option (implicit enumeration) with all characters unordered. Tree statistics generated from HENNIG86 include the tree length (L), the ensemble consistency index (CI), and the retention index (RI). The ensemble consistency index (CI) is a measure of character fit on a scale of 0 to 1 and the ensemble retention index (RI) is the fraction of apparent synapomorphy in a character that is retained as synapomorphy on the tree (Farris, 1989). The genus *Lycium* was chosen as the outgroup for this analysis based on the cpDNA phylogenies produced for the Solanaceae in which *Lycium* is the sister group to the clade containing *Atropa* and *Hyoscyamus* (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press).

RESULTS AND DISCUSSION**Tree topology**

The HENNIG86 analysis produced a single most parsimonious tree of L=109, CI=52, and RI=58 (Fig. 2). The group can be broadly divided into two clades: the *Hyoscyamus* + *Physochlaina* clade and the rest of the genera (see Fig. 2). The *Hyoscyamus* + *Physochlaina* clade is defined by the following suite of synapomorphies: cordate leaves (character 24), very small seeds (character 29), glandular hairs with uniseriate and multiseriate glands (character 33), and pollen with isolated scabrate supratectal elements (character 38). A close relationship between *Hyoscyamus* and *Physochlaina* has been pointed out by previous authors (Lu & Zhang, 1986). The genus *Physochlaina* is not, in our tree, a monophyletic group. This could be used as evidence for the suggestion that this genus should be reduced to synonymy within *Hyoscyamus*. The position of *P. praealta* does agree with the observations of Zhang & Lu (1984) who suggest this species may be intermediate between the two genera. The characters linking *P. praealta* to *Hyoscyamus* include the shape of the calyx and the fruit. However, if the pattern of branching is altered, such that the two species of *Physochlaina* do form a monophyletic group, then the tree is only one step longer. Clearly, this analysis does not provide convincing evidence either for the lumping of these genera or for keeping them separate.

The clade consisting of the rest of the genera in the tribe is defined by the following suite of synapomorphies: a racemose inflorescence (character 0), a medium length calyx (character 6, also present in *Hyoscyamus*) and corolla (character 12, occurring in many places on the tree), basal filament insertion (character 14), stamens included in the corolla tube (character 15), and non-compressed seeds (character 27). Within the clade, the only consistent groupings are *Scopolia* + *Anisodus* and *Atropa* + *Mandragora* (see p. 19). Relationships of the other genera are somewhat ambiguous, although *Przewalskia* is basal to the clade. Contrasting this with the proposed phylogeny of Lu & Zhang (1986) illustrates an important aspect of cladistics which distinguishes it from other purportedly phylogenetic approaches. Lu & Zhang (1986) hypothesize that *Przewalskia* is the

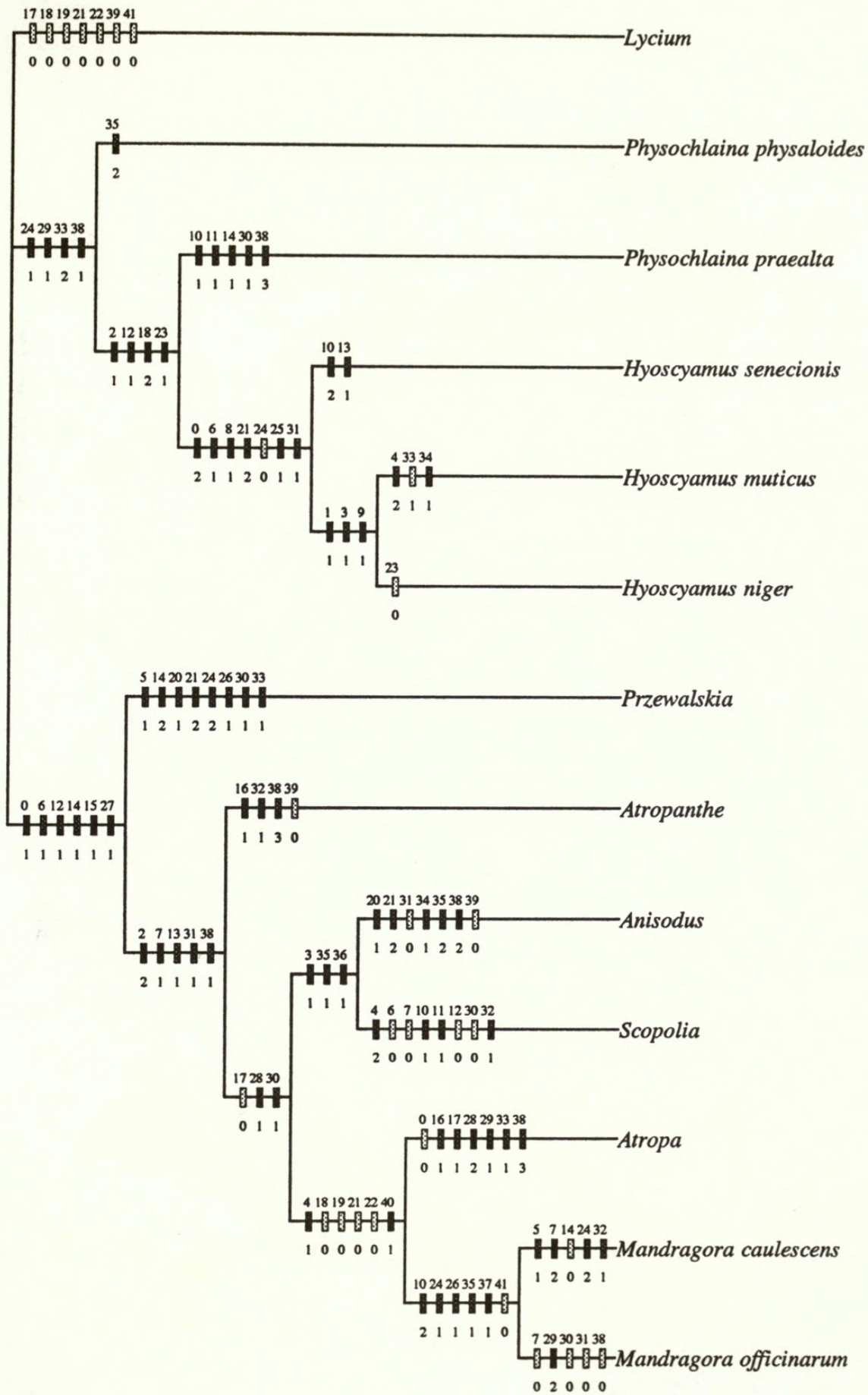
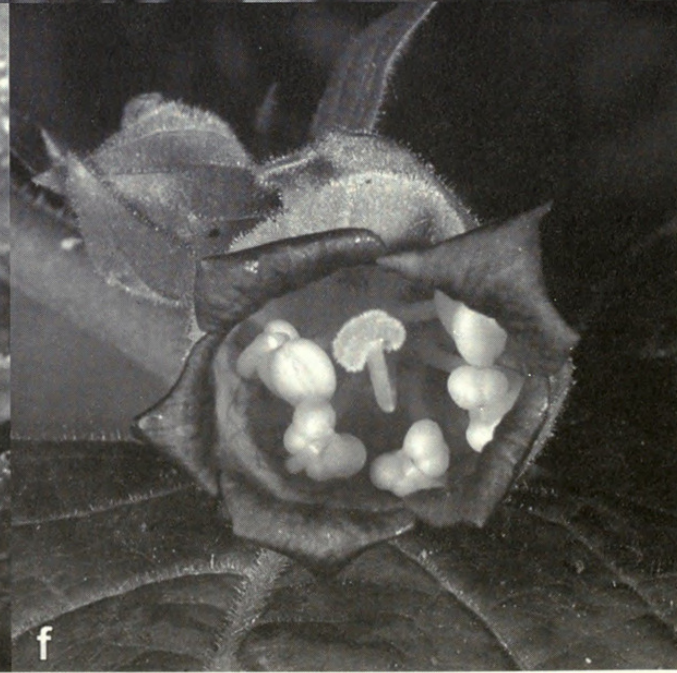
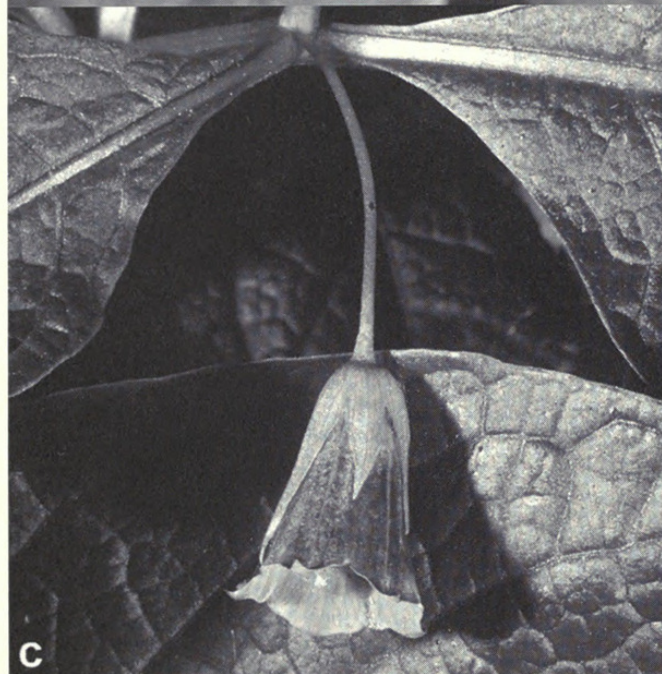
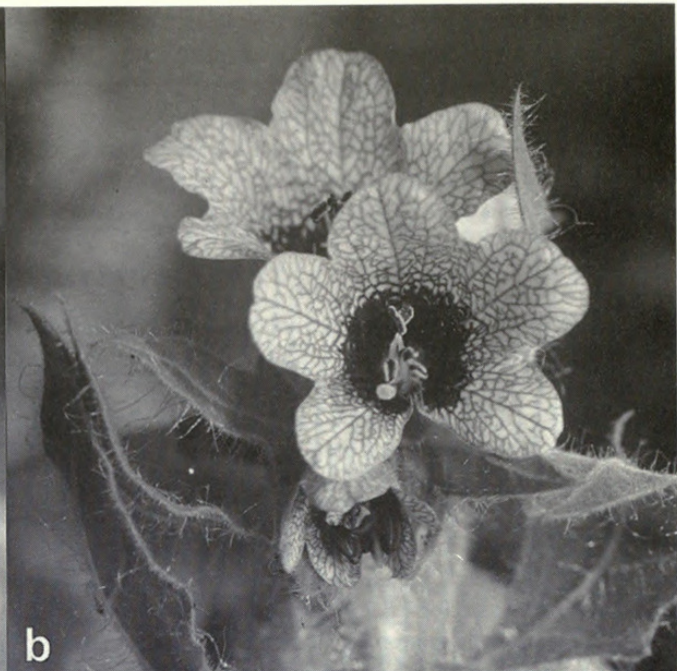


Fig. 2 The single most parsimonious cladogram from the HENNIG86 analysis. The characters are discussed in the text, and character states are shown in Table 2. For characters marked on the branches of the cladogram: unshaded marks indicate synapomorphies, stippled marks indicate reversals and parallelisms (homoplasy), and solid marks non-homoplastic synapomorphies.



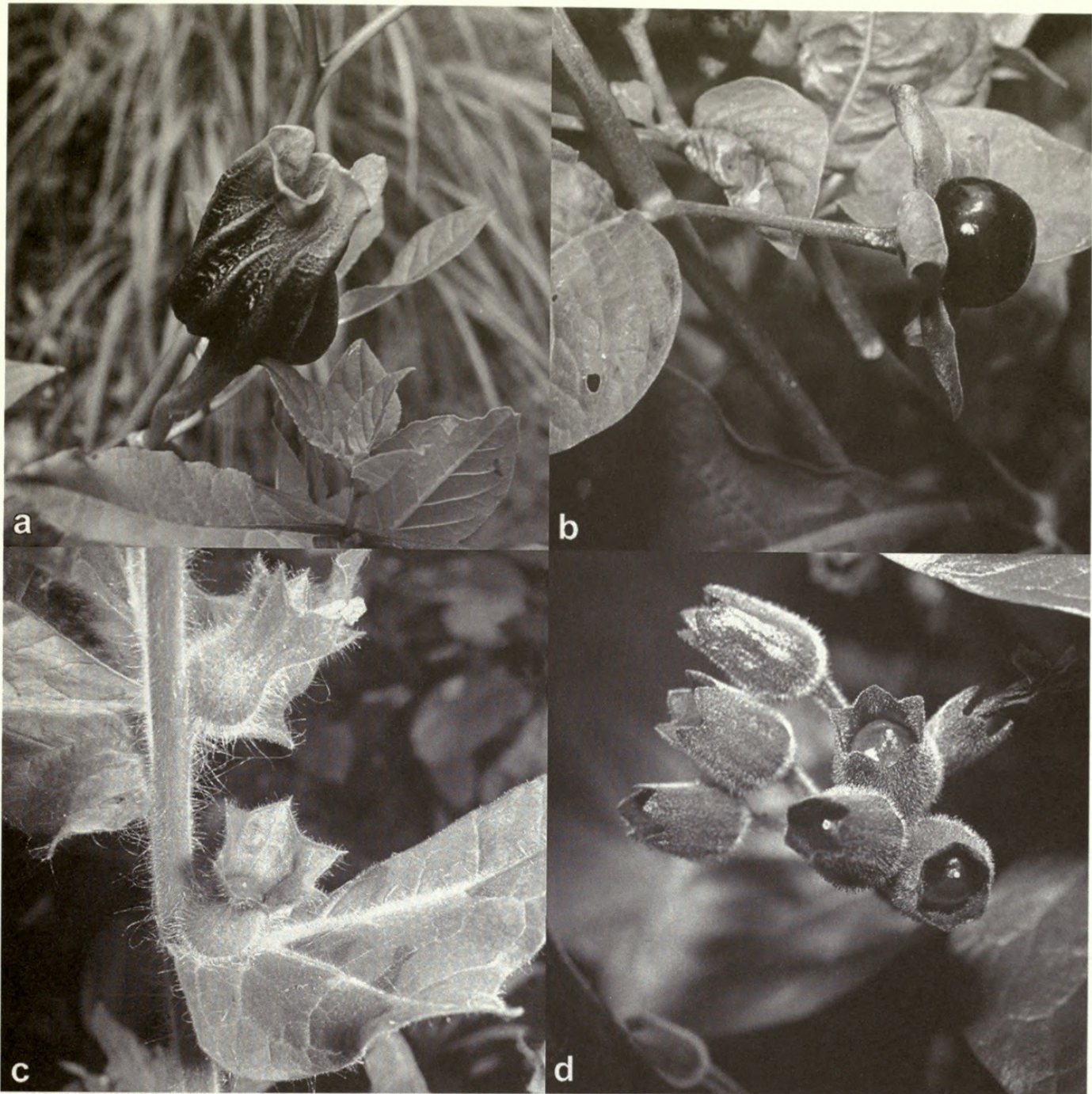


Fig. 4 a) Fruit of *Anisodus tanguticus* (photograph courtesy of M. Gilbert), b) Fruit of *Atropa belladonna*, Chelsea Physic Garden, c) Fruit of *Hyoscyamus niger*, Chelsea Physic Garden, d) Fruit of *Physochlaina orientalis*, RBG Kew.

most 'advanced' and thus, according to them, derived, taxon of the group. However, in our tree, this genus usually occurs at the base of the clade. This radical difference in placement is most likely due to the large number of autapomorphies (see Fig. 2) which distinguish *Przewalskia*. Automorphies are not informative about relationships.

Atropa and *Mandragora* cluster together and are nested well within the tribe as a whole. This is in agreement with Tétényi's (1987) system. Earlier classifications had not included *Atropa* or *Mandragora* within the tribe simply on the basis that they bear berries and not capsules. Characters which unite the two genera

include those of the fruiting calyx (shape, inflation, and texture), fruit type, and the presence of belladonnine. The close relationship of these two genera was implied in the classifications of some of the early botanists: Miers (1849), Dunal (1852), and Bentham (1876) all placed these two genera in the same tribe or subtribe. This link is also reflected in the naming of some of the species, for example, Linnaeus had described *Mandragora officinarum* in *Species plantarum* (1753), but in later editions he changed the name to *Atropa acaulis* (1762, 1764).

Fig. 3 a) Flowers of *Physochlaina orientalis*, RBG Kew, b) Flowers of *Hyoscyamus niger*, Chelsea Physic Garden, c) Flowers of *Scopolia carniolica*, Chelsea Physic Garden, d) Flowers of *Anisodus luridus*, RBG Kew, e) Flowers of *Mandragora autumnalis*, RBG Kew, f) Close-up of the flower of *Atropa belladonna* showing declinate stamens, Chelsea Physic Garden (photograph courtesy of J. Vogel).



Fig. 5 a) Fruiting plant of *Przewalskia tangutica* (photograph courtesy of M. Gilbert), b) Fruit of *Przewalskia tangutica* showing dehiscence (photograph courtesy of M. Gilbert), c) Fruit of *Mandragora officinarum*, RBG Kew, d) Fruiting plant of *Mandragora chinghaiensis* (photograph courtesy of M. Gilbert).

Character analysis

Rather than discussing in detail all of the characters and their distribution on the tree, we have chosen a few to discuss in detail. Some of these are characters that show little homoplasy on the tree, while others are those that surprisingly do not provide any phylogenetic evidence.

Morphological characters

3. CALYX SYMMETRY. An actinomorphic calyx is plesiomorphic in the tribe. This finding is contrary to studies completed for the family as a whole, with the most basal members possessing zygomorphic flowers (see Olmstead & Palmer, 1992; Olmstead et al., in press). Zygomorphy occurs twice on the tree, once in *Hyoscyamus* and as a

synapomorphy uniting *Scopolia* and *Anisodus*. In *Scopolia* and *Anisodus* the calyces are symmetrical except in their lobing. In *Scopolia*, one lobe is usually enlarged (Fig. 3c), and in *Anisodus* the lobing is very irregular (Fig. 3d, 4a). However, in the two species of *Hyoscyamus*, the asymmetry is manifested differently. In these species the calyx tube is curved, and the lobes show a gradation in size. The zygomorphic calyces of *Hyoscyamus* should probably not be equated with those of *Anisodus* and *Scopolia*. A more meaningful coding of this character may be to represent these as two independent states, or it could be divided into two characters; symmetry of the calyx lobes and of the calyx tube.

7. COROLLA SHAPE. A flared corolla is the plesiomorphic state for the tribe. Within the *Hyoscyamus/Physoclaina* clade, this character is conservative. In contrast to this, in the rest of the tribe, corolla

shape shows much homoplasy. It was difficult to divide shape into discrete states, although the cup-shaped flowers of *Mandragora caulescens* were quite distinct. Shape may in fact represent several independent characters, and so would be better coded as such. The problem then lies in determining just what these characters should be.

14. FILAMENT INSERTION. Lu & Zhang (1986), in their study of the Chinese members of this tribe, presumed that stamens inserted at the base of the corolla tube were a primitive feature. This analysis suggests that this should actually be regarded as a derived trait, occurring in two places on the tree. Basal stamen insertion is a synapomorphy of the *Przewalskia* clade (uniting all the genera save *Hyoscyamus* and *Physochlaina*) and occurs in *Physochlaina praealta*.

16. ARRANGEMENT OF THE STAMENS. Declinate stamens are found in both *Atropa* and *Atropanthe*. Consequently, this character is not indicative of shared ancestry and, in this analysis, is uninformative about generic relationships. It is possible that this feature is an adaptation for improving pollen deposition on insect pollinators. The flowers of these genera are held horizontally or are nodding, and the position of the anthers is such that they would brush the bodies of insects entering them (see Fig. 4f).

19. INFLATION OF THE FRUITING CALYX. An inflated fruiting calyx (Figs 4c, d, 5a) is a synapomorphy of the tribe in this analysis. The non-inflated calyx found in *Atropa* and *Mandragora* (Figs 4b, 5c, d) must therefore be considered to be derived within the tribe and is probably related to the method of seed dispersal in these plants. Both these genera produce fleshy or juicy berries. Those of *Atropa* are black and shiny when ripe, and are eaten by birds. The fruits of *Mandragora* are whitish, greenish, yellow, orange or purple, and are borne close to the ground, frequently hidden by leaves. These are eaten by small mammals or reptiles. In the other members of the tribe seed dispersal is effected by the seeds being shaken from the capsules. The fruits of *Przewalskia* become detached and behave as tumble weeds, releasing seeds as they are blown about by the wind (M. Gilbert, pers. comm.).

21. TEXTURE OF THE FRUITING CALYX. A subcoriaceous calyx is plesiomorphic in the tribe. *Atropa* and *Mandragora* are united by having membranous calyces. This seems to provide some support for the suggestion that the calyx has a protective function in other members of the tribe. Thickening of the calyx occurs in three places on the tree, in *Anisodus*, *Przewalskia*, and as a synapomorphy of *Hyoscyamus*.

26. LEAF ARRANGEMENT. A rosette arrangement of leaves occurs twice on the tree, in *Przewalskia* and *Mandragora*. The rosette habit has been thought to be an adaptation to habitat (Lu & Zhang, 1986), providing protection from wind and grazing animals, and ensuring maximum exposure to the sun. *Przewalskia* is found at high altitudes in arid grasslands and areas of frost heave (Fig. 5a), while *Mandragora* (see Fig. 5d) occurs in a wider range of habitats, which include stony slopes and screes in mountainous regions, grassland, and ruderal habitats.

27. SEED COMPRESSION. Compressed seeds are confined to the *Hyoscyamus* + *Physochlaina* clade, and so supports the division of the tribe into two groups. Non-compressed seeds are a synapomorphy of the other clade and are generally uncommon in the family (see Knapp, 1991). This character may be related to the development of the seeds, and possibly to seed dispersal.

29. SEED SIZE. Small seed size is a synapomorphy of the *Hyoscyamus* + *Physochlaina* clade, but is also found in *Atropa*. Small

seeds are often associated with capsular fruit in the Solanaceae (Souèges, 1907), but in the Hyoscyameae this ecological distinction appears not to hold true.

30. SEED COLOUR. In contrast to the genus *Solanum* and other tribes in the family (see Knapp, 1989; Knapp et al., in press; Knapp & Helgason, in press) seed colour provides little support for the tree topology, and has frequently changed in the Hyoscyameae. The explanation for this may lie in the function of the seed colour, or may reflect the ease with which these changes can occur.

32. SPERMODERM CELL WALLS. Whether the cell walls of the spermoderm are straight or sinuate is uninformative with respect to generic relationships, since straight walls are autapomorphic in both *Scopolia* and *Mandragora caulescens*. This is in contrast to the utility of cell wall shape as a character in studies of other groups of Solanaceae (Knapp & Helgason, in press).

34. PRESENCE OF DENDRITIC HAIRS. Dendritic hairs occur in both clades, in *Physochlaina* and *Anisodus*. This high level of homoplasy is also found in many other groups of Solanaceae (Knapp, 1991). Trichomes can have a multitude of functions, for example, protection against desiccation, ultra-violet radiation, and insect attack (Metcalf & Chalk, 1983). Dendritic hairs, in comparison to simple hairs, may have advantages in any of these roles but no evidence exists for an adaptive role.

Pollen characters

35. NUMBER OF APERTURES. Triaperturate pollen grains are plesiomorphic in the tribe, as they are thought to be for the family Solanaceae and dicotyledons in general. This is contrary to the suggestion of Lu & Zhang (1986) that inaperturate pollen grains are ancestral in the Hyoscyameae. They (Zhang & Lu, 1984; Lu & Zhang, 1986) identified the pollen grains of *Anisodus tanguticus*, *A. luridus* (as *A. mairei*), *A. carniolicoides* (as *Scopolia carniolicoides*), and *A. acutangulus* as inaperturate, while our results clearly show (Fig. 7b) the grains of *A. luridus* to be porate. The potentially cryptic nature (see *Mandragora* p. 27, and Diez & Ferguson, 1984) of the apertures in the pollen grains of *Anisodus* needs further study. The two species which have pollen with more than three apertures, *Anisodus luridus* and *Physochlaina physaloides*, are unrelated. Increase in aperture number must therefore have occurred independently in these two taxa. Distribution of apertures in these two taxa differs radically. In *A. luridus* the six apertures are distributed randomly on the pollen grain, and the grains are pantoporate (Fig. 7b), whereas in *P. physaloides* the apertures are confined to the equator (Fig. 6a).

The principal functions of the pollen aperture are protection, harmomegathic responses (alterations in form accompanying changes in pollen grain hydration, see Blackmore & Barnes, 1986), ion exchange, and pollen tube germination. The significance of the number of apertures to each of these functions is unclear. Increase and irregularities in number of apertures does seem to be related to polyploidy, but cytological information is lacking for both these species (see Table 4).

36. LENGTH OF APERTURES. The presence of pores, rather than colpi, is a synapomorphy which unites *Anisodus* and *Scopolia* (see Fig. 7a, b). Reduction of aperture size may have occurred in response to an increasingly arid environment, reducing the risk of desiccation of the pollen grains. However, the ecology of these genera does not fit in with this, as they are typically plants of moist environments. This highlights the fact that we should be wary of making simplistic explanations about the adaptive significance of

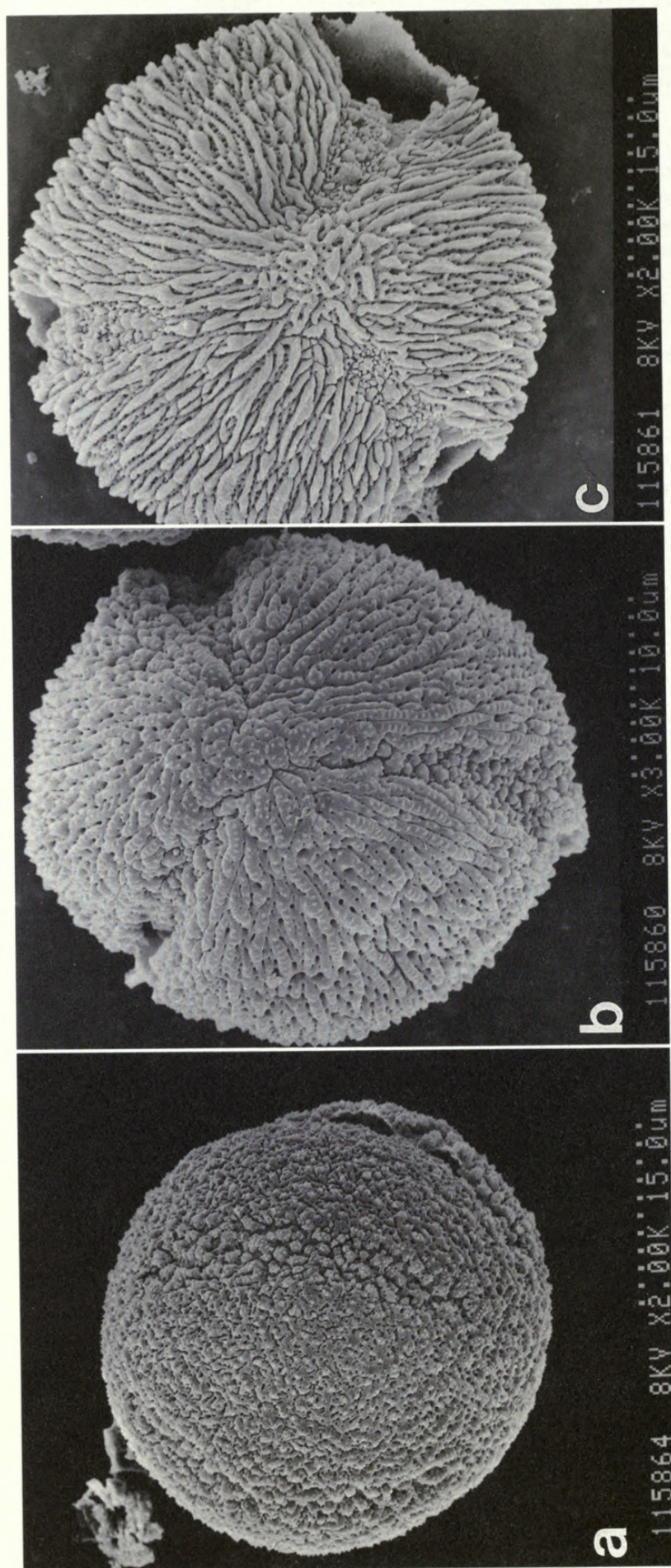


Fig. 6 Pollen morphology of the Hyoscyameae. Scale bars beneath photographs. a) *Physochlaina praealta*, b) *Physochlaina physaloides*, c) *Atropanthe sinensis*.

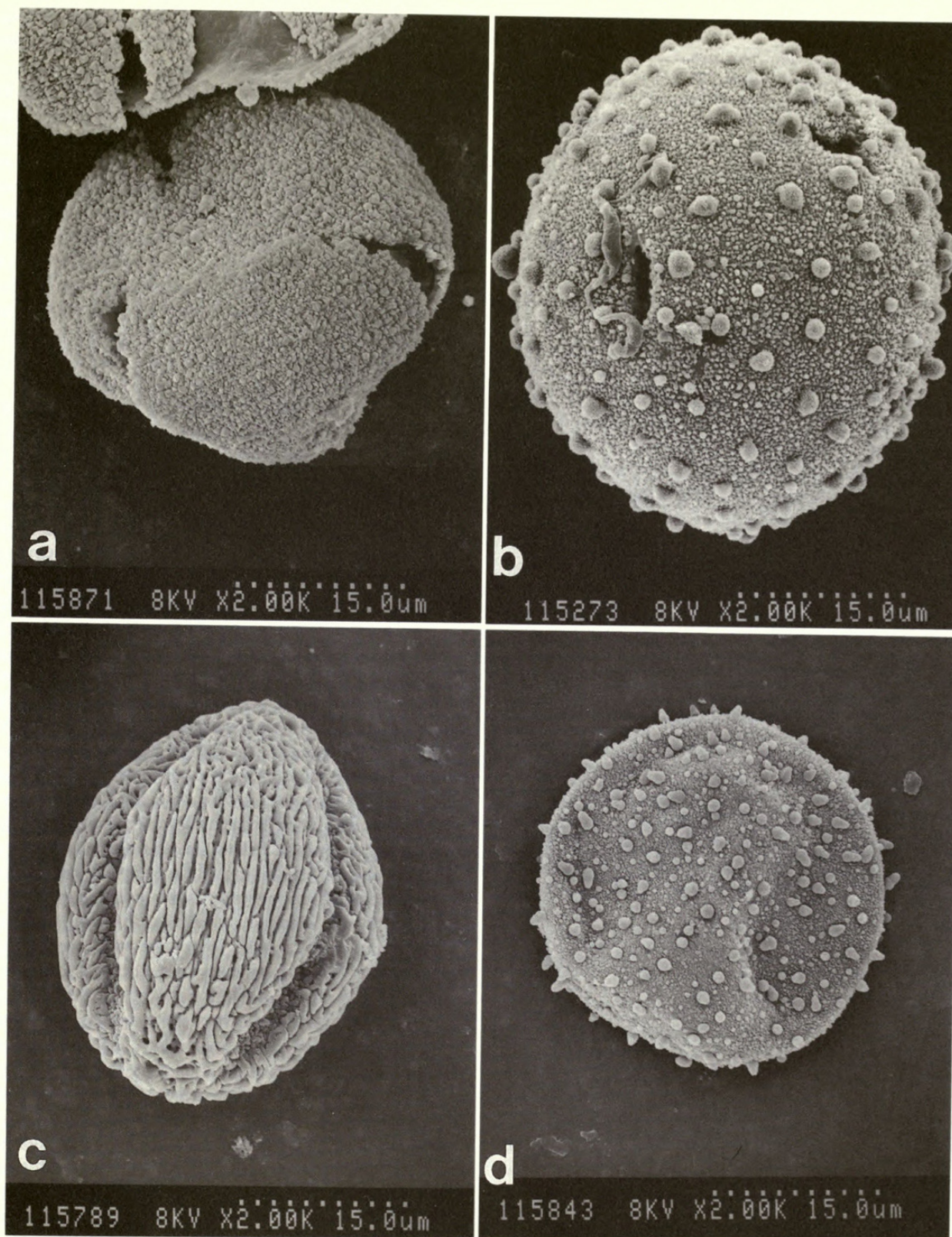


Fig. 7 Pollen morphology of the Hyoscyameae. Scale bars beneath photographs. a) *Scopolia carniolica*, b) *Anisodus luridus*, c) *Atropa belladonna*, d) *Mandragora caulescens*.

characters. Multiple functions of characters considerably complicate the issue. This is undoubtedly true for pollen apertures, where complexity of structure and a variety of alternative strategies make simplistic adaptive explanations unrealistic.

37. OCCURRENCE OF A TECTUM. The only taxa in which intectate pollen occurs, are the two species of *Mandragora*. This type of pollen is believed to be primitive for the angiosperms as a whole (Zavada, 1986). Lack of a tectum is perhaps related to the cryptaperturate condition in *Mandragora* (Diez & Ferguson, 1984).

The structure of the ectexine affects the physical properties of the wall, and this must influence the durability of the pollen and the exchange of materials across the wall.

38. SUPRATECTAL ORNAMENTATION. There is little concurrence between this character and the tree topology. This may be for two reasons. One possibility is that the ornamentation of the pollen grain may not be useful in revealing phylogenetic relationships in this group because of parallel evolution. This analysis does suggest that pollen with a reticulate pattern may have arisen independently in

Table 4 Chromosome numbers which have been recorded for the Hyoscyameae.

Species	Chromosome number	Reference
<i>Atropa belladonna</i>	2n = 72	Vasudevan, 1975
<i>Hyoscyamus muticus</i>	2n = 28	Al-Musawi, 1979
<i>Hyoscyamus niger</i>	2n = 34	Al-Musawi, 1979
<i>Hyoscyamus senecionis</i>	2n = 34	Al-Musawi, 1979
<i>Mandragora autumnalis</i>	2n = 96	Murin, 1978
	2n = 84	Hawkes, 1972
<i>Physochlaina praealta</i>	n = 41	Vasudevan, 1975
<i>Scopolia carniolica</i>	2n = 48	Vasudevan, 1975
		Hawkes, 1972

three lineages. The selection pressures which may have led to this are not known. The function of pollen sculpturing has been thought to be related to the pollen vector (Hemsley & Ferguson, 1985; Ferguson & Pearce, 1986), although in some groups of plants there is no apparent correlation between the vector and ornamentation type (Thanikaimoni, 1986). An alternative explanation is that the delimitation of the character states is not meaningful. This seems likely in view of the difficulty in deciding on character states due to uncertainty about pattern homology. For example, pollen grains which were scabrate and those with isolated granules were coded together, but perhaps these should have been coded separately. Pollen of *Anisodus* was unique in being scabrate with isolated gemmae (see Fig. 7b). This was coded separately from simply scabrate pollen. The importance of this distinction is unclear. Investigation into the development of sculptural patterns may shed some light on this area, and so help in the interpretation of changes in ornamentation type.

Chemical characters

39. PRESENCE OF 3-TIGLOYLOXYTROPANE. Prescence of this compound is a synapomorphy for the tribe, but the distribution of the character on the tree is homoplasious. Either the ability to produce this compound has arisen up to four times in the tribe, or there have been reversals in *Anisodus* and *Atropathe*.

40. PRESENCE OF BELLADONNINE. This character is a synapomorphy of *Atropa* + *Mandragora*.

41. PRESENCE OF TROPINE. The occurrence of tropine is a synapomorphy of the tribe in this analysis. However, there has been a reversal in this character in *Mandragora*.

Lu & Zhang (1986) identified a number of characters which they considered to be 'primitive' for the tribe. Among these were actinomorphic and solitary flowers, stamens inserted at the base of the corolla tube, and inaperturate pollen. They provided no explicit reasoning for their choices, and tried to place taxa on a gradient of 'advancement'. This analysis suggests that many of these features should be viewed as derived within the tribe. This draws attention to the futility of deciding *a priori* on criteria of 'advancement'. Decisions based on phylogenetic analyses rather than on intuition can be more easily justified.

The diversity of pollen types in the Hyoscyameae means that such characters cannot be used as synapomorphies of the group. Similarly, this source of data provides little information about generic relationships in the tribe. The differences in pollen morphology between some of the genera have been used in the past as evidence for their continued recognition (Zhang & Lu, 1984; Sandina & Tarasevich, 1982). Thus, the separation of *Scopolia*, *Atropathe*, and *Anisodus* is supported by the palynological evidence. However, this is insufficient evidence on its own, because similar levels of varia-

tion are found within other genera such as *Physochlaina* (Zhang & Lu, 1984). There is no justification for emphasizing one source of data at the expense of others.

Chromosome numbers have not been used in this analysis, but may perhaps be of use in future work on this group. Initial work on the cytology of these plants suggests that this may be informative. The chromosome counts which have been completed are listed in Table 4. A chromosome number of $x=12$ is widely held to be primitive for the Solanaceae, with aneuploid reduction to $x=7$ in many lineages (Goodspeed, 1954; Olmstead & Palmer, 1992). Polyploidy is common and possibly has been an important factor in the evolution of the tribe. Whether ploidy levels in the Hyoscyameae are due to allopolyploidy or to simple chromosome doubling is not known.

Biogeography

The biogeography of the Hyoscyameae is of great interest because it is the only exclusively Eurasian group in the family, the rest of which is largely Gondwanan in distribution (see Symon, 1991). Two theories have been proposed for the origin of the Hyoscyameae. Lu & Zhang (1986) drew attention to the diversity of the tribe in south-western China. Eleven of the forty species of the Hyoscyameae are found here, five of which are endemic to this area (see Fig. 1). On this basis, they concluded that this area was probably 'the birthplace of hyoscyaminous plants'. However, there is a fundamental flaw in equating the centre of origin of a group with its centre of diversity: centre of origin arguments are often flawed (Humphries & Parenti, 1986) and these dispersal hypotheses always require external, often ad hoc, causes to explain patterns. Linking distribution with the history of the earth has proved a powerful method for understanding the processes that influence the patterns we observe (Nelson & Platnick, 1981; Humphries & Parenti, 1986). An alternative scenario to the centre of origin idea of Lu & Zhang (1986) was proposed by Symon (1991). He considered the distribution of this tribe to be consistent with the ancestral group being rafted north on the Indian plate. On meeting Eurasia, the group evolved in the developing Himalayas, and subsequently spread from there.

The geological history of the area occupied by members of the Hyoscyameae is remarkably complex. Although the group is largely Eurasian in distribution at present, the main areas occupied by the genera of the Hyoscyameae were once part of the Gondwana supercontinent. Much of South East Asia, including southern China, consists of terranes rifted from the margins of eastern Gondwana some time during the Jurassic (Hallam, 1994). The southern part of Tibet in the Himalayan mountains is thought to have been the southern margin of the Tethys Sea or still moving to collide with the Laurasian supercontinent in the early to mid Jurassic, while the northern part of the area is more consistent with a non-Gondwanan, Eurasian position. The Lhasa block collided with the other rifted terranes in the late Jurassic to early Cretaceous (Dewey, 1988). Apulia, including Turkey and present day Italy, was connected to Africa during the early Cretaceous, and rotated to collide with Eurasia about 80 million years ago (Hallam, 1994). The Indian plate is thought to have broken away from the Gondwanan land mass last of all, some time near the Cretaceous/Tertiary boundary between 65 and 60 million years ago (Hallam, 1994). The Eurasian-African collision closing the seaway to the Indo-Pacific occurred in the early Miocene, and brought the Middle East into contact with the major land masses of Eurasia. Climate change during the Neogene was probably important to the evolution and distributional patterns of land plants in these areas. The Himalayas have continued to uplift long after the initial collision event between India and Asia (Hallam, 1994) and this may have been a major factor in the general cooling of climate in the Neogene. The general pattern of the break-up of the

continents over geological time is thus consistent with the Hyoscyameae being a primarily Gondwanan group which has radiated extensively in Eurasia in more recent times.

The two main clades within the tribe have broadly overlapping distributions centred in the Himalayan and South China area. Distribution patterns within the *Hyoscyamus*/*Physochlaina* clade are somewhat confused due to widespread human utilization and distribution of these species. The genus *Physochlaina* is found in much of China, reaching north into Siberia and as far west as the Himalayas. Species of *Physochlaina* are predominantly plants of montane habitats. A possible scenario is that this genus arose with adaptation to high altitudes or to colder climates. This may have occurred during the development of the Himalayas, or alternatively this group might have evolved at low altitudes during later glaciations in the Quaternary. *Hyoscyamus* shows a much wider distribution and ecological amplitude. The majority of the species occur in the Middle East and the Mediterranean region, and it has been suggested that its occurrence in North Africa and northern Europe is a result of human dispersal (Symon, 1991). All species of *Hyoscyamus* occurring in India occur in Kashmir and the north of the country, perhaps lending support to the idea of a very early origin for the group. Adaptation to more arid and mediterranean climates seems to have occurred in many of the species. This may have arisen as the genus spread into more arid areas or during a period of increased aridity. Such conditions are thought to have developed in central Asia following the uplift of the Himalayas and the Tibetan plateau (Manabe & Broccoli, 1990). However, any hypotheses of biogeography and evolutionary history of *Hyoscyamus* will need to be tested using an in-depth phylogenetic analysis of the entire genus.

Within the other clade of the Hyoscyameae, similar ecological factors seem to have been important. The genera in this clade are largely isolated ecologically, growing in different elevational ranges and often in quite different microhabitats. *Przewalskia* is a narrow endemic from the Qinghai-Xizang Plateau of western China and Tibet, growing between 3200 and 5000 m. The evolution of *Przewalskia* may have occurred during the uplift of this region (Lu & Zhang, 1986). The timing of the Himalayan orogeny is uncertain. One theory is that the main orogenic events occurred in the Oligocene, at the same time as the Himalayas developed. Alternatively, uplift may have continued well into the Pliocene and palynological evidence supports this (Ruddiman et al., 1989). The prolonged uplift of the Himalayas (Ruddiman et al., 1989) and the concomitant expansion of grassland habitats at the expense of forests will have had a profound effect on the evolution of plants found in these areas.

The widely disjunct distribution of *Scopolia* (see Fig. 1) suggests that it was once more widespread. This explanation is favoured over one of long-distance dispersal because capsular fruits and small unornamented seeds, which are found in these plants, tend to be locally dispersed (Olmstead & Palmer, 1992). Lu & Zhang (1986) suggest that this genus was widespread during the Tertiary, but became much more restricted with the advance of ice-sheets over the continent during the Quaternary.

Atropa and *Mandragora* are both very widespread genera, occurring from southern Europe across to the Himalayas and the mountains of western China. Their animal-dispersed fruits and their widespread human use may have helped to expand their ranges considerably.

The analysis presented above is a first attempt at a complete phylogenetic classification of the Hyoscyameae. The resultant cladogram shows that two lineages can be identified within the group, one clade consisting of *Hyoscyamus* + *Physochlaina* and the other containing *Przewalskia* + the rest of the genera. Within the *Przewalskia* clade the relationships of the genera are somewhat

ambiguous, although *Anisodus* + *Scopolia* and *Atropa* + *Mandragora* always group together. The position of *Atropa* and *Mandragora*, clustering well within the tribe, provides evidence for including them in the Hyoscyameae and supports Tétényi's (1987) grouping. This is further corroborated by their distribution, since they form a phytogeographically coherent group with the Hyoscyameae (Symon, 1991).

GENERIC CONSPECTUS

This conspectus is intended as an overview of the taxonomy of the genera, but may require revision as more species are studied in detail. The synonymy has been taken in large part from recent floristic or monographic treatments, which are acknowledged and cited as part of each description. Much work remains to be done with the taxonomy and phylogeny of each of these genera and we hope that this conspectus will help future workers in these groups. Distributions for each of the species are given in general terms. More complete descriptions, especially for species occurring in China, can be found in the floristic works cited.

Artificial key to the genera of the Hyoscyameae

1. Fruit a fleshy or juicy berry, white, green, yellowish orange, purplish or black 2
Fruit a dry capsule, usually circumscissile 3
2. Berry white, green, purplish or yellowish orange at maturity, fleshy, usually held beneath the leaves; acaulescent (occasionally shortly caulescent) herbs with enlarged tap roots; flowers deeply lobed, actinomorphic 5. **Mandragora**
Berry black and juicy at maturity; plant an erect perennial to 1 m tall; flowers shallowly lobed, the stamens declinate 2. **Atropa**
3. Flowers solitary or in short inflorescences of 2–3 flowers 4
Flowers in elongate or branched inflorescences, the inflorescence usually with more than 5 flowers 7
4. Acaulescent herbs with long, fleshy taproots; leaves sessile; corolla narrowly tubular 7. **Przewalskia**
Erect, often branched perennials with well-developed above-ground stems; leaves variously petiolate; corolla not narrowly tubular 5
5. Corolla slightly zygomorphic, one petal larger than the rest; calyx lobes equal in size; anthers declinate at anthesis 3. **Atropanthe**
Corolla actinomorphic; calyx lobes usually unequal in size; anthers not declinate at anthesis 6
6. Corolla campanulate-urceolate, as wide as long, greenish; calyx lobes rounded at the tips 1. **Anisodus**
Corolla flaring, longer than wide, usually purplish without; calyx lobes strongly pointed, especially the elongate one 8. **Scopolia**
7. Inflorescences markedly one-sided, usually unbranched; corolla zygomorphic; calyx lobes spiny at the tips in fruit 4. **Hyoscyamus**
Inflorescences not markedly one-sided, usually branched; corolla actinomorphic; calyx lobes not spiny at the tips in fruit 6. **Physochlaina**

1. **Anisodus** Link, in Sprengel, *Syst. veg.* **1**: 699 (1825). Type: *Anisodus luridus* Link.

Figs 3d, 4a.

Robust subshrubs or perennial herbs, at least sometimes with a massive softly woody rootstock; glabrous or pubescent. Leaves alternate, petiolate, entire or dentate; sympodia difoliate. Inflorescences of solitary flowers borne in the leaf axils. Flowers

subactinomorphic; calyx campanulate-funnelform to funnelform, the lobes unequal in length and variable in shape, usually rounded at the tips; corolla campanulate, longer than or equal in length to the calyx; stamens inserted near the base of the corolla tube; pollen hexapantoporate with slightly elongated pori with rounded ends and scabrate-gemmate ornamentation (Fig. 7b); ovary bilocular, with a disc-like nectary. Fruit a globose or ovoid capsule, with circumscissile dehiscence; fruiting calyx much enlarged, sometimes enclosing the fruit and prominently ribbed, often laterally compressed. Seeds numerous, not markedly compressed. Grasslands and woodland edges, occasionally ruderal around towns and villages; 2800–4500 m.

LIST OF SPECIES (Zhang et al. 1994). *Anisodus acutangulus* C.Y. Wu & C. Chen, China; *Anisodus carniolicoides* (C.Y. Wu & C. Chen) D'Arcy & Zhang (*Scopolia carniolicoides* C.Y. Wu & C. Chen), S. China; *Anisodus luridus* Link (*Anisodus fischerianus* Pascher, *A. luridans* Link & Otto, *A. mairei* (H. Lev.) C.Y. Wu & C. Chen, *A. stemonifolius* G. Don, *A. stramonifolius* (Wall.) G. Don, *Nicandra anomala* Link & Otto, *Physalis stramonifolia* Wall., *P. stramonifera* Wall., *Scopolia anomala* (Link & Otto) Airy Shaw, *S. lurida* (Link) Dunal, *S. mairei* H. Lev., *S. stramonifolia* (Wall.) Shrestha, *Scopolina stramonifolia* (Wall.) Kuntze), *Whitleya stramonifolia* (Wall.) Sweet, India, Bhutan, Nepal, and China; *Anisodus tanguticus* (Maxim.) Pascher (*Scopolia tangutica* Maxim.), Nepal, China.

2. *Atropa* L., *Sp. pl.* 1: 181 (1753). Type: *Atropa belladonna* L. Figs 3f, 4b.

Perennial herbs; glabrous or slightly pubescent. Leaves alternate, petiolate, simple and entire. Inflorescences of solitary flowers borne in the leaf axils. Flowers actinomorphic; calyx campanulate; corolla tubular-campanulate, twice as long as the calyx, greenish purple or yellow; stamens inserted near the base of the corolla tube, declinate; pollen trizonocolporate with long, distinct colpi with sunken margins and striate-rugulate ornamentation (Fig. 7c); ovary bilocular, with an annular receptacular disc. Fruit a black, juicy berry; fruiting calyx somewhat enlarged but not enclosing the berry. Seeds numerous, sublenticular. Woodland and other shady habitats, rocky screes; 0–1800 m. (Hawkes, 1972; Schönbeck-Temesy, 1972).

LIST OF SPECIES (Harborne & Khan, 1993; Pojarkova, 1955; Schönbeck-Temesy, 1972; Baytop, 1979). *Atropa acuminata* Royle ex Lindl., Asia (India, Pakistan, Afghanistan, Mongolia, Iran); *Atropa baetica* Willk., Spain and Morocco; *Atropa belladonna* L. (*Atropa caucasica* Kreyer, *A. komarovii* Blin. & Schal., *A. lutescens* Blin. & Schal., *A. pallidiflora* Schönb.-Tem., *A. paschdewiczii* Kreyer), widespread in Central Europe and Asia to Iran.

3. *Atropanthe* Pascher in *Öesterr. Bot. Zeitschr.* 59: 329 (1909). Type: *Atropanthe sinensis* (Hemsl.) Pascher (basionym *Scopolia sinensis* Hemsl.).

Subshrubs or perennial herbs; glabrous. Leaves alternate, petiolate, simple and entire. Inflorescences of solitary flowers borne in the leaf axils. Flowers subactinomorphic; calyx tubular-campanulate; corolla slightly zygomorphic, with one petal lobe enlarged, tubular-campanulate, twice as long as the calyx; stamens inserted near the base of the corolla tube, declinate; pollen trizonocolporate with short, distinct colpi and striate-rugulate ornamentation (Fig. 6c); ovary bilocular with an annular disc. Fruit a globose capsule, with circumscissile dehiscence; fruiting calyx inflated, abruptly inserted on the pedicel. Seeds rectangular and somewhat compressed. Forest and ditches; 1400–3000 m. (Zhang et al. 1994).

LIST OF SPECIES (Zhang et al. 1994). *Atropanthe sinensis* (Hemsl.) Pascher (*Anisodus sinensis* Hemsl.), China.

4. *Hyoscyamus* L., *Sp. pl.* 1: 179 (1753). Type: *Hyoscyamus niger* L.

Figs 3b, 4c.

Annual, biennial or perennial herbs; variously pubescent. Leaves alternate, sometimes forming a rosette, petiolate and simple, variously sinuate to dentate, rarely entire. Inflorescences of solitary flowers in the leaf axils, condensed to form usually secund, scorpioid cymes. Flowers zygomorphic, sessile or shortly pedicellate; calyx tubular-campanulate or urceolate, the lobes often spine-tipped; corolla campanulate or funnelform, the lobes unequal; stamens inserted near the base of the corolla tube; pollen trizonocolporate with long, distinct colpi and weakly striate ornamentation; ovary bilocular with an indistinct disc. Fruit a globose or ovoid capsule, with circumscissile dehiscence; fruiting calyx enlarged, enclosing the fruit, the lobes spine-tipped. Seeds reniform or discoid, strongly compressed. Fields, waysides, and hedges; 0–3600 m. (Zhang et al. 1994; Hawkes, 1972; Al-Musawi, 1979).

LIST OF SPECIES (Schönbeck-Temesy, 1972; Al-Musawi, 1979; Feinbrun-Dothan, 1978). *Hyoscyamus albus* L. (*Hyoscyamus arenarius* Dunal, *H. canariensis* Ker-Gawl., *H. clusii* G. Don, *H. major* Mill., *H. minor* Mill., *H. varians* Vis.), Mediterranean to Iraq and Egypt; *Hyoscyamus aureus* L., E. Mediterranean to NW Iraq, Sinai, and Egypt; *Hyoscyamus flaccidus* Wright, Arabia; *Hyoscyamus gallagheri* A.G. Mill. & J.A. Biagi, Oman; *Hyoscyamus grandiflorus* Franch., tropical Africa; *Hyoscyamus insanus* Stocks (*Hyoscyamus angulatus* Griff., *H. nutans* Schönb.-Tem., *H. orthocarpus* Schönb.-Tem., *H. rosularis* Schönb.-Tem., *H. tenuicaulis* Schönb.-Tem.), N. Africa and the Middle East; *Hyoscyamus leptocalyx* Stapf., W. Iran; *Hyoscyamus longipedunculatus* Townsend, Iraq; *Hyoscyamus malekianus* Parsa, Iran; *Hyoscyamus muticus* L. (*Hyoscyamus betaefolius* Lam., *H. boveanus* (Dunal) Ascher & Schweinf., *H. datora* Forsk., *H. falezlez* Coss., *Scopolia boveana* Dunal, *S. datora* (Forsk.) Dunal, *S. mutica* (L.) Dunal), N. Africa and the Middle East; *Hyoscyamus niger* L. (*Hyoscyamus agrestis* Kit., *H. auriculatus* Tenore, *H. bohemicus* F.W. Schmidt, *H. lethalis* Salisb., *H. pallidus* Waldst. & Kit., *H. persicus* Boiss. & Buhse, *H. pictus* Roth, *H. syspirensis* C. Koch, *H. verviensis* Lej.), widespread in temperate Eurasia; *Hyoscyamus pusillus* L. (*Hyoscyamus micranthus* Ledeb., *H. pungens* Griseb.), Egypt to SW and C. Asia; *Hyoscyamus reticulatus* L. (*Hyoscyamus afghanicus* Pojark., *H. arachnoideus* Pojark., *H. camerarii* Fisch. & Mey., *H. coelosyriacus* Bornmuller, *H. issa-sadiqui* Parsa, *H. kopetdaghi* Pojark., *H. kotschyanus* Pojark., *H. kurdicus* Bornmuller, *H. leucanthera* Bornm. & Gauba, *H. multicaulis* Rech. f. & Edelb., *H. pinnatifidus* Schldl., *H. pojarkovae* Schönb.-Tem., *H. purpureus* Griseb., *H. squarrosus* Griff.), Egypt to SW Asia; *Hyoscyamus senecionis* Willd. (*Hyoscyamus pinnatisectis* Boiss.), Egypt through the Middle East; *Hyoscyamus tibesticus* Maire (*Hyoscyamus cylindrocalyx* Rech. f., *H. desertorum* (Asch.) Täckh.), N. Africa in Sahara to the Arabian peninsula; *Hyoscyamus turcomanicus* Pojark., Trans-Caspian area in Iran, Uzbekistan.

5. *Mandragora* L., *Sp. pl.* 1: 180 (1753). Type: *Mandragora officinarum* L.

Figs 3e, 5c, d.

Perennial herbs from enlarged taproots; variously pubescent. Leaves alternate, forming a dense basal rosette, very short petiolate or sessile, simple, entire or dentate. Inflorescences of solitary flowers

in the leaf axils. Flowers actinomorphic; calyx flared or cup-shaped, deeply lobed, the lobes long-triangular; corolla flared or cup-shaped, deeply lobed; stamens inserted in proximal part of the corolla tube; pollen cryptaperturate with symmetrical pattern of endoaperture thinnings and gamete-baculate ornamentation (Fig. 7d); ovary bilocular, with an indistinct disc. Fruit a globose or ovoid, fleshy berry, yellow-orange, greenish or white flushed with purple, usually borne beneath the leaves; fruiting calyx slightly enlarged, not enclosing the berry. Seeds reniform, very large. Grasslands, woods, hedges and waysides, stony hillsides and scree; 0–4200 m. (Zhang et al., 1994; Hawkes, 1972).

LIST OF SPECIES (Pojarkova, 1955; Schönbeck-Temesy, 1972; Jackson & Berry, 1979; Zhang et al., 1994). *Mandragora autumnalis* Bertol. (*Mandragora femina* Gersault, *M. microcarpa* Bertol., *M. officinalis* Moris., *M. officinarum* Bertol., *M. officinarum* L. pro parte), Mediterranean; *Mandragora caulescens* C.B. Clarke (*Anisodus caulescens* (C.B. Clarke) Diels, *A. mariae* Pascher, *Mairella yunnanensis* H. Lev., *M. tibetica* Grubov.), Himalayas in India, Nepal, Bhutan, and China; *Mandragora chinghaiensis* Kuang & A.M. Lu, China, restricted to pika warrens (fide M. Gilbert); *Mandragora officinarum* L. (*Atropa acaulis* L., *Mandragora acaulis* Gaertn., *M. haussknechtii* Heldr., *M. hispanica* Vierhapper, *M. mas* Gersault, *M. neglecta* G. Don, *M. officinalis* Mill., *M. praecox* Sweet, *M. vernalis* Bertol.), widespread in Eurasia; *Mandragora turcomanica* Mizg., Turkmenistan near Caspian Sea, Russia.

6. **Physochlaina** G. Don, *Gen. Hist.* **4**: 470 (1837). Type: *Physochlaina physaloides* (L.) G. Don (basonym *Hyoscyamus physaloides* L.). Figs 3a, 4d.

Perennial herbs; glabrous or variously pubescent. Leaves alternate, petiolate, simple, entire to sinuate. Inflorescences axillary or terminal, branched several times. Flowers actinomorphic; calyx tubular-campanulate to tubular-urceolate; corolla campanulate or funnellform, purplish; stamens inserted midway up the corolla tube; pollen either pentacolporate, occasionally tetracolporate, with long, indistinct colpi and scabrate ornamentation or trizonocolporate with long, distinct colpi and striate-rugulate ornamentation (Fig. 6a, b); ovary bilocular, with a fleshy, annular disc. Fruit a globose or oblong capsule, with circumscissile dehiscence; fruiting calyx subcoriaceous and inflated, longer than the capsule. Seeds reniform, compressed. Grasslands and forest edges; 800–4500 m. (Zhang et al., 1994; Pojarkova, 1955).

LIST OF SPECIES (Zhang et al., 1994; Kuang & Lu, 1981; Schönbeck-Temesy, 1972; Pojarkova, 1955). *Physochlaina capitata* A.M. Lu, China; *Physochlaina infundibularis* Kuang, China; *Physochlaina macrocalyx* Pascher, China; *Physochlaina macrophylla* Bonati, China; *Physochlaina orientalis* G. Don (*Hyoscyamus orientalis* (G. Don) Bieb., *Physochlaina dubia* Pascher, *Scopolia orientalis* (G. Don) Dunal), Caucasus to Iran; *Physochlaina physaloides* (L.) G. Don (*Atropa physaloides* Georgi, *Hyoscyamus physaloides* L., *Physochlaena dahurica* Miers, *Physochlaina physaloides* (L.) Miers, *P. pseudophysaloides* Pascher, *Scopolia physaloides* (L.) Dunal), China, Mongolia, Russia (Siberia); *Physochlaina praealta* (Dcne.) Miers (*Belenia praealta* Dcne., *Hyoscyamus praealtus* (Dcne.) Walp., *Physochlaina grandiflora* Hook., *P. urceolata* Kuang & A.M. Lu, *Scopolia praealta* (Dcne.) Dunal), China, Nepal, Pakistan, and India (Kashmir); *Physochlaina semenowii* Regel, central Asia.

7. **Przewalskia** Maxim. in *Bull. Acad. Petersb.* **27**: 507 (1881).

Type: *Przewalskia tangutica* Maxim.

Figs 5a, b.

Perennial herbs, from an elongate fleshy taproot; pubescent, the trichomes glandular. Leaves alternate, forming a dense basal rosette, simple, entire. Inflorescences of clusters of flowers in the leaf axils. Flowers actinomorphic; calyx tubular-campanulate; corolla tubular-funnelform, greenish yellow or violet; stamens inserted in the distal part of the corolla tube; pollen trizonocolporate with long, distinct colpi and reticulate ornamentation; ovary bilocular, with an annular disc. Fruit a globose capsule, with circumscissile dehiscence; fruiting calyx much enlarged and the tube inflated with prominent reticulate veins, completely enclosing the much smaller fruit, the lobes constricted with incurved lobes. Seeds reniform. Open habitats on the Qinghai-Tibet plateau, sand dunes, road margins and areas of frost heave; 3200–5000 m. (Zhang et al., 1994).

LIST OF SPECIES (Zhang et al. 1994). *Przewalskia tangutica* Maxim. (*Mandragora shebbearei* C. Fischer, *Przewalskia robo-rowskii* Batalin, *P. shebbearei* (C. Fischer) Grubov), China.

8. **Scopolia** Jacq., *Obs. Bot.* **1**: 32 (1764). Type: *Scopolia carniolica* Jacq. Fig. 3c.

Perennial herbs; glabrous to minutely pubescent. Leaves alternate, petiolate, simple, entire. Inflorescences of solitary flowers in the leaf axils. Flowers subactinomorphic; calyx cup-shaped with irregular lobes, one usually much longer than the rest; corolla campanulate-funnelform, greenish yellow to reddish purple; stamens inserted near the base of the corolla tube; pollen trizonocolporate with long, indistinct colpi and scabrate ornamentation (Fig. 7a); ovary bilocular, with an annular disc. Fruit a globose capsule, with circumscissile dehiscence; fruiting calyx somewhat enlarged, enclosing the fruit. Seeds subreniform. Woodlands; 500–1500 m. (Lu & Zhang, 1986; Pojarkova, 1955).

LIST OF SPECIES (Sandina, 1980; Lu & Zhang, 1986). *Scopolia carniolica* Jacq. (*Hyoscyamus scopolia* L., *Scopolia atropoides* Bercht. & Presl, *S. caucasica* Kolesn., *S. hladnikiana* Fleishm., *S. parviflora* (Dunal) Nakai, *S. trichotoma* Moench, *S. tubiflora* Kreyer, *Scopolina atropoides* Schult.), Alps, Carpathian mountains, Caucasus; *Scopolia japonica* Maxim., Japan, Korea.

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APPENDIX I

Specimens examined for pollen analysis (all BM).

- Anisodus luridus* Link – Beer et al. 9410 (Nepal).
Atropa belladonna L. – Mohamed 146 (Morocco).
Atropanthe sinensis (Hemsl.) Pascher – Wilson 2594 (China, Hupeh).
Hyoscyamus muticus L. – Hildebrandt 71 (Egypt).
Hyoscyamus niger L. – Davis 52541 (Algeria).
Hyoscyamus senecionis L. – Thesiger 189 (Afghanistan).
Mandragora caulescens C.B. Clarke – Gardner 479 (Nepal); Polunin et al. 4696 (Nepal).
Physochlaina physaloides (L.) G. Don – Heward s.n., July 1847 (India).
Physochlaina praealta (Dcne.) Miers – Stachey & Winterbottom s.n. (China, Tibet).
Przewalskia tangutica Maxim. – Richardson 56 (China, Tibet).
Scopolia carniolica Jacq. – Harris Garden, University of Reading



Hoare, Alison L and Knapp, Sandra. 1997. "A phylogenetic conspectus of the tribe Hyoscyameae (Solanaceae)." *Bulletin of the Natural History Museum. Botany series* 27(1), 11–29.

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