Hybridization between *Heracleum mantegazzianum* Somm. & Lev. and *H. sphondylium* L. (Umbelliferae) in the British Isles

by

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ABSTRACT

The objective of this study of hybridization between H. mantegazzianum Somm. & Lev. and H. sphondylium L. in Britain was to provide evidence for the existence of hybrids from field observations and experimental crosses. H. sphondylium is native to the British Isles; H. mantegazzianum was introduced to Europe from the Caucasus in 1895. During the nineteenth century several species of Heracleum were cultivated in Britain, but only H. mantegazzianum is now widely naturalized along rivers and on waste ground in south-east Scotland.

In 1976 and 1977 several sites in south-east Scotland were surveyed for hybrids. Mass collections and morphometric measurements were made in the field. Principal components analysis and summary statistics were used to demonstrate the existence of an intermediate group of low fertility. A detailed comparison of plants at one site showed that for the putative hybrids the length of pollen grains and of leaf hairs on the lower epidermis of the leaf was discrete.

The H. sphondylium x H. mantegazzianum cross set 23% seed which was 73% viable. Attempts to synthesize hybrids on H. mantegazzianum failed on six of nine plants, and gave an average 1% seed set. Both species set more seed on intraspecific crosses between plants, but on selfing H. sphondylium set only 16% seed, and H. mantegazzianum proved to be fully protandric within the primary umbel. Pollen transferred from secondary to primary umbels of the

same H. mantegazzianum plant set 68% seed; there was no evidence of a self-incompatibility system, or inbreeding depression.

In the field the flowering time of both parents and hybrids overlap. A single backcross on H. sphondylium with hybrid pollen gave 14% seed set which was 77% viable, but from the survey there was no noticeable increase in variation between pure and mixed populations of either species that might indicate introgression. Putative hybrids were rare, and only found where populations of both species grew interspersed.

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CHAPTER I

Introduction

The hybrid Heracleum mantegazzianum Somm. & Lev. x H. sphondylium L. was described by McClintock as:

> "Intermediate in size of stem, leaf and umbel, in leaf outline, in the shape and length of the fruit and vittae, in the hairiness of the stem and sheath and in the smell when bruised. Hybrids have reduced or no fertility."

This entry in "Hybridization and the Flora of the British Isles" (Stace 1975) and the previous notes of McClintock (1974) provide the only published description of Heracleum hybrids in Britain. Reference to the hybrid in the field was made by Praeger (1951) for Ireland, and by Perring and Walters (1964) for two sites in Cambridgeshire. Kent (1975) lists several sites for the putative hybrid in Middlesex, where M.G. Collet and R.K. Brummitt recorded the hybrid along the banks of the River Brent near Ealing in 1962 and 1967. Specimens collected in 1969 by P.H. Davis and C.W. Muirhead from a mixed population of H. mantegazzianum and H. sphondylium growing on the Mound in Edinburgh were sent to the Russian authority Mandenova for determination, and were returned with the comment: "Il est bien probable que c'est une forme hybride". Hybrids have also been collected by Brummitt from a colony near Heathrow (Stace 1975) and by McClintock from Coldstream in south-east Scotland. Also in Scotland records have been made at Black Isle (Muirhead 1974), Caithness (McClintock 1974) and in Morayshire

(McCallum Webster 1978). Despite the number of records and the interest shown in hybrids, no detailed study of the relation between the introduced *H. mantegazzianum* and the indigenous *H. sphondylium* has yet been made.

In the family Umbelliferae, to which *Heracleum* belongs, there have been very few experimental studies of hybridization. Bell (1955) examined five putative hybrids of the *Sanicula crassicaulis* complex in North America. He dismissed two as minor variants of their diploid species, made two species in their own right, and maintained only one, the octoploid *Sanicula crassicaulis* var *tripartita* as hybrid in origin. Extensive attempts to produce a hybrid between cultivated plants failed. Owens (1974) also failed to induce interspecific crosses in *Daucus*, or intergeneric crosses between *Daucus*, *Astrodaucus* and *Orlaya*. However, sub-specific crosses within the *Daucus carota* complex, and between *D. gingidium*, *D. capillifolium* and the closely related cultivated carrot have been made (McCollum 1975, 1977).

Although interspecific hybrids have not been artificially produced in the Umbelliferae, there are a number of field records for intermediate types that are thought to be of hybrid origin. Of the 43 genera recorded from this family in Britain, only 15 are represented by more than one species. Of these, 7, or about 50%, do have records for natural hybrids, though not all from Britain. *Apium* x *moorei* (Syme) Druce (*Apium inundatum* (L.) Reichb. f. x *A. nodiflorum* (L.) Lag. both 2n=22) is the most widely recognised (Clapham et al. 1962). It flowers less freely than its parents and appears to be completely sterile. It occurs with both parents in shallow water on damp mud, is very local in eastern central England, but frequent and widespread in Ireland. Diploid *Apium* hybrids have also been noted in New Zealand, between *A. australe* Thovars and *A. filiforme* (A. Rich) Hook.f., both 2n=22, at South Brighton, Canterbury (Beuzenberg & Hair 1963). Other hybrids between species which occur in Britain have been recorded from abroad. *Eryngium campestre* L. x *E. maritimum* L. (2n=14 and 2n=16) have been recorded from France (Stace 1975). Constance (1978) has observed a spontaneous hybrid between *Eryngium pandanifolium* C. & S. from Uruguay and *E. alternatum* C. & R. from Mexico grown in cultivation (all hexaploid n=24 and fertile), and Reese (1969) described in detail a hybrid between *E. campestre* L. (2n=14) and *E. planum* L. (2n=16). *Pimpinella saxifraga* L. (2n=18,36), Burnet Saxifrage which grows in dry grassy places, and *P. major* (L.) Huds. (2n=18) the Greater Burnet Saxifrage of grassy places, margins of woods and hedgebanks, are recorded as the hybrid *P.* x *intermedia* Figert from Austria, Czechoslovakia and Germany (Stace 1975). Angelica, *Angelica archangelica* L. (2n=22), formerly cultivated and now naturalized on river banks and in waste places, and the common indigeneous species of damp meadows, woods and fens, *A. sylvestris* L. (2n=22) are recorded as hybridizing in Roumania (Stace 1975). There is one intergeneric hybrid recorded from France;

x *A. loretii* (Rouy & Camus) P. Fourn. between the widespread *Anthriscus sylvestris* (L.) Hoffm. (2n=16) and *Chaerophyllum aureum* L. (2n=22) which is introduced in Britain and naturalized in meadows in a few places in Scotland (Stace 1975). *Hydrocotyle*, with only one species in Britain, has a recorded hybrid from South America. Rodriguez (1960) described, using a hybrid index, *Hydrocotyle mexicana* Cham. and Schlecht. x *H. pusilla* A. Rich, which occurs where the range of the two parent species overlaps in an intermediate habitat in the central highlands of Costa Rica.

Heywood (1978) notes "A curious feature of the Umbelliferae is the apparent rarity of interspecific hybridization". An interspecific hybrid, however, may be easily recognised only if the distinction between the two parents is concise. In *Heracleum* distinction between species is often confused by variation within each taxa. *Heracleum* is a reputably difficult genus of more or less indistinct morphological species some of which have been narrowly defined, such as the species described by Mandenova (1950) as endemic to the Caucasus, and others, in particular *H. sphondylium* L. described by Brummitt (1968) in "Flora Europaea", given a broad basis. The many variants of *H. sphondylium* L. which had at one time specific rank, were included by Brummitt as subspecies of *H. sphondylium* L. *H. alpinum* L. and *H. pyrenaicum* Lam. are now *H. sphondylium* subsp. *alpinum* (L.) Bonnier & Layens, and subsp. *pyrenaicum* (Lam.) Bonnier & Layens, and show considerable morphological intergradation. An interspecific hybrid would therefore only be noticeable in the field between individuals of very different taxa such as the giant *H. mantegazzianum* and smaller *H. sphondylium*. The paucity of recorded hybrids at least in *Heracleum* is therefore not surprising.

The existence of intermediate plants on its own does not constitute proof of hybridization. A combination of field studies and experimental work on floral biology is required to provide sufficient evidence to make this decision (Stace 1975). As few Umbelliferae genera have been investigated in this way the limits of biological species groups in the family are not well known and putative *Heracleum* hybrids could, as in Bell's (1955) study of *Sanicula*, be resolved as variants.

The objective of this investigation of hybridization between *H. sphondylium* and *H. mantegazzianum* was therefore to describe in more detail the extent of hybridization in the field and the variation that might be expected in natural populations of *H. mantegazzianum* and *H. sphondylium*, and then to provide evidence for the existence of hybrids by controlled pollinations of plants in cultivation and by germination of hybrid seed. The morphological studies are described in Chapter III, the controlled crosses and floral biology in Chapter IV and seed germination in Chapter V. The practical work was limited to populations of *H. mantegazzianum* and *H. sphondylium* growing in south-east Scotland, and at a few selected sites in north-east Scotland. All *Heracleum* sites in Scotland mentioned in the text are listed with grid references in Appendix II.

H. sphondylium is native to the British Isles (Clapham et al. 1962) and is commonly found by roadsides, woods, hedgerows and in grassy places (Fig.2.2). In fact it is widely distributed through most of the north-temperate regions, but shows its greatest variation in Europe (Brummitt 1971). Nine geographical variants are recognized as subspecies in Europe (Brummitt 1968) of which subsp. *sphondylium* is the lowland type distributed mainly in North West Europe and extending to Scandinavia, East Central Europe and the Mediterranean region. The variation within the group is being analysed by Weimarck (1978). *H. mantegazzianum*, however, is not an indigenous species in Britain. It was introduced as a garden plant and has subsequently become naturalized. Other species of giant *Heracleum* have been grown in Europe; the "Flora of the British Isles" mentions *H. persicum* (Clapham et al. 1962) and Brummitt (1968) in "Flora Europaea" refers to *H. lehmannianum* Bge. and *H. laciniatum* auct. Scand., non Hornem., and concludes that "The taxonomy and nomenclature of the naturalized plants from South West Asia requires further investigation". Chapter II is an attempt to show which species of large *Heracleum* may be found in Britain by comparing historical accounts of Giant Hogweed in Britain and Europe with the taxonomic literature on *Heracleum*.

Finally, Chapter VI discusses the significance of the conclusions on hybridization between *H. mantegazzianum* and *H. sphondylium* for the genus *Heracleum.*

CHAPTER II

An Historical Review of Giant Hogweed

The many different names which have been used to describe the Giant Hogweed in Britain may be found by searching the local floras, old gardening journals, the publications of the Royal Horticultural Society and cuttings files and seed lists of botanical gardens. The first section of this chapter (2.1) describes the results of a short search of this nature made in 1975 at the Royal Botanic Gardens at Kew and Edinburgh. In Section 2.2 these historical details are used to help explain discrepancies in the taxonomic literature between Giant Hogweed which grows in South West Asia and the naturalized populations in Europe today. More evidence for the spread of H. mantegazzianum was obtained by tracing some of the large established riverside colonies of Giant Hogweed in Britain to their original point of introduction in cultivation. This information described in Section 2.3 was needed for the study of variation in Chapter III. Conclusions are listed in Section 2.4.

2.1 Local floras, horticultural journals and seed lists

Local floras

The earliest record in the local British floras refers to H. persicum collected in 1828 in Cambridgeshire (Perring & Walters 1964). This specimen is kept at the

Cambridge Herbarium and was renamed H. mantegazzianum by Perring & Walters for the Cambridge Flora. A more substantial description is given in the Manchester Flora (Grindon 1859):

> "... and that prodigeous plant, the siberian Cow Parsnip ... the largest discovered plant of the family, the stem rising 8 or 10 feet high and umbels measuring nearly 1 yd across. It is now becoming common in gardens and has been grown in public parks. Two species are distinguished, the H. giganteum, a biennial, with umbels somewhat convex, and H. sibiricum, which is perennial and has umbels flat-topped".

and under H. giganteum Fisch. in the Bristol Flora (White 1912):

> "An ornamental alien which has been known for 50 years or more about the Great Western railway at Keynsham and Saltford but is now disappearing".

Other "ornamental aliens" have been mentioned as growing in Britain before the 1900's about Silloth dock entrance, Cumberland in 1868 (Hodgson 1899), near Ellacombe, Gloucestershire in 1883 (Riddelsdell et al. 1948), near Moffat, Dumfriesshire in 1893 (Scott Elliott 1896) and as a roadside escape in Kent (Hanbury et al. 1899) and Surrey (Salmon 1931). Many of these references do not describe the plant clearly, but specimens have been collected for plants at Ashford Dale, Derbyshire in 1869 (Clapham 1969) and in Warwickshire in 1888 (Birmingham Natural History Society 1965).

From these early records until about the 1950's the various names used for Giant Hogweed in the local floras are:

H. persicum (Perring & Walters 1964)
H. giganteum (Grindon 1859, Scott-Elliott 1896)
H. sibiricum (White 1912)
H. hirsutum (Hodgson 1899)
H. villosum Fisch. (Hanbury et al. 1899, Salmon 1931, Keble-Martin 1939, Druce 1926, 1927)
H. giganteum Fisch. (Druce 1927, Wilson 1938)
H. giganteum Hort. non Fisch. (Green 1933)
H. mantegazzianum S. & L. (Horwood et al. 1933, Druce 1927, Grose 1957, Lees 1941)

There is no doubt, therefore, that a large species of Heracleum was widely naturalized in Britain before 1900, and around Manchester and Bristol as early as 1850. Although a number of names were used before the mid 1930's, thereafter the alien from the Caucasus naturalized in the British Isles was referred to in local British floras as H. mantegazzianum, (Wade 1970, Bowen 1968, Petch 1968, Kent & Lousely 1953, May 1967, Allen 1969, Graham et al. 1972, Savage et al. 1963, Newton 1971).

Literature on cultivated plants

As well as the brief references in early floras, more detailed descriptions and often illustrations can be found in the early literature on cultivated plants. Loudon's Hortus Britannicus published in 1839 lists 29 species of Heracleum among the "plants indigenous, cultivated in or introduced to Britain". These include all the species mentioned in the local floras with the exception of H. hirsutum, H. persicum and H. mantegazzianum. The year of introduction and native country of H. giganteum is given as 1820, Siberia, and of H. villosum as 1826, Siberia. *H. sibiricum* is mentioned as a small Siberian species with green flowers. Although *H. persicum* is not included (the type was described later in 1841) three other related species (see Fig.2.1) are named: *H. caucasicum* Steven, 1818, Caucasus; *H. pubescens*, 1823, Caucasus; and *H. laciniatum*, 1819, Siberia.

From the often effusive articles in the gardening magazines of the nineteenth and early twentieth centuries it is obvious that several different types of Giant Hogweed were in cultivation at that time, but that the most popular was the plant variously called *H. giganteum* or *H. villosum*, said to have been introduced from the Caucasus or Siberia in 1820. An illustration of this plant may be found in *Gardeners Chronicle* 14.2.1925. p.113; *The Field* 19.4.1919; *Country Life* 17.9.1921; and *The Garden* 10.1.1880, p.33. Seeds of *H. giganteum* are listed for sale in the 1895 catalogue of James Backhouse & Sons, York, and plants of *H. giganteum* in the 1900 catalogue of T. Ware Ltd., Hale Farm Nurseries, Feltham. One article, in *The Garden* 15.10.1904, p.259, describes and clearly illustrates a plant called *H. lehmannianum* from Turkestan having 2-3 or 4 pinnate leaves and ovate segments. Another, in *The Garden* 14.4.1900, p.269, gives an interesting account of *H. persicum* found growing on waste land in the West End of London and originally thought to come from India. A partial umbel collected by Druce in Dagenham, Essex, now in the Royal Botanic Garden Herbarium, Edinburgh, has been determined *H. persicum* by Mandenova.

In The Garden 2.3.1872, p.326, there is a reference to H. wilhelmsii. Other earlier names represented by Loudon; H. caucasicum, H. pubescens and H. laciniatum, are not mentioned.

After the cultivation of H. mantegazzianum by Correvon in 1895 (see Section 2.2) this name also appears in the gardening journals. The first article was published in 1901 (The Garden 2.3.1901, p.148) and pictures may be found in The Garden 2.3.1901; Gardeners Chronicle 24.8.1966, p.17; and Gardening Illustrated 13.10.1928. It was said that:

> "The older Heracleum giganteum was a grand thing, but H. mantegazzianum surpasses it, not only in actual size, but in ornamental detail, for the edges of the leaves are more sharply and handsomely toothed, and the whole plant is of a livelier and more glossy green".
>
> (Gardening Illustrated 13.10.1928)

Despite its attractive appearance H. mantegazzianum did not completely replace H. villosum which was mentioned as late as 1937 (Gardeners Chronicle 30.1.1937) and pictured in Gardeners Chronicle 14.2.1925, p.113. A specimen of H. villosum Fish. collected at Mildenhall, Suffolk, 1916, now in the Edinburgh Herbarium has been determined H. mantegazzianum by Mandenova.

Even though it is quite likely that the names for these closely related species were confused by amateur gardeners, it still appears from the literature that at least two types of Giant Hogweed were introduced, an earlier H. villosum or H. giganteum type, and a later

H. mantegazzianum type. Amongst other names, H. lehmannianum and H. persicum were obviously different plants in cultivation but not widely distributed. These four names are described in the Royal Horticultural Society's Dictionary of Gardening (1956):

> "H. villosum: Perennial up to 12ft.h. l. sinnuately pinnatifid, long pointed, sharply toothed, woolly beneath. fl. white or whiteish in many-rayed umbels. fr. ciliate, woolly on back. Caucasus. Syn. H. giganteum.
>
> H. persicum: Biennial up to 12ft.h. l. pinnate or 2 pinnate, large glabrous above, shortly hairy beneath; lobes in 3 or 4 pairs, lower stalked, all cut into lanceolate, long-pointed segs. fl. white in large hairy umbels. Persia c. 1888.
>
> H. lehmannianum: Stout biennial; 3 to 7ft.h. l. glabrous above, hairy beneath; lower l. pinnatisect; segs in 2 or 3 pairs, lobes shortly ovate, acute, coarsely toothed. fl. many, dull pink; umbels large. Turkestan.
>
> H. mantegazzianum: Cartwheel flower. Gigantic perennial up to 12ft high. Stem coppery red. l. 3ft. long forming a tuft 12ft. across: deeply cut lobes, oblong, notched. fl. white, very numerous (up to about 10,000), in umbels 4 to 4½ft. across. Caucasus 1893."

The gardening journals also contain references to these plants as troublesome weeds. Of H. giganteum it was said:

> "This plant, however, should only be introduced to cultivated grounds or even woods with due caution as it spreads so rapidly and is so vigorous in growth".
>
> (The Garden 10.6.1876, p.540)

Similar warnings appear in The Garden 5.7.1894, p.13; Country Life 17.9.1921; and Gardeners Chronicle 30.1.1937. If the earlier names, H. giganteum and H. villosum really refer to a different type of *Heracleum* from *H. mantegazzianum*, then these species were naturalised in Britain, as recorded in the early floras, before the introduction of *H. mantegazzianum* in 1895, although Clapham et al. (1962) mention only *H. mantegazzianum* and *H. persicum* as possible garden escapes in the British Isles today.

Seed Lists at Kew

The earliest references to *Heracleum* in the Record Books at Kew read as follows:

Year	Seeds received
1814	Sir Joseph Banks has presented to the Royal Gardens the following seeds sent to him from Vienna by Prof. Jacquard: H. tauricum Jacq.
1817	Received from the Royal Botanic Gardens at Berlin p. favour of Mr. Otto: 1944 H. speciosum
1817	"Seeds for the Royal Gardens at Kew from the Gorenki Botanic Gardens presented to the Protector of Botany the Right Hon. Sir Joseph Banks with the particular suit to grant his kind benevolance intercession and protection to the Gorenki Gardens by Dr. G.D. Fisher: 2151 Heracleum Giganteum. Caucasus
1818	The following Russian seeds received per favour of Mr. Martin Call: 1916 Heracleum giganteum Caucasus

1819 Seeds from Vienna Baron Jacquin:
The following collection of seeds received from Baron Jacquin from Vienna through the hands of the Right Hon. Sir Joseph Banks:

853 Heracleum giganteum
854 Heracleum laciniatum

1819 The following collection of seeds received from Prof. Fischer at Moscow through the hands of Dr. Lyall:

1538 H. giganteum villosum
H. giganteum caucasicum
H. tauricum

1824 From Professor Steven of Sympheropole in the Crimea. Collected on the Altaic and Caucasian Mntns. Rec'd favor of A.P. Hove Esq.:

1785 H. Gummiferum
1786 H. pubescens
1787 H. pyrenaicum Steven
1758 H. ligusticifolium

1820 Dr. Alexan. Creighton "collected in the Russian territories and May from the borders of the Caspian".:

1350 H. Tauricum

1820 Prof. Steven Caucasian seeds

1997 H. Tauricum

1820 Seeds from Paris M. Thouin

3262 H. tauricum Horn.

1821 Per favour of A.P. Hove Esq. from Vienna:

1816 H. tauricum

1823 A.P. Hove Esq.:

1284 H. tauricum

1824 The following from M. Fischer of Goettingen:

2013 H. villosum

1824 The following Russian seeds per favour of Dr. Fischer of St. Petersburg

3883 H. tauricum

Records prior to the 1800's are barely legible and are not systematically arranged according to latin names. Subsequent to the 1824 catalogue, record entries are more frequent, and sometimes seed lists are not given in full, presumably because the number of seed packages arriving was too great. At about the 1840's entries in the outwards and inwards books are made for exchanges with the larger botanic gardens in Britain.

The seed lists at the Royal Botanic Garden , Edinburgh (seeds available) list the following names:

Year	
1888	*H. giganteum*
1890	*H. villosum* Fisch.
1891	*H. giganteum* Fisch.
1892	*H. giganteum* var. *purpurea* Hort.
1894	*H. giganteum* var. *H. Leichtlini* Hort. *H. villosum* Fisch.

Plants of Giant Hogweed were therefore being sent to Britain from at least the early 1800's onwards. Moreover, by the 1840's, these seeds were in circulation between botanic gardens and probably through commercial firms as well. If seed was sent to Sir Joseph Banks at Kew from the botanical explorers in Russia it was probably sent, or passed on, either to George Loddiges or one of the other large horticultural firms interested in importing new foreign plants. The year 1820 mentioned in the gardening journals and Loudon's Hortus Britannicus for the introduction of Giant Hogweeds to cultivation in Britain is therefore more or less correct.

The seed lists also show quite clearly that there was not just one introduction to this country of two or three species from a single gathering in Russia, but a number of acquisitions of seeds from diverse sources which were referred to by different names. In 1817 when Dr. Fischer sent seeds of *H. giganteum* to Britain there was no widely circulated comprehensive account of the genus *Heracleum*. A few early names had been published by different authors: *H. giganteum* Fisch. (1812), *H. speciosum* Weinmann (1810), *H. caucasicum* Steven (1812) and *H. laciniatum* Hornem (1813), which were later revised by Thellung (1924) (Section 2.2). Bieberstein's "Flora Taurico-Caucasica" (1819) brought together five species:

H. sibiricum L.
H. asperum M.B.
H. pubescens M.B.
H. pyrenaicum M.B.
H. ligusticifolium M.B.

It was not until 1844-1849 that Ledebour's "Flora Rossica II" was published with 23 species including:

H. trachyloma Fisch. et Meyer
H. brevivittatum Ledeb.
H. Wilhelmsii Fisch. et Lallem
H. pubescens M.B.
H. caucasicum Steven
H. villosum Fisch. (syn. *H. speciosum* Rud.,
H. giganteum Hornem,
H. laciniatum Hornem,
H. pyrenaicum M.B.,
H. panaces Pall.,
H. subvillosum Steven)

H. persicum Desf. from the northern Iranian province of Azerbaijan was first described in Ind. Sem. Horti. Petrop. 7:50 (1841) by F.E.L. Fischer, C.A. Meyer and J.L.E. Ave-Lallemant. H. lehmannianum Bge. collected by Alexander Lehmann on a journey from 1839-1842 through Turkestan was described by A.L. Bunge in 1851.

Of these earlier names, H. villosum Fisch. was retained in Boisser's Flora Orientalis (1872) (Section 2.2) while H. giganteum remained in common use for cultivated plants in Europe as a natural synonym for the Giant Hogweed.

2.2 Taxonomic Literature

The Description of H. mantegazzianum

The description of H. mantegazzianum was the last and most comprehensive account to be published in Europe of an introduced Heracleum from Russia. The account appeared in 1895 (Sommier & Levier, Nuovo Gior. Bot.Ital. nov. ser., 2:79 (1895)) and is reproduced below:

> "Giganteum viride, caule crasso profunde sulcato basi glabrato superno breviter papilloso-pubescente asperulo; foliis amplissimis supra glabris subtus sub lente valida minutissime puberulis pinnatisectis, inferioribus 2-3 jugis, segmentis elongato-lanceolatis acutis vel acuminatis in lobos triangulari-lanceolatos acutos vel plus minus longe acuminatos crenato et mucronulato-denatos pinnatifidis, segmentis binis inferioribus a superioribus remotis sat longe petiolutatis lamina in petiolulo unilateraliter decurrente, segmentis

coeteris confluentibus, foliis superioribus in vagina ampla sessilibus; umbellis permagnis ultra 50 radiis non involucratis, lateralibus centralem superantibus, radiis papilloso-pubescentibus sulcatis, involucelli phyllis circa 8 lineari-subulatis, umbellulis sub50radiis; calyce quinquedentato, petalis radiantibus profunde bipartitis cum lacinula inflexa, antheris dilute olivaceis, ovario dense papilloso-hirsuto; fructu elliptico basi non vel vix attenuato apice non vel vix emarginato, dorso papilloso-pubescente, margine levi vel parce et brevissime aculeolato, vittis valde clavitis, dorsalibus ad $\frac{3}{4}$ pericarpii perductis, duabus centralibus longioribus, commissuralibus binis pericarpium medium subaequantibus vel brevioribus; stylis reflexis stylopodio conico basi crenato multo longioribus. Tota planta, praesertim fructus, anisum redolens, inter herbas «macroflorae» statura et umbellarum amplitudine praeeminens.

Legimus in alveo fluminis Seken Abchasiae, socia Tommasinta purpurascente, 900 m., 25 Aug. fr. tantum, et ad specimen Genevae in horto Correvoniano eductum descripsimus. - Ad ripam dextram fluminis Kliutsch, 1700-1800 m., 26 Aug., fr. (planta in loco natali $2\frac{1}{2}$ m. alta).

Caulis ultra 2 m. altus; folii inferioris petiolus in specimino culto, nobis a cl. Correvon misso, 30 cm. longus brunneo-maculatus, lamina 65 cm. longa 50 lata, laciniae ultra 50 cm. longae, earum decurrentia unilateralis 3-5 cm. longa; pelioluli maculati 9 cm. longi; rachis nuda inter segmenta inferiora et superiora 18 cm. longa; rami inflorescentiae ultra 50 cm. longi; umbellae centralis radii 13-20 cm. longi; umbellularum radii longiores $2\frac{1}{2}$ cm., fructus 12-14 mm. longus 6-8 latus.

Inter Heraclea Florae Orientalis affinitatem majorem praebet cum H. Persico Desf. cujus odorem anisoidem gravem exhalat, sed a quo differt statura procerrima, foliis subtus glabratis aliter sectis, segmentis minus profunde incisis praeter par infimum approximatis basi late confluentibus, inferioribus in petiolulum unilateraliter late decurrentibus, petiolis non hepatici coloris, ovario brevius lanato, fructu maturo elliptico rarius parum obovato margine levi vix aculeolato. - Ab H. pubescente M.B. longius distat glabritio, statura gigantea, segmentis foliorum lanceolatis longe acuminatis.

> Amicissimo Paulo Mantegazza, qui de florum venustate venuste scripsit, speciem miram et myriantham dicamus."

Paolo Mantegazza was an Italian naturalist who used to accompany M. Sommier and M. Levier on their travels to Europe and Asia (Thellung 1926). In 1892 M. Levier, a Swiss doctor, and M. Sommier, a French amateur botanist, explored the central Caucasus, and brought back seeds of H. mantegazzianum. M. Levier wrote of the journey in "A travers le Caucase, notes et impressions d'un botaniste" (1894) which includes a photograph of "Herbes géantes du Caucase (Vallée de la Nakra)"; a large unnamed Umbellifer with lanceolate leaves fills the foreground. The collection taken to Europe was made in the adjacent valley to the Nakra, the Seken, Abkhasia, where Levier (1894) explains: (p.207)

> "Malgré l'éxubérante végétation qui orne les rives du Séken, nos récoltes sont de la dernière pauvreté. Sur de longs espaces nous n'apercevons pas une seule fleur, et celles que nous notons sans les cueillir, épilobes, laitues, lapsanes, géranium de Robert, sont presque toutes aussi répandues en Europe que dans le Caucase. Une seule fait exception: c'est une ombellifère géante, affectionnant le voisinage de l'eau, et facilement reconnaissable à la forme de ses fruits, qui rappellent ceux de son unique congénère d'Europe (Tommasinia purpurascens Lall.)."

The seeds were sown in 1893 by Henry Correvon in the Jardin d'Acclimation at Geneva (The Garden 2.3.1901) and flowered in 1895. Seeds were then distributed "to the trade and to amateurs". An addendum to the type description states:

> "Osserv. L'esemplare coltivato a Ginevra fu scelto fra i più piccoli. Abbiamo calcolato che non portava meno di 10,000 flori. Il sig. H. Correvon ci scrive che gli steli avevano in media 2 metri di altezza, un diametro di 10 centimetri alla base, che la lamina delle foglie oltrepassava 1 metro di lunghezza, e che l'infiorescenza raggiungeva dimensioni ancora più colossali di quelle dell' *Heracleum* che si coltiva a Ginevra sotto il nome di *H. giganteum* (=*H. villosum* Fisch.). I frutti della nostra specie somigliano del tutto a quelli del *H. villosum*, il quale però ne è perfettamente distinto per le sue foglie non pennatosette e per la sua villosità."

M. Sommier and Levier were therefore of the opinion that their *H. mantegazzianum* was a new species which differed from the giant *Heracleum* already in cultivation in Europe.

Thellung's description of *Heracleum* introduced to Europe

Thellung (1926) has made the only attempt to sort out the nomenclature of the *Heracleum* introduced to Europe. His valuable account of the history of a number of species was published in Hegi's "Flora von Mitteleuropa" in 1926. He reduced many names to synonomy, these are listed in Fig. 2.1, and compared with related taxa in the earlier Flora of Boissier (1872),"Flora of the Caucasus"(Grossheim 1967)"Flora of the USSR"(Komarov 1951) and "Flora Europaea"(Brummitt 1968). Of the 12 introduced species described by Thellung (1926) seven do not concern Giant Hogweed. *H. platytaenium* is a distinctive plant with woolly ternate leaves and wide

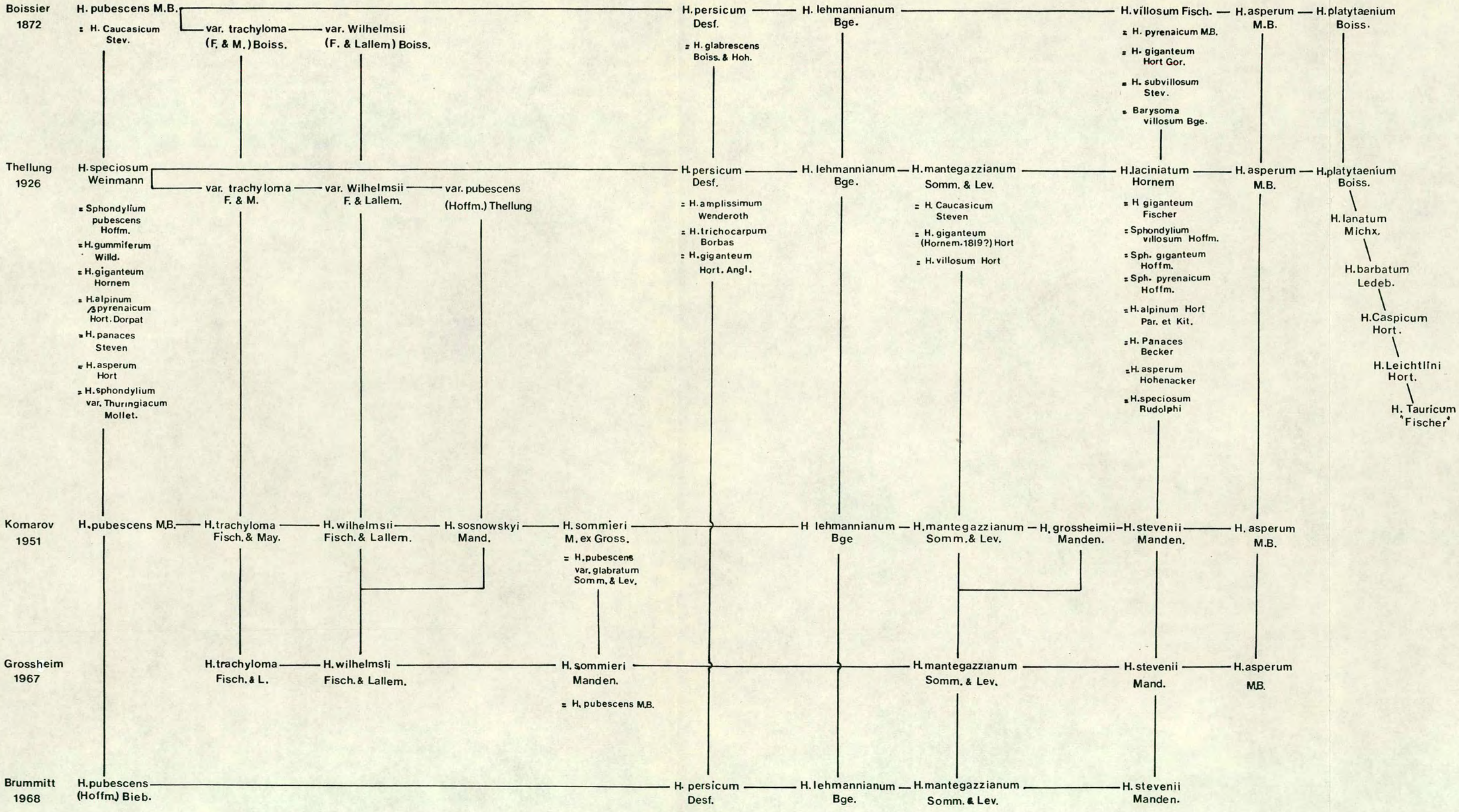


Fig. 2.1 Thellung's treatment of Heracleum species introduced to Europe

vittae endemic to Anatolia (Davis 1972), H. lanatum is from North America and similar to H. sphondylium (Brummitt 1971), H. barbatum is also similar to H. sphondylium (Komarov 1951) as is H. caspicum (Thellung 1926). H. asperum, H. leichtlini and H. tauricum are rare or insufficiently known species. This leaves:

H. laciniatum
H. lehmannianum
H. mantegazzianum
H. persicum
H. speciosum

which, with synonyms, account for the species mentioned in the history of British Giant Hogweed (Section 2.1).

Thellung was aware of the problem of which plants were introduced to Britain and of the confusion over the names H. villosum: "H. mantegazzianum das in den Gärten auch unter der falschen Bezeichnung H. villosum geht" and H. giganteum: "Namentlich unter H. giganteum werden verschiedene Arten verstanden". In his opinion the picture of H. giganteum in Gardener's Chronicle 1923 most closely resembles H. persicum Desf. He was also critical of the original descriptions of these names and pointed out that even those species described by him were not distinct. He says of the H. speciosum and H. persicum group that: "Die Formenkreise der beiden

Arten (?) H. persicum and H. speciosum (pubescens) sind uberhaupt sehr unsicher begrenzt und umschrieben und durften vielleicht später verschmolzen werden mussen". One exception is, however, made clear, that H. lehmannianum was distinct from the other species, with a perennial nature and green leaves kept later in the year, although it lagged behind the other species in height and beauty.

Most important of all, Thellung, who, working in 1924, must have been very familiar with natural and cultivated plants of Giant Hogweed in Europe at that time, was of the opinion that H. mantegazzianum had been introduced to Europe before Sommier and Levier brought the plant to Correvon in Geneva. He mentions an example of H. giganteum Fisch. collected by J.J. Vetter in 1884 in Orbe as being the same as H. mantegazzianum. If this is true, then the earlier names must have been used indiscriminately, and it will be extremely difficult to resolve the exact year of introduction of individual species of giant Heracleum to Europe or Britain.

Mandenova and Grossheim's treatment of Caucasian Heracleum

Since Thellung's work in 1926 in Europe, two relevant studies have been published in Russia. The first was Mandenova's monograph on the genus Heracleum in the Caucasus, (Mandenova 1950). The system of classification which she drew up was used in Komarov's "Flora of the USSR" and Section Pubescentia is shown in Fig. 2.1. The second was the recent treatment of Heracleum in"Flora of the Caucasus "(Grossheim 1967), also shown in Fig. 2.1, in which H. grossheimii I. Mand. was joined with H. mantegazzianum, H. wilhelmsii Fisch. et Lallem with H. sosnowskyi I. Manden., and H. pubescens M.B. with H. sommieri Manden. Furthermore, according to the distribution maps in Grossheim (1967) (Fig. 2.2) and Kulieva (1974) the distribution of H. mantegazzianum, H. wilhelmsii and H. trachyloma Fisch. et Lall. in the Caucasus is continuous. These plants form a series from tall glabrous H. mantegazzianum, with lanceolate leaves, growing in the deep valleys of the Caucasus, through finely pubescent H. wilhelmsii, fruit with "sparse long hairs on dorsal surface", to a hairier plant H. trachyloma, with fruit "dorsal surface densely covered with long scarious hairs and leaves with ovate-oblong acuminate lobules". H. sommieri, of limited distribution in the Caucasus which overlaps with H. mantegazzianum (Fig. 2.2), is a smaller plant, said by Mandenova (1950) to be derived from a single specimen only. This was collected at high altitude by Sommier and Levier, and thus may correspond to H. mantegazzianum rather than H. pubescens.

The number of taxa of Giant Hogweed in their natural habitat may be summarized as follows:

(1) The Mantegazzianum - Wilhelmsii - Trachyloma type
(2) A smaller species, H. pubescens, from the Caucasus
(3) H. persicum which grows in Northern Iran
(4) H. lehmannianum from Turkestan

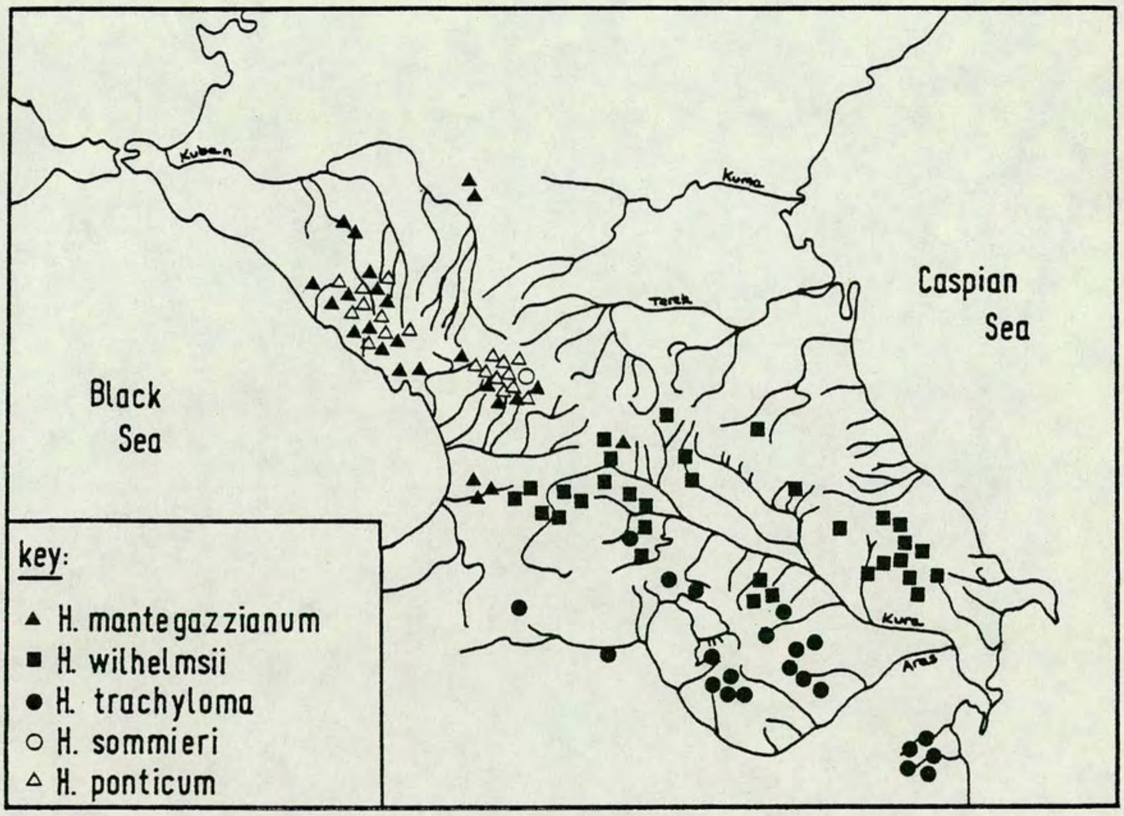


Fig. 2.2 The distribution of H. mantegazzianum, H. wilhelmsii, H. trachyloma, H. sommieri and H. ponticum in the Caucasus

H. lehmannianum Bge according to the type description "differt insuper a H. persico et Wilhelmsii fructibus exacte oblongis, vel lato-ellipticis, nec basi attenuatis obovatis, parce pilosis, aculeolis nec in dorso, nec in margine ullis, vittisque angustioribus longioribus", although Temirbekov (1977) says that H. lehmannianum fruit has circular, obovate, oval, egg-shaped and oblongate oval forms, covered sparsely or thickly with monocellular filaments. It may be related to H. laciniatum in Scandinavia (H. Myras, pers. comm.) (Fig. 2.3). H. persicum Desf. ex Fischer, Meyer et Lallem. may still be in cultivation in Europe (McClintock 1968) (see Fig. 2.4). Of H. pubescens M.B., Boissier (1872) considered both H. wilhelmsii Fisch. et Lallem. (= sosnowskyi) and H. trachyloma Fisch. et Meyer varieties, but Mandenova (1950) states that H. sosnowskyi "has often been collected and described as H. pubescens which sensu stricto is a much smaller plant".

Within the H. mantegazzianum group Mandenova (1950) described six species of sect. Pubescentia from the Caucasus (Fig. 2.1). Of these, H. trachyloma is easily distinguished by its pubescence and H. sommieri by its small stature. The key characteristics of the remaining four are listed below:

Fig. 2.3 The leaf of the type specimen of H. lehmannianum Bge. (a) compared with a leaf of H. laciniatum from Leiden (b), (photograph by Dr. Fischer)

Fig. 2.4 *Heracleum* growing in cultivation at Platt, Kent. (Photograph by permission of D. McClintock)

	Elliptical Fruit	Wide Leaf	Rays & leaf downy	Short petal	Style length (x length of stylopodium)		
					2-3	3	3-4
H. grossheimii							+
H. mantegazzianum	+					+	
H. wilhelmsii			+		+		
H. sosnowskyi		+		+	+		

The two species H. sosnowskyi and H. wilhelmsii, later combined by Grossheim (1967), differ from H. mantegazzianum in that they have shorter styles, and either wide leaves and short petals, or very downy leaves and rays. H. grossheimii has exceptionally long styles.

A difference in style length has been noted in south-east Scotland. Short styles are found on plants at Coldstream and Biel Water. In the present study this has not been found to be associated with increased pubescence. In fact, plants with styles 3 to 4 x length of the stylopodium found at Riddell, Hopetoun and Currie have both more pubescent rays and lanceolate leaves. There are no plants resembling the description of H. wilhelmsii in Scotland. Plants from Biel Water resemble the description of H. sosnowskyi in that they have short styles, short petals and broad leaf segments, but do not have the appropriate fruit shape. Their fruits resemble those of H. mantegazzianum at Kale Water. This population is mentioned in Section 2.3 as being of different origin from the rest of H. mantegazzianum in south-east

Scotland, but was not included in this study and will not be discussed further here.

The taxonomic problem which has yet to be resolved is how these recognised Russian species relate to those names in the history of Giant Hogweed in Europe: H. giganteum, H. villosum, and from Scandinavia, H. laciniatum. This confusion in nomenclature will be difficult to disentangle as older herbarium specimens of Heracleum are often in poor condition and are not representative samples from one plant. In the absence of any definitive treatment of introduced Heracleum species in Europe the conclusions in section 2.4 have been adopted for this study.

2.3 The present distribution of Giant Hogweed in the British Isles

The distribution map of H. mantegazzianum (Perring & Walters 1976) is shown in Fig. 2.5. Site types for Giant Hogweed are typically river banks, roadsides or waste ground in urban areas. In Scotland the largest populations are found naturalized along the banks of the River Tweed and its tributaries in south-east Scotland, on waste ground and beside rivers in the Edinburgh area, and along the rivers of the north-east coast, in the Moray Nairn region. On the west coast some colonies are found in Glasgow by the River Cart, and further south near Ayr, and beside the River Nith, Dumfriesshire. Records for

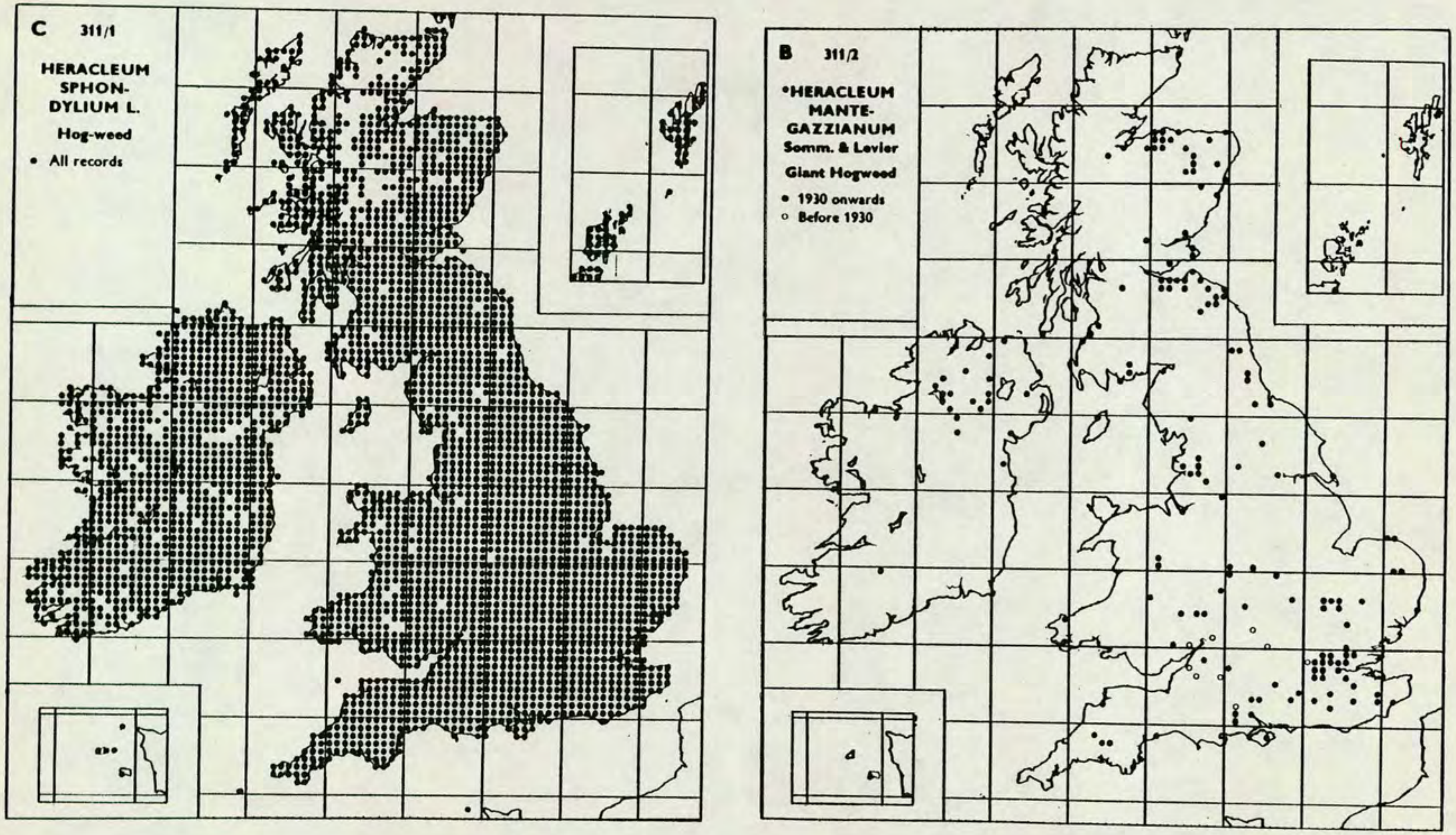


Fig. 2.5 The distribution of Heracleum in the British Isles
(a) H. sphondylium (b) H. mantegazzianum

the islands, Mull and Shetland, refer to groups of a few plants only.

The several discrete areas of hogweed colonies in the north-east and south-east of Scotland, and the south-east of England, suggest that H. mantegazzianum was introduced and subsequently became naturalized in a number of different localities. Clegg & Grace (1974) showed that Heracleum seeds could float for several days in water and discovered a population of H. mantegazzianum near Dalkeith which had become established after a flood. For the present study a careful survey was therefore made of south-east Scotland to try to locate places where H. mantegazzianum was originally introduced. A history of these naturalized plants could help to explain variation between distant populations of Giant Hogweed or by date of origin suggest affinities with other Heracleum species. The centres of spread which have been traced for Scotland are listed below.

The origins of some naturalized populations of Giant Hogweed in south-east and north-east Scotland

A list of contributors to the survey is given in Appendix I, and grid references for survey sites in Appendix II.

TWEED RIVER SYSTEM

Riddell Estate, by Melrose. A few plants were introduced to the wild garden from Blair House, near

Dalry, Ayrshire, about 1910 (Sprot, pers. comm.). A small burn flows through the garden and across open parkland to the Ale Water, tributary of the River Teviot which flows into the River Tweed at Kelso. After 1948, when the large house on the estate burnt down, the garden became overgrown, and Giant Hogweed is now naturalized along the banks of Ale Water, the River Teviot and the River Tweed. Large colonies of Hogweed have been growing on the Monteviot Estates beside the River Teviot since the 1940s.

Abbey St. Bathans. A few plants have been growing in the saw mill yard for at least 30 years (Gillon, pers. comm.). Small groups of Giant Hogweed are found alongside the Whiteadder Water, with large populations at Edrom near the confluence with the River Tweed.

Giant Hogweed also grows beside the River Till which joins the River Tweed just above Norham. These plants may come from Till House, or have spread along the roadside from Coldstream. Giant Hogweed in the lower Tweed basin is very "weedy" and can be found spreading along many side roads away from the river system. A few plants grow opposite the sewage works on waste land at Selkirk (Smith, pers. comm.). The origin of these is unknown, as is the origin of the colony reputed to grow beside St. Boswells West Burn in 1926 (Robb, pers. comm.). Hogweed grows in the backwaters of Mertoun House below

St. Boswells, but is not cultivated there. Populations on the River Tweed are therefore of mixed origin, but on the River Teviot and Ale Water, and on Whiteadder Water, they are descended from one introduction only.

BIEL WATER, EAST LOTHIAN

Giant Hogweed was introduced into the Whittingehame Estate, and now grows beside Biel Water to Dunbar. There is a record in the herbarium of Miss I.M. Balfour (1871-1873) to *H. giganteum* on the Whittingehame Estate. (Beattie, pers. comm.).

RIVER ESK, DALKEITH

Plants along the River North Esk which flows through the Dalkeith Estate to the sea at Musselburgh are now spreading from a ruined cottage garden by Park Burn next to Dobbie's Nurseries outside Dalkeith. The origin of this colony is unknown. There is a specimen in the Edinburgh Herbarium of a Giant Hogweed labelled *H. villosum* Linn. = *H. giganteum* Hort, and subsequently *H. mantegazzianum*, collected from the riverside at Musselburgh on 25.6.1936. A plant from Cockenzie shore collected in 1963 by Miss Muirhead seen by Mandenova "Ab H. mantegazziano foliorum forma et petalio subradiantibus differt".

EDINBURGH

Laverockdale House, Colinton. H. mantegazzianum was introduced as a 'jungle plant' to the water garden, formed around an artificial pool in Bonally Burn, probably soon after the house was built in 1910. From there it has spread to waste land beside the Braid Burn which flows through the city of Edinburgh, and probably colonized the derelict site at Fairmilehead. A specimen from here has been determined as H. mantegazzianum by Mandenova.

Kinleith Mill, Currie. Between 1910 and 1920, the mill owner, Mrs. Patrick Bruce, set up a water garden around the cottage at the mill (Brownlie, pers. comm.). Both house and garden are now abandoned, and H. mantegazzianum is naturalized on waste ground beside the mill. Seeds from this population may at one time have been distributed by the Water of Leith to Hogweed sites downstream. This may be the origin of the Giant Hogweed plants in Warriston Cemetary.

Hopetoun House, Queensferry. A large population of Giant Hogweed is naturalized in the wood at Hopetoun. The date of introduction of these plants to the garden where they still grow is not known. This population is local and has not spread outside the grounds.

Southfield House, Longniddry. Another local population, date of introduction unknown, which has spread down a small burn towards the sea.

NORTH EAST SCOTLAND

McCallum Webster (1978) notes the following introductions in north-east Scotland:

Glenferness House. Introduced c. 1890 by Ronald Earl of Leven to an ornamental pool at Glenferness House from whence it has escaped to the banks of the River Findhorn. Probably also distributed at the same time to Kellas House, where it is naturalized beside the River Lossie, Culloden House, Abriachan, and Tomatin House, 1920.

2.4 Conclusions

(1) At least four types of Giant Hogweed were introduced to Britain in cultivation:

1. *H. mantegazzianum* Somm. et Lev.
2. *H. villosum* Fisch. (*H. giganteum* Hornem)
3. *H. persicum* Desf. ex Fisher, Meyer et Lallem
4. *H. lehmannianum* Bge.

Both 1 and 2 have been recorded as naturalized in Britain, 3 is recorded as naturalized in Germany and 4 may be naturalized in Scandinavia.

(2) Although H. lehmannianum cannot be confused with H. mantegazzianum, other names may have been used interchangeably.

(3) The earliest dates for introduction are:

1820 for H. giganteum

1895 for H. mantegazzianum

(4) Populations used for this study of hybridization in Heracleum originated in the 1900's and are considered to be typical H. mantegazzianum, as are the populations at Fairmilehead, Hopetoun, Currie and in Moray-Nairn.

(5) Other populations in south-east Scotland could be of older origin, especially along the River Esk and Biel Burn, and could therefore be H. giganteum or H. villosum, but are not included in this work.

(6) Both of these introduced Heracleum are considered sufficiently closely related to both H. mantegazzianum and H. sosnowskyi for comparison with these plants growing in Russia.

CHAPTER III

Observations in the Field

3.1 Introduction

Objectives

As there were few specimens of hybrids available for study and only a limited number of references in the literature, the first objective of the field survey was to find hybrids and describe their morphology in more detail. Hybrids had previously been described as intermediate between the two parent species (McClintock in Stace 1975). However, as *H. sphondylium* is extremely variable and the characteristics of *H. mantegazzianum* growing in this country are not well known, it was difficult to be certain of identifying an intermediate type in the field. It was therefore decided that, as a second objective, some assessment of the variation in parent populations should be made.

Consequently in the summer of 1976 a number of sites were visited in order to examine pure and mixed populations of *Heracleum* species. The results of the preliminary survey have been published (Grace & Stewart 1978, appended). Only the observations at Riddell, Roslin, Coldstream and Kale Water are described here. In 1977 a second assessment of hybridization was made in detail at Kale Water only. At each site a number of morphological characters were measured for selected plants and when possible mass collections or voucher specimens were retained. These are held by the Department of Forestry and Natural Resources, University of Edinburgh.

Choice of Characters

Mandenova (1950) has reviewed the choice of characters in the classification of the genus *Heracleum* and concluded that there are no clear morphological differences between species in any one character. Mandenova (1950) therefore used a number of "slight but sufficiently stable" features such as the segmentation of the leaf or the colour of the flowers to distinguish species, with emphasis on the shape of the disc and characters of its surface. In the key for Komarov's "Flora USSR" (1951), Mandenova separates *H. sphondylium* (Sect. *Euheracleum*) from *H. mantegazzianum* (Sect. *Pubescentia*) on the following dichotomy:

> " 5. Dorsal canals proximally narrow, with abrupt large sacciform expansion, commisural canals broad, clavate, leaves ternate or pinnate compound
>
> Section 2 *Pubescentia*
>
> Dorsal canals broad or narrow, gradually slightly expanded at lower end; leaves simple, ternate or pinnate-compound"

In the key for "Flora Europaea" (Brummitt 1968) these two species are distinguished in the same way.

In the field differences between H. mantegazzianum and H. sphondylium have already been mentioned by McClintock (1973), are listed in Table 3.1, and the two species illustrated in Fig.3.1. H. sphondylium is smaller than H. mantegazzianum, with slender, more acute branching, smaller, more pubescent leaves and has ripe fruit with slender or only slightly expanded vittae. H. mantegazzianum is monocarpic with a single flowering stem bearing more lateral umbels than the perennial H. sphondylium which produces several flowering stems from the same root system in successive years.

For the morphometric study, characters were chosen, according to the definition of Marsden-Jones & Turrill (1954) as "any describable structure or behaviour or range of such that can be used to define or differentiate taxa". Thus the classical attributes of leaf shape, pubescence, fruit and flower structure were combined with the differences between parent taxa listed in Table 3.1. In addition an attempt was made to describe the form of the plants, which, because of the large size of Heracleum species, had previously been neglected in taxonomic studies (Thellung 1926).

A chemical analysis of roots collected from Kale Water in 1977 is being undertaken by Dr. F. Fischer of the University of Leiden, (Fischer et al. 1978b). A study of the chemical constituents of H. mantegazzianum by Jossang et al. (1969) led to the isolation of several furannocoumarins and long chain esters and alcohols from different parts of the plant and from the oils of the fruit.

Table 3.1. Differences between H. sphondylium and H. mantegazzianum (table reproduced from McClintock 1973)

Character	H. sphondylium	H. mantegazzianum
DURATION	Perennial	Monocarpic
ODOUR	Faint or none	Pungent
HEIGHT	2 ft. - 7 ft.	8 ft. - 18 ft.
HABIT	Branches at a fairly acute angle	Branches at a very much broader angle, often almost horizontal
UMBEL SIZE	1 in. - 4 in.	6 in. - 18 in.
LEAVES	Pinnate with about 5 separate segments	Pinnate with 3 segments only the bottom one clearly separate
LEAF SIZE	to c. 15 in.	to 4 ft.
LEAF DIVISIONS	comparatively round edges	pointed edged
LEAF SHEATHS	Hispid - shaggy	More or less glabrous
STEMS	Green, hairy	Red blotched, more glabrous
STEM DIAMETER	to $\frac{3}{4}$ in.	to 5 in.
RAYS OF UMBEL	15 - 45	50 - 150
OUTER PETAL SIZE	to 10 mm	to 12 mm
FLOWERING TIME	July - Sept.	June to July
FRUIT SIZE	7 - 10 mm	to 12 mm
VITTAE	to 0.4 mm not or hardly swollen below	0.5 mm to 1.0 mm swollen below

Fig. 3.1 (a) H. sphondylium at Roslin and
(b) H. mantegazzianum at Riddell

Furannocoumarins are especially interesting compounds as they may invest Heracleum species with allelopathic properties (Zhamba 1972, Junttila 1975) and resistance against fungal attack (Fischer et al. 1978a). The natural occurrence and physiological activity of coumarins has been reviewed by Soine (1964). Furannocoumarins have also been used for systematic studies. Molho et al. (1971) found that chemical analysis of furannocoumarins of H. mantegazzianum from Kew, Brunoy and Samoëns all gave different results, and Fischer et al. (1978b) that Scottish H. mantegazzianum had slightly fewer coumarins than the same species from Leiden, but the same as H. sphondylium. A comprehensive review of well identified constituents of Heracleum and other species in the tribe Peucedaneae has been compiled by Carbonnier, et al. (1978).

Material collected from Kale Water in 1977 has been investigated by Dr. G. Weimarck of the University of Lund in a related cytological study. The results are discussed in Chapter VI. The published chromosome number for both species is 2n=22 (Maude 1939, 1940, Hakansson 1953, Bell & Constance 1966, Gagnidze & Chkheidze 1974, 1975).

Choice of Numerical Method

It has been suggested (Stace 1975) that simple hybrid indices or pictorialized scatter diagrams are adequate for describing hybrid plants from morphological observations. At the beginning of the study it was thought that scatter diagrams would not be suitable for a description of hybrids in Heracleum as no two or three characters were expected to distinguish clearly between the two parent taxa and an intermediate type. Hybrid indices, although able to combine information from a larger number of characters, are time consuming to construct and were never intended to outlive numerical methods (Anderson 1953). Therefore it was decided to use multivariate techniques which can rapidly summarize statistics for several variables.

Several types of multivariate analysis have been used for Numerical Taxonomy. This approach to classification is described by Sokal and Sneath (1963), Blackith and Reyment (1971), Jardin and Sibson (1971), Sneath and Sokal (1973), and Clifford and Stephenson (1975), and reviewed by Moss and Hendrickson (1973). Not all of these methods are suitable for a study of hybrids. The detection of intermediate groups requires a technique which does not involve an a priori definition of groups. For this reason, methods such as discriminant analysis and canonical variates analysis are not suitable (Dancik 1975).

Principal component analysis provides a method which can be used to reveal structure in a population where taxa are difficult to identify because it ordinates all plants in a multidimensional space on the basis of a comparison of all characters for each plant. There is no comparing means or clustering into groups before the analysis. The basic data matrix X of character values for p plants and n characters:

$$X = \begin{bmatrix} x_{11} \cdots\cdots x_{1p} \\ \vdots \\ x_{n1} \cdots\cdots x_{np} \end{bmatrix}$$

is transformed to a symmetric matrix A of correlation coefficients between characters:

$$A = \begin{bmatrix} a_{11} \cdots\cdots a_{1n} \\ \vdots \\ a_{n1} \cdots\cdots a_{nn} \end{bmatrix}$$

The principal components F_{1-n} are calculated so that the first principal component accounts for as much of the variability between variates as possible. Mathematically this is achieved by finding the eigenvectors B of the correlation matrix A (Jeffers 1964):

$$B = \begin{array}{c} \underline{F_1 \cdots\cdots F_n} \\ \begin{bmatrix} b_{11} \cdots\cdots b_{1n} \\ \vdots \\ b_{n1} \cdots\cdots b_{nn} \end{bmatrix} \end{array}$$

These values relate the n characters to the components F_{1-n} (Orloci 1966). The coordinates of each plant on each component are found by linear combinations of the coefficients and the original variables:

$$\begin{aligned} F_{j1} &= b_{11}x_{1j} + b_{21}x_{2j} \,\cdots\cdots\, b_{n1}x_{nj} \\ &\vdots \\ F_{jn} &= b_{1n}x_{1j} + b_{2n}x_{2j} \,\cdots\cdots\, b_{nn}x_{nj} \end{aligned}$$

Thus the loadings on the principal components are:

Plant No.	1st component	....	nth component
1	F_{11}		F_{1n}
$\vdots$	$\vdots$		$\vdots$
p	F_{p1}		F_{pn}

The method of principal components has been used by Schilling and Heiser (1976) for a numerical taxonomic study of *Solanum* including hybrids (although Edmonds (1978) maintains that non-hierarchical methods of cluster analysis give equally satisfactory results for *Solanum*), by Whiffin (1977) for *Correa aemula* and *C. reflexa* (Rutaceae) hybrids, and by Hall et al. (1976) for the *Bulbostylis* complex in Nigeria.

A further advantage of component analysis is that those characters which are most important for the calculation of component loadings (F_{ij}) can be identified. Generally it is the character with the highest eigenvector (b_{ij}) for each component (F_{1-n}) (Isebrands and Crow 1975). Characters thus selected may not have any biological significance as they relate to numerical attributes of the basic data set, but they may also point out relationships between plants which are not normally apparent from observation alone.

A risk associated with a numerical method is the possibility of excluding essential features of the plants at the first stage of the analysis. A large number of characters are required for Numerical Taxonomy, at least 60 are recommended by Sneath and Sokal (1973), and are all *a priori* considered of equal weight in creating natural taxa. A discussion of the aims of Numerical Taxonomy may be read in Johnson (1970) and Ruse (1973), and the practical disadvantages are outlined by Moss and Hendrickson (1973). While collecting large amounts of data small but significant features can be overlooked. This has brought criticism to a numerical study of the Ericales (Burtt et al. 1970). Numerical methods are perhaps best used as an adjunct to classical techniques to help clarify problems in classification, as in the recent study by Rahn (1974) on *Plantago* sect. *Virginica*. Therefore it was decided to combine principal component analysis of the morphometric data with summary statistics and a record of observations of hybrids in the field.

There is one numerical method that might have analysed the *Heracleum* data in a more satisfactory manner than the use of principal component analysis and descriptive statistics. It is the correspondence analysis described by Benzecri (1973) which has been applied to palynological studies in France (Hideux 1977). This type of analysis may be used on both quantitative and qualitative data or both, and therefore resembles the extension to principal component analysis proposed by Hill (Hill & Smith 1976). The larger number of characters which can thereby be included in the numerical analysis make this technique suitable for multidisciplinary studies. A recent survey of the genus Bupleurum (Cauwet et al. 1978) provides an example of this technique using 135 populations and 128 characters: 25 morphological, 23 anatomical fruit characters and 78 chemical characters.

3.2 Materials and methods

Sites

A number of sites were surveyed in 1976 for pure and mixed populations of Heracleum species, and plants of intermediate stature. Site grid references are listed in Appendix II with a map of their location in south-east Scotland. At Riddell H. mantegazzianum grows in a woodland clearing (Fig.3.1) beside a burn which disperses seed downstream to sites such as Kale Water and Coldstream, where H. mantegazzianum has become established with H. sphondylium on low lying land beside the River Teviot and the River Tweed. At Roslin, H. sphondylium grows in scrub woodland beside the River North Esk (Fig.3.1) about 5 km from the nearest known populations of H. mantegazzianum at Park Burn, by Dalkeith.

In 1977 a detailed study was made of the mixed population at Kale Water which was thought to include plants of hybrid origin. A plan of the site is shown in Fig.3.2. The site is a partial island of low lying land,

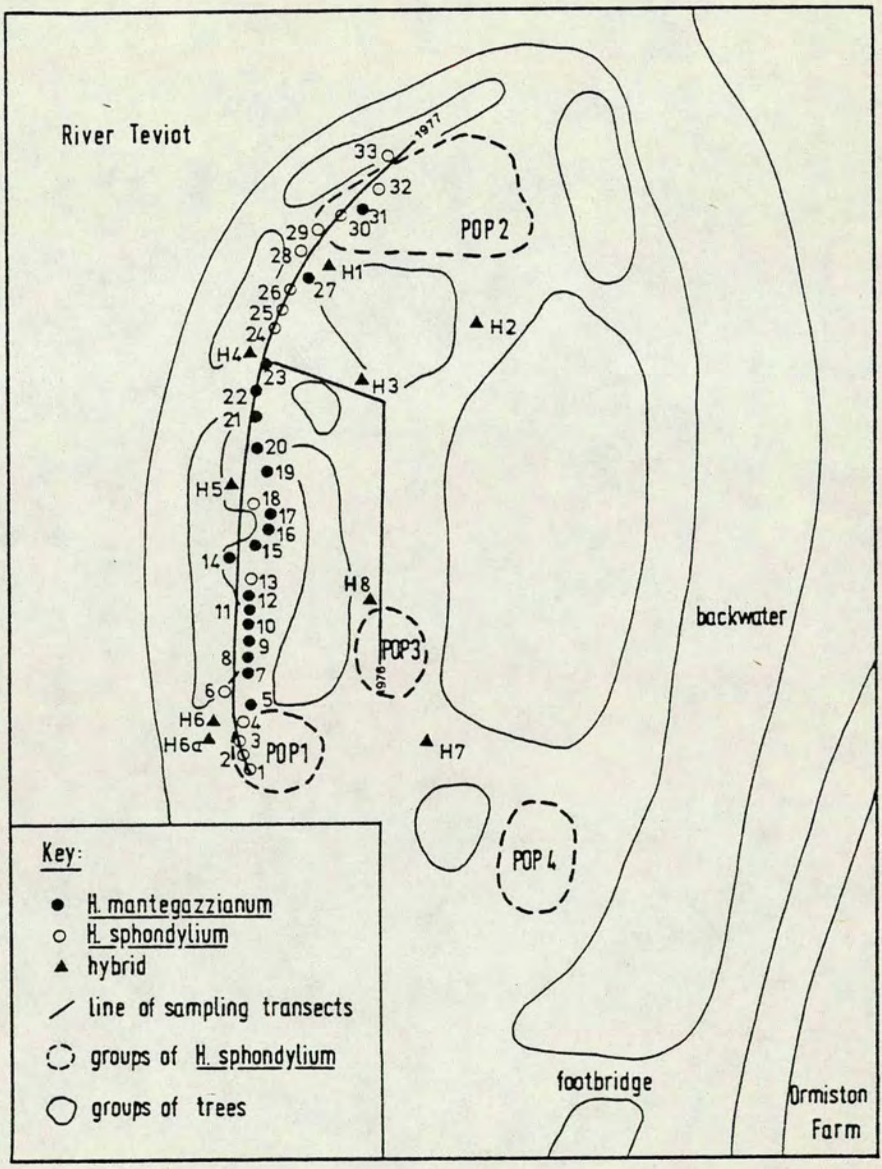


Fig. 3.2 Plan of Kale Water site showing relative position of numbered plants in 1977 survey

liable to flooding, formed by a backwater of the River Teviot just below its confluence with Kale Water. A footbridge connecting the site to the road provides access to fishermen, occasionally cattle cross the backwater to graze, but otherwise the site is undisturbed. A large population of H. mantegazzianum has become established on the island forming dense stands between the few groups of trees and leaving only isolated clearings where populations of H. sphondylium grow (Fig. 3.3). Plants of H. sphondylium are found amongst stands of H. mantegazzianum and individual Giant Hogweed plants are isolated in the large population of H. sphondylium at the head of the island (POP2 in Fig.3.2). Hybrid plants are scattered throughout the site; six were found in 1976, nine in 1977 and eight in 1978.

Sampling

In 1976 all sites were visited once for morphological measurements and a number of plants selected for study along a transect at 1 m intervals. Sample size and date for each site are listed below:

Site	Number of plants in sample	Date of sampling
Coldstream	31	1st 4th, 7th July 1976
Riddell	20	25th July 1976
Roslin	16	16th July 1976
Kale Water	31	11th July 1976

Fig. 3.3 *H. sphondylium* population 3 at Kale Water towards line of 1976 transect through *H. mantegazzianum*

Later in the year ripe fruits were collected from five plants of each type at Riddell, Roslin and Kale Water.

In May 1977, 42 plants at Kale Water were labelled for intensive study. A line transect was drawn from POP1 to POP2 (Fig.3.2), and individual plants labelled at 3 m intervals until a total of 18 H. mantegazzianum and 15 H. sphondylium plants had been selected. Nine putative hybrid plants were found on the site; these too were labelled. The relative position of numbered plants is shown in Fig. 3.2. Plants were marked by tying labels loosely with wire around the base of the flowering stem. Numbered plants were sampled repeatedly through June and July for the following collections:

(1) Flowers in bud from primary and secondary umbels for chromosome analysis by Weimarck

(2) Material preserved in FAA (Formalin, glacial acetic acid, 70% alcohol 5:5:90)

a. Flowers from primary and secondary umbels
b. 2 cm lengths of petiole from a cauline leaf
c. Sections of leaf lamina - 2 cm^2 cut from the midpoint of proximal segment of outer edge of cauline leaf

(3) Herbarium samples:

a. Central, middle and outer umbellets from primary and secondary umbels
b. Cauline leaf from midpoint of stem
c. Bud sheath - inflated petiole of peduncle subtending leaf (see Fig.3.4)

(4) Chemical samples

Plants were sampled for root material to be sent to Fischer

The main stem and umbels were left standing until fruit were ripe in August, when the terminal and one secondary umbel were harvested complete, and 10 cm lengths collected from the midpoint of the stem and dried.

Morphological measurements

The following measurements were made on plants from Kale Water 1977. A list of those characters measured at other sites is given in Appendix III. Terminology for the inflorescence (reviewed by Jury 1978) is described in Fig. 3.4, leaf characters are illustrated in Fig. 3.5 and fruit morphology in Fig. 3.6.

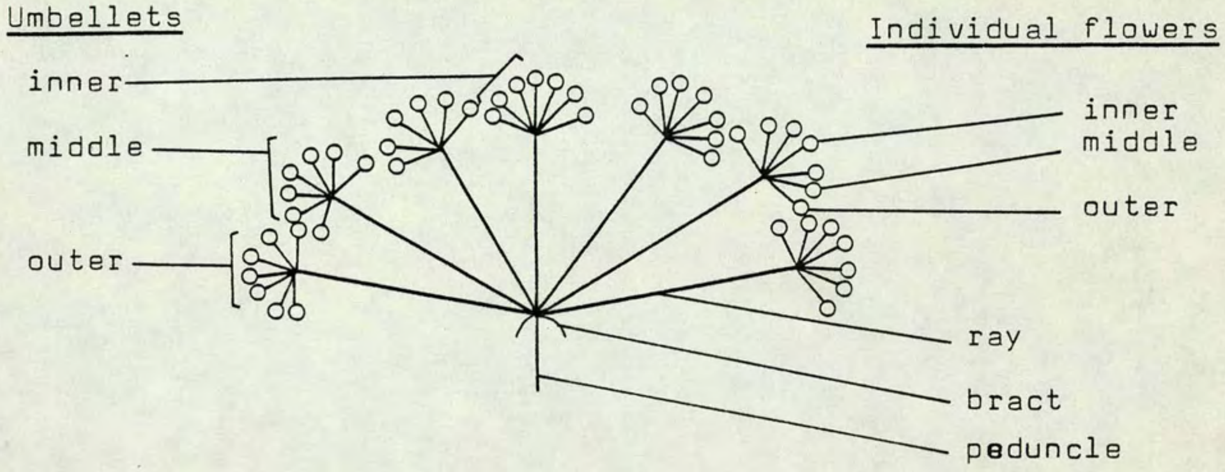
Morphological characters measured in the field

1. HEIGHT - Height of plant from ground level to top of terminal umbel
2. TSD - Diameter of peduncle directly below rays of terminal umbel
3. BSD - Diameter of stem at ground level
4. 1^{o} DIAM - Diameter of terminal umbel
5. NO. RAYS - Number of rays in terminal umbel
6. ANGLE 1^{o} & 2^{o} - Angle between peduncle of terminal umbel and first branch of secondary umbel
7. NO. of 2^{o} - Number of secondary umbels in first whorl below terminal umbel
8. NO. BRACTS - Number of bracts

Fig. 3.4 Terminology for the inflorescence

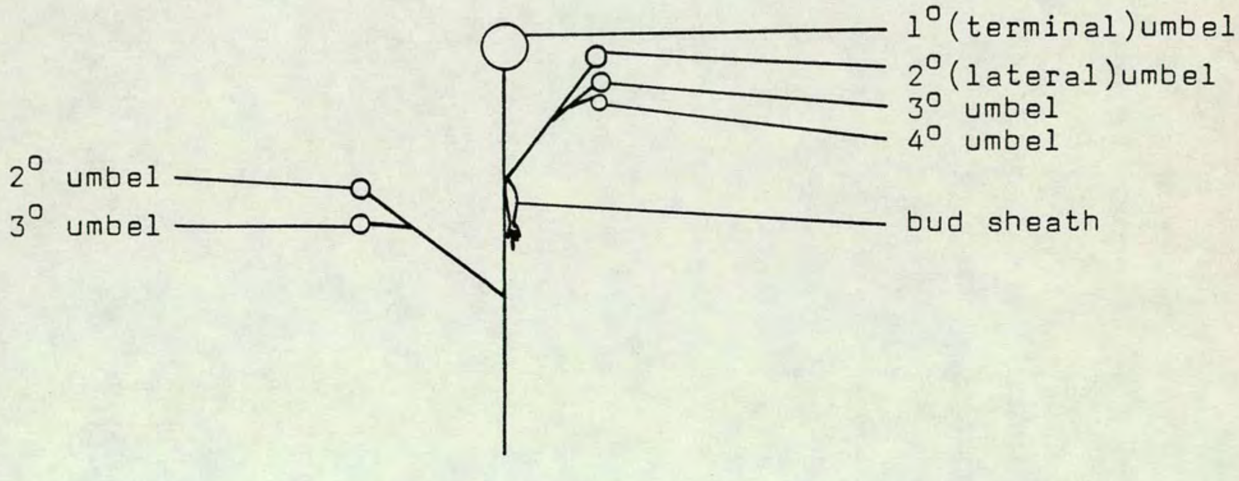
Individual flowers of Heracleum are grouped into umbellets, and several umbellets form a single compound umbel

A single compound umbel of Heracleum



Several compound umbels are grouped on a single flowering stem;

A single flowering stem of Heracleum



Leaf characters measured on herbarium specimens

9. L - Length of lamina (leaf excluding petiole)
10. W1 - Width of leaf across 1st pair of leaflets
11. W2 - Width of leaf across 2nd pair of leaflets
12. R1 - Length of rachis between 1st and 2nd pair of leaflets
13. R2 - Length of rachis between 2nd and 3rd pair of leaflets
14. d1 - Depth of incision of proximal segment of outer edge of leaf
15. d2 - Length of proximal segment of outer edge of leaf from apex to midrib of leaflet
16. b - Width (at widest point) of proximal segment of outer edge of leaf
17. n.s. - Number of pairs of leaflets
18. a - Angle of tip of proximal segment of outer edge of leaf
19. ax - Angle between segment midrib and midrib of leaflet
20. bsl - Bud sheath length (inflated petiole of peduncle subtending leaf which encloses the inflorescence in bud)
21. bsb - Bud sheath breadth

Floral characters

22. %pf

Pollen fertility was calculated as the percentage of pollen stained dark blue by lactophenol cotton blue (1%). For

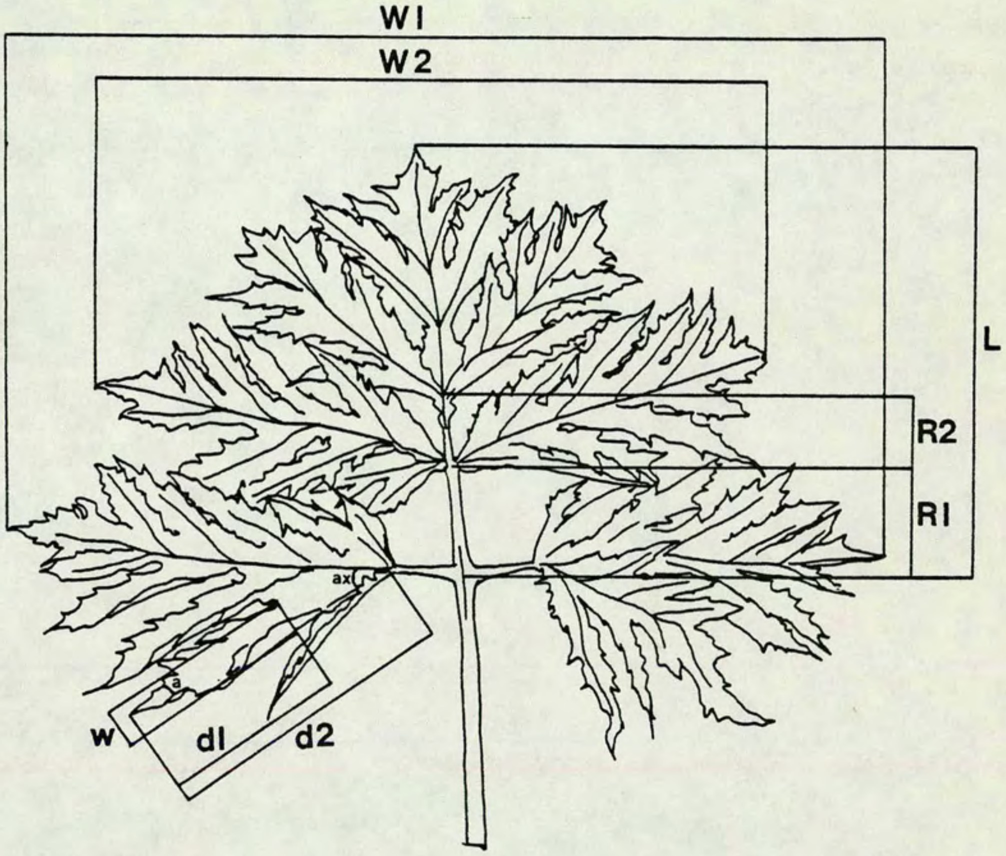


Fig. 3.5 Leaf characters

each plant one dried flower from each of an inner, middle and outer umbellet was brushed in a drop of water on a clean glass slide to disperse the pollen load. A drop of stain was mixed with the pollen suspension and after 15 minutes the number of stained pollen grains in a sample of 200 was counted.

23. %ss

Seed set was calculated for the terminal umbel of each plant as the number of mericarps containing an endosperm at least half developed in size as a percentage of the number of perfect flowers in the umbel. For H. mantegazzianum these numbers were estimated: a sample of 4 - 8 umbellets selected from centre to outside of the terminal umbel was found to give an estimate of the number of perfect flowers for a whole umbel accurate within 10% when the sample average for one umbellet was multiplied by the total number of rays in the umbel. A subsample of 400 seeds selected by the method described in Section 5.2 was used to estimate the number of mericarps containing an endosperm.

24. Style length

A preliminary survey showed that the length of the style at maturity was the most reliable character to measure for a comparison of floral morphology since the styles of Heracleum remain attached to the ripening fruit.

25. Pollen length

Measured on stained preparations for pollen fertility counts. Only stained grains were measured, ten for each plant.

Fruit characters

Ten mericarps chosen at random from the seed collection for each plant were measured for the following characters:

26. WT - Air dry weight of mericarp

27. L - Length from top of stylopodium to base of fruit

28. W - Width of mericarp at widest point

29. dvl - Length of longest dorsal vittae from tip to point of insertion in stylopodium

30. cvl - Length of commisural vittae from tip to base of stylopodium

31. dvw - Width of dorsal vittae at widest point

32. cvw - Width of commisural vittae at widest point

34. stl - Length of stylopodium from base to base of style

35. stb - Width of stylopodium at base

36. wb - Breadth of wing of mericarp

33. NO. VITTAE - Number of dorsal vittae

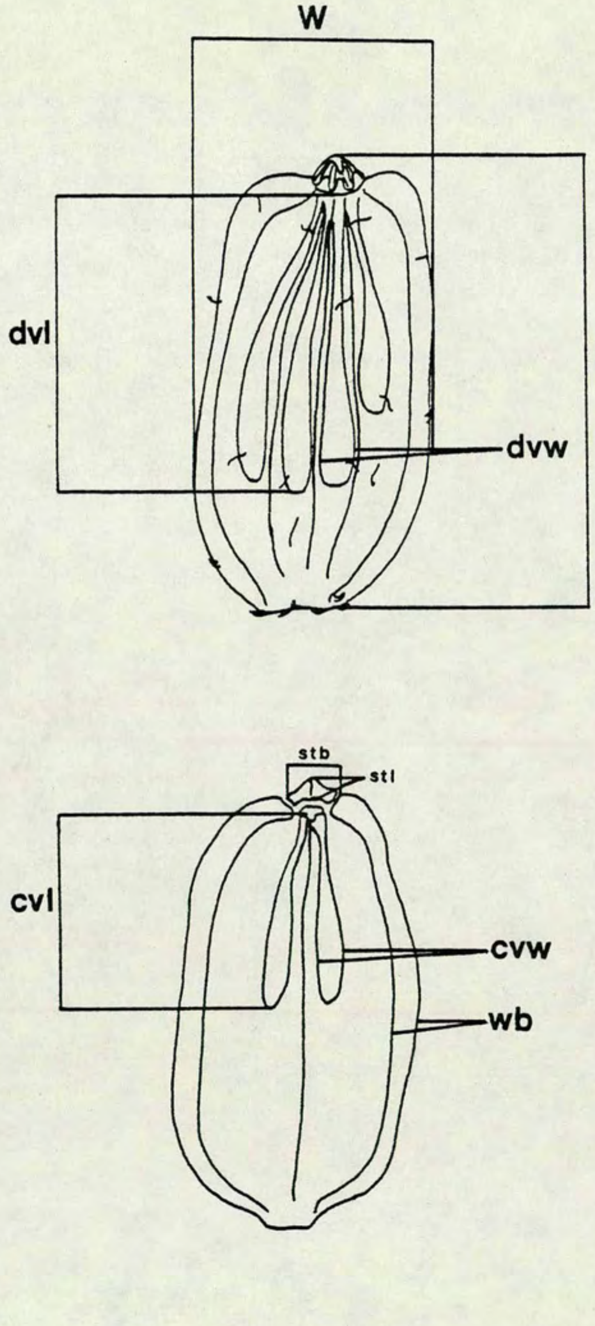


Fig. 3.6 Fruit characters

Leaf characters measured on material preserved in fluid

37. Hair length

38. Hair breadth

The length and breadth of hairs on the lower epidermis of the leaf were measured on epidermal peels taken from material preserved in FAA. A preliminary survey from different sections of an entire leaf showed that variation in hair length between species was greater than could be expected over the leaf surface of any one plant. The method of Sokal and Rohlf (1969 p.247) was used to calculate the number of replicates needed to detect a 30% difference between means at a significance level of 0.05 assuming a probability of 0.9. A total of 30 hairs were measured from preserved material for each plant, and means calculated.

Methods of analysis

Plants from Riddell, Roslin and Coldstream surveyed in 1976 and from the single site at Kale Water in 1977 were examined by principal component analysis of morphometric data to look for evidence of a separate hybrid group. The Genstat computer program (available from Rothampstead Experimental Station, Harpenden, Herts.) was used with the PCP directive on a correlation matrix of the basic data set.

Interpretation of the eigenvectors in the principal component analysis, summary statistics and observations in the field were used to describe:

(1) Characters which distinguish hybrid from parent plants at Kale Water in 1977.

(2) Variation between H. sphondylium and H. mantegazzianum at different sites and between 1976 and 1977.

3.3 Results

All measurements for individual plants at all survey sites are tabulated in Appendix IV. Mean, range, standard deviation and coefficient of variation are listed for groups of H. sphondylium, H. mantegazzianum and putative hybrids at Roslin, Riddell, Kale Water and Coldstream in Appendix V.

Delimitation of groups: principal component analysis

A principal component analysis of data collected in 1976 from Roslin, Riddell, Kale Water and Coldstream produced the scatter of plants between the first and second component axes shown in Fig.3.7. Plants thought to be hybrid are intermediate in position but vary continuously with either parent. A similar analysis, using more complete data collected at Kale Water in 1977 produced the scatter of plants between the first and second component axes shown in Fig. 3.8. Putative hybrids lie to the left of and intermediate between the parent groups. They are quite distinct from H. mantegazzianum, but less definitely separated from H. sphondylium.

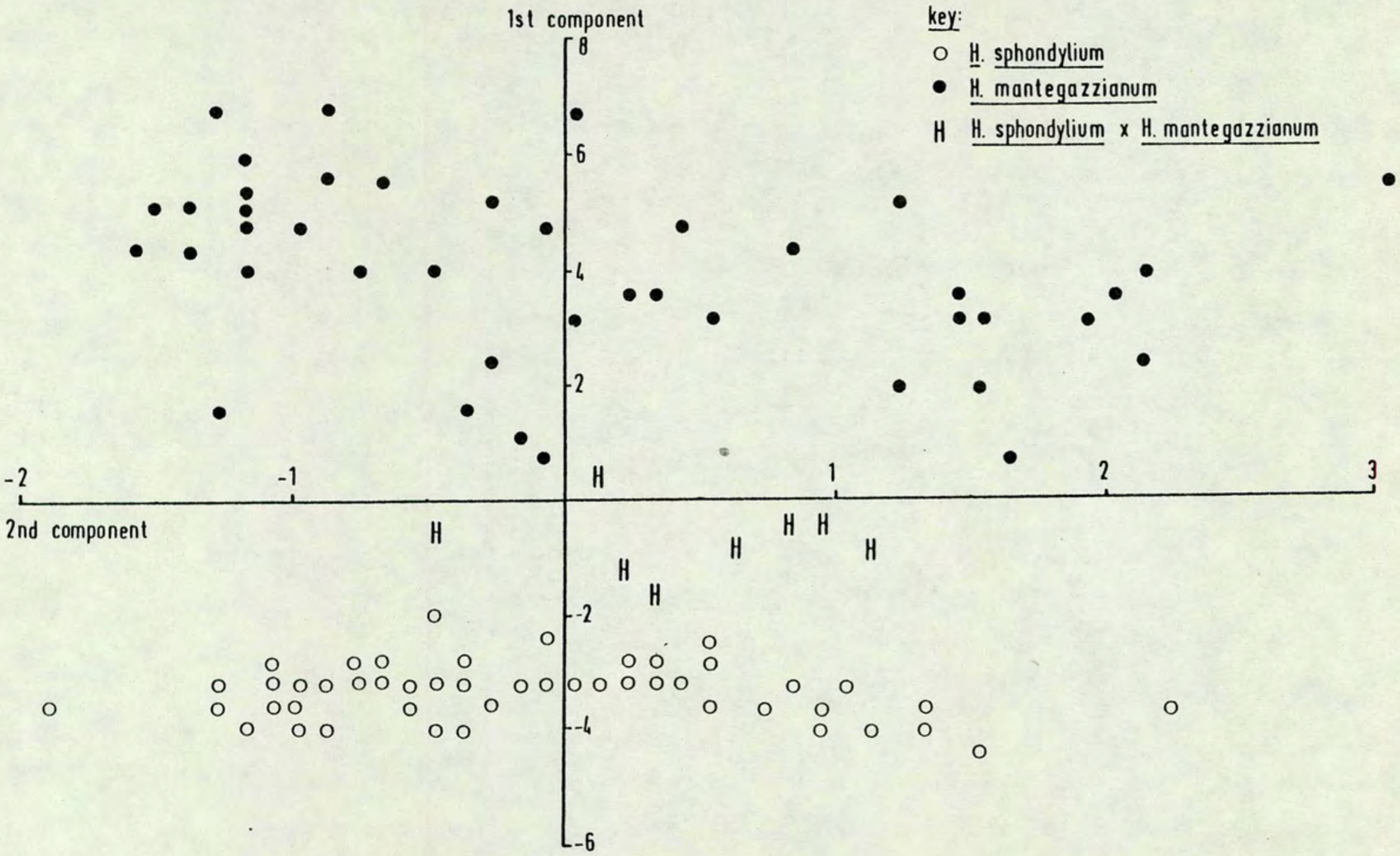


Fig. 3.7 Scatter of plants between first and second components: data collected in 1976

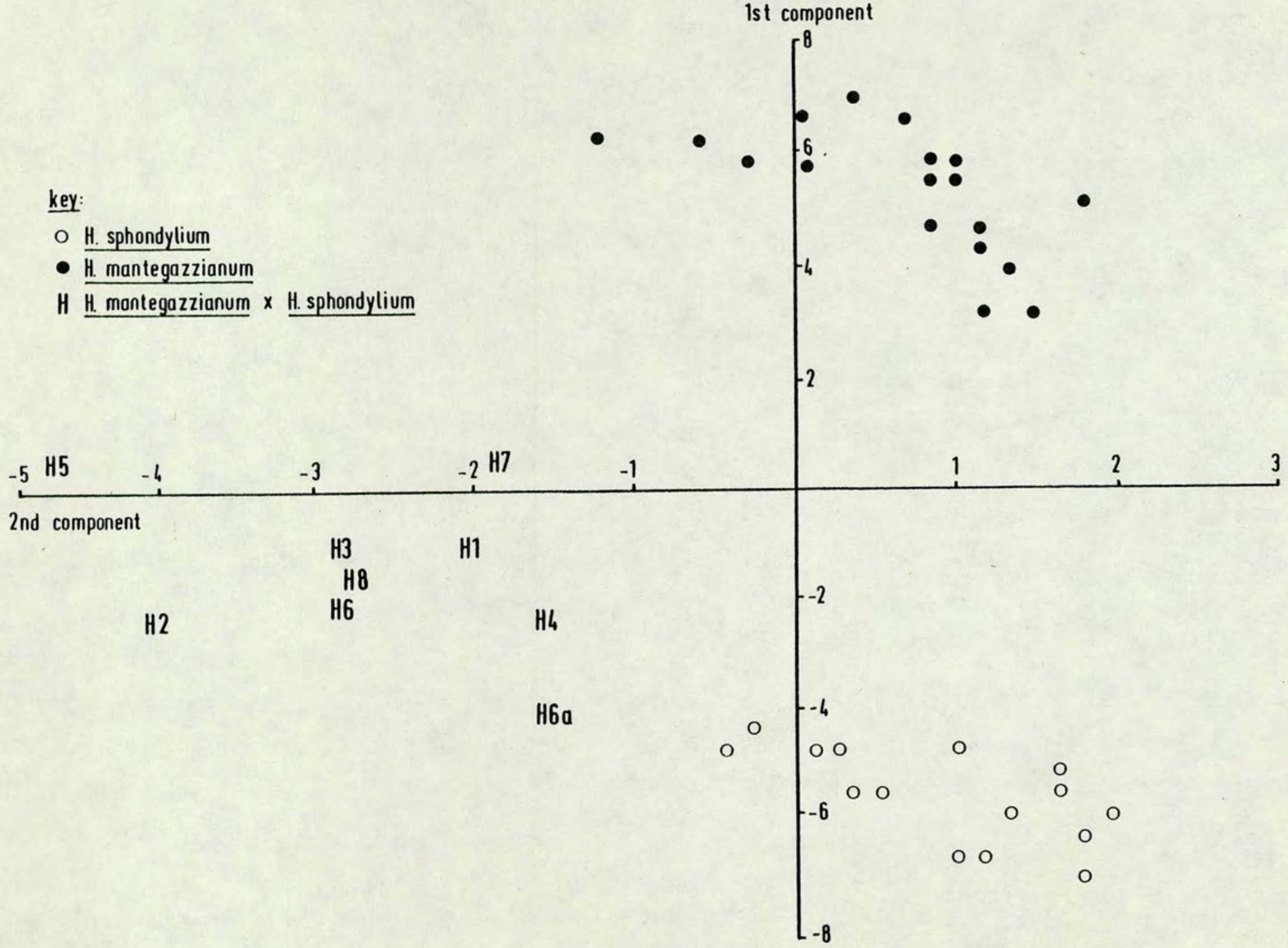


Fig. 3.8 Scatter of plants between first and second components:
Kale Water 1977

Nevertheless, the multivariate analysis suggests that putative hybrids can be recognised in the field.

Analysis of the eigenvectors by isolating coefficients with highest values for each component (Isebrands & Crow 1975), underlined in Table 3.2 and 3.3, suggests that the first component of each analysis may be attributed to a general size vector, particularly the length and width of the leaf. Hybrids are intermediate in stature between parent plants. For the 1976 analysis, the second component, associated with the angle between the leaf lobe and the axis of the lateral segment, did not distinguish hybrid from parent plants. Only eighteen morphometric characters were used for this analysis; they are listed in Table 3.2 and Appendix III. The 38 characters used for the 1977 analysis are listed with eigenvectors in Table 3.3. Five components have eigenvalues greater than 1.0 and account for 86% of the variance between the plants. Components 2 to 5 may be attributed to pollen fertility, number of vittae and stylopodium length which were not measured in 1976, and angle between the segment midrib and midrib of leaflet.

Of those characters important for the principal component analysis only the general size vector and pollen fertility were useful for identifying hybrids. At least 40% of H. sphondylium pollen and 75% of H. mantegazzianum pollen stained with lactophenol cotton blue, whereas only a maximum of 7% of pollen grains of hybrid plants took up the stain (Table 3.4). Seed set was also low in hybrid plants, 3% at the most.

Table 3.2 Eigenvectors for the first two components in the analysis of 1976 data

Eigenvectors corresponding to component:

	1	2
NO. 2^{o}	0.2215	-0.1642
NO. BRACTS	0.2197	0.1456
HEIGHT	0.2528	0.1676
BSD	0.2532	0.2057
TSD	0.2575	0.1391
1^{o}DIAM	0.2558	0.2021
RAYS	0.2534	-0.1263
R1	0.2398	-0.1364
LEAF W2	0.2469	-0.2497
W1	0.2605	-0.0763
ns	-0.1593	-0.0441
bsl	0.2428	-0.0736
bsb	0.2330	0.0461
d2	0.2635	0.0041
b	0.1989	0.2606
d1	0.2573	0.0638
ax	-0.0989	0.7937
Leaf L	0.2621	-0.0838
Eigenvalue for component:	13.5343	1.0863
% of variance for component:	75.1903	6.0351

Table 3.3. Eigenvectors for the first five components in the analysis of Kale Water 1977 data

	Eigenvectors corresponding to component no:				
	1	2	3	4	5
HEIGHT	0.1790	0.0513	-0.0102	0.0045	0.0405
TSD	0.1828	0.1299	-0.0565	0.0208	-0.0185
BSD	0.1894	0.0824	0.0166	-0.0006	0.0302
1^o DIAM	0.1875	0.1002	-0.0316	0.0239	0.0174
NO. RAYS	0.1836	0.1301	-0.0267	0.0508	-0.0512
_ 1^o & 2^o	0.1533	0.1044	0.1372	-0.0915	0.3564
NO. 2^o	0.1424	0.0581	0.0336	0.1014	-0.3735
NO. BRACTS	0.1758	0.0590	0.0881	0.0922	0.0609
LEAF L	0.1852	-0.0508	0.1428	-0.1067	-0.0302
W1	0.1871	-0.0089	0.0979	-0.1140	-0.0930
W2	0.1872	0.0202	0.0946	-0.0940	-0.0022
R1	0.1278	-0.2793	0.3103	-0.2695	-0.0375
R2	0.1839	-0.0435	0.1111	-0.0583	-0.0698
d1	0.1814	-0.0043	0.1121	-0.2045	-0.0196
d2	0.1850	-0.0187	0.0871	-0.1614	-0.0655
b	0.1764	-0.0900	0.0789	-0.1500	-0.0603
ns	-0.1203	-0.0356	0.2940	-0.0567	0.1922
a	-0.1698	-0.0098	0.1035	-0.0138	-0.0830
ax	0.0949	0.3020	0.1534	-0.1856	0.4023
bsl	0.1644	-0.0163	0.0571	-0.2118	0.3127
bsb	0.1830	0.0834	0.0362	-0.0537	-0.0310
%pf	0.0547	0.4996	-0.0553	0.0820	-0.1512
%ss	0.1547	0.3076	0.0146	0.0677	-0.1731
style L	0.0881	-0.3132	-0.1515	0.1799	-0.0483
pollen L	0.1857	-0.0289	-0.0539	0.0214	0.0412
mericarp wt	0.1451	-0.1916	-0.0575	0.3100	0.2340
L	0.1622	-0.2302	0.0251	0.1725	0.1045
W	0.1537	-0.2443	-0.0752	0.1942	0.1759
dvl	0.1760	-0.1598	-0.0456	0.1658	-0.0122
cvl	0.1743	-0.1234	-0.1443	0.1209	-0.0463
dvb	0.1883	0.0262	-0.1020	0.0881	0.0123
cvb	0.1808	0.0572	-0.0867	0.1027	0.0016
NO. VITTAE	0.0044	-0.0839	0.6872	0.2936	-0.2973
stl	0.0550	-0.2622	-0.2642	-0.5625	-0.2834
stb	0.1601	0.1299	-0.1364	-0.0447	-0.1928
wb	0.1741	0.0222	-0.1591	0.0897	0.0524
hl	-0.1835	0.0851	0.0396	-0.0313	-0.0289
hb	-0.1643	-0.0117	-0.0252	-0.0489	0.1732
Eigenvalue for component	26.4210	2.7760	1.3282	1.1286	1.0702
% of variance for component	69.5289	7.3053	3.4952	2.9700	2.8163

Table 3.4. Group means, ranges, and coefficients of variation (SD as % of mean) for characters used to distinguish hybrids (H) from H. sphondylium (S) and H. mantegazzianum (M) plants at Kale Water 1977

	S	H	M
% pf	79 (40-94)	3 (0-7)	91 (75-97)
% SS	25 (0-51)	1 (0-3)	84 (62-94)
Hair length (μm)	551 (506-638) 9%	274 (202-385) 19%	110 (96-123) 8%
Pollen length (μm)	44.7 (41.7-47.1) 3%	54.9 (52.5-57.3) 3%	65.3 (60.4-70.0) 4%
Dorsal vittae width (mm)	0.29 (0.25-0.43) 16%	0.64 (0.44-0.98) 29%	1.25 (1.10-1.50) 8%
No. rays	19 (13-25) 18%	33 (25-54) 27%	107 (79-144) 16%
Mericarp Length (mm)	8.58 (6.90-11.00) 13%	11.67 (9.05-13.60) 12%	12.40 (10.05-14.00) 8%
Leaf Width (mm)	280 (190-380) 19%	520 (260-770) 34%	950 (650-1200) 17%
a (^{o})	42 (25-60)	30 (22-40)	16 (10-18)

H. sphondylium seed set could be equally low, but ranged to a maximum of 51%. *H. mantegazzianum* seed set was highest, between 62% and 94% (Table 3.4.).

Discrimination between groups: Kale Water 1977

For group means and ranges of characters measured at Kale Water in 1977 (Appendix V), there are four variables whose values for parent and hybrid plants do not overlap. They are:

Length of hairs on the lower surface of the leaf
Pollen length
Width of vittae on the dorsal surface of the fruit
Number of rays in the terminal umbel

and are listed in Table 3.4. Of these, pollen length shows least variation, with S.D.s' 3%, 3% and 4% for the three groups respectively, while the field characters of leaf width and number of rays are most variable.

A scatter diagram of pollen length against leaf hair length for individual plants at Kale Water in Fig.3.9 shows that these two characters alone suffice to distinguish clearly between *H. mantegazzianum*, *H. sphondylium* and the hybrid. *H. sphondylium* at Kale Water has long slender hairs on the lower epidermis of the leaf, on average 551 µm long, whereas *H. mantegazzianum* has short pointed hairs, of mean length 110 µm. Hairs measured for Kale Water hybrids vary between 202 µm to 385 µm in length (Table 3.4).

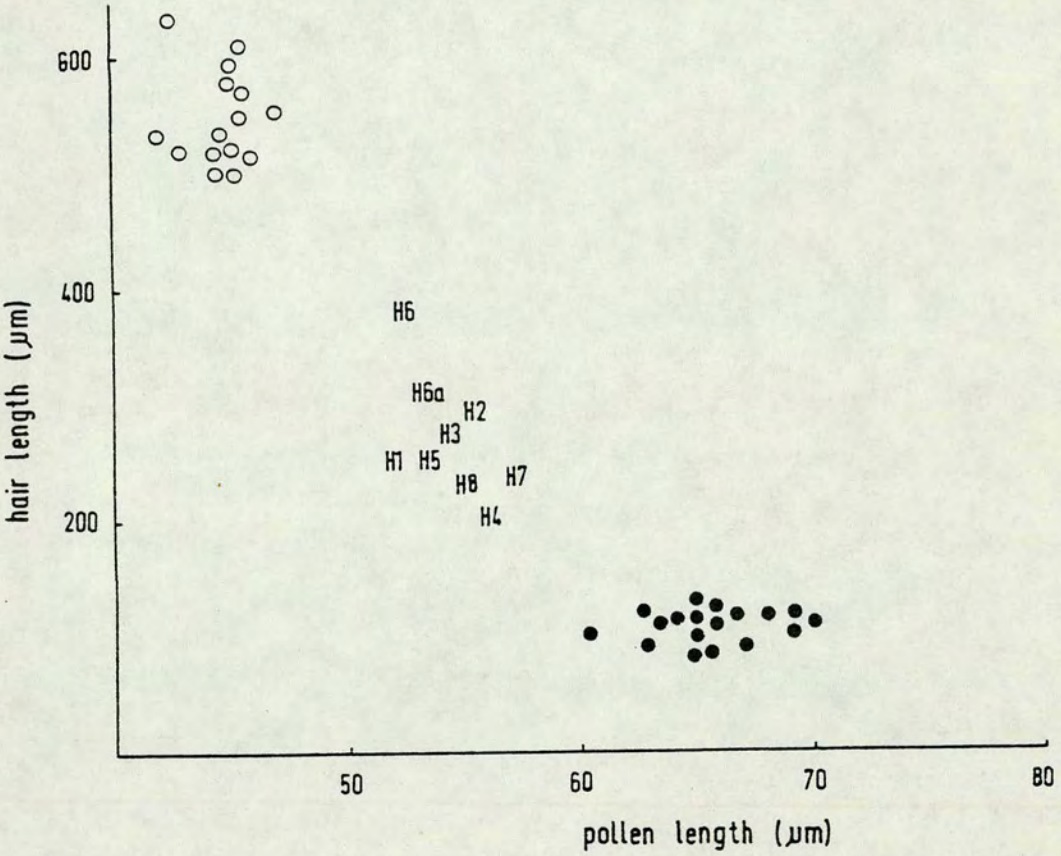


Fig. 3.9 Scatter diagram of pollen length and hair length for H. mantegazzianum (●), H. sphondylium (o), and hybrids (H) at Kale Water 1977

The three types of indumentum produced by these different hair lengths are illustrated in Fig.3.10. They can be distinguished in the field: H. mantegazzianum appears almost glabrous, H. sphondylium is softly pubescent, while the lower surface of the hybrid leaf is setaceous or shortly pubescent.

The hairs on H. sphondylium and H. mantegazzianum leaf surfaces also differ in structure. H. sphondylium has long, slender, unicellular or bicellular hairs, apparently thin walled and with a blunt but tapered apex. The hairs collapse quickly under the scanning electron microscope if fresh specimens are used without treatment (Fig.3.11). There are very few pits in the walls of H. sphondylium leaf hairs compared with those of H. mantegazzianum (Fig.3.12) which have a tuberculate and pitted surface, easily visible on epidermal peels viewed through the light microscope. H. mantegazzianum hairs are short, narrowly pointed, mostly unicellular and thick walled. Hybrid hairs are longer, have pointed tips and thickened walls characteristic of H. mantegazzianum, but resemble H. sphondylium in their smoother surface (Fig.3.13).

H. mantegazzianum pollen, between 60.4 µm and 70.0 µm long, is larger than both H. sphondylium pollen of length 41.7 µm to 47.1 µm and hybrid pollen which is 52.5 µm to 57.3 µm long (Table 3.4). All three types of pollen are similar in shape, although differences between the fine structure of H. sphondylium and H. mantegazzianum pollen have been described (Cerceau 1971).

a
x38

c
x38

Fig. 3.10 Lower surface of the leaf under SEM for (a) H. mantegazzianum, (b) H. sphondylium and (c) hybrid plants

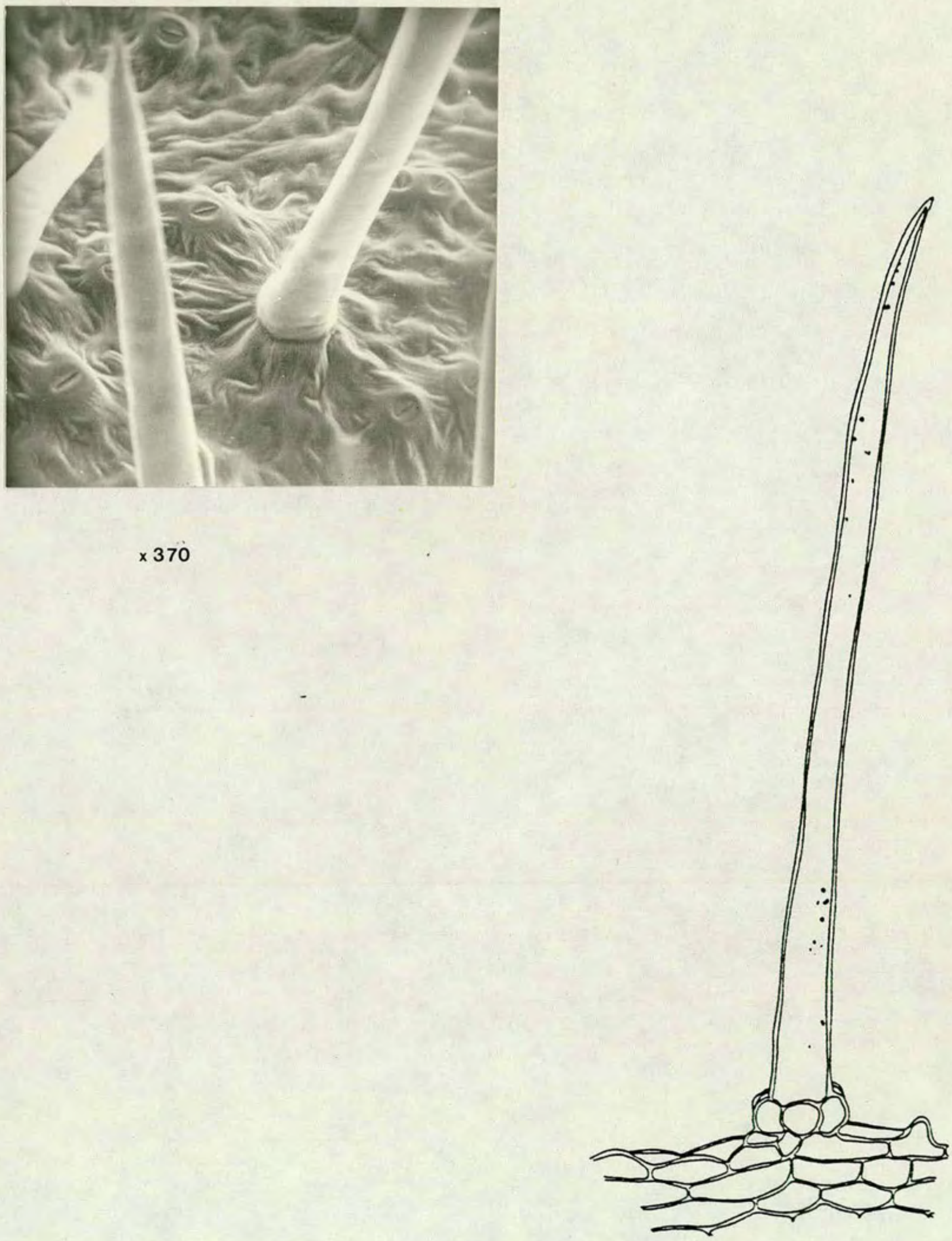


Fig. 3.11 Hairs on lower epidermis of the leaf: <u>H. sphondylium</u>

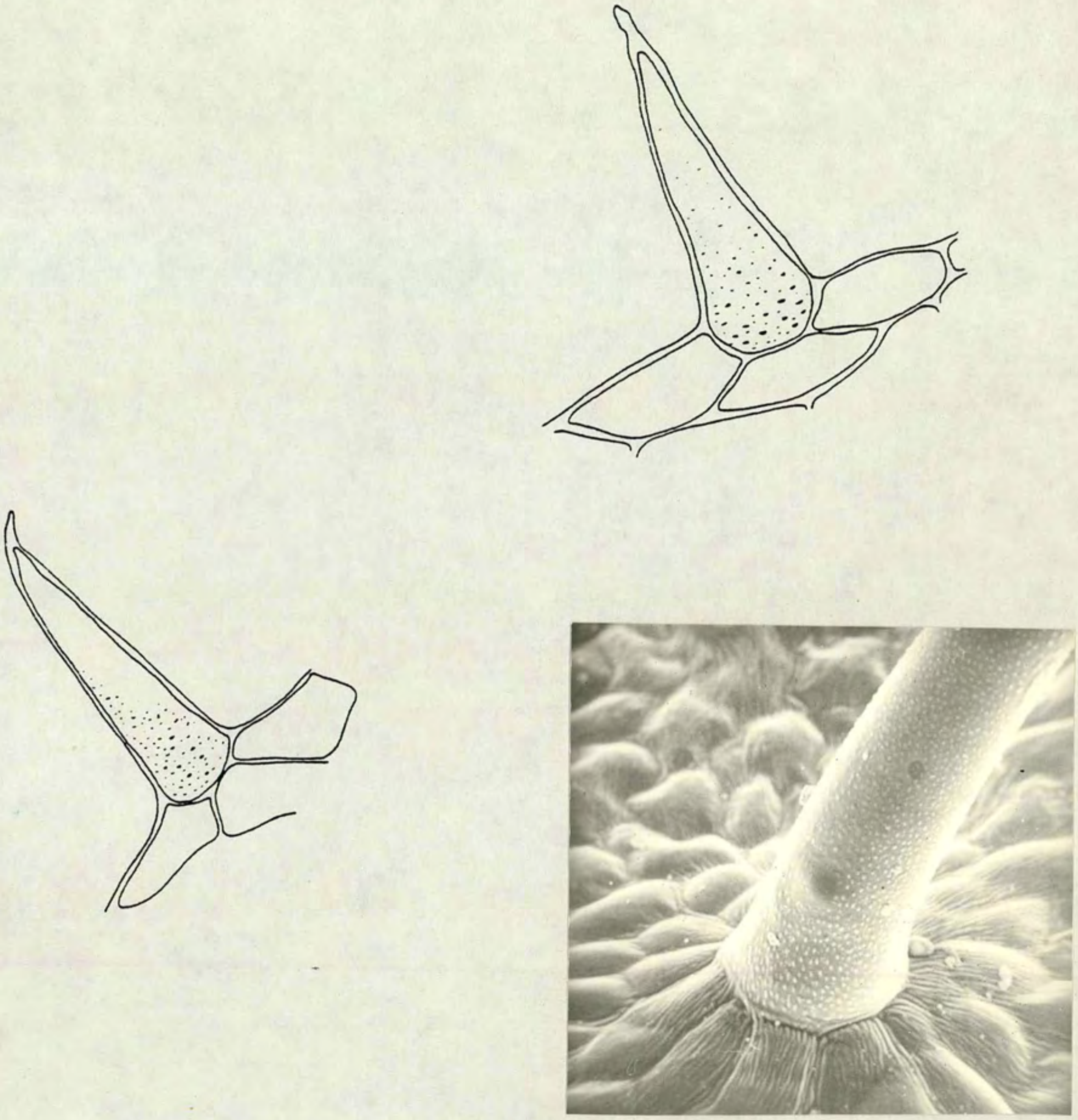


Fig. 3.12 Hairs on lower epidermis of the leaf: <u>H. mantegazzianum</u>

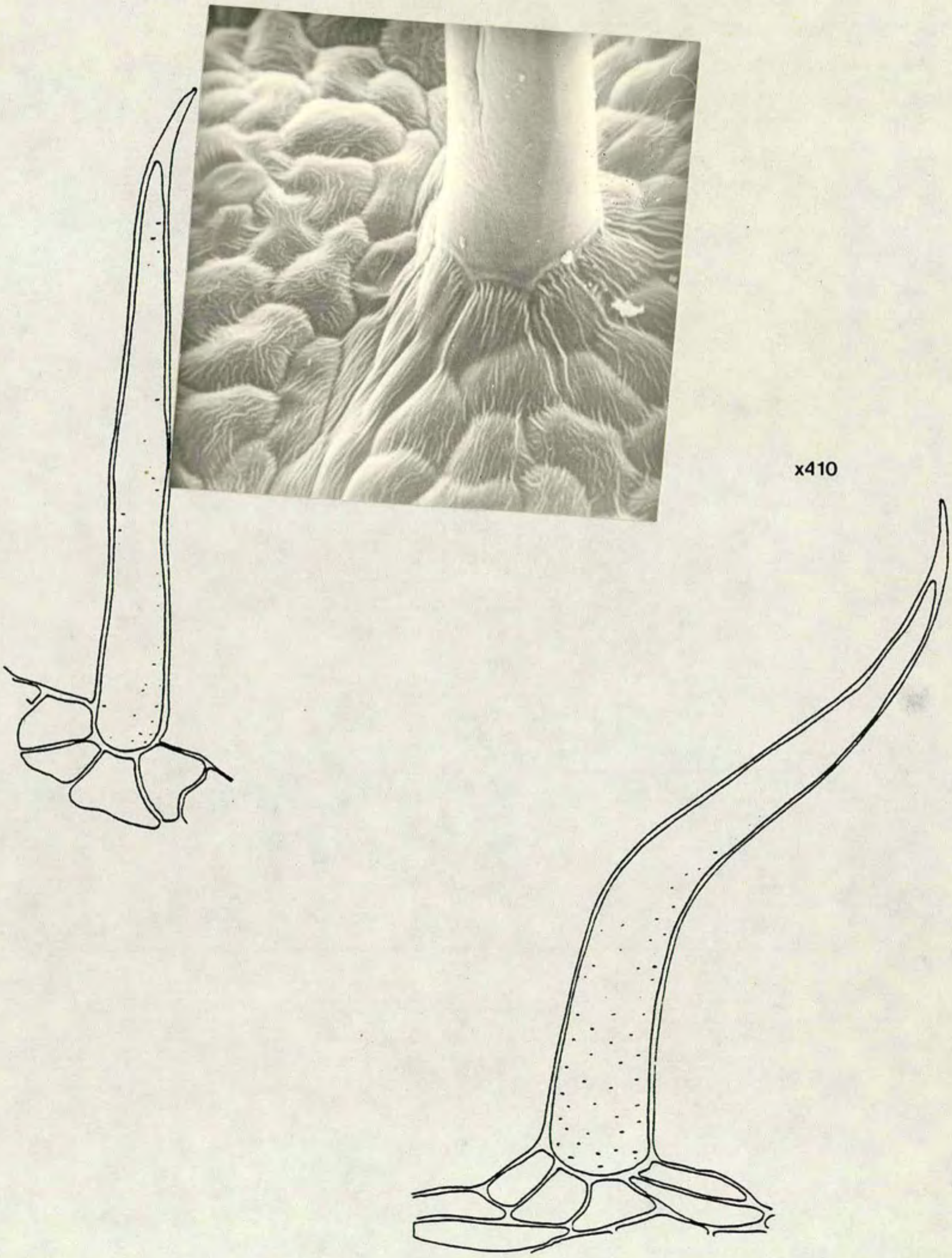


Fig. 3.13 Hairs on lower epidermis of the leaf: <u>H. mantegazzianum</u> x <u>H. sphondylium</u>

At Kale Water H. mantegazzianum had a mean vitta width of 1.25 mm, while H. sphondylium vittae were only 0.29 mm wide on average (Table 3.4). Hybrids have slender not very expanded vittae which are quite broad on account of the large size of their mericarps. A scatter diagram of width of dorsal vittae against length of the mericarp for Kale Water plants in Fig. 3.14 shows that most of the putative hybrids measured in 1977 had fruits as long as those of H. mantegazzianum, but which differed from that parent in their narrower vittae, ranging in width between 0.44 mm and 0.98 mm (Table 3.4).

Mericarps from hybrid plants can be identified at a glance because, though large, their vittae are narrow, not clavate. This is clearly illustrated in Fig.3.15. For the other descriptive characters used in the identification of Heracleum fruits (Koval 1975) differences between the two parent species are not so concise. Both H. sphondylium and H. mantegazzianum have a varying covering of thin scarious hairs on the dorsal surface of the fruit. H. mantegazzianum has scattered short spines on the edge of the fruit, which were also found on one hybrid and two plants of H. sphondylium. In H. mantegazzianum fruits the surface of the disc is more deeply rugose, hemispherical in shape and set slightly above the wing border of the mericarp. H. sphondylium has a conical disc, generally but not always set into a depression in the wing margin, smoother in surface, and with a distinct annular ring. Hybrids vary in appearance between the two parental extremes.

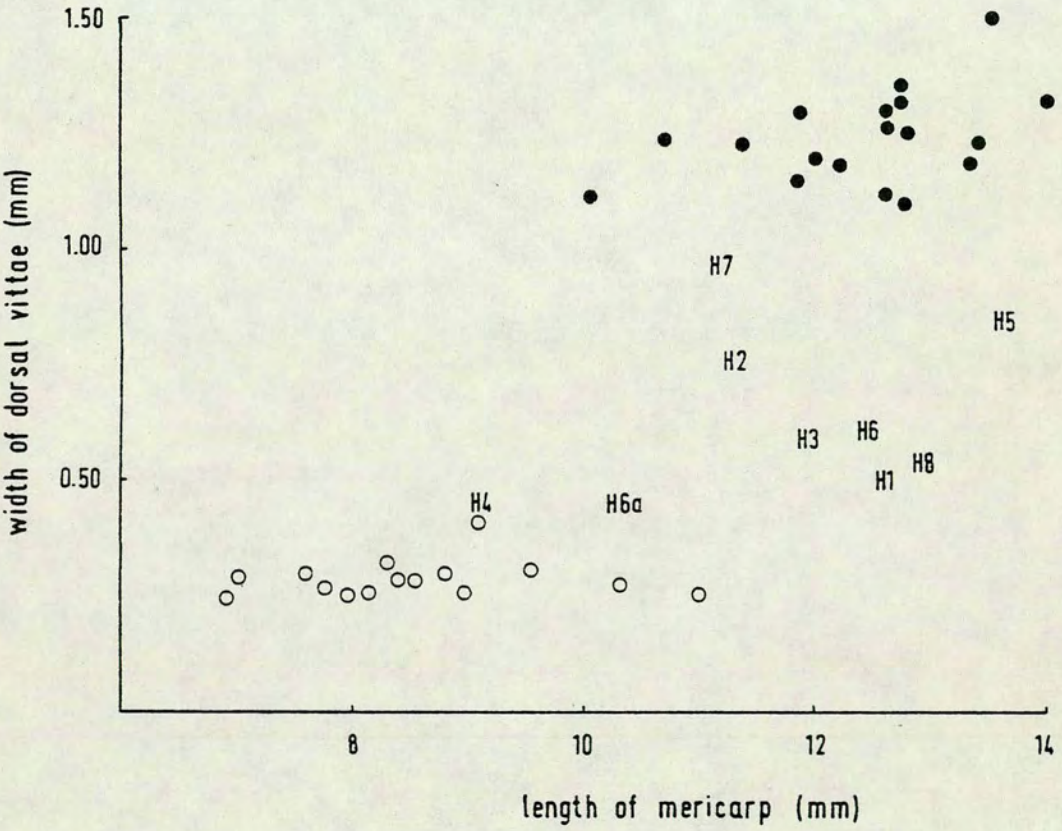


Fig. 3.14 Scatter diagram of width of dorsal vittae and length of mericarp for H. mantegazzianum (●), H. sphondylium (o) and hybrids (H) at Kale Water 1977

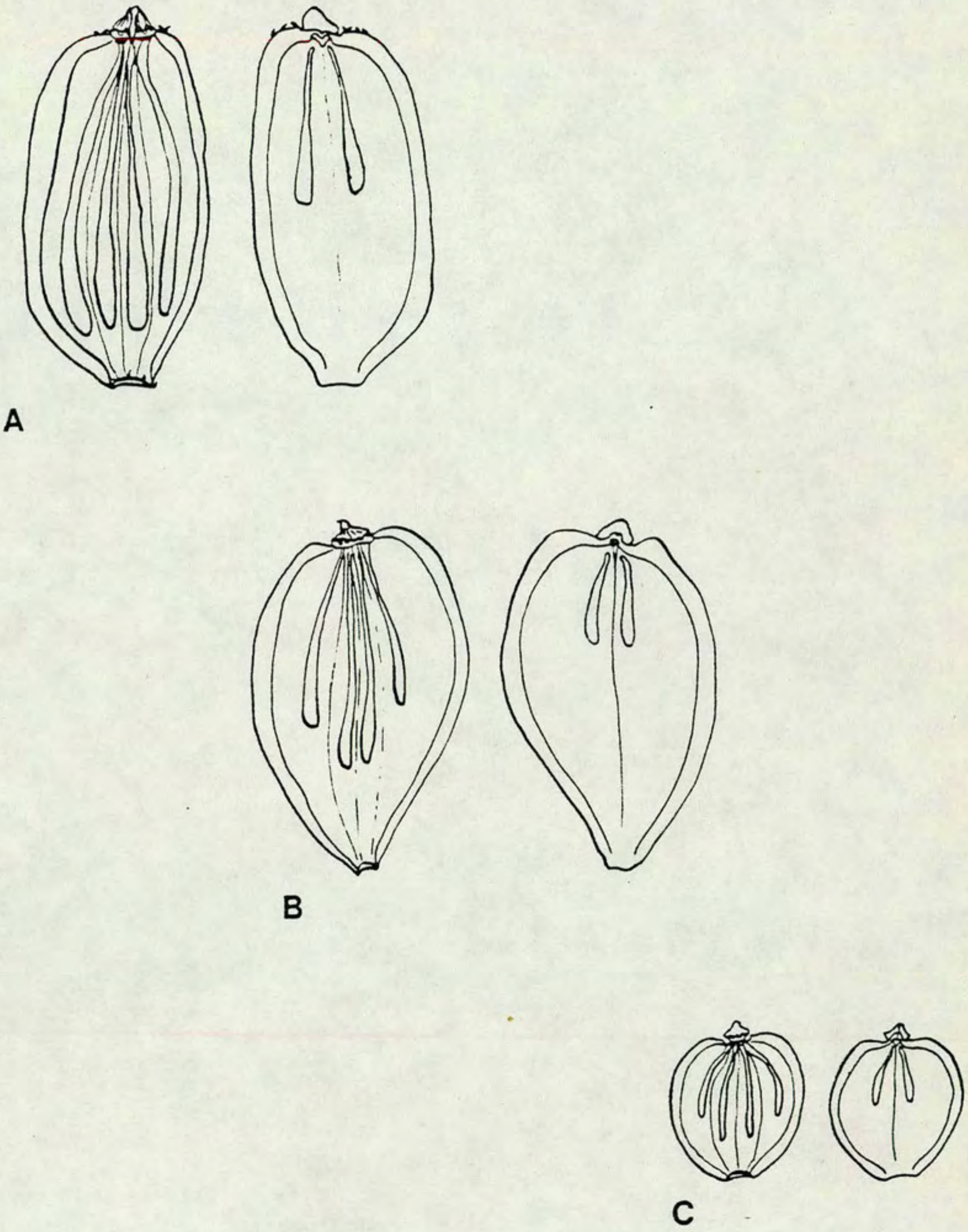


Fig. 3.15 Mericarps of H. mantegazzianum (A), H. sphondylium (C) and hybrid (B) plants

In the field the microcharacters of hair and pollen length and the morphology of the fruit are not as useful for identifying hybrids as the discrete character of ray number, and the overall size of the plant (which contributed most to the variation of the first component of the analysis in Table 3.3). In Fig.3.16 the plants at Kale Water in 1977 are scattered according to the number of rays and the width of the leaf, an indication of size. Plants which are intermediate in stature between H. sphondylium and H. mantegazzianum and are considered hybrids have 30 - 50 rays and leaves which are larger, of mean width 520 mm, than those of H. sphondylium, of mean width 280 mm (Table 3.4). The number of rays, although very much greater for H. mantegazzianum with 78 rays or more, is not really discrete between H. sphondylium and the putative hybrid, since the ranges are continuous, from 13 to 25 and 25 to 45 (Table 3.4). In the scatter diagram in Fig.3.16 two hybrids have grouped with H. sphondylium plants. These two characters alone, although more practical in application, do not separate the hybrid group as clearly as leaf hairs (Fig.3.9) or fruit morphology (Fig.3.14).

Leaf characters, though not discrete between the three groups, are illustrated for each plant at Kale Water 1977 in the photograph series in Fig.3.17. In the vegetative state, leaf and indumentum type are the only morphological characters for identifying hybrids. The photographs show that it is the triangular outline of the H. mantegazzianum leaf that distinguishes it most

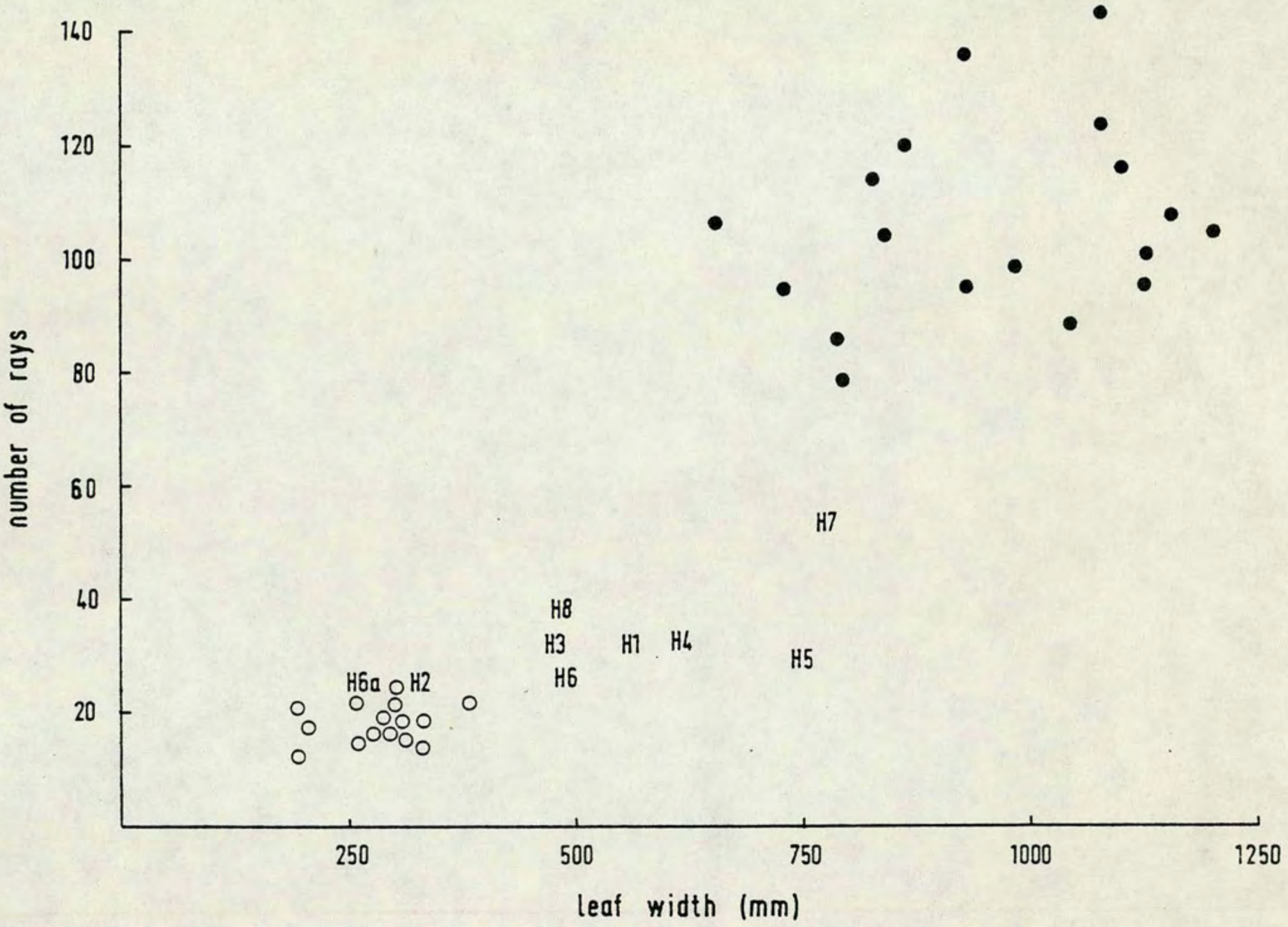
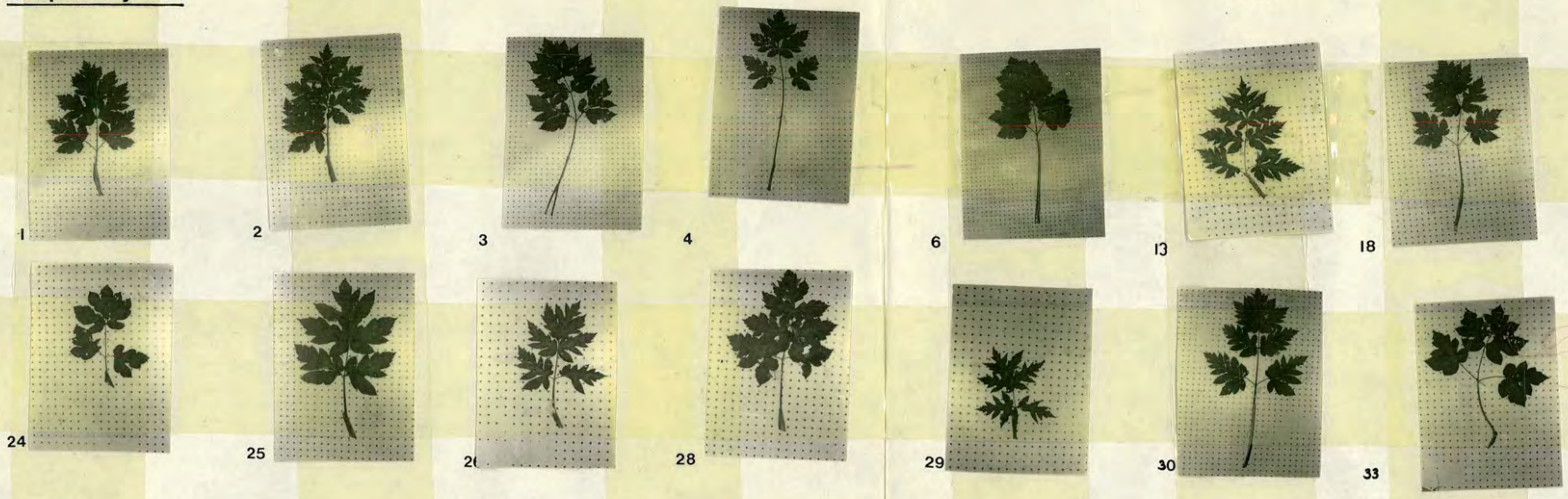


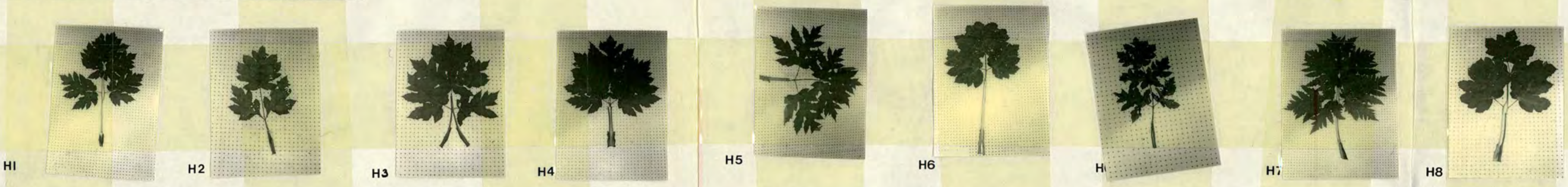
Fig.3.16 Scatter diagram of number of rays and leaf width for H. mantegazzianum (●), H. sphondylium (o) and hybrids (H) at Kale Water 1977

Fig. 3.17 Leaf photographs (of herbarium specimens)

H. sphondylium



H. mantegazzianum x H. sphondylium



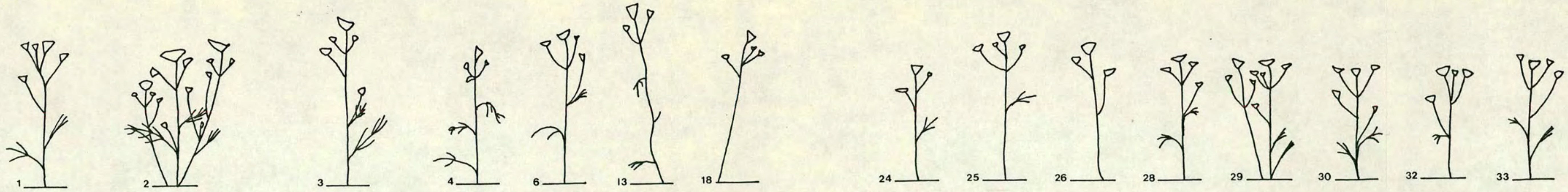
H. mantegazzianum

readily from the oblong 1-2 pinnate H. sphondylium leaf, rather than the shape of the leaf segments. The angle of the segment tip is also a better quantitative character than the dissection of the leaf. H. mantegazzianum has distinctly acuminate tips to each segment, between 10° and 18°; for H. sphondylium the angle is more obtuse, between 25° and 60°. Hybrids do not overlap the range for H. mantegazzianum in this character, yet the angle of the leaf tip may be more acute than H. sphondylium, between 22° and 40° (Table 3.4). Their leaves are large, triangular or oblong in outline, with one or two pairs of leaflets, ovate to lanceolate segments, are dull green in colour and shortly pubescent on the lower surface of the leaf.

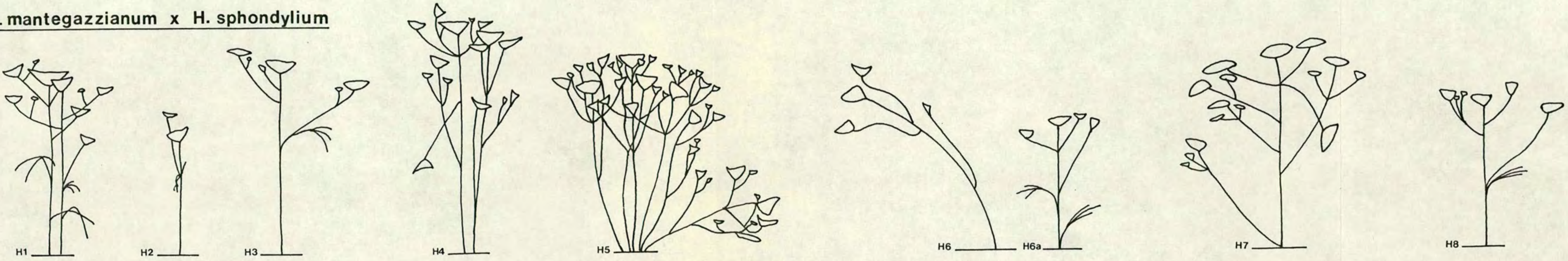
In fact, in the field, ray number and leaf width are combined with a complex of characters describing plant form to identify flowering hybrid plants. Some of these (height, basal stem diameter, top stem diameter, diameter of primary umbel, number of secondary umbels) were measured in the morphometric survey, but do not show discrete differences between the three groups of plants. Other differences due to length and angle of branching, the total number of subsidiary umbels and the number and position of flowering stems per plant were not measured for plants at Kale Water. Instead, the shape of each individual is presented as an ideogram (Bell 1955) in Fig.3.18. H. mantegazzianum bears additional subsidiary shoots from the base of the main stem, rather than producing two or more flowering stems from the same

Fig. 3.18 Ideograms for Heracleum plants at Kale Water 1977

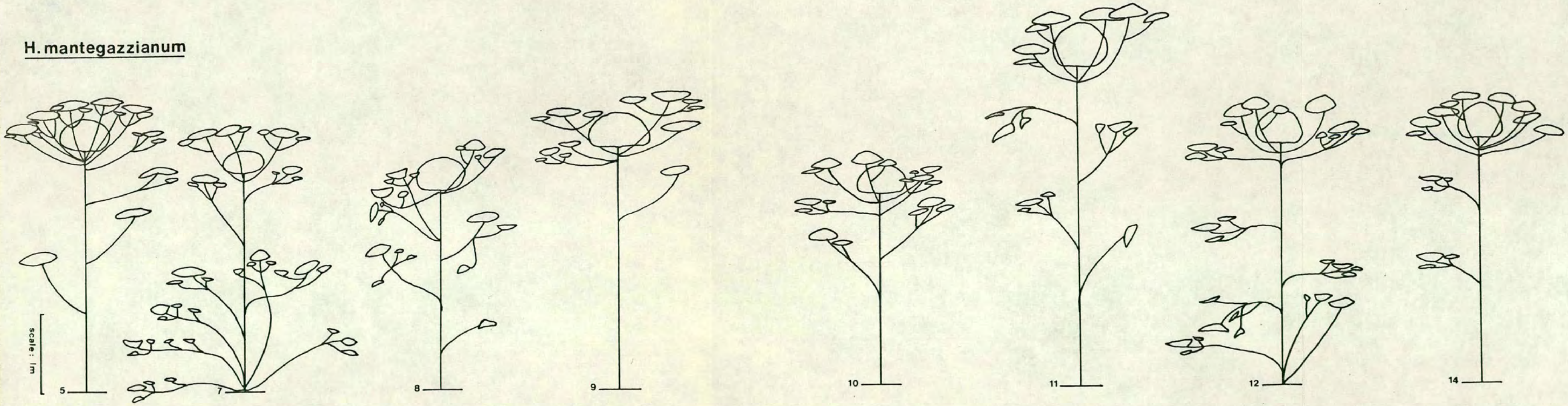
H. sphondylium



H. mantegazzianum x H. sphondylium



H. mantegazzianum



root system as in *H. sphondylium*. Hybrids resemble *H. sphondylium* in flowering stem form, but have secondary umbels as large as primary umbels, and weak stems or branches which collapse easily at seed set (Fig.3.19). Neither *H. mantegazzianum* nor *H. sphondylium* show this structural weakness, they are to be found as rigid dried flowering stems still standing in late autumn after foliage has died.

From Fig.3.18 it is immediately apparent that although the evidence from principal component analysis suggests that there is a definite hybrid group, H2 and H6a superficially resemble *H. sphondylium*. These two plants also grouped with *H. sphondylium* on the basis of leaf width and ray number (Fig.3.16). H6a and H4 were associated with *H. sphondylium* when compared with width of dorsal vittae and length of mericarp (Fig.3.14). Evidence from all four types of character: size (height of plant),fruit morphology (dorsal vittae width), leaf shape and floral morphology (style length) are combined in Fig.3.20 to show the variation in hybrid types at Kale Water compared with the range for parental species. H6a is the only hybrid which closely resembles one parent, *H. sphondylium*, in all four characters.

Fig. 3.19 Putative hybrids at (a) Kale Water
(b) Warriston Cemetary

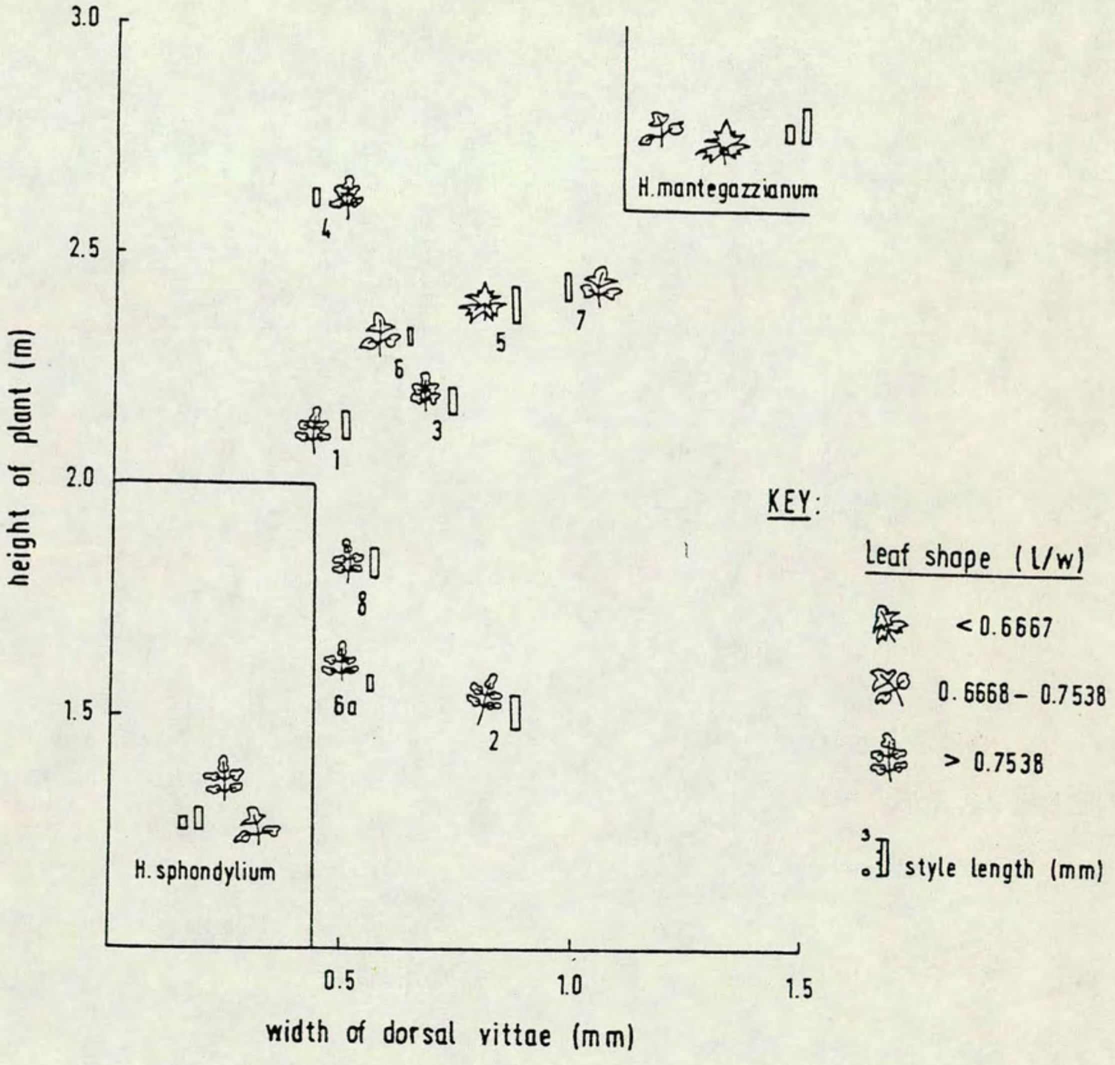


Fig. 3.20 Variation in hybrids:
Kale Water 1977

Variation between sites and years

Fruit characters

At Kale Water, Riddell and Roslin, five plants were sampled for fruit characters in 1976. The group means for mericarp length and dorsal vittae width are compared with values for Kale Water measured in 1977 in Table 3.5.

Table 3.5. Mean values for mericarp length and dorsal vittae width for H. mantegazzianum, H. sphondylium and hybrid plants at Roslin, Riddell and Kale Water 1976 and 1977.

	Mericarp length (mm)		Dorsal vittae width (mm)	
H. sphondylium				
Roslin	8.00		0.31	
Kale Water 1976, 1977	8.37	8.58	0.26	0.29
Hybrid				
Kale Water 1976, 1977	12.29	11.67	0.70	0.64
H. mantegazzianum				
Kale Water 1976, 1977	12.10	12.40	1.08	1.25
Riddell	10.92		0.77	

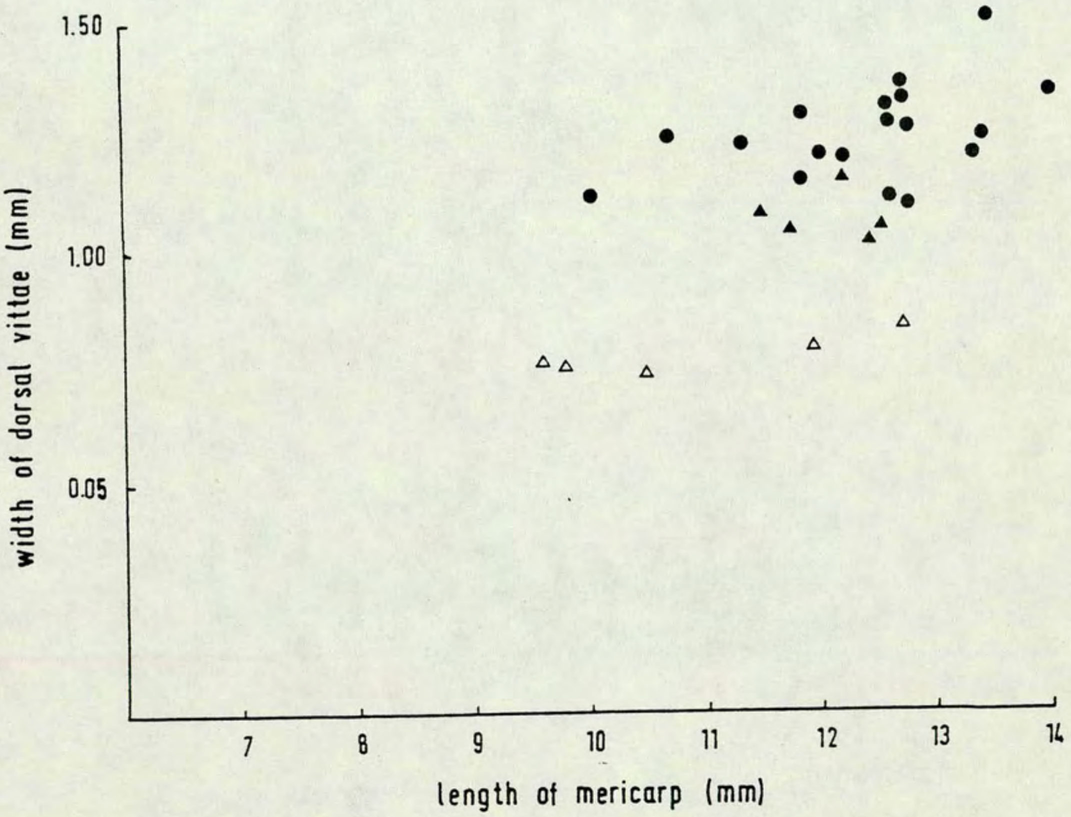


Fig. 3.21 Scatter diagram of width of dorsal vittae and length of mericarp for <u>H. mantegazzianum</u> plants at Kale Water 1977 (●) Kale Water 1976 (▲), and Riddell 1976 (△)

There is little difference between means for these characters from 1976 to 1977 at Kale Water, or between values for pure populations of H. sphondylium at Roslin and H. sphondylium growing with hybrids. However, fruits collected at Riddell in 1976 were much smaller, with a mean length of 10.92 mm, than fruits of mean length 12.20 mm harvested at Kale Water in the same year. The position of Riddell plants on a scatter diagram of width of dorsal vittae against mericarp length (Fig. 3.21) would overlap with the scatter of hybrid plants at Kale Water (Fig. 3.14). The size of the fruit and width of the dorsal vittae for H. mantegazzianum therefore varies as much between sites as between hybrid and H. mantegazzianum groups, although at one site values have remained constant from one year to the next.

Ray number and width of leaf

For H. mantegazzianum the mean number of rays was lower at Coldstream and Kale Water than at Riddell, and also varied from 1976 to 1977 at the one site at Kale Water (Fig.3.22), although the minimum value was always greater than any count made for hybrid plants. The change in ray number was not associated with change in plant height (Fig.3.22). For H. sphondylium the mean ray number remained constant from site to site and between years, but the range of values at Coldstream, where plants were on average smaller in height, was greater

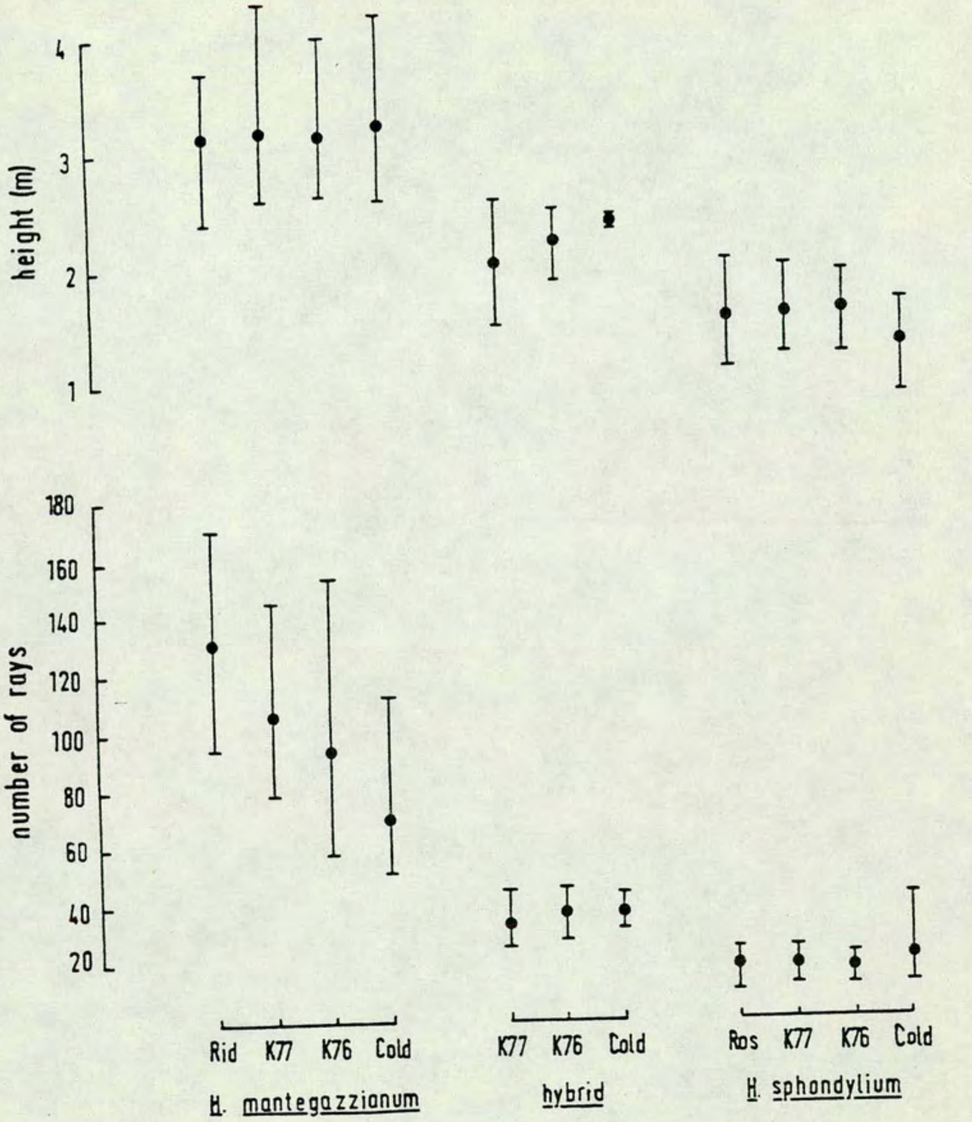


Fig. 3.22 Comparison of mean and range for height and number of rays of H. mantegazzianum, H. sphondylium and hybrid plants at Riddell, Roslin, Kale Water 1976 and 1977 and Coldstream

than at any other site. The range of H. sphondylium ray number overlaps with the number of rays for hybrid plants when several sites are considered. In the scatter diagram in Fig. 3.23 all plants of H. sphondylium and hybrid origin surveyed in 1976 and 1977 are positioned by ray number and leaf width as for Kale Water plants in Fig. 3.16. Two hybrids from Kale Water are within the scatter of H. sphondylium plants, and there is less separation between the two groups, even though leaf width values show little overlap. The means and coefficients of variation for leaf width at all sites are as follows (Table 3.6):

Table 3.6. Mean leaf width and coefficient of variation for H. sphondylium, H. mantegazzianum and hybrid plants at Riddell, Roslin, Coldstream and Kale Water, 1976 and 1977

	S	H	M
Roslin (pure H. sphondylium)	26 (24%)		
Riddell (pure H. mantegazzianum)			151 (22%)
Kale Water 1977	28 (19%)	52 (34%)	95 (17%)
Kale Water 1976	27 (29%)	63 (16%)	105 (28%)
Coldstream	27 (26%)	46	105 (27%)

H. sphondylium leaf width remained constant for different sites, and from one year to the next. H. mantegazzianum leaf width was more variable, both in mean value and in the coefficient of variation between sites and years.

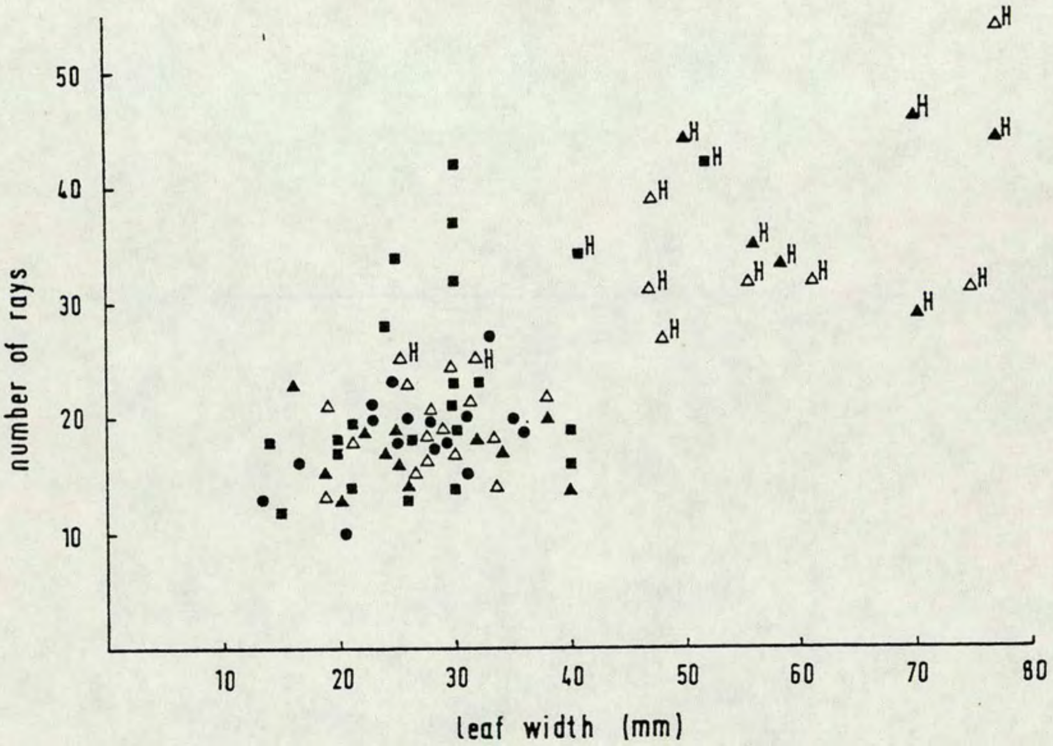


Fig. 3.23 Scatter diagram of number of rays and leaf width for plants of H. sphondylium at Roslin (●), and H. sphondylium and hybrids (H) at Kale Water 1976 (▲) and 1977 (△), and Coldstream (■)

Summary

The morphological measurements for all 63 H. sphondylium, 60 H. mantegazzianum and 17 hybrids in the survey are summarized in Table 3.7 as the range over all sites for those quantitative characters most often mentioned in taxonomic literature (Brummitt 1968, Mandenova 1950, Clapham et al. 1962, Koval 1975).

Table 3.7. Range of values of 12 morphometric characters for all H. sphondylium (S), H. mantegazzianum (M), hybrid (H) plants surveyed in 1976 and 1977

	S n=63	H n=17	M n=60
Height (m)	0.9 - 2.05	1.5 - 2.6	2.4 - 4.30
B.S.D. (mm)	10 - 25	18 - 49	40 - 110
No. of rays	10 - 42	25 - 42	52 - 169
Umbel diameter (mm)	65 - 250	160 - 440	420 - 740
Leaf length (mm)	110 - 390	300 - 620	320 - 1250
Leaf width (mm)	140 - 400	260 - 770	340 - 2240
Mericarp length* (mm)	6.90 - 11.00	9.05 - 13.60	9.65 - 14.00
Mericarp breadth (mm)	5.40 - 7.25	6.90 - 8.65	5.50 - 9.35
Dorsal vittae width (mm)	0.25 - 0.43	0.44 - 0.98	0.74 - 1.50
Commissural vittae width (mm)	0.23 - 0.50	0.40 - 0.81	0.58 - 1.28
Dorsal vittae length/mericarp length	0.56 - 0.77	0.59 - 0.75	0.67 - 0.77
Commissural vittae length/mericarp length	0.43 - 0.61	0.46 - 0.63	0.45 - 0.53

* Mericarp characters calculated from Roslin, Riddell, Kale Water, 1976 and 1977 only (not including Coldstream).

3.4 Discussion

The existence of a group of plants intermediate between *H. sphondylium* and *H. mantegazzianum* which could be considered as hybrid was satisfactorily demonstrated by the principal component analysis of Kale Water data collected in 1977. Intermediacy does not give proof of hybridization, but provides a criterion for allocating plants to taxa so that the characters differentiating groups can be described. Ordination of the data from 1976 suggests that it is difficult to distinguish hybrids in an analysis of measurements from more than one population, but for field observations it matters only that hybrids are correctly identified at any one site. The results of the principal component analysis suggest that at Kale Water all putative hybrids were recognized in the field.

A better separation between groups in the 1976 analysis might have been obtained by including a larger number of characters, particularly the assessment of fertility, micromorphology and fruit characters which were added to the list in 1977. Vegetative characters alone can differentiate taxa in numerical studies of some species. Fifteen OTUs (operational taxonomic units) of *Allium* were distinguished by the two axes attributable to scape/sheath length ratio, leaf number and shape, and to bulb and leaf diameter in a principal coordinates analysis of 49 morphometric characters (El-gadi & Elkington 1977). For Limnanthaceae, two artificial hybrids among 21 OTUs were associated with different parents if the analysis was based on vegetative characters or included floral parts (with a total of 35 characters) (Ornduff & Crovello 1968). Vegetative characters alone have not yet been found sufficient for a numerical classification of the Umbelliferae. McNeill et al. (1969) working with 83 characters from 27 OTUs from the tribe Caucalidae found that with a centroid sorting strategy leaf characters contributed virtually nothing to the resultant classification, while fruit characters and unexpectedly floral characters were relatively important. From the second principal component analysis of this study it would appear that fruit and floral characters are equally important for a numerical analysis of hybrids between H. mantegazzianum and H. sphondylium.

On the other hand adding characters to the 1977 data set is more difficult to justify, given the limited objective simply to indicate the existence of a hybrid group. Hall et al. (1976) has tried varying character sets with a principal component analysis. Data for 107 OTUs of the Bulbostyis/Fimbristylis (Cyperaceae) complex in Nigeria was split into 8, 12, 16, 20 and 24 random character samples of the total 55 presence/absence characters from all parts of the plant. With a reduction in character number the scatter on the first and second principal components from analysis of weighted similarity coefficients of the data became more compact, but groups separated on the first component remained distinguishable, even if only 8 characters were used. It is interesting to note that Hall found a more distinct separation of groups on the first component. In the analysis of the 1976 data only the first component was associated with a character which separated groups. Quality of data rather than quantity is much more likely to change the results of an analysis. This has been demonstrated by Bisby and Nicholls (1977) who ran six different sets of morphometric data for 175 species of the tribe Genistae with different definition and selection of characters through a single linkage clustering program and obtained very different results. Therefore, although the 38 character set of the 1977 analysis is to be preferred to the 18 character set of the 1976 analysis because of the inclusion of floral and micromorphological characters, further additions to make up the 60 characters required for a numerical study (Sokal & Sneath 1973) are not needed to distinguish the hybrid group, and in fact the final data set could be considerably reduced and still retain a separation between species.

Although the multivariate analysis was able to identify a group of intermediate plants, the interpretation of eigenvectors was not particularly helpful in choosing characters to describe hybrids. The general size of plants and their pollen fertility (Table 3.3) were the most biologically meaningful characters associated with components. In contrast, the simple descriptive statistics of each of the three groups confirmed by the principal component analysis showed that four characters were discrete: pollen length, hair length, dorsal vittae width and the number of rays. Of these pollen length and hair length were least variable, but were studied for Kale Water plants only. Dorsal vittae width and number of rays, which were less consistent, differed between sites and years.

All four characters have already been studied for species of *Heracleum*. Pollen shape has been carefully described in the work of Cerceau (1962, 1959) on the Umbelliferae. Cerceau's (1959) value of 64 µm compares well with *H. mantegazzianum* at Kale Water in 1977 with a pollen length between 60.4 µm and 70.0 µm, of mean length 65.3 µm. *H. sphondylium* at the same site, with a mean pollen length of 44.7 µm and a range from 41.7 µm to 47.1 µm, resemble the *H. sphondylium* in the study on *Tetrataenium* (Mandenova et al. 1978) with a mean pollen length of 43.0 µm but not Cerceau's early work (1959) where pollen length for *H. sphondylium* was 38.5 µm.

It is important that pollen samples are taken from the same order umbel in the Umbelliferae. With *Eryngium maritimum* (Sub-family Saniculoideae (Tutin et al. 1968))a difference was found between pollen on tertiary and primary inflorescences with inhibited growth and secondary inflorescences with normal growth (Van der Pluym & Hideux 1977a). Abnormal pollen was also found on secondary umbels of *Peucedanum palustre* (Sub-family Apioideae (Tutin et al. 1968)) and less matured pollen grains were found towards the centre of the umbel (Hideux et al 1978, Nigaud 1978). At Kale Water estimates of pollen length per plant were made from 10 measurements only, taken from a sample of grains from central, middle and outer umbellets of the terminal umbel.

However, pollen size measured at Kale Water in 1977 probably does not adequately represent the range of values for either species from different populations in south-east Scotland. The amount of variation in pollen length for one population has been found to depend on the species studied for the Umbelliferae. Bell (1955) found too much variation between populations for pollen length to be of use in determining the polyploid level for the Sanicula crassicaulis complex and later (Bell 1959) suggested that mineral nutrition might affect the variation in pollen size. For Eryngium maritimum (in the same sub-family as Sanicula) pollen length was found statistically homogeneous for one population but not for plants from several geographical locations (Van der Pluym & Hideux, 1977b. Mean pollen length for E. maritimum over all sites was 48.01 µm ± 0.18 µm with a range from 41.2 µm to 55.9 µm. For Peucedanum palustre (Nigaud 1978) the mean for seven different sites was 30.91 µm with range from 29.40 µm to 32.92 µm and for Seseli the range over ten species was from 22.0 µm to 32.0 µm (Pardo 1978). The range in pollen length for H. mantegazzianum at one site Kale Water in 1977 from 60.4 µm to 70 µm was therefore large compared with P. palustre and Seseli species from several sites, but not as great as the variable E. maritimum. H. sphondylium at Kale Water had a narrow range of pollen lengths from 41.7 µm to 47.1 µm but almost certainly may be expected to vary from site to site, if not in south-east Scotland, then in Britain. Gawlowska (1961) obtained a range of values from 29.7 µm to 45.9 µm for H. sphondylium var. chaetocarpoides at different sites in Poland. Means and ranges are listed below:

Site	Mean (µm)	Min-Max (µm)	No. of grains	No. of plants
Krakow I	35.75	29.7 - 40.5	100	5
Krakow II	41.93	32.4 - 45.9	90	5
Maluszyn	39.96	29.7 - 33.2	92	5

Despite variation of this magnitude which may be expected between populations of H. sphondylium in Scotland, it would still be possible to distinguish H. sphondylium pollen from hybrid pollen which has a range from 52.5 µm to 57.3 µm in length.

Pollen length, although significant for this regional study, is not a certain diagnostic character. Cerceau (1971) has given the length of H. lanatum pollen as 60.0 µm. Brummitt (1971) has included this species with H. sphondylium subsp. montanum, yet its pollen length approaches that of H. mantegazzianum and exceeds the length of hybrid pollen. It is probably important to quote pollen lengths at sub-specific level for the sphondylium complex.

Cerceau has used tectal surface structure to separate Himalayan and South Indian species of Heracleum from Eurasian relatives (Mandenova et al. 1978): South Indian species have surface "tectale striée-rugulée à striée", while *H. sphondylium*, the Eurasiatic relative, has "surface tectale cérébroïde a rugulée aux pôles". However, *H. mantegazzianum* has been described (Cerceau 1971) as "surface tectale striato-rugulée" and is supposedly a Eurasiatic species also. Structure of the tectal surface has also been used as a diagnostic character in *Eryngium* (Van der Pluym & Hideux 1977b) and *Pterolobium* (Hul Thol 1977) but examination of this character requires scanning electron microscopy, transmission electron microscopy and associated techniques for splitting pollen grains (Cerceau 1971), in order to view columnar structure of the tectum. The easy to measure character of pollen length may be of limited application in distinguishing *Heracleum* species, but when combined with an assessment of pollen fertility it is both practical and sufficient for identifying hybrids from a limited geographical area.

Leaf hairs have recently been investigated as a diagnostic character for *Heracleum* taxonomy by Guyot (Mandenova et al. 1978, Guyot 1978) as part of the study on *Tetrataenium*. Other leaf surface structures, stomatal type and density, were found to be homogeneous for *Heracleum*. The structure of leaf hairs is thought to be a more dependable character than their density which may vary with growing conditions (Grace & Russell 1977). Traditionally plant pubescence has been associated with a response to dry environments; the ecological aspects of pubescence have been reviewed recently by Johnson (1975). The surface structure of hairs, the pitting or roughening of the outer cell wall, is the result of changes in mycofibril orientation during growth as well as the deposition and accumulation of carbonates, silicates etc. (Johnson 1975). The variable ornamentation of leaf hairs was thought to be of secondary importance for the taxonomy of the genus compared with the form of the apex. At Kale Water the surface structure for hairs on the lower leaf surface was consistently tuberculate for H. mantegazzianum and smooth or only slightly pitted for H. sphondylium. Ornamentation must indeed be a variable character for Heracleum as Guyot states that "H. sphondylium et H. afghanicum présentent des poils striés, plus ou moins couverts de tubercules, de forme aiguë, qui les différencient nettement de ceux des Tetrataenium qui, en général, sont lisses."

Hair length may be more dependable. For H. mantegazzianum at Kale Water 1977 the range was 96.0 µm to 123 µm, while that of H. sphondylium was 506 µm to 638 µm and the hybrid 202 µm to 385 µm. Guyot quotes a wider range of lengths for H. sphondylium: 300, 400-800 µm, but these included hairs on the nerves which are much longer, and were not part of the Kale Water calculations. At any one site, the length of hairs on the lower epidermis of the leaf which may be assessed accurately by microscopy or approximately in the field, is a very satisfactory character for distinguishing hybrids.

Fruit morphology was most recently described by Koval (1975). His results are listed in Table 3.8.

Table 3.8. Ranges of values for fruit characters for H. sphondylium and H. mantegazzianum from Koval (1975)

	H. mantegazzianum	H. sphondylium
length (cm)	9-14	6-7
breadth (cm)	6-8	5-6
dvw (mm)	1	0.25
dvl/l	0.8	0.6
cvw (mm)	1	0.25+
cvl/l	0.5-0.67	0.5-0.67
wing breadth (cm)	0.75	0.5

Fruits of H. mantegazzianum in south-east Scotland (Table 3.7) conform with Koval's description of H. mantegazzianum except that the vittae are slightly shorter and wider, and the fruit wing more broad. According to Koval's key these plants with dorsal vittae width greater than 1.25 mm would be H. sosnowskyi or H. pubescens. However, in Scotland, plants from the same origin growing at Kale Water and Riddell (Section 2.3) have dorsal vittae widths varying from 0.75 mm to 1.50 mm. Moreover, fruits from Kale Water closely resemble those of H. mantegazzianum described by Koval (1975) and fruits collected from the garden of H. Correvon in Geneva (p.19) in all other respects: elliptical shape, style three times the length of the stylopod, papillose pubescence on the dorsal surface, fruit apex barely emarginate, disc conical. Dorsal vittae width is not a good character for separating the large Heracleum species.

H. sphondylium from south-east Scotland not only has wider dorsal vittae than those measured by Koval, but also longer mericarps (Table 3.7). They are larger also than measurements made by Gawlowska (1961) on *H. sphondylium* in Poland of length 4.7-8.2 mm, and breadth 3.5 mm to 5.6 mm, but are not exceptional for Great Britain. Ripe fruits collected on waste ground in Bradford, Yorkshire, were 5 mm to 11 mm in length, 3 mm to 8 mm in width (Bradley & Fell 1966). Although Clapham et al. (1962) quote fruit length for *H. sphondylium* as 7 mm to 8 mm, Brummitt (1968) describes them as "(5-)7-10(-12) mm, elliptical or suborbicular, glabrous, vittae rather slender, up to 0.4 mm wide", which encompasses the range of lengths of 6.90 mm to 11.0 mm and dorsal vittae width of 0.25 mm to 0.43 mm for south-east Scotland plants.

Fruits of *H. mantegazzianum* may also vary by 5 mm in length. Sommier and Levier's (1895) original description was 12 mm to 14 mm, greater than the (7)9-11 mm quoted by Brummitt (1968). Mandenova (1950) gave 10-11 mm as the length of *H. mantegazzianum* fruits in the Caucasus, and those of *H. grossheimii* as 12-14 mm. These two species were combined as *H. mantegazzianum* in Grossheim (1967). Therefore the length of 9-14 mm for fruits from south-east Scotland (Table 3.7) is similar to measurements for the same species in the Caucasus and probably represents the range of variation that may be expected in the species in response to environmental stress (Section 4.4).

Fruit length and dorsal vitta width do not remain discrete for hybrid plants when the variation in parent species is considered, either from south-east Scotland (Fig. 3.14) or from the European Floras. Hybrid fruits may be described as having a large size relative to dorsal vittae width compared with parent species, but other characters, such as the fact that a very few seeds (0-3% Table 3.4) on a hybrid umbel are actually fully developed with endosperm, give better evidence of hybrid status.

Ray number and other characters measured in the field (Table 3.7) may be compared with the few dimensions in the type description of H. mantegazzianum (Sommier and Levier 1895) and a fairly complete description by Brummitt (1968) (Table 3.9).

Table 3.9. Morphological measurements: H. mantegazzianum described by Brummitt (1968) and Sommier and Levier (1895)

	Somm & Lev.	Brummitt
Height	2m+	2-5 m
BSD		10 cm
Leaf l x b	65 x 50 cm	to 300 cm
segment l	50 cm	130 cm
umbel diam.		50 cm
No. of rays	50+	50-150

H. mantegazzianum in south-east Scotland exceeds upper limits for ray and umbel diameter given by Brummitt (1968). H. sphondylium also exceeds the maximum of 25 for subsp. sphondylium (Brummitt 1968). More rays than 30 per umbellule have been counted for individuals in pure H. sphondylium populations at Farfield and Jedburgh in 1975, and at mixed sites such as Coldstream as well, but are within the range of 45 for the species. Subspecies of Torilis arvensis (Umbelliferae) cannot be separated by ray number either, and in Daucus carota ray number and number of flowers produced per umbellet has been found to increase with decreasing temperature (Quagliotti 1967). Ray number also varied between sites (Fig.3.22) possibly in response to environmental stress (Section 4.4). Therefore a wide difference in the number of rays per plant may be expected, within a limit of about 50 for the minimum number of rays for a primary umbel of a single flowering stem of H. mantegazzianum and 45 as the maximum for H. sphondylium.

H. mantegazzianum in south-east Scotland is also tall. Sommier and Levier (1895) say "Planta in loco natali 2½ m alta". This was at 900 m in Seken, Abkhazia, and at 1700-1800 m by Kliutsch. However, a photograph taken at the Gumista Reservation, Abkhazia (Sakhokia 1961) shows H. mantegazzianum growing at least 5 m tall. The highest site for this survey was at Riddell at an altitude of 170 m where plants grew to 3.15 m in height.

Observations on H. sphondylium in south-east Scotland also support Brummitt's (1971) contention that specific limits cannot be drawn within this complex on the basis of leaf form. Plants may have ternate leaves or pinnate leaves with 2 pairs of leaflets. The photographs in Fig.3.17 when compared with leaf drawings by Briquet (1903) and Thellung (1926) are found to include all types of leaf dissection from lanceolate to ovate and very broadly ovate which were previously used to distinguish subspecies.

Other Umbelliferae have been found to show considerable variation in leaf outline. In Torilis arvensis there may be a transition from 2-3 pinnate to ternate or 3 lobed leaves at different heights on a single plant (Jury 1978). In some species this variation is ecotypic. Forms of Anthriscus sylvestris (L.) Hoffm. with narrow leaf shape were associated with dry sites, and large leaf types with fertile localities (Petersen 1915). A recent biosystematic study of 11 populations of Heptaptera in Israel (Hermstadt and Heyn 1971) demonstrated that two groups of plants were associated with altitude. At high altitudes Heptaptera have 3-4 pairs of segments per leaf, and shorter and fewer rays, while low altitude forms have 5-8 segments per leaf which are more dissected. Bell (1955) after examining leaf variation in Sanicula decided that a foliar classification would be "a guide to population and ecotype variants rather than a key to polyploidy". Similarly Webb (1977) found that populations of Gingidia enysii maintained differences in leaf shape when grown in a uniform environment, but concluded that "the variation is continuous and that varietal rank of any of the forms unwarranted."

Bradshaw (1965) has pointed out that plasticity evolves separately in related taxa and may not have adaptive significance. Although narrow leaves are associated with dry sites in some Umbelliferae, the subspecies sphondylium appears to be polymorphic for leaf type and shows a wide variation from ovate to lanceolate shapes at each site. However, it is possible that within the broad definition of H. sphondylium by Brummitt (1968) leaf division does show ecotypic variation. This is being investigated by Weimarck (Fischer et al. 1978, Weimarck 1978).

However variable the leaf characters and general features of Heracleum, field recognition of hybrids depends largely on the shape of plants as illustrated in the ideograms (Fig. 3.18) and their noticeably low fertility, either as unusual floral morphology, or low seed set. The large leaves of hybrids, of a slightly dull sheen compared with the glossy leaves of H. mantegazzianum, and yet not as noticeably pubescent as H. sphondylium provides a further check of intermediate status, which may be confirmed by detailed comparison of hair length and pollen length for plants from one site.

Phenetic evidence of hybridization is also inherent in the variability of a group of hybrid plants (Schueler & Rising 1976). Hybrids at Kale Water are more variable than either parent in number of rays, leaf width, dorsal vittae breadth and hair length (Table 3.4). In general, H. mantegazzianum was less variable than the polymorphic H. sphondylium, (Table 3.4 and Appendix IV) showing only slight variation between populations that could be attributed to site type. No differences could be found between H. mantegazzianum at Kale Water, and at Coldstream, where plants of different origin were thought to grow (Section 2.3). H. mantegazzianum in south-east Scotland is remarkably uniform in appearance, and closely resembles the description of plants from the Caucasus. There was no noticeable increase in variation or change in morphology between pure and mixed populations of either species that might indicate introgression. However, backcrosses may have been included in the intermediate plants classed as hybrids. In the illustration of variation in Kale Water hybrids (Fig. 3.20) H7 and H5 most closely resemble H. mantegazzianum and H6a H. sphondylium. H7 and H5 were growing amongst H. mantegazzianum plants (Fig.3.2) while H6a was on the edge of H. sphondylium population I and adjacent to hybrid H6. Further evidence for backcrossing is discussed in Chapter VI.

CHAPTER IV

Floral Biology and Experimental Crosses

4.1 Introduction

Objectives

The experimental crosses were designed to provide evidence for the existence of hybrids between *H. sphondylium* and *H. mantegazzianum*. They are described in Section 4.3. An understanding of the floral biology of the two species was needed to carry out the work, this is explained in Section 4.2.

Transplants

Observations on floral biology and experimental crosses were made on *H. sphondylium* and *H. mantegazzianum* transplants from a number of sites around Edinburgh. Plants in the rosette stage were dug out in March or early April and settled immediately in tubs with their own soil. Those which flowered were brought into the greenhouse in early June for experimental work. *H. sphondylium* plants collected in 1976 overwintered in cultivation and flowered again the following year. *H. mantegazzianum* are monocarpic and new plants had to be transplanted each spring. Table 4.1 lists the date and origin of each provenance, the number of transplants, and the number of plants finally used for the controlled crosses. Losses in flowering material were greater than 50%. They were due to plants remaining in the vegetative state (none of the hybrid plants flowered) and to predation by the larvae of Depressaria pastinacella, the parsnip flat-bodied moth.

These very active larvae were the only serious pest for Heracleum cultivated in the greenhouse. Aphid and mildew infestations were controlled by spraying regularly with "Primor", "Milgo", "Zinab" and Nicotene. Spraying for the larvae was not possible because of their behavioural pattern. Depressaria pastinacella, a species with a holarctic distribution, pupates in July or August in the hollow stems of Heracleum, Pastinaca or Angelica, or in the ground, hibernates overwinter in houses and outbuildings, mates the following spring and lays its eggs on the unopened umbels of new host plants (Thompson & Price 1977, Thompson 1978). The larvae have vivid markings: a black head and black base of hairs on a pale body. Also known as the parsnip webworm, they bind together several young umbellets with webbing to form an enclosure within which they feed. On Heracleum plants, unlike Pastinaca (Thompson 1978) several larvae may be found in a single umbel. Once Heracleum plants have become host to D. pastinacella larvae only rigorous attention to infested buds, either by removing them completely or searching carefully for larvae with a pair of sharp forceps, will prevent the extremely active larvae from migrating to other flower buds on the same or adjacent plants. In 1977 nearly all plants moved into the greenhouse were host to the larvae. Only three H. mantegazzianum inflorescences were so badly infested that they failed to open at all, but 10 *H. sphondylium* plants lost all their flowering stems. Plants from Roslin and Slitrig were particularly badly infested, and a number of secondary umbels from *H. mantegazzianum* plants and single stems of *H. sphondylium* had to be removed. Cultivated *Heracleum* should be kept in an insect free environment from early spring to late June to avoid infestation with these larvae.

Table 4.1 Number and date of transplants for each provenance used for experimental crosses

Date of Transplant	Origin	Number of transplants	Number flowered and used for crosses
H. sphondylium			
1975	Park Burn	7	2
13 March 1976	Farfield	10	14
23 May 1976	Farfield	10	
5 June 1976	Slitrig	10	3
5 April 1977	Roslin	10	0
		47	19
H. mantegazzianum			
18 March 1977	Hopetoun	10	8
23 March 1977	Riddell	10	1
		20	9
H. mantegazzianum x *H. sphondylium*			
23 March 1977	Riddell	3	0

4.2 Description of Flowering in Heracleum

Heracleum flowers are protandric, anthers dehisce and pollen is shed before the stigma becomes receptive. Individual flowers open in successive mornings across the primary umbel and then in sequence through the secondary and tertiary umbels. Most flowers are hermaphrodite, but an increasing proportion of male flowers are found in lower order umbels.

Pollen presentation and pollen collection has been described by Percival (1949) for H. sphondylium and the characteristics of flowering in H. sosnowskyi by Shumova (1970). Ponomarev (1960) recorded a distinct separation of sexual stages on primary and secondary umbels of Libanotia intermedia, Carum carvi, Chaerophyllum Prescottii, Conium maculatum, Libanotis buchtarmensis, Pastinaca silvestris, Pimpinella saxifraga, Seseli strictum, and Silaus Besseri. The only species without synchrony where all primary and secondary umbels flowered by protandry in unison was Peucedanum Lubimenkoanum. An account of flowering in plants used for experimental crosses follows.

Individual flowers

The individual Heracleum flowers have five petals and five stamens inserted alternately below the rim of a conical stylopodium. Petals are zygomorphic, outer flowers of outer umbellets have the most enlarged outer petals. Two filamentous styles merge with the two halves of the fleshy stylopodium. The two ovules are inferior and encased by a green receptacle which later enlarges to form the seed coat. Male flowers have a smaller receptacle with reduced or no stigma and stylar tissue. Male sterile flowers similar to those found in Daucus carota (Braak and Kho 1958) are found very rarely in H. sphondylium or H. mantegazzianum in south-east Scotland Figs. 4.1 to 4.4 show the development of individual flowers of H. sphondylium and H. mantegazzianum. For both species four stages may be discerned:

1. In bud

Petals and filaments are furled over the immature anthers (Fig. 4.1). The tip of the stigma surfaces are slightly exserted at the centre of the bud. H. mantegazzianum buds are yellow-white, those of H. sphondylium slightly green and pink. Buds lighten colour slightly the day before opening.

2. Dehiscence

Petals uncurl and white filaments hook outwards as the flower opens. When petals have unfurled the filaments straighten one by one, the olive green or red-brown anthers tip upwards, and each of the two anther lobes splits longitudinally along the side (Fig.4.2.). The anther wall rolls back to expose the oily yellow pollen load. Time taken from flower opening to dehiscence varies from one to several hours according to the time of day and temperature. Twenty four hours after pollen presentation the filaments collapse and anthers fall below the petal surface (Fig.4.3.).

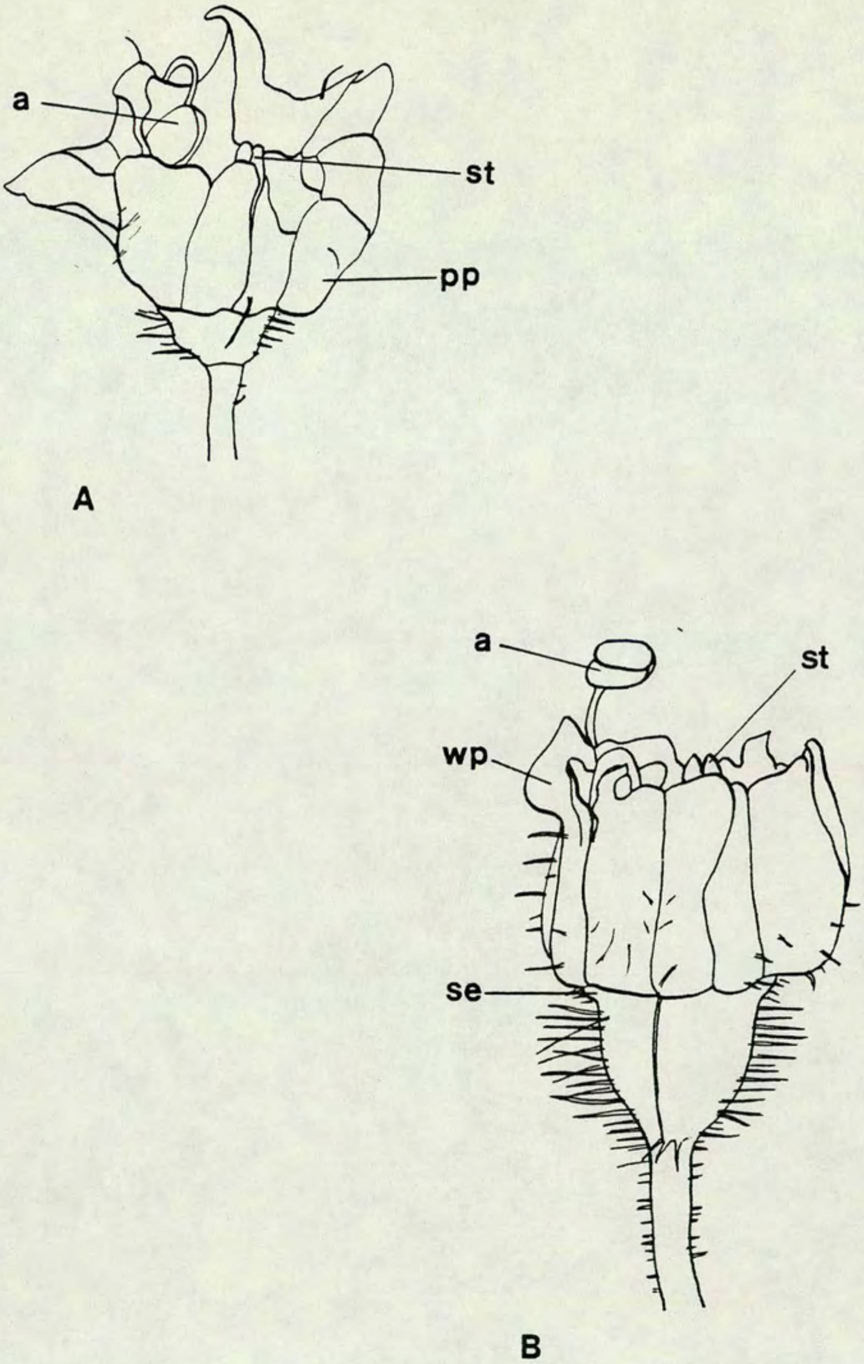


Fig. 4.1 Buds. A. *H. sphondylium*
B. *H. mantegazzianum*
a, anther; pp, pink-tinged petals; se, sepal; st, stigma; wp, white petals

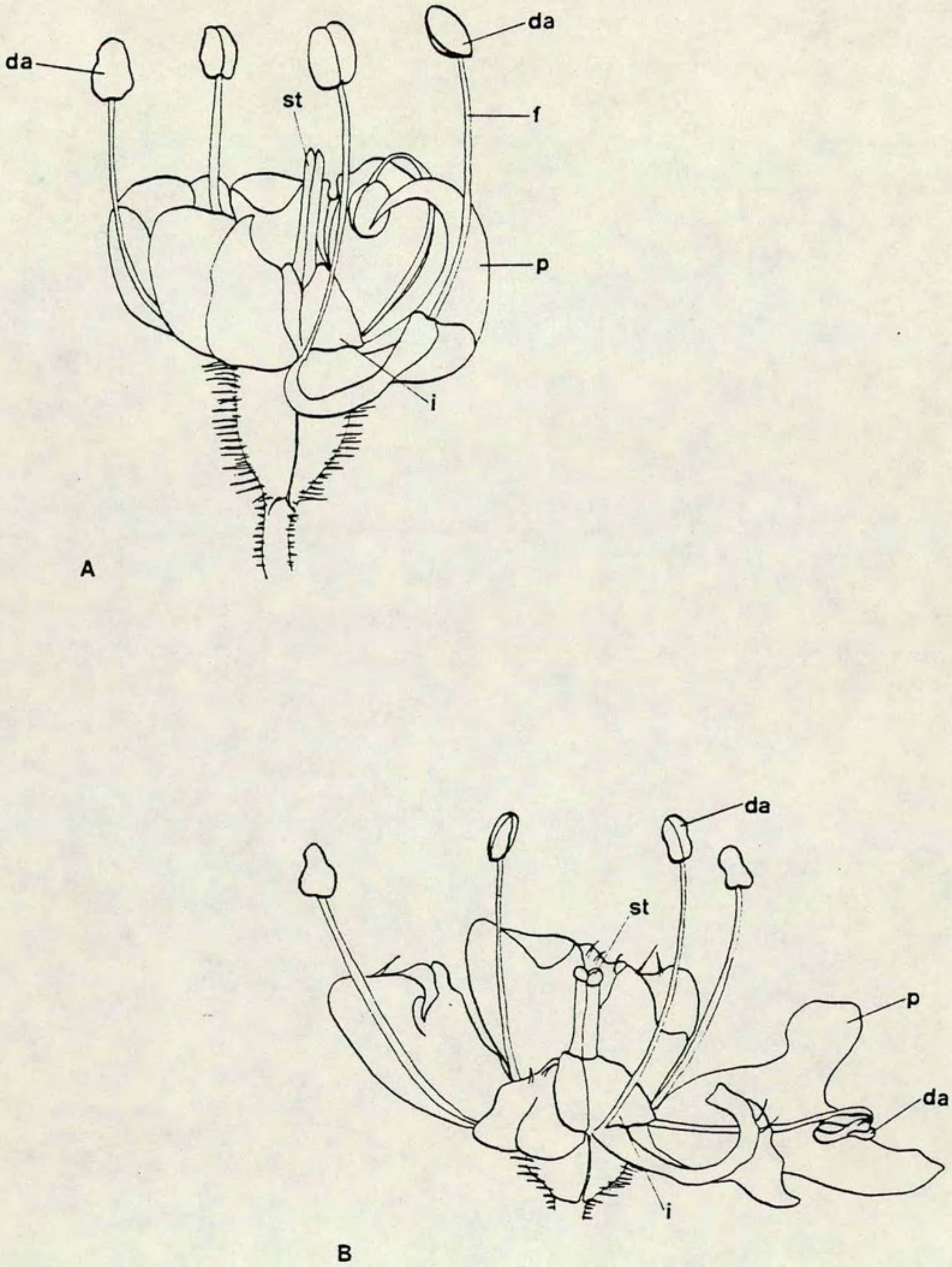


Fig. 4.2 Dehiscence A. *H. mantegazzianum*
B. *H. sphondylium*
a, anther; da, dehisced anther; f, filament;
i, indumentum; p, petal;
st, stigma

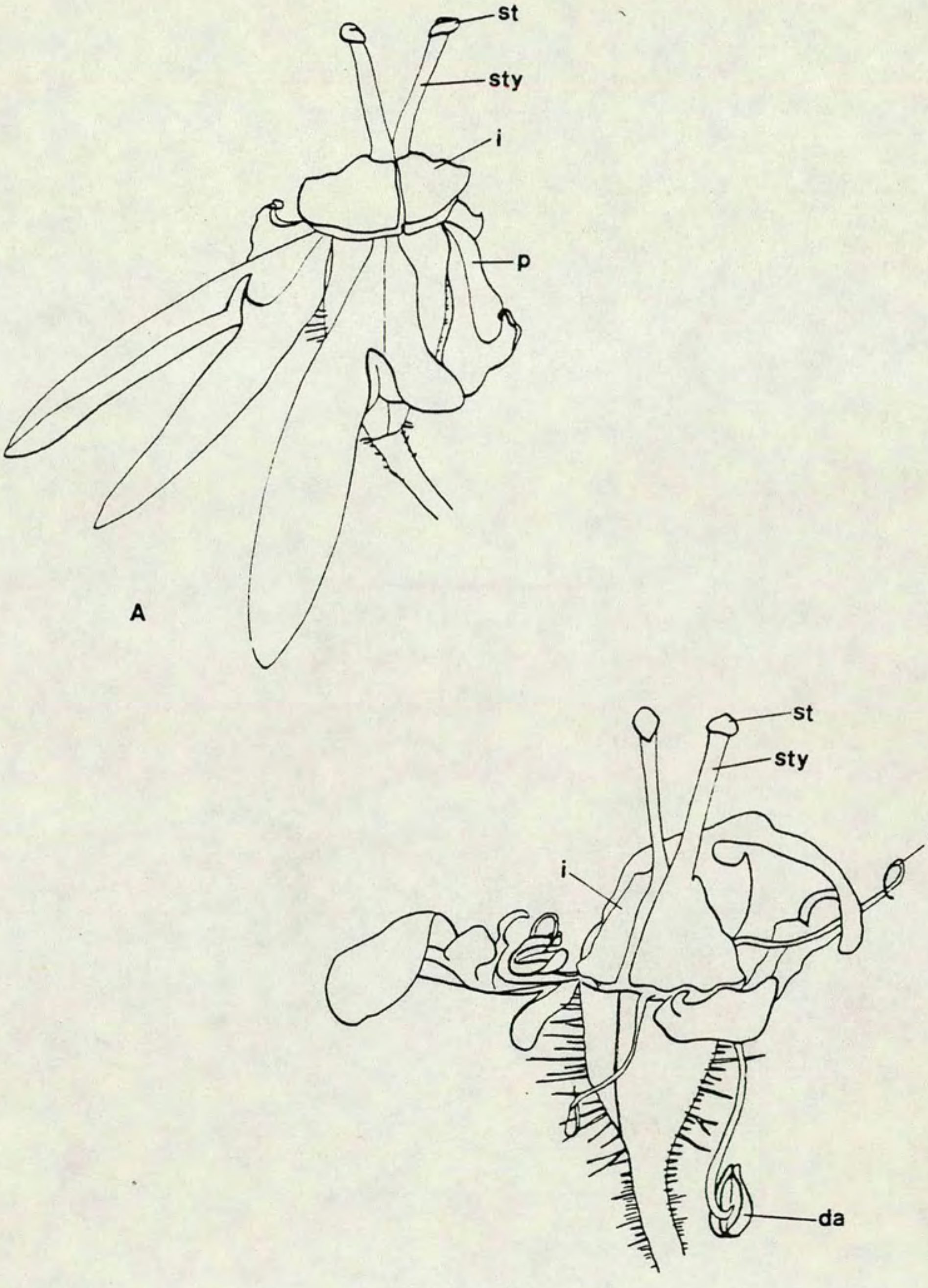


Fig. 4.3 Receptive flowers A. *H. sphondylium*
B. *H. mantegazzianum*
da, dehisced anther;
f, filament;
i, indumentum; p, petal;
st, stigma; sty, style

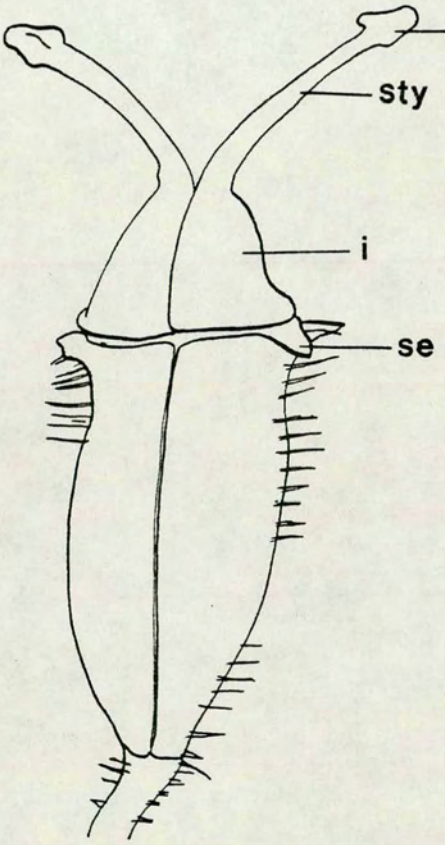


Fig. 4.4 Young fruit <u>H. mantegazzianum</u>
i, indumentum; se, sepal;
st, stigma; sty, style

3. Receptive

At dehiscence the exposed stigma are immature. Each pair lies with styles and stigma surface touching. Over a period of one to five days the styles elongate, part, and bend back to expose the stigma surface. In H. sphondylium the stigma is rounded (Fig.4.3.), in H. mantegazzianum it is elongated (Fig.4.3.). At maturity the stigma surface becomes sticky, sometimes slightly tinged with pink, and a drop of nectar forms an arc between the filamentous style and the indumentum surface. In H. sphondylium the petals are bent back slightly at maturity (Fig.4.3.) and shed after pollination. In H. mantegazzianum the petals are retained horizontal to the receptive flower (Fig.4.3.).

4. Young fruit

After fertilization, the indumentum surface dries out and darkens in colour. The fruit begins to elongate and flatten in a dorso-ventral plane (Fig.4.4). When ripe, the two mericarps are held by a central commissure.

The Inflorescence

Individual flowers open in sequence across a single compound umbel. The outer flowers of outer umbellets open first, followed by the outer flowers of middle umbellets. The middle flowers of outer and middle umbellets, and the outer flowers of inner umbellets open next, and finally, about four to five days later, the inner flowers of all umbellets open together. This is shown graphically in Fig.4.5 for H. sphondylium (No.26) using approximate divisions for flower categories in Fig.3.4. Most flowers open early in the morning, and very few after midday. Percival (1949), describing an H. sphondylium stand flowering in south Wales from 24th July to 8th August, reported 61% of the day's flower production complete by 8 a.m. Shumova (1970), for H. sosnowskyi flowering in late June, described flower opening between 6 a.m. and 7 a.m., followed by dehiscence at 9 a.m. Of the plants used for experimental crosses, dehiscence was most regular in H. mantegazzianum where anthers presented pollen more or less at the same time with the first warm sunlight after 7 a.m. H. sphondylium spread flower opening over the day; so that some flowers dehisced early in the morning at 5 a.m., and others late at night. In 1976, when the weather was exceptionally warm, dehiscence began at 4 a.m.

After the last flower on a compound umbel opens there is a pause of 24 hours or more before the flowers become receptive. This delay can only be approximated from the change in morphology of the flower and for the plants cultivated in 1977 appeared to vary from one to four days, with two days usual for H. mantegazzianum and two to three days for H. sphondylium. Shumova (1970) reports a 24 hour delay for H. sosnowskyi, which coincides with the start of the male phase of the secondary umbels.

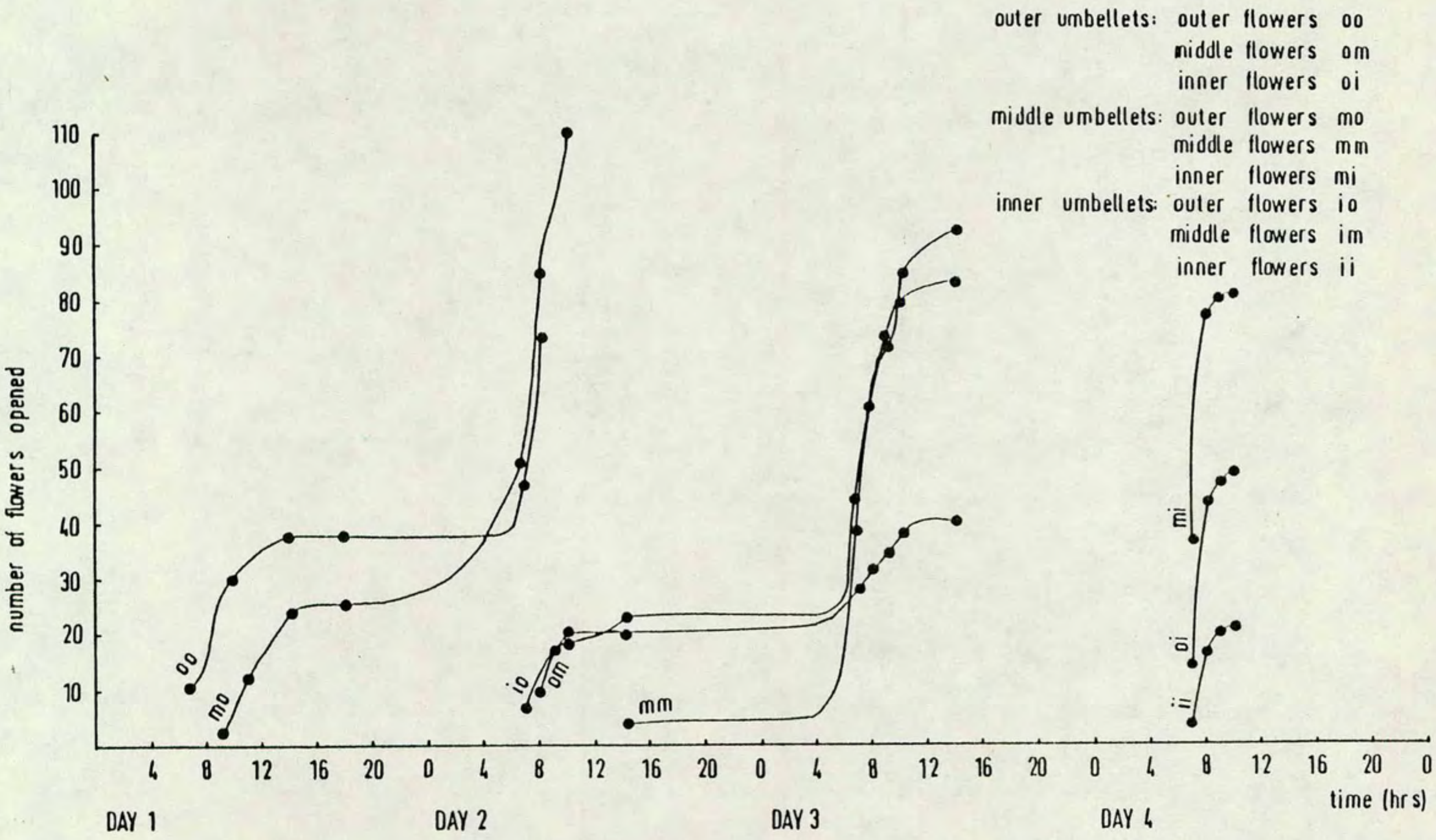


Fig. 4.5 Timing of flower opening: <u>H. sphondylium</u>

The flowering sequence is repeated for the total number of sub-umbel orders, secondary umbels flower next, then tertiary umbels etc. The separation between the male phase of primary and secondary umbels varies between plants. The frequency of the duration of each phase is shown in Fig.4.6 for all plants studied in 1977. The male phase lasts approximately four to five days in primary and secondary umbels for both species, but the interval between pollen presentation in different order umbels was only two or at most four days for *H. mantegazzianum*, while secondary umbels of *H. sphondylium* flowered up to seven days after the end of the male phase of the primary umbel. Across the whole inflorescence of a flowering *H. mantegazzianum* there will therefore be receptive stigmas at the same time as pollen presentation on lower order umbels, while for *H. sphondylium* some plants may be strictly protandric, with female stage complete on one umbel before flowering commences on the next. Flowering of secondary umbels in greenhouse plants was not exactly synchronized, sometimes one or two days separated the beginning of the male phase in several secondary umbels.

Effective protandry is also reduced in *H. sphondylium* by the out of sequence flowering of inflorescences on separate flowering stems from a single plant. Most plants of *H. sphondylium* in the greenhouse produce two or more flowering shoots from the same plant, and these usually flowered one to two or three days out of sequence so that

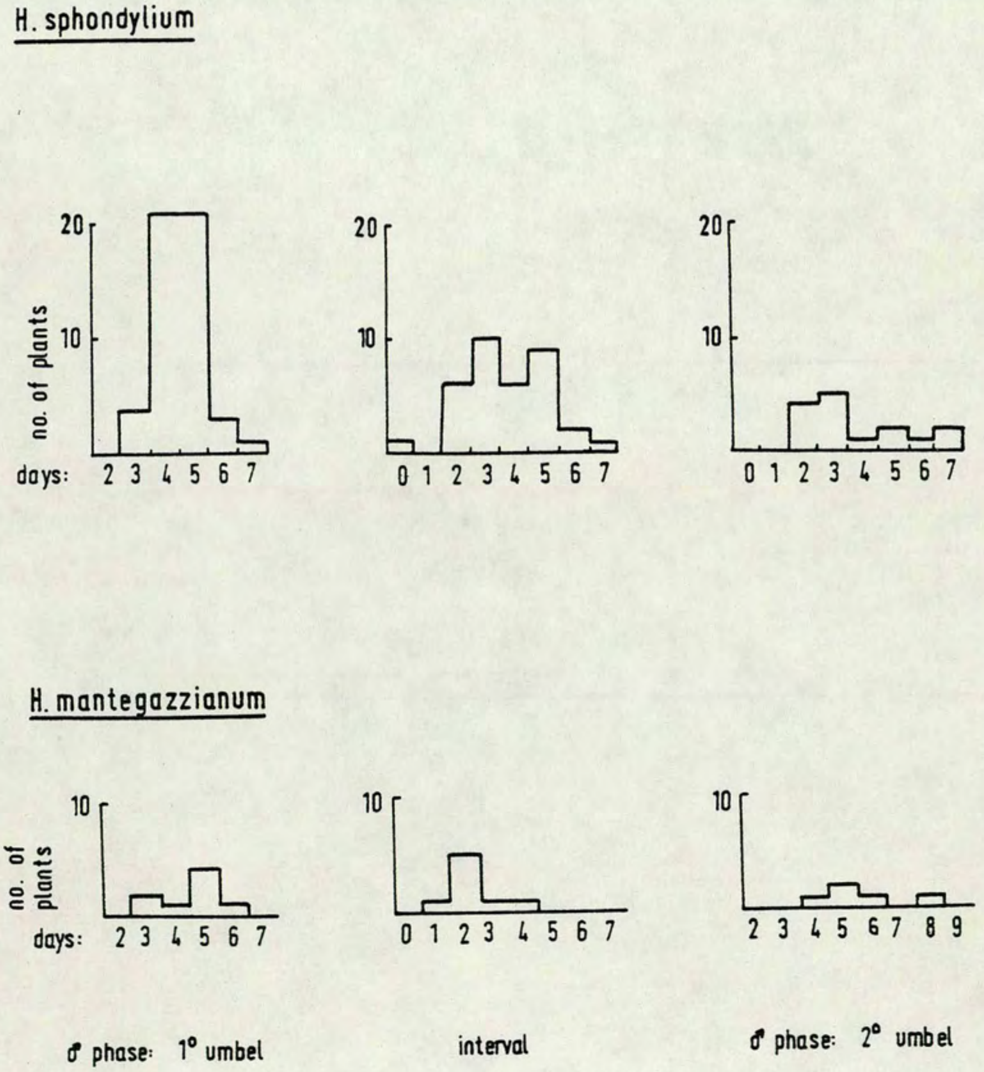


Fig. 4.6 Duration of male phase in primary and secondary umbels and interval between the two: H. sphondylium and H. mantegazzianum

male and female stages overlapped on different flowering stems of the same plant. This does not apply to H. mantegazzianum which produces only one flowering stem.

4.3 Experimental Crosses

Materials and Methods

Plants used for experimental crosses are listed in Table 4.2 with provenance number referred to in the presentation of results. In 1977, of the plants brought into the greenhouse on 6th June, the H. sphondylium flowered from 19th June to 11th July, and the H. mantegazzianum from 28th June to 4th July. Only primary umbels were used with a minimum of 70 flowers (140 stigmas) for each type of cross. Experimental flowers were enclosed in lens tissue paper bags (Shepherd 1975). Large squares were used to cover a whole umbel of H. sphondylium and narrow rectangles to enclose individual umbellets of H. mantegazzianum. Each bag was sealed on three sides with "Sellostick" or "Pritt" and tied at the open end with thread and label ties (Fig. 4.7).

Flowers used for outcrosses or controls were emasculated as petals unfurled using fine forceps to pull out the hooked filaments or strip off anthers before they dehisced. For H. mantegazzianum about seven umbellets provided sufficient flowers for one treatment in one morning, between 7 a.m. and 9 a.m., the remaining unopened flowers were cut away and each umbellet bagged and left for

Fig. 4.7 Lens tissue paper bags on <u>H. sphondylium</u>

pollination. Central umbellets of H. mantegazzianum umbels were left to flower undisturbed. For H. sphondylium the whole umbel had to be carefully emasculated over the entire period of the male phase from 5 a.m. to 9 p.m. over several days. Flowers opening on the last day, which included male flowers, were cut out and not used.

On H. mantegazzianum a single terminal umbel was large enough for controls to be included with all types of cross on each plant (Table 4.2). However, a single H. sphondylium primary umbel could accommodate one cross type and a control only, or one selfing. More than one type of cross on each H. sphondylium plant (Table 4.2) was made when more than one flowering stem and therefore more than one primary umbel was produced per plant. The random allocation of self, out and hybrid treatments between umbels for each H. sphondylium plant is shown in Table 4.2. A few additional crosses were made using hybrid pollen and pollen from secondary umbels.

Flowers to be selfed were not emasculated but left enclosed in bags until the last day of the male phase for that umbel. Pollen was then transferred from adjacent central flowers of the umbel or umbellet which were then cut out as in preparation for other types of cross. For H. mantegazzianum numbers 41 and 43 selfs were made at the time of stigma maturity using pollen from secondary umbels.

Stigmas were pollinated by gently brushing a dehisced anther across the stigma surface until a clump of yellow pollen could be seen adhering to the tips of the styles.

Table 4.2 Plant provenances and allocation of treatments

H. sphondylium

Stobs	2			H/C	
	5		O/C		
	7	S			
Farfield	21	S	O/C	H/C	
	22	S	O/C	H/C	
	24	S	O/C	H/C	
	25	S	O/C	H	
	26	S	O/C	H/C	
	29		O/C		
	31	S	O/C	H/C	
	32	S		H/C	
	34			H/C	
	35	S		H/C	
	36	S		H/C	
	37		O/C	H/C	
	38	S	O/C		
	39	S		H/C	B/C
Park Burn	40(1)	S	O/C	H	

H. mantegazzianum

Hopetoun	41	S	O	H	C	S(2^{o})	
	42	S	O	H	C		
	43	S	O	H	C	S(2^{o})	
	44	S	O	H	C		
	45	S	O	H	C		O(2^{o})
	48		O	H	C		
	49	S	O	H	C		
	50	S	O	H	C		
Riddell	51	S	O	H	C		

Self (S) intraspecific outcross (O) hybrid cross (H) control (C) backcross to hybrid (B) self with 2^{o} pollen (S(2^{o})) intraspecific outcross with 2^{o} pollen (O(2^{o}))

The pollen for all experimental crosses was from umbels cut and brought in water from H. sphondylium plants growing at Roslin and H. mantegazzianum (Park Burn provenance) grown in an experimental garden outside the greenhouse. Pollinations were made at any time of day, but not between the hours of 9 p.m. and 8 a.m. Before outcrosses were made on H. sphondylium umbels a sheet of lens tissue was lodged between the two halves of the umbel to separate treatment from control within each lens tissue bag. After pollination umbels were left bagged until seed harvest.

When the fruit were ripe umbels were cut on 18th and 26th August, 1977 and left two to four weeks to dry at room temperature. Mericarps were then stripped off and stored in paper bags.

For seed counts, mericarps were passed over a light table and only those with at least 2/3 developed endosperm were scored as 'seed set'.

A check was made on pollen tube growth in the style of Heracleum flowers. Cut umbels of H. sphondylium (from Roslin) and H. mantegazzianum (from lateral shoots of Warriston Cemetary plants) were kept in water in late July, 1977. Flowers were emasculated, enclosed in lens tissue bags, and pollinated on successive days from flower opening to petal fall, with intraspecific or interspecific pollen. Each day selected flowers from each cross type and day of pollination were stained by the lactophenol cotton blue method of Datta & Naug (1967), and the growth of pollen tubes relative to the length of the style recorded.

Results

Controls

The number of seed set for each treatment is shown in Tables 4.3, 4.4. Controls for outcross plant No.32 and hybrid cross No.34 were unacceptably high, and these values are not included in the tables of percentage seed set, Tables 4.5, 4.6.

Self

H. sphondylium is not self incompatible and set overall 16% seed on selfing. The proportion of seed set was variable, as low as 1% or as high as 40% (Table 4.6). H. mantegazzianum appears to have more effective protandry in the primary umbel as pollen from the male phase of the umbel showed an almost negligible (1%) seed set on selfing (Table 4.5). Within the plant there is however no incompatibility system as pollen from secondary umbels gave a consistently high seed set not significantly different from the seed set from an intraspecific cross (Table 4.8). Geitonogamy is not possible within a single umbel of H. mantegazzianum, but provided pollen is transferred from lower order umbels autogamy can take place.

Intraspecific outcross

Both H. mantegazzianum and H. sphondylium showed high seed set on outcrossing. H. mantegazzianum set 64% seed (Table 4.5), H. sphondylium 67% (Table 4.6) but both species also showed considerable variation between plants in the degree of outcrossing success. For H. sphondylium values were greater than for selfing and ranged between 43% and 99%. For H. mantegazzianum the lowest value of 15% for No.42 seems exceptionally low compared with the range of 47% to 85% for the remaining plants. This particular cross may have been made too late for successful fertilization as the stigma seemed drier than usual at the time pollination took place.

Hybrid cross

The hybrid cross with H. mantegazzianum mother failed to set any seed at all for five of the nine replicates. Of the remainder, three gave a 1% seed set that could be due to contamination with self pollen, and only one, plant No.51, gave a 15% seed set (Table 4.5). This was the only plant of Riddell provenance, other H. mantegazzianum were from Hopetoun. In comparison, the H. sphondylium hybrid cross was successful. Overall a 23% seed set was obtained (Table 4.6). Again, the range of values between plants was variable, between 4% and 51%. Although as great as the range for percentage seed set on selfing, no hybrid cross on H. sphondylium set as much

Table 4.3. Results of controlled crosses: NUMBER OF SEED SET

H. mantegazzianum ♀

(1) No. of stigmas pollinated
(2) No. of seeds set

Plant No.	SELF		OUTCROSS		HYBRID		CONTROL	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
41	144	9	114	97	216	3	150	1
42	150	0	162	25	176	0	174	0
43	158	0	162	116	180	0	154	0
44	150	0	160	111	176	2	166	0
45	154	0	160	90	162	1	172	3
48			164	125	158	0	154	2
49	172	0	184	152	162	0	168	0
50	168	0	152	72	142	0	126	0
51	166	6	168	129	166	24	168	0

	SELF(2^o)		OUTCROSS(2^o)	
	(1)	(2)	(1)	(2)
41	192	122		
43	172	125		
45			170	141

Table 4.4. Results of controlled crosses: NUMBER OF SEED SET

H. sphondylium ♀

(1) No. of stigmas pollinated
(2) No. of seeds set

Plant No.	SELF		OUTCROSS		CONTROL		HYBRID		CONTROL	
	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
2							228	116	202	0
5			196	131	196	0				
7	448	12								
21	486	26	156	79	138	0	160	16	82	1
			160	95	38	0				
22	244	24	156	122	184	0	156	6	140	0
24	276	22	200	96	156	1	266	48	248	9
25	300	12	176	174	172	2	236	89		
26	698	210	224	168	150	2	252	51	150	2
			198	126	168	12	228	65	168	12
29			248	173	176	4				
31	220	3	196	116	150	0	196	26	156	5
32	228	75	158	30	64	28	166	6	158	0
							160	48	40	0
34							154	0	246	12
35	220	14					194	17	152	0
36	200	50					150	70	108	0
37			160	140	22	4	166	21	76	0
38	270	38	184	142	192	6				
39	166	48					160	32		
							140	34	32	0
40(1)	276	109	176	75	150	0	168	39		

Plant No.	BACKCROSS		CONTROL	
	(1)	(2)	(1)	(2)
39	150	21	46	1

Table 4.5. Results of controlled crosses: PERCENTAGE SEED SET

H. mantegazzianum ♀

Plant No.	SELF	OUTCROSS	HYBRID
41	6	85	1
42	0	15	0
43	0	72	0
44	0	69	1
45	0	56	1
48		76	0
49	0	83	0
50	0	47	0
51	4	77	15
TOTAL:	1	64	2

	SELF(2^{o})	OUTCROSS(2^{o})
41	64	
43	73	
45		83
TOTAL:	68	83

Table 4.6. Results of controlled crosses: PERCENTAGE SEED SET

H. sphondylium ♀

Plant No.	SELF	OUTCROSS	HYBRID	BACKCROSS
2			51	
5		67		
7	3			
21	5	55	10	
22	10	78	4	
24	8	48	18	
25	4	99	38	
26	30	70	24	
29		70		
31	1	59	13	
32	33		17	
35	6		9	
36	25		47	
37		88	13	
38	14	77		
39	29		22	14
40(1)	40	43	23	
TOTAL:	16	67	23	14

seed as the maximum values for intraspecific outcrossing. Nevertheless, the results confirm that hybrid seed can be produced.

Comparison between crosses

H. mantegazzianum set most seed by the single intraspecific outcross to secondary umbel pollen which gave 85% seed set (Table 4.8). Seed set from selfing within the same umbel was negligable and only one plant gave a low amount (15%) of hybrid seed. H. mantegazzianum also gave a high seed set from the intraspecific outcross, or selfing to secondary umbels. Using the χ^2 test of significance, there is no significant difference between the results of these two crosses, they are both high (64% and 68%) (Table 4.8).

H. sphondylium set most seed on outcrossing, but could also set seed from self pollination or a hybrid cross. There was considerable variation in the response of individual plants to the cross type. A χ^2 test for homogeneity showed that the proportion of seed set was dependent on plant number within each cross type (Table 4.7). There was no consistent response to treatment type, No.40 gave almost equal percent seed set for both self and outcross, with a lower value for the hybrid cross (40%, 43%, 23%) while No.25 with 99% outcross and 38% hybrid cross, gave a low value, 4%, for selfing (Table 4.6). On average the hybrid cross set more seed

Table 4.7. Values of χ^2 for the null hypothesis that the proportion of seed set is independent of the plant number within each cross type

CROSS TYPE	d.f.	$\chi^2(p=0.05)$	χ^2
H. sphondylium ♀			
SELF	12	21.03	500.319
OUTCROSS	10	18.31	237.898
HYBRID	12	21.03	281.657
H. mantegazzianum ♀			
OUTCROSS	8	15.51	268.868
SELF (2^o)	1	3.84	3.063

Table 4.8. Values of χ^2 for the null hypothesis that the proportion of seed set is independent of cross type for each combination of crosses

CROSS COMBINATION	d.f.	$\chi^2(p=0.05)$	χ^2
H. sphondylium ♀			
SELF, OUT, HYBRID	2	5.99	2,020.453
SELF, OUT, HYB, BACK	3	7.82	2,120.059
SELF, HYBRID	1	3.84	49.739
H. mantegazzianum ♀			
OUT, OUT(2^o),SELF(2^o)	2	5.99	24.278
OUT,SELF(2^o)	1	3.84	0.789

than selfing, but less than the intraspecific outcross. A two-way analysis of variance (Table 4.10) for those plants with all three treatment types (Table 4.9) on an arcsin transformation of the percentage data (Sokal and Rohlf 1969) gave a significant difference in seed set attributable to cross type but not, as might be expected from the χ^2 test, to plant number. The one backcross using hybrid pollen from Fairmilehead set as much seed as a hybrid or self cross.

Pollen tube growth in the style

On cut flowers kept in water *H. sphondylium* pollen tubes could grow from 1.0 mm to 1.5 mm in *H. mantegazzianum* styles which were 2.0 mm to 2.5 mm long (Fig.4.8). *H. mantegazzianum* pollen tubes in *H. sphondylium* styles grew at least to the level of the indumentum, a distance of about 2.0 mm.

Few flowers pollinated during the male phase (day 1 to 5) showed germinating pollen on the stigma surface (Fig. 4.8). Once the styles had elongated and the stigma surfaces bent back, pollen tubes were clearly visible in the style for intraspecific crosses, although the lacto-phenol-cotton blue method was not able to show pollen tubes entering the ovule. Unfortunately three of five *H. sphondylium* umbels, and one of two *H. mantegazzianum* umbels, did not complete the female stage successfully, styles did not extend fully and bend back as in normal receptive flowers. These results are therefore incomplete.

Table 4.9. Percentage seed set for plants used for all three treatments

Plant No.	SELF	OUTCROSS	HYBRID
21	5	55	10
22	10	78	4
24	8	48	18
25	4	99	38
26	30	70	24
31	1	59	13
40	40	43	23
Average:	14	65	19

Table 4.10. ANOVA table for an arcsin transformation of percentage seed set shown in Table 4.9

Source of variation	d.f.	s.s.	m.s.	F_s
CROSS TYPE	2	5171.9952	2585.9976	18.4269
PLANTS	6	944.1505	157.3584	1.1213
ERROR	12	1684.0533	140.3378	
TOTAL	20	7800.1990		

$F_{0.05}(2,12) = 3.8853$ $F_{0.05}(6,12) = 2.9961$

Fig. 4.8 Growth of (a) *H. sphondylium* pollen tubes in *H. mantegazzianum* style and (b) *H. mantegazzianum* pollen on *H. mantegazzianum* stigma

4.4 Discussion

The experimental crosses have shown that hybrid seed can be produced by artificial pollination of H. sphondylium stigmas with H. mantegazzianum pollen. The percentage seed set is not as high as seed set from outcrossing, but is at least as great as seed set from selfing within the primary umbel. A backcross with hybrid pollen was also produced on the H. sphondylium stigmas. It is possible that hybrid seed can also be made by the H. mantegazzianum x H. sphondylium cross, but probably in smaller quantities. H. mantegazzianum is strongly protandric and can only set a high proportion of seed if selfed from the secondary umbels.

The performance of H. mantegazzianum plants in cultivation was poor compared with seed set for plants growing wild at Kale Water. H. mantegazzianum is potentially very sensitive to environmental stress at flowering, because of its capacity to change from hermaphrodite to male flowers. Liehr (1927) managed to reduce the number of hermaphrodite flowers in the primary umbel of cultivated H. mantegazzianum from 100% to 0% by nutrient deficiency. It is not unusual for plants with mixed inflorescences to vary the number of fully fertile flowers. Wakhloo (1975) has shown a reduction of the percentage of fully developed flowers of Solanum sisymbrifolium Lam. from 95.2% at high levels of foliar potassium in the plant to 64.9% at low levels of foliar K. The transition from hermaphrodite to staminate flowers is not abrupt, but occurs by gradual reduction in the length of the ovary and style. Flowers which appeared hermaphrodite and were used for the experimental crosses may in fact have been sterile. In general, before a flowering shoot is fully developed, reproductive output can be controlled by the plant in response to environmental stress by reducing the number of inflorescences per plant or the future seed weight (Cook 1975). Later, when flowering has started, stress usually leads to abortion or reduction in final seed number rather than changes in the seed weight or number of flowers (Harper 1977). The low percentage of hybrid seed set may therefore be an underestimate of the hybridization potential of H. mantegazzianum.

A hybrid pollination may fail at any stage in the progress of the pollen tube from activation and germination on the stigma surface to fertilization of the ovule, or by abortion of the developing embryo. The mechanisms of interspecific incompatibility may resemble self-incompatibility systems (Heslop-Harrison 1975) when there is a specific inhibitor either on the stigma surface or in the style, or incongruity systems (Hogenboom 1975) if there is simply a mis-matching of genetic information between pollen and pistil. In Heracleum there is no evidence for a fully effective self-incompatibility system. Individual plants of both species were able to set seed from their own pollen. The low seed set on selfing primary umbels of H. mantegazzianum with pollen from the same umbel must be due to rapid loss of viability of

H. mantegazzianum pollen since pollen from secondary umbels presented at the same time as maturity of the primary umbel stigma on the same plant was able to set 68% seed. The 16% seed set obtained on selfing primary umbels of H. sphondylium must mean that either H. sphondylium pollen lives longer than that of H. mantegazzianum, or H. sphondylium stigma are receptive at the same time as pollen is shed.

Heracleum pollen is trinucleate (Heslop-Harrison 1977) and would therefore be expected to show reduced longevity (Hoekstra and Bruinsma 1978). Trinucleate pollen has a high rate of respiration, and rapid tube growth, but loses viability quickly and is difficult to germinate "in vitro". Attempts to germinate Heracleum pollen in sucrose solutions of varying concentrations with or without pollen germination media all led to burst pollen grains or short but ruptured pollen tubes. The short life of Heracleum pollen grains may also explain the nature of the male phase in umbels where fresh pollen is presented every morning for three to five days. Day old anthers are eliminated from the new pollen source as their filaments collapse and fall below the petal surface after 12 - 24 hours. A similar flowering sequence is found in the Composite inflorescence which produces a new whorl of florets every day and which is considered an adaption to the trinucleate pollen type (Hoekstra & Bruinsma 1978).

Usually trinucleate pollen is associated with "dry" stigma types (Heslop-Harrison 1975) which would be expected to show inhibition of incompatible pollen at the stigma surface. However, Heracleum stigma are of the "wet" type (Heslop-Harrison 1977) more often associated with binucleate pollen, where inhibition occurs in the style. This anomolous combination of trinucleate pollen and wet stigma type is not unique, neither to Heracleum nor to the Umbelliferae. Associated families in this category surveyed by Heslop-Harrison (1977) include the Caprifoliaceae, Cactaceae, Escalloniaceae, Lentibulariaceae, Melastomataceae and Pittosporaceae. The sphorophytic system of individual interaction between pollen grains and the cells of the dry stigma surface is not possible with receptive wet stigmas where pollen grains are rapidly submerged in copious free-running secretions, and individual cells of the stigma surface are non-papillate and often dead at maturity. The scanning electron micrograph of the stigma surface of H. mantegazzianum by Heslop-Harrison (1977) illustrates the depth of the surface exudate relative to the size of the pollen grain. Although Heracleum pollen is difficult to germinate and may be sensitive to the composition of this surface exudate, inhibition of pollen in interspecific crosses is more likely to take place in the style or by abortion of the developing embryo.

The evidence from staining selected flowers of Heracleum with lactophenol cotton blue suggests that inhibition of H. sphondylium pollen tubes occurs in the style of *H. mantegazzianum*. For cut umbels kept in water *H. sphondylium* pollen tubes could grow to ½ to ¾ the length of the *H. mantegazzianum* style. *H. mantegazzianum* pollen tubes were able to grow at least to the level of the indumentum of *H. sphondylium* flowers. The reduced seed set for interspecific hybrid crosses in *H. sphondylium* was therefore more probably due to failure just before or during fertilization, or to early abortion of the developing zygote through hybrid weakness.

With attempted interspecific crosses in *Daucus*, none of which set seed, Owens (1974) also found inhibition of pollen tube growth in the style for all crosses where pollen was placed on the stigma of either subspecies of *D. carota*. In addition pollen was inhibited in the stigma for the *D. muricatus* x *D. aureus* and *D. blanchei* x *D. carota* crosses. *Daucus* therefore exhibits a reciprocal relationship between species which is similar to, but more restrictive than, that of *H. mantegazzianum* and *H. sphondylium*. Owens (pers. comm.) has suggested that this relationship may be explained by the incongruity system of Hogenboom (1975). According to this hypothesis pollen is thought to have a gene or gene complex for penetrating the genetically determined barrier capacity of the pistil. Only fully matching systems will enable pollen to pass through all the potential barriers from activation on the stigma surface to penetration of the embryo sac and bring about successful fertilization. When the relationship between pistil and pollen of two species is not reciprocal, then the pistil of one species may have a low barrier capacity which can accept many types of pollen, as in H. sphondylium and D. carota, while the pistil of the other species has a high capacity to exclude pollen types as in H. mantegazzianum and D. blanchei. The ability of H. sphondylium pistil to accept a wider range of pollen types than that of H. mantegazzianum would be expected since H. sphondylium is polymorphic for a number of characters such as leaf shape and flowering time, whereas H. mantegazzianum is much less variable.

The perpetuation of a matching pistil pollen relationship depends on their co-evolution: changes in the type of barrier in the pistil will rapidly select for a particular type of pollen, or if the barrier is made less specific, will enable a more heterogeneous pollen population to evolve. Thus the incongruity system also explains apparent differences in fertility between separated populations of the same species as well as how interspecific sterility may evolve. Hogenboom (1975) found that inbreeding and selection of Lycopersicum peruvianum lowered the barrier capacity of some lines to the level of penetration of L. esculentum pollen, and unilateral incongruity between these two species was broken. H. mantegazzianum, with the largest flowers of all Heracleum species and effective protandry within each umbel, probably usually reproduces by outcrossing. Several examples may be cited of small flowers which are inbreeders with closely related larger flowers which reproduce by outcrossing, including the small flowered inbreeding D. montanus and D. subsessilis and the closely related large flowered Orlaya daucorlaya which shows more characteristics of outbreeding (Owens 1974). When brought into cultivation and distributed as small groups of plants in widely separated localities, H. mantegazzianum may in some places have been forced to inbreed, with consequent changes in the pistil pollen relationship between populations. This may explain the success of the H. mantegazzianum hybrid cross on the single plant from Riddell, compared with the failure to set hybrid seed on plants from Hopetoun. Throughout Britain the ability to form hybrids by the H. mantegazzianum x H. sphondylium cross probably varies between populations of different origin.

In the field this potential for hybridization may be considerably reduced by ecological and ethological isolation of the two species. Flowering times may not overlap or pollen may seldom be transferred between the two species. If mixed pollen loads are obtained, plants may be able to select for domestic pollen in favour of hybrid progeny as in Zea, Gossypium, Streptocarpus and Gilia (Ornduff 1969, Baker 1951, Stebbins 1971).

Pollen transfer between H. mantegazzianum and H. sphondylium and time of flowering has been studied by Grace (unpublished). The flowering period of both species in Britain overlaps. H. sphondylium flowers from June to September, H. mantegazzianum from late June to early July (Clapham et al. 1962). At Kale Water in 1977 H. mantegazzianum began flowering on 25th June. The adjacent H. sphondylium began the male phase on 7th July, when 5 of the 18 H. mantegazzianum were at the female receptive stage in the primary umbel. By the 12th July, H. mantegazzianum was presenting pollen on the lowest order umbels while only 5 of the 15 H. sphondylium had reached the receptive stage. Therefore only one third of the H. sphondylium plants examined could have received pollen from the opposite species, while all H. mantegazzianum plants could receive H. sphondylium pollen at any time during their receptive female stage. H. mantegazzianum finished flowering on the 28th July, and H. sphondylium on the 4th August.

Grace (unpublished) found traces of H. sphondylium pollen on insects caught on H. mantegazzianum plants but not vice versa, suggesting that in nature the hybrid seed would form on H. mantegazzianum umbels. However, in the experimental crosses the H. mantegazzianum x H. sphondylium cross gave a low seed set. It seems more reasonable to assume that hybrids are formed by pollen transferred from lower order H. mantegazzianum umbels to early receptive stigma of H. sphondylium even though pollen transfer in this direction was not observed. At this stage the size and height above ground of the lateral H. mantegazzianum umbels is similar to the form of H. sphondylium primary umbels and the distance between species is therefore reduced. Large numbers of hybrids are often found on sites within Edinburgh which are cleared of Giant Hogweed by the Corporation in early July. The main stems of H. mantegazzianum are cut, leaving lateral shoots which flower in late July. At Warriston and Fairmilehead within the city, stands of Giant Hogweed are cleared annually and in late July many Heracleum plants of intermediate morphology can be found in flower. These sites - one an abandoned gravel pit, the other an overgrown graveyard - may support more hybrids than can be found in natural populations not only because of increased opportunity for interspecific pollination through interference by man, but also because they provide a mixed edaphic site, the classic hybrid habitat of Anderson (1953).

Contrary to early opinion that the Umbelliferae are pollinated by a great variety of insects (Bell 1971) it has recently been observed that in Thapsium barbinode, Zizia trifoliata, Angelica tringuata and A. venosa very few of the many insect visitors are effective in pollination (Bell & Lindsey 1978). Grace (unpublished) found that for Heracleum, too, very few insects carried large pollen loads. Many different thrips, bugs, beetles and flies visit Heracleum umbels (Proctor & Yeo 1973), but probably few are effective pollinators. Those insects that do bring about cross fertilization are quite likely to visit both species. It is well known that many pollinating insects are polytropic and that introduced species, such as H. mantegazzianum, are readily visited by the native insect fauna (Valentine 1978b).

The amount of pollen transferred between H. mantegazzianum and H. sphondylium will depend on the foraging behaviour of the insects which visit these flowers. Honeybees (Apis mellifera), for instance, are known to be fairly consistent in the species visited on the same or successive flights, while bumblebees (Bombus) search individually for flowers and are therefore more likely to carry mixed pollen loads (for a review see Free 1966). All types of pollinators, however, show greater consistency when there are large areas of an attractive species (Levin 1978). Thus, on the lower reaches of the River Tweed and along the mouth of the River Findhorn, where large stands of H. mantegazzianum are contiguous but not intermixed with populations of H. sphondylium, there are very few hybrids and probably very little pollen is transferred between the adjacent populations. At Warriston and Fairmilehead, where individual plants are interspersed with the same number of the other species, insects are more likely to visit different types of flowers, and it is here that the most hybrids have been found.

It is possible that at some sites, such as at Kale Water, where there is a larger area of H. mantegazzianum than H. sphondylium, the smaller species has to compete for pollinators when flowering times overlap. This may be why the H. sphondylium flowering at Kale Water in 1977 set only 40% seed, far below the species maximum of 90%. It is tempting to suggest that the smaller umbel is less attractive to pollinators. Outbreeding umbels have been correlated with conspicuous flowers (Jury 1978), but Bell and Lindsey (1978) found that removal of up to 50% of the umbel of Daucus carota had no apparent effect on fruit set. Bees are attracted by the appearance of flowers, but the stimulus to alight comes from their sense of smell, and

H. mantegazzianum umbels are very heavily scented. Competition for pollinators between H. sphondylium and H. mantegazzianum could lead to selection for later flowering H. sphondylium in those populations where the two species have grown side by side for several years. H. sphondylium has a very variable flowering time. Jaeger (1963) recorded two ecotypes in meadows in France, one early the other late flowering in response to selection by haymaking in June. Local adaption to competition for pollinators is not unknown. Centaurea nigra, a very variable species, has radiant capitula and flowers later when growing with C. scabiosa (Lack 1976), although, as a self-incompatible species with slow vegetative reproduction, C. nigra would be subject to greater selection pressure from poor pollination than the perennial self-compatible H. sphondylium.

At present it must be assumed that there are few barriers to the transfer of pollen between species and hybrids of Heracleum. The slightly out of phase flowering of both species excludes interspecific pollen transfer between early flowering H. mantegazzianum and late flowering H. sphondylium; the tendency of H. mantegazzianum to grow in monospecific stands reduces the chance of an insect visiting both species in succession. Where populations of both species are mixed and interspecific pollen transfer can take place the results of the experimental crosses suggest that there are additional barriers to successful hybridization. Both interspecific crosses set less seed than on intraspecific outcrossing, either from failure of the pollen tubes to grow beyond the base of the style, failure during fertilization or early abortion of the developing embryo.

CHAPTER V

Seed Germination

5.1 Introduction

Objectives

Seeds from the experimental crosses and ripe fruits harvested at Kale Water were set out to germinate to determine the viability of hybrid seed and compare its germination rate with that of parent species.

Seeds of Heracleum are known to require a period of cold treatment before germination takes place (Stokes 1952a, b, 1953a, b, Ivanova 1971). During this period insoluble amino acids in the endosperm are converted to a soluble form which can be taken up by the developing embryo as it grows (Stokes 1953b). The reaction is not reversible, seeds brought to room temperature do not lose their accumulation of soluble amino acids. The optimum time and temperature needed for recorded germination rates is:

Temperature	Species	Time (months)	% germination	Reference
2°C	H. mantegazzianum	1 - 2.5	92	Ivanova 1971
5°C	H. mantegazzianum	1 - 2.5	81.3	Ivanova 1971
2-5°C	H. sphondylium	3	90	Stokes 1952,3

5.2 Materials and Methods

All seeds from experimental crosses were set out to germinate. Trials with Kale Water seed in 1976 indicated that a 90% germination could be expected from *H. mantegazzianum* seed after two months at 2°C and a 70% for *H. sphondylium* after three months at 2°C. A sample of 400 seeds would therefore be needed to give a 99% chance of detecting a significant difference between 80% and 90% germination at 0.1p (Sokal and Rohlf 1969). A sample of 400 seeds was taken from the 1977 seed harvest of each *H. mantegazzianum* plant studied at Kale Water by the random cups method (International Seed Testing Association 1976). Neither the *H. sphondylium* nor the hybrid seed harvested from Kale Water in 1977 could provide this sample size per plant; the maximum number to the nearest multiple of 50 was used instead. The trials included 50 seeds from each of a random selection of five *H. mantegazzianum* and five *H. sphondylium* secondary umbels.

Ripe fruits were weighed and set out on sterile agar plates to germinate. Mericarps were first sterilized in round bottomed flasks (100 ml and 500 ml) with a solution of sodium hypochlorite(1 vol. + 3 vols. water) and then rinsed with sterile water. Mechanical shakers were used for wash times:

sodium hypochlorite	10 mins	
Water wash	1	30 mins
	2	30 mins
	3	30 mins

All glassware was sterilized for 20 mins. before use and seeds were plated out in a sterile cabinet onto 0.5% water agar (Davis Standard Agar, Davis Gelatine Ltd., Leamington Spa, England) (5g Agar/l of de-ionized water) at the following densities:

H. sphondylium	25-30 seeds/8.5 cm diameter plate
H. mantegazzianum and hybrid	50 seeds/14 cm diameter plate

To reduce the information that would be lost if plates became badly infected, seeds from each cross type were allocated to plates at random in units of 10 H. sphondylium and 25 H. mantegazzianum seeds to each plate.

Plates were stacked in two Gallenkampf incubators regulated at 2°C without light for six months. Heracleum seeds will germinate at 2°C, but more slowly than at 20°C, as the growth of the embryo is retarded by the low temperatures (Stokes 1952). These seeds were left at 2°C to completely cover the dormancy period of H. sphondylium, i.e. until the percentage of seed germinated had stabilized.

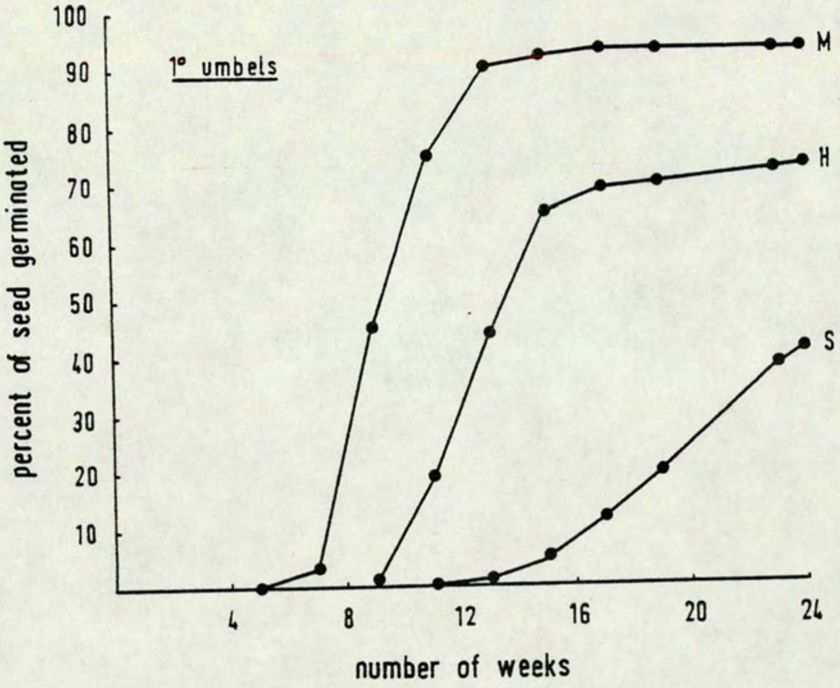
At two week intervals plates were checked at room temperature for the number of germinated seeds and were watered, if necessary, using sterile water from a syringe. Seeds which had "germinated" by exserting the tip of the radicle were removed with sterile forceps, laid on sand over a seed tray of compost and left on the greenhouse mist bench to develop cotyledons. Seedlings were checked at the first leaf stage for evidence of inbreeding depression and a selected number from each cross type kept for further observations.

5.3 Results

After six months at $2^{0}C$ all seed lots had reached a more or less stable germination total except those from H. sphondylium, Kale Water. After a further two weeks at $20^{0}C$ the number of these seeds germinating was still slowly increasing, while all other seed groups had reached a maximum. Seed which had not developed was mostly found to contain a rotting undeveloped embryo.

Seed of H. mantegazzianum began germinating at seven to nine weeks (Fig.5.1 and 5.3) and reached a maximum at 15 weeks. H. sphondylium began germinating at 11 weeks (Fig.5.1 and 5.2) and reached a maximum at 22 weeks. Both required more time than anticipated. H. sphondylium seed used by Stokes (1952) reached a maximum germination percentage after 18 - 20 weeks, and H. mantegazzianum after 10 weeks at $2\text{-}5^{0}C$ (Ivanova 1971). Seed collected from hybrid plants at Kale Water showed characteristics intermediate between H. sphondylium and H. mantegazzianum. Germination commenced at nine weeks and reached a maximum at 17 weeks (Fig.5.1). Seed from hybrid crosses showed the same dormancy requirement as parent plants but germinated more rapidly at first (Fig.5.2).

The maximum germination percentages attained by these seeds on agar plates (Table 5.1) compares favourably with expected germination of Heracleum seeds from experimental work. H. mantegazzianum from Kale Water gave 93% germination of seed from primary umbels, 94% from secondary umbels, which is almost the same as 92% quoted by Ivanova



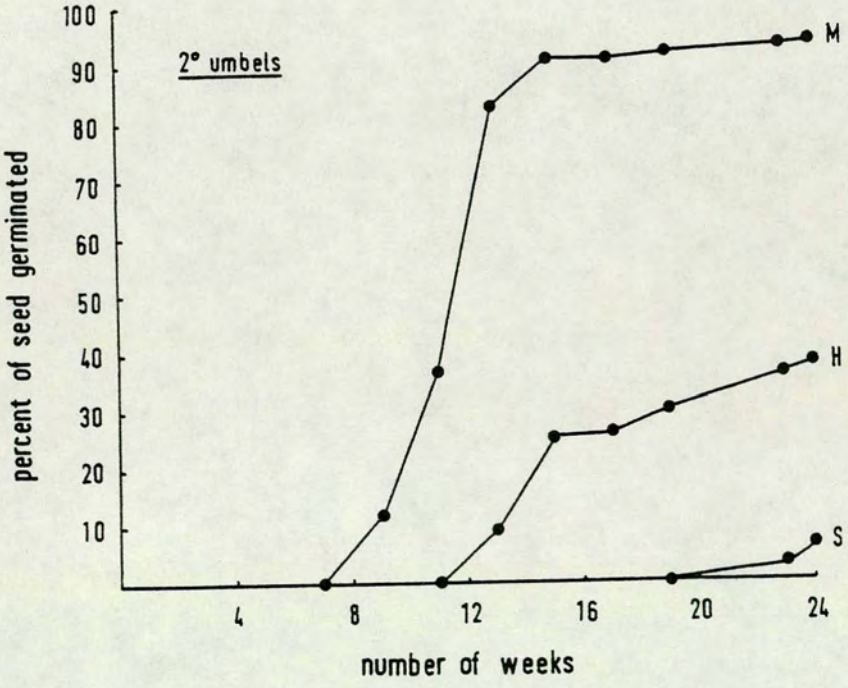


Fig. 5.1 Total germination percent at 2 week intervals for 6 months at 2°C: Seed from primary and secondary umbels of H. sphondylium (S), H. mantegazzianum (M) and hybrid (H) plants at Kale Water 1977

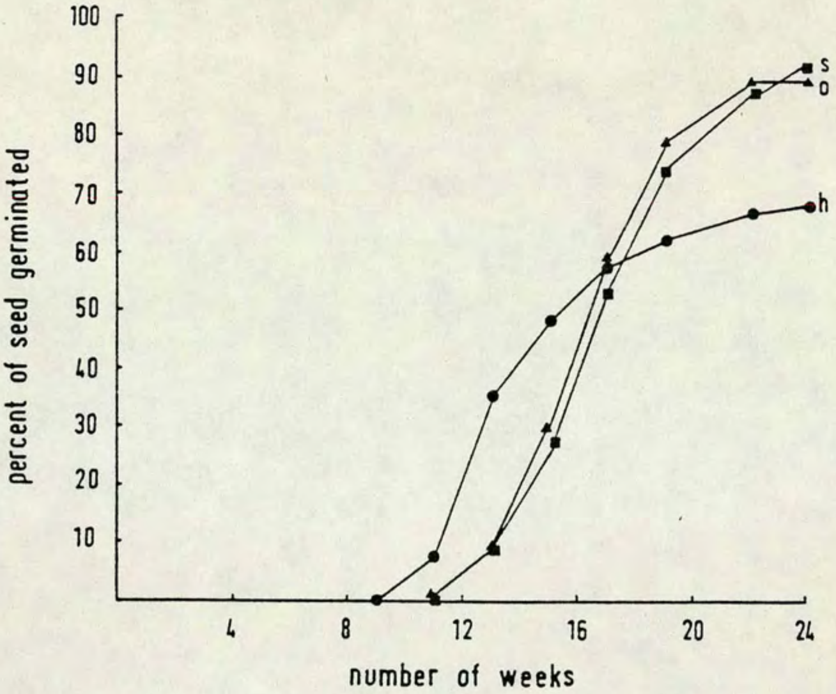


Fig.5.2 Total germination percent at 2 week intervals for 6 months at 2°C: Seed from H. sphondylium experimental crosses. Outcross (o), Self (s), hybrid (h)

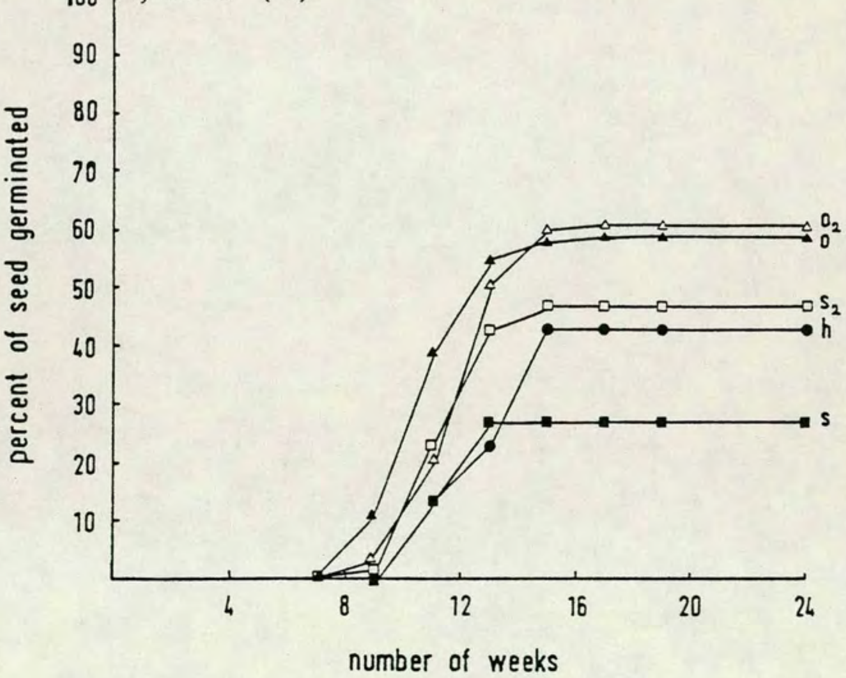


Fig.5.3 Total germination percent at 2 week intervals for 6 months at 2°C: Seed from H. mantegazzianum experimental crosses. Outcross (o), Outcross 2° umbel pollen (O_2) self (s), self 2° umbel pollen (S_2), hybrid (h)

Table 5.1. Total germination percent after 6 months at 2°C

CONTROLLED CROSSES

	SELF	OUT-CROSS	HYBRID	BACK	SELF 2°	OUT 2°
H. sphondylium	91	91	73	77		
H. mantegazzianum	27	59	45		52	60

KALE WATER PLANTS

	1° umbel	2° umbel
H. mantegazzianum	93	94
H. sphondylium	41	6
Hybrid	73	38

(1971) for H. mantegazzianum in the U.S.S.R. H. sphondylium reached a maximum of 91% for experimentally produced seed, similar to percentages determined for H. sphondylium fruits collected from near Bristol and north London (Stokes 1952).

Final germination percentages were not uniformly high for all collections. Notably H. mantegazzianum seed set in the greenhouse failed to give more than 59% germination, and seeds from H. sphondylium at Kale Water, as well as germinating slowly, had only reached a maximum of 41% after six months. These lower values were not noticeably due to infected plates, small differences in washing seed batches or the stacking of plates in the incubator.

Hybrid seed collected at Kale Water gave an intermediate 73% germination for seed from primary umbels, exactly the same as the total germination for hybrid seed from the H. sphondylium mother, and close to the 77% for for backcross (Table 5.1).

The overall values for germination percentages conceal a wide variation between plants which is shown most clearly by the total germination percent at two week intervals for individual plants from each cross type and collection at Kale Water in Figs. 5.4 to 5.13. Of the three groups with the very high overall germination of 90%: H. sphondylium outcross seed (Fig. 5.6) and seed from H. mantegazzianum at Kale Water (Fig. 5.11), both have relatively uniform germination totals over the same time period, while seed from H. sphondylium selfing (Fig. 5.4) and H. sphondylium at Kale Water (Fig. 5.10) have a wider interval between the start of germination in seed batches

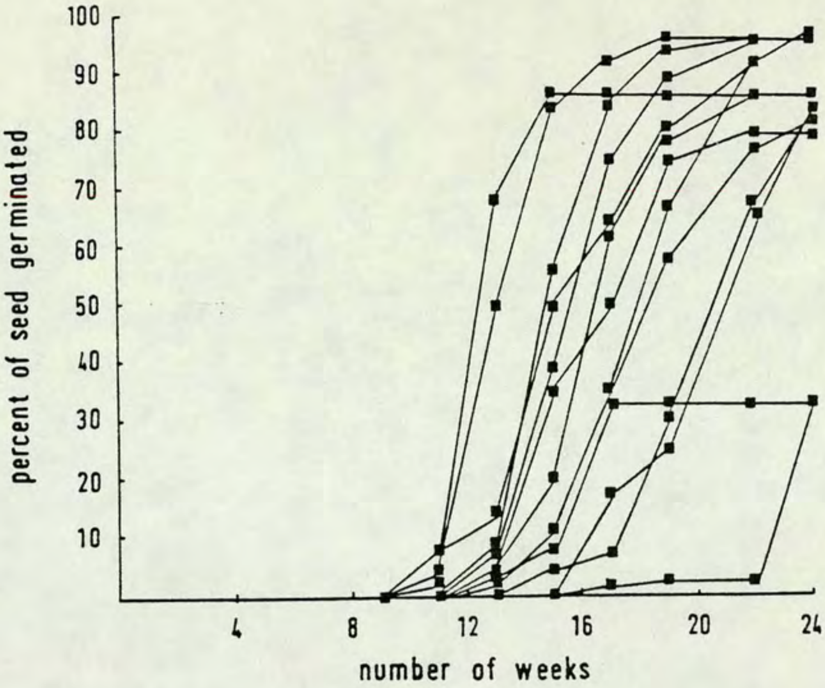


Fig. 5.4 Total germination percent at 2 week intervals for 6 months at 2°C. Seed from individual H. sphondylium plants used for experimental crosses: SELF

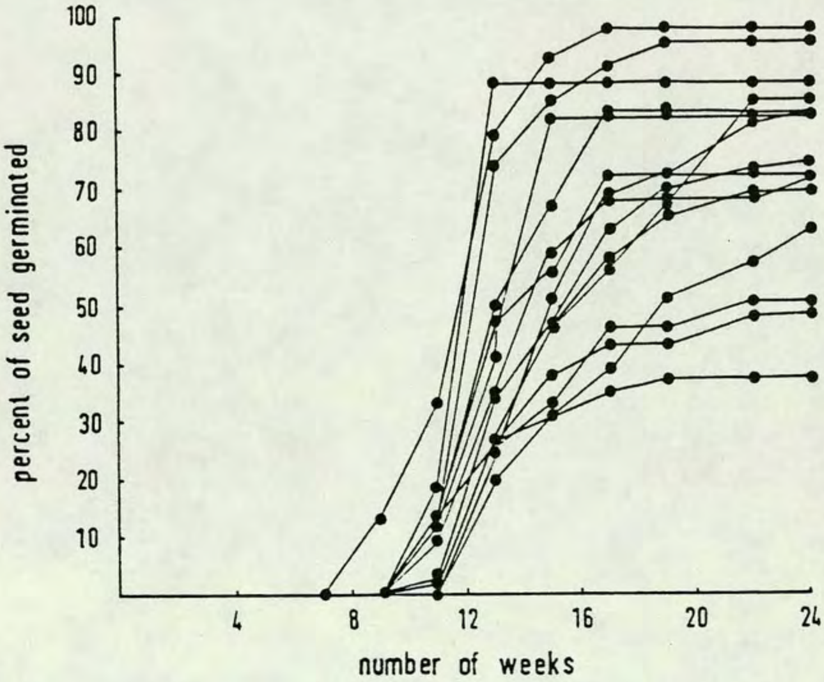


Fig. 5.5 Total germination percent at 2 week intervals for 6 months at 2°C. Seed from individual H. sphondylium plants used for experimental crosses: HYBRID

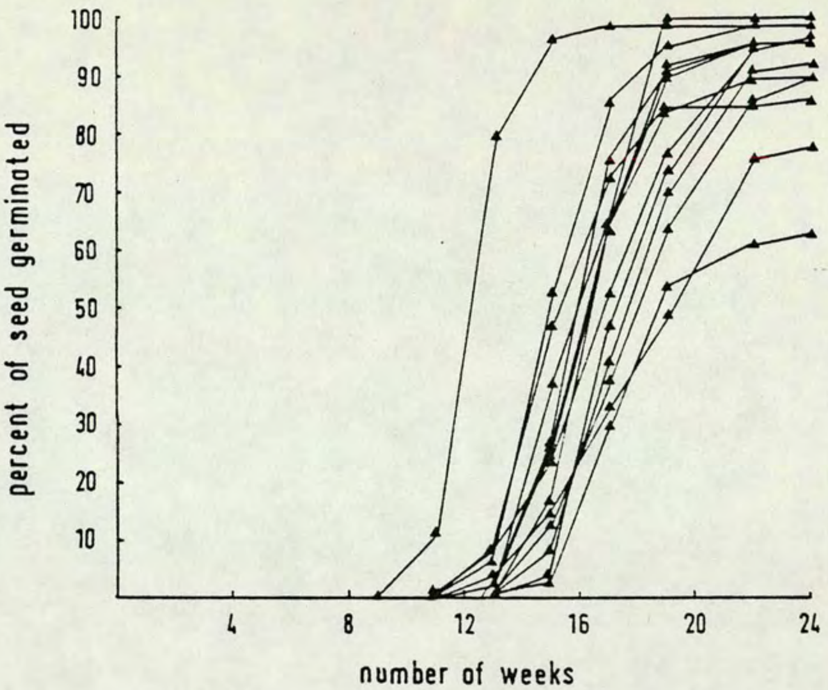


Fig. 5.6 Total germination percent at 2 week intervals for 6 months at 2°C. Seed from individual <u>H. sphondylium</u> plants used for experimental crosses: OUTCROSS

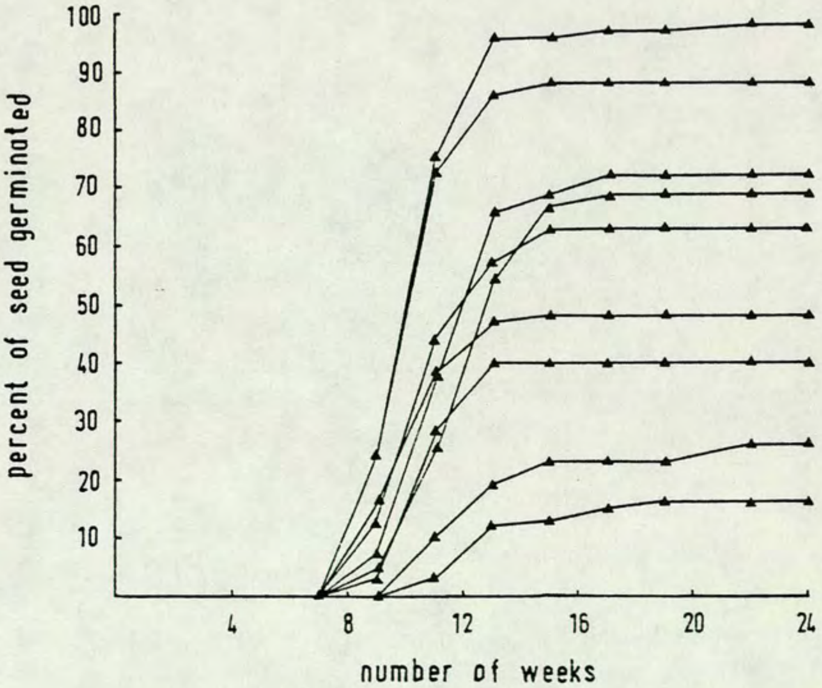


Fig. 5.7 Total germination percent at 2 week intervals for 6 months at 2°C. Seed from individual <u>H. mantegazzianum</u> plants used for experimental crosses: OUTCROSS

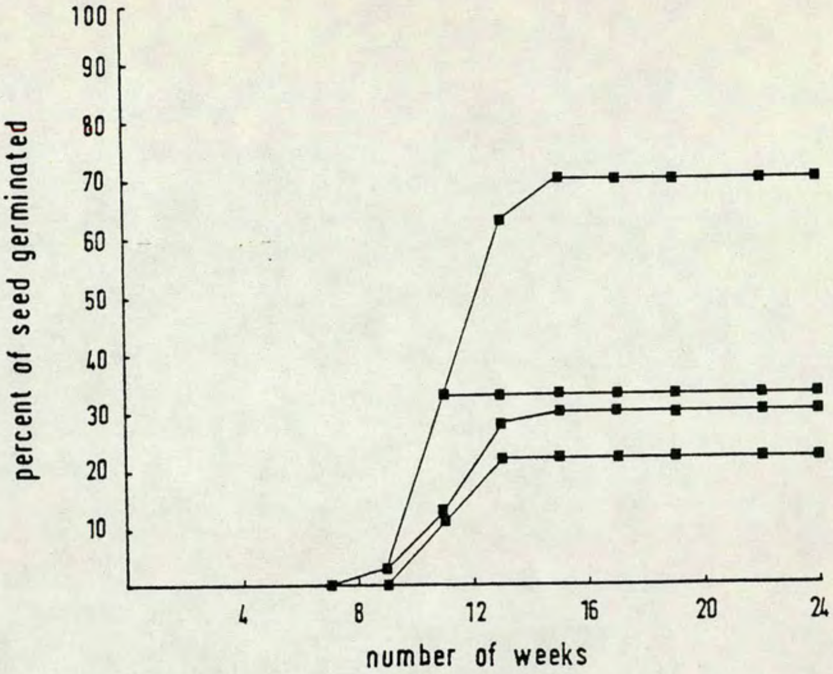


Fig. 5.8 Total germination percent at 2 week intervals for 6 months at 2°C. Seed from individual H. mantegazzianum plants used for experimental crosses: SELF

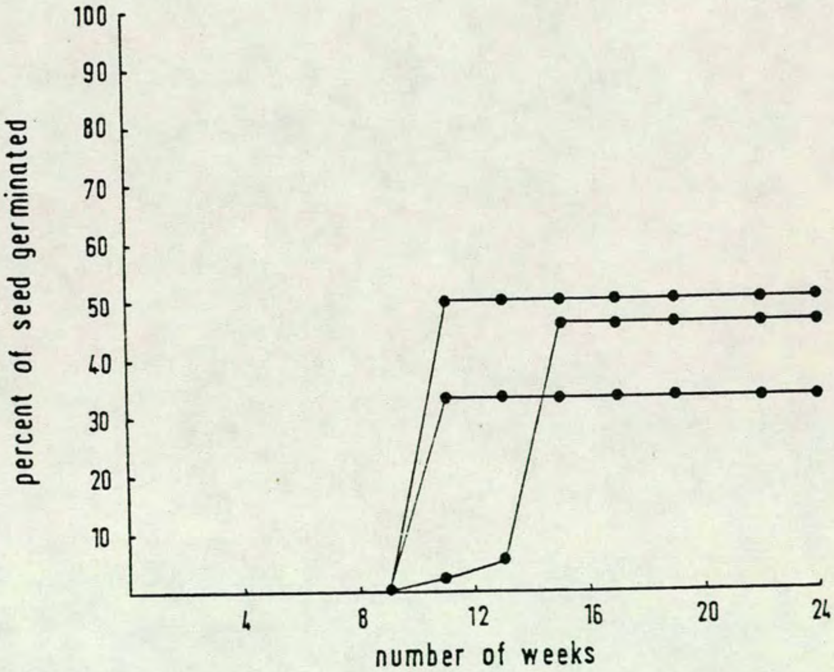


Fig. 5.9 Total germination percent at 2 week intervals for 6 months at 2°C. Seed from individual H. mantegazzianum plants used for experimental crosses: HYBRID

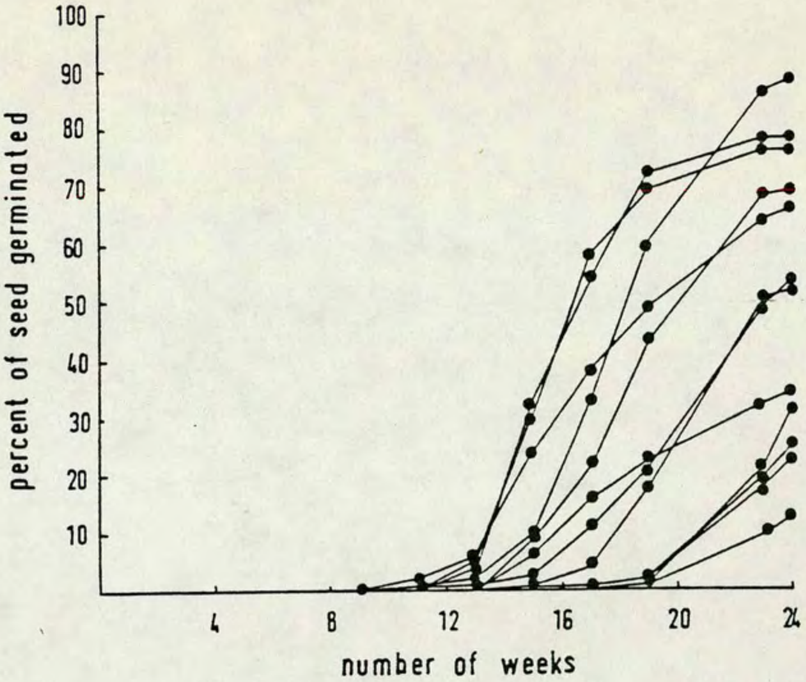


Fig. 5.10 Total germination percent at 2 week intervals for 6 months at 2°C: Seed harvested from primary umbels of H. sphondylium at Kale Water 1977

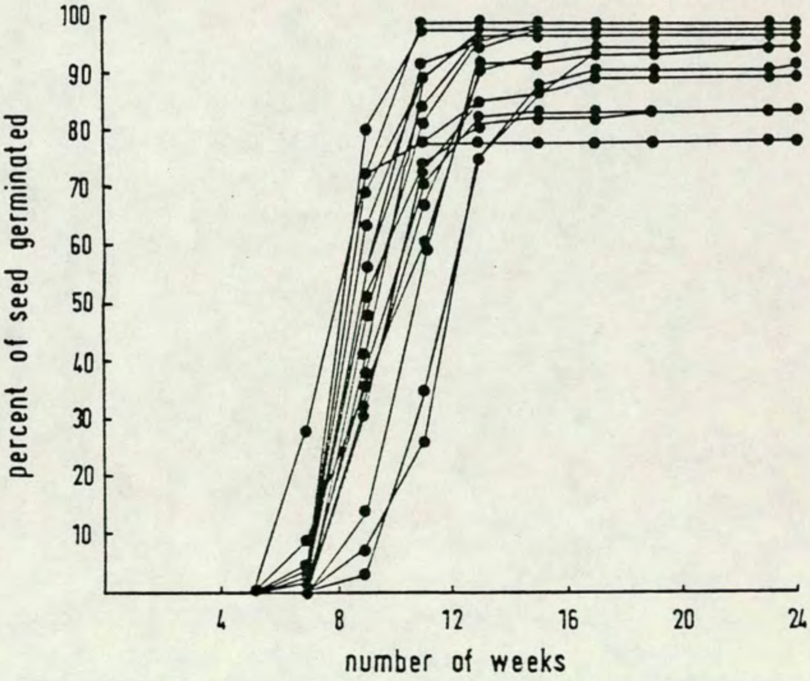


Fig. 5.11 Total germination percent at 2 week intervals for 6 months at 2°C: Seed harvested from primary umbels of H. mantegazzianum at Kale Water 1977

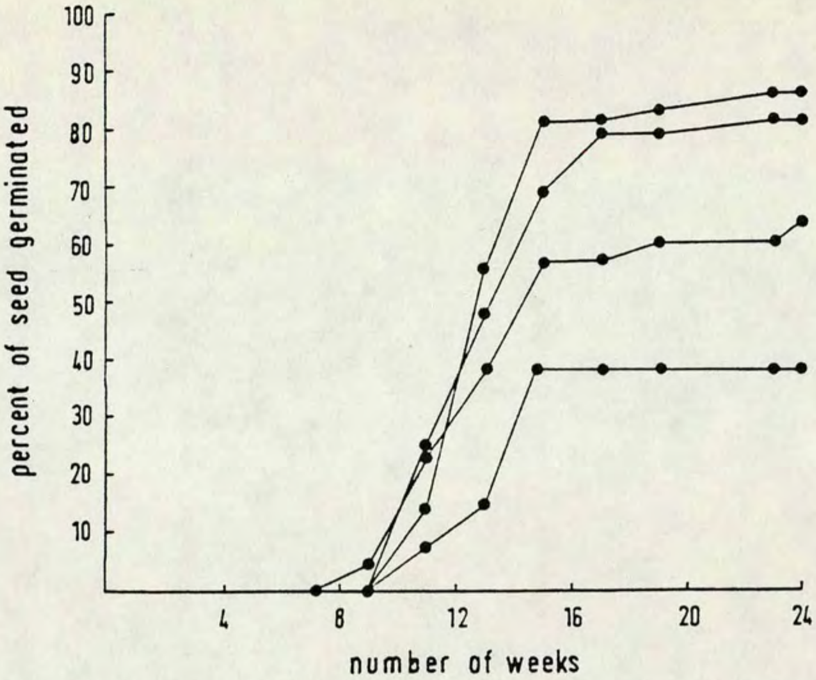


Fig. 5.12 Total germination percent at 2 week intervals for 6 months at 2°C: Seed harvested from primary umbels of hybrids at Kale Water 1977

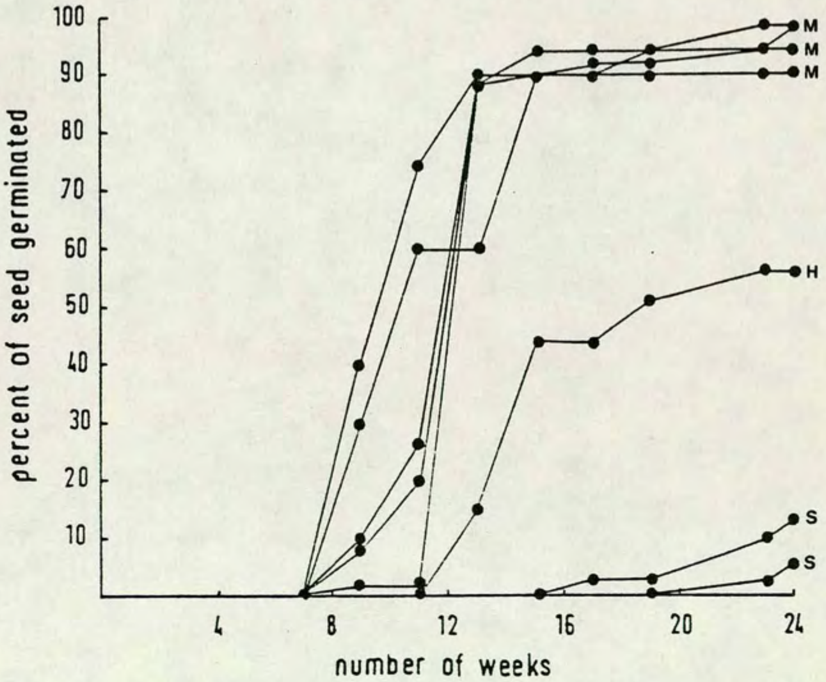


Fig. 5.13 Total germination percent at 2 week intervals for 6 months at 2°C: Seed harvested from secondary umbels of *H. mantegazzianum*(m), *H. sphondylium*(s) and hybrids(h) at Kale Water 1977

from different plants. The two plants with very low germination totals in Fig.5.4 were those with low numbers of seeds (12 and 3). Here percentages are misleading, Tables 5.2 to 5.4 give absolute values for all crosses and plants from Kale Water. Graphs for seeds from individual H. mantegazzianum plants used for self and hybrid crosses (Figs. 5.8 and 5.9) are also based on low numbers.

The variation in final germination percent for individual plants is demonstrated by the X^2 test for homogeneity in Table 5.5. All groups were heterogeneous. However, a two-way analysis of variance (Table 5.8) on an arcsin transformation (Sokal and Rohlf 1969) of the reduced dataset for H. sphondylium crosses (Table 5.7) suggests that there is no significant difference between the final germination percent of out, self or hybrid cross seed which may be attributed to either cross type or plant number. The percentage seed germination for self, out and hybrid seed from this reduced dataset is 79%, 90% and 79% respectively. This contradicts a X^2 test on the totals (Table 5.1) of 90%, 90% and 73%. (Table 5.6). There is no distinct difference between the final germination percentages for seeds from any cross type or plant provenance. Numbers of seed germinating from any one seed batch vary as much between plants as between species or cross type. The significant difference between groups is that most H. mantegazzianum seed germinates at least a month before seed of H. sphondylium and two weeks before seed from hybrid plants. Artificially produced hybrid

Table 5.2. Results of germination trials: Numbers of seed germinated after 6 months at 2°C

H. mantegazzianum ♀

	OUTCROSS		HYBRID		SELF	
Plant No.	(1)	(2)	(1)	(2)	(1)	(2)
41	16	81	1	2	2	7
42	10	15				
43	83	33				
44	98	13	1	1		
45	61	28				
48	29	96				
49	73	79				
50	45	27				
51	125	4	11	13	2	4

	SELF(2°)		OUTCROSS(2°)	
	(1)	(2)	(1)	(2)
41	192	122		
43	172	125		
45			170	141

(1) number of seeds germinated
(2) number of seeds not germinated

Table 5.3. Results of germination trials: Number of seed germinated after 6 months at 2°C

H. sphondylium ♀

	SELF		OUTCROSS		HYBRID	
Plant No.	(1)	(2)	(1)	(2)	(1)	(2)
2					25	43
5			120	11		
7	4	8				
21	22	5	165	10	14	2
22	19	5	104	17	5	1
24	19	3	75	21	24	24
25	10	2	159	5	74	15
26	201	9	230	47	32	19
29			155	18		
31	1	2	113	3	18	8
32	71	4			47	7
35	12	2			14	3
36	48	2			52	18
37			134	6	10	11
38	37	1	141	1		
39	39	9			47	19
40	104	5	73	2	38	1

	BACK	
	(1)	(2)
39	19	2

(1) number of seeds germinated
(2) number of seeds not germinated

Table 5.4. Results of germination trials: numbers of seed germinated after 6 months at 2°C

KALE WATER PLANTS

	1° umbel		2° umbel	
Plant No.	(1)	(2)	(1)	(2)
H. sphondylium				
2	0	300		
3	187	163		
4	19	131		
6	233	217		
13	46	104	6	94
24	88	12		
25	151	49		
26	39	11		
28	66	34		
29	17	33		
30	104	46		
32	99	301		
33	45	155		
H. mantegazzianum				
5	331	69		
7	313	87	45	5
8	390	10	45	5
9	356	44		
10	333	67	47	3
11	392	8		
12	390	10		
14	382	18		
15	387	13	49	1
16	376	24		
17	385	15	49	1
19	363	37		
20	382	18		
21	377	23		
22	384	16		
23	389	11		
27	385	15		
31	394	6		
Hybrid				
H3	30	17	22	17
H5	39	9	4	26
H7	5	8		
H8	31	5		

(1) number of seeds germinated
(2) number of seeds not germinated

Table 5.5. Values of χ^2 for the Null Hypothesis that the proportion of seed germinated is independent of plant number within each cross type

Cross Type	d.f.	$\chi^2_{0.05}$	χ^2
H. sphondylium ♀			
SELF	12	21.03	89.737
OUTCROSS	10	18.31	81.643
HYBRID	12	21.03	94.250
H. mantegazzianum ♀			
OUTCROSS	8	15.51	277.099
SELF 2^o	1	3.84	33.337
Kale Water			
Hybrid	3	7.82	14.642
H. mantegazzianum	17		384.754
H. sphondylium	12	21.03	673.962

Table 5.6. Values of χ^2 for the Null Hypothesis that the proportion of seed germinated is independent of cross type or species for each cross/species combination

Cross/species combination	d.f.	$\chi^2_{0.05}$	χ^2
H. sphondylium ♀			
SELF, OUT, HYBRID	3	7.82	154.499
SELF, OUT, HYBRID, BACK	3	7.82	155.615
SELF, HYBRID			
H. mantegazzianum ♀			
OUT, HYBRID, SELF	2	5.99	8.453
OUT, SELF 2^o, HYBRID	2	5.99	5.447
Kale Water			
H. mantegazzianum *H. sphondylium*, hybrid	2	5.99	2,776.982

Table 5.7. Percentage seed germination for plants used for all three treatments

Plant No.	SELF	OUTCROSS	HYBRID
21	81	95	88
22	79	86	83
24	86	78	50
25	83	97	83
26	96	80	80
31	33	97	69
40	95	97	97
mean	79	90	79

Table 5.8. ANOVA table for arcsin transformation of percentage seed germination of *H. sphondylium* plants used in all three treatments (Table 5.7)

Source of variation	d.f.	s.s.	m.s.	F
CROSS TYPE	2	371.1629	185.5815	1.6883
PLANTS	6	1036.419	172.7365	1.5715
ERROR	12	1319.0586	109.9216	
TOTAL	20			

$F_{0.05}(2,12)=3.8853$ $F_{0.05}(6,12)=2.9961$

seed commences germination at the same time as seed from parent plants, but the numbers of seed germinating increases more rapidly than for seed from H. sphondylium intraspecific crosses (Fig.5.2.).

Seed weights

The mean seed weight for the hybrid cross was greater than that of either self or outcross (Table 5.9) for both H. sphondylium and H. mantegazzianum. A two-way analysis of variance for plants with all three treatment types (Table 5.10) gave a significant difference between mean seed weights attributable to cross type but not plant number (Table 5.11).

5.4 Discussion

The potential for natural hybridization between H. sphondylium and H. mantegazzianum was further substantiated by the successful germination of hybrid seed produced from both parent plants. Hybrid seedlings grew vigorously, and at the first leaf stage could be readily distinguished from either parent by their intermediate size and pubescence on the upper leaf surface (Fig.5.14). Seed produced by backcross of hybrid pollen onto H. sphondylium stigmas and collected from hybrid plants at Kale Water also germinated, thus providing evidence for an F2 hybrid generation or backcrossing in the field.

Table 5.9 Results of controlled crosses: MEAN SEED WEIGHT FOR EACH TREATMENT (mg)

	SELF	OUT-CROSS	HYBRID	BACK	SELF 2^o	OUT 2^o
H. sphondylium	10.8	9.6	13.2	13.4		
H. mantegazzianum	29.2	27.1	30.3		28.6	27.3

Table 5.10. Mean seed weight for each plant used for all three treatments (mg)

Plant No.	SELF	OUTCROSS	HYBRID
21	12.6	5.2	13.1
22	14.0	14.8	15.2
24	15.6	10.6	14.4
25	14.2	12.8	16.1
26	7.8	9.2	9.8
31	7.2	8.6	16.1
40	11.6	9.7	11.4
mean:	11.9	10.1	13.7

Table 5.11. ANOVA table for mean seed weights shown in Table 5.10

Source of variation	d.f.	s.s.	m.s.	F
Cross type	2	4,538.38	2,269.19	4.27
Plants	6	9,111.62	1,518.60	2.86
Error	12	6,370.95	530.91	
Total	20	20,020.95		

$F_{0.05}(2,12)=3.8853$ $F_{0.05}(6,12)=2.9961$

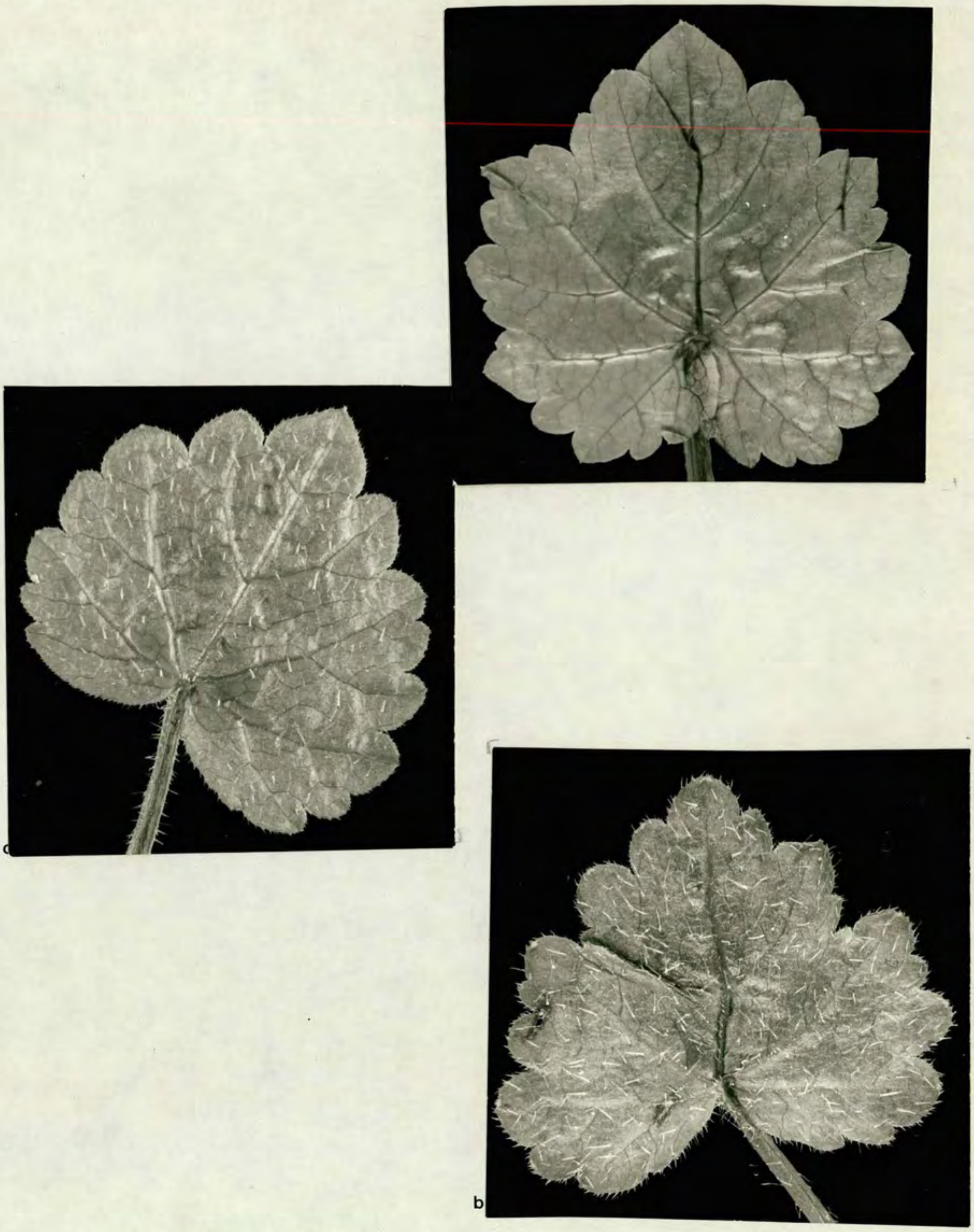


Fig. 5.14 First leaf of seedlings of (a) H. mantegazzianum, (b) H. sphondylium and (c) hybrid (photographs by W. Foster)

Hybrid seed did not, however, give a final germination percent as great as that from *H. sphondylium* intraspecific crosses. Although most seeds which did not develop were found to have decayed or decomposed and rotting embryos, some of the interspecific crosses and the hybrid plants from Kale Water had seeds with misshapen embryos. This postzygotic hybrid failure contributed to the lowered germination response in the F1 and F2 seeds; 20% below the optimum for both *Heracleum* species. Hybrid seedlings which did emerge were not noticeably abnormal in the early stages of growth when compared with other *Heracleum* species.

Whether or not the hybrid seedlings would become established as adult plants would depend on their ability to germinate in the sites available to them in the field, and to compete effectively with associated species or either *Heracleum* parent during the growth of the seedlings and young plants. Their germination requirements and percentage viability will determine the hybrid's chance of occupying suitable sites in the environment, while length of dormancy and rate of growth will affect seedling survival in competition.

Heracleum hybrids at Kale Water were found growing either on the boundary of one of the populations of *H. sphondylium* or within the population of *H. mantegazzianum* (Fig. 3.2). Typically, *H. sphondylium* grows in grassy places, roadsides, by hedges and in woods, while *H. mantegazzianum* is a plant of waste ground and riversides

(Clapham et al. 1962). Hybrids have not been found in the wettest habitat of H. mantegazzianum, in the sand and gravel backwaters of Kale Water, nor on the driest field sites of H. sphondylium where H. mantegazzianum does not grow. Hybrid regeneration sites are therefore in the damp grass community of H. sphondylium, or the edge of the more open H. mantegazzianum habitat. Within this environment hybrid seeds, capable of a high germination percent and with the typical chilling requirements of Heracleum, probably have as much chance of successful germination as parent plants.

It has been suggested that the settlement of Heracleum in plant communities is assisted by the furanocoumarin content of seeds, and that this has an allelopathic effect on the surrounding vegetation (Zhamba 1972). Junttila (1975) has shown that seeds of H. laciniatum Horn. inhibited the germination of lettuce, Lactuca sativa L. cv. Maikonig, Salix pentandra L., and radish, Raphanus sativus L. cv. København Torg, but had no effect on the germination of spruce, Picea abies (L.) Karst. Coumarin content varies between species of Heracleum (Molho et al. 1971) and might be expected to confer an advantage to certain species. However, Myras (pers. comm.) working on the invasion of H. laciniatum Horn. to grassland in north Norway, thinks that although there is some evidence for the leaching of toxins from the roots of Heracleum, competition for light accounts for 90 - 100% of reduction of plant population production under stands of H. laciniatum and that inhibition by chemicals probably plays a minor role in the establishment of the plant.

The dormancy requirements of Heracleum hybrids are intermediate between those of the two parent species. In this respect they resemble other known hybrids. Those of the Xanthium strumarium complex (McMillan 1975) show the broader temperature tolerances of the American parent when crosses with plants of Asian origin. Xanthium species also thrive in habitats disturbed by man where photoperiod and temperature response ensures survival in normally diverse environments. Hybrid seeds intermediate in dormancy requirements have also been noted in the genus Amaranthus (Frost & Cavers 1975). Seed from the backcross of hybrid pollen to H. sphondylium stigma germinated at the same rate as seed from the hybrid cross, while seed from plants collected in the field began germinating earlier than any artificially produced seed, suggesting that seed set in the wild may be of H. mantegazzianum backcross origin.

In cultivation hybrid seed from experimental crosses began germinating at the same time as that of H. sphondylium, but at 3½ months 40% had germinated whereas only 20% of H. sphondylium seed had germinated in the same time. The time required by individual hybrid seed lots to start germinating was much less variable than those of H. sphondylium, though both reached a maximum after six months at 2-5°C. H. mantegazzianum, in contrast, had a much more uniform germination response, began germinating two weeks to one month earlier than H. sphondylium and reached a maximum at 2 - 3.5 months.

H. sphondylium seeds from Kale Water were extremely slow to break dormancy. After six months at 2°C seeds from plant No.13 and 4 were still germinating, while Nos. 24, 25 and 26 had already stabilized about 75% germination. It is not unusual to find variations in germination response, and this is well documented in cultivated plants. In the Umbelliferae poor germination is a common occurrence for cultivated carrots *Daucus carota*, celery *Apium graveolens*, parsley *Petroselinum crispum* and parsnips *Pastinaca sativa* (Robinson 1954). A difference in temperature sensitivity has been noted within a single carrot cultivar (Hegarty 1973). In natural populations the only extensive study of germination in the Umbelliferae is on *Torilis japonica*, the only biennial species in *Torilis*, and has shown that seeds which did not germinate in the autumn of the first year were induced into dormancy until autumn of the following year (Baskin & Baskin 1975). In a more general survey of the family perennial species were found to require several months and annual or biennial species only five days to one month for germination at normal temperatures (Cerceau 1962). None of the *Heracleum* species from south-east Scotland germinated this rapidly. Of the genera studied by Cerceau (1962) they may best be compared with *Neogaya mucronata* from Turkestan, which germinated after five months at low temperatures. The pattern of interspecific variation in germination requirements in *Heracleum* resembles that of *Amaranthus* (Amaranthaceae). Six collections of *A. powellii* showed considerable intraspecific diversity both in rate and percent germination, while five collections of *A. retroflexus* were more uniform in their time taken to germinate (Frost & Cavers 1975). Despite their potential for variation, the minimum recorded dormancy requirement for H. sphondylium of three months (Stokes 1952) is still longer than that of *H. mantegazzianum* 2.5 months (Ivanova 1971).

The difference in germination response of *H. sphondylium* and *H. mantegazzianum* is part of the difference in life cycles between these two species. *H. mantegazzianum* is extremely successful at colonizing new habitats as is evident from its distribution in Britain. In terms of population dynamics (Harper 1977) it is an "r" selection species, with high fecundity, a large seed resource and competitive ability, but no protection against predators. Although said by Mandenova to be perennial, plants from south-east Scotland were predominantly monocarpic when grown in the experimental garden. Nine of ten plants died after flowering, one flowered again the following year. A small proportion of plants are recruited to the population each year. Plants which are to flower can be recognised early in the season from their significantly large rosette size. Probably a critical rosette size must be reached before flowering can take place, as for *Dipsacus fullonum* (Werner 1975), and *Pastinaca sativa* (Thompson 1978). Observations of fixed quadrats at Hopetoun and Park Burn confirm a high mortality rate for seedlings and juveniles. Plants seldom become established on meadows because they cannot withstand grazing.

H. sphondylium is a "K" selection species, a perennial with fewer seeds per plant and a long life and juvenile period. The life cycle of *H. sphondylium* subsp. *sibiricum* has been followed over several years by Rabotnov (1956). This subspecies, similar to subsp. *sphondylium*, but with a North Europe and Asian distribution, has a 13-15 year life-span, and flowers at irregular intervals. About 20% of the population was monocarpic. *H. sibiricum* flowers first after 2-4 years, but may extend the juvenile period as long as 10 years. Similarly a population of *H. lehmannianum* (Sect. *Pubescentia*) was found by Temirbekov (1977) to be 5% monocarpic, with most plants flowering in their third year, and a small number (10%) remaining virginal to their fifth year. Mortality in *H. sibiricum*, like *H. mantegazzianum*, was greatest (49.4%) in young plants up to one year old, and very low (10%), among plants which had reached flowering. In exceptional circumstances plants may live for 20 - 25 years, but the population studied by Rabatnov was eradicated by frost and flooding of the River Oka in 1952. In 1953 new plants germinated, but the composition of the meadow community had changed in favour of grasses. *H. sphondylium* is therefore apparently not as successful at recolonization as *H. mantegazzianum* but may be better able to survive interspecific competition. The variable dormancy requirements of *H. sphondylium* seeds ensures that seedlings are continuously germinating, thereby increasing the chance of some occupying a suitable regeneration site in closed communities.

"r" and "K" concepts are generalizations which help to make predictions about the fitness of life cycles for survival in different environments. They do not take into account the specialized adaptions of plants; differences in structure which affect the ability of seeds to take up water (Oomes & Elberse 1976, Sheldon 1974), and physiological responses to increased density which are negative for some weedy species, positive for others of closed communities (Linhart 1976). Germination on agar at uniform density is only part of the potential for establishment. Furthermore, although the "regeneration niche" is undoubtedly important for diversity and speciation (Grubb 1977), interspecific and intraspecific competition must also play a part. Two examples may be found in biennial Umbelliferae. On the introduction of Daucus carota (Holt 1972) to the early stages of succession in a community, mortality of seedlings was greater on herbage than on bare ground, but also the presence of associated vegetation delayed the onset of flowering for four or five years. In patches of Pastinaca sativa (Thompson 1978) the slower growth of plants in the centre which were subject to increasing intraspecific competition led to "the dissolution of the patch in time".

There is not enough information on the population dynamics of Heracleum to draw conclusions on the fitness of the hybrid from germination counts alone. The hybrid does have an advantage over H. sphondylium in its slightly shorter dormancy requirements, and over H. mantegazzianum

by its slightly heavier seed (Harper 1977, Salisbury 1974). Once mature the adult hybrid may live for several years; at Kale Water in 1978 four of nine hybrids flowered for the second time. Thus it is intermediate between "r" and "K" taxa. Exactly what contribution natural selection makes to the postzygotic isolation between these two Heracleum species is not possible to say, but, with the evidence of the viability of the seed from the H. sphondylium hybrid cross on the one hand, and the numbers of hybrids at Kale Water on the other, Karlson's comment on the relationship between introduced and indigenous Euphrasia in Sweden may provide an appropriate conclusion: (Karlsson 1976).
"Thus has nature in an enormous experiment tested the taxonomic status of the biological units, more rigorously than we can ever hope to do in our experimental gardens."

CHAPTER VI

Discussion & Conclusions

Occasional hybrids were identified in mixed populations of *H. mantegazzianum* and *H. sphondylium* in Scotland during the period 1974-78, but during that time the specific characters of the parents remained discrete; there was no evidence of widespread introgression. Attempts to synthesize the hybrid by the *H. mantegazzianum* x *H. sphondylium* cross failed on 6 of 8 plants of Hopetoun provenance, but gave 15% seed set on the plant from Riddell. The *H. sphondylium* x *H. mantegazzianum* cross set 23% seed overall, which was 73% viable. Seed set from an artificial intraspecific *H. sphondylium* cross was 91% viable, but at Kale Water in 1977 only 9 hybrid plants were found in a mixed population of several hundred *Heracleum* of both species. Either the F1 hybrid progeny die before they reach the adult stage, or there is a barrier to cross fertilization in pollen transfer between species or certation, or all these factors work together to keep the two species relatively isolated.

The hybrid in the field is 0-7% pollen fertile and sets at the most 3% seed. An explanation for the partial sterility is provided by the description of meiosis in the hybrids from Kale Water (Weimarck et al. to be published). All plants studied by Weimarck were diploid, 2n=22, and had at most one chiasmata per chromosome. Weimarck concluded that the high degree of sterility could be explained by segregational aberrations due to structural heterozygosity: the parents probably differed karyologically by:

(1) 2 translocations involving 3 chromosome pairs

(2) 2 inversions of different length and in different pairs

(3) At least 1, maybe up to 3 visibly different chromosome arms belonging to chromosomes whose other arm was capable of regular chiasma formation

(4) Perhaps a number of small chromosomal differentiations reducing fertility in the hybrids

The H. mantegazzianum plant No. 23, with 85% fertility, had 11 bivalents and balanced segregation at Anaphase I, but one bridge without a fragment and one lagging chromatid at Anaphase II. Two of the H. sphondylium plants with 87% pollen fertility formed a quadrivalent at Diakinesis, but segregated normally at Anaphase I. Translocation heterozygosity is apparently common in H. sphondylium sens. lat. The hybrids H1 and H4 with 3% and 10% fertility, had a higher proportion of multivalents at Diakinesis, including hexavalents which were broken up at Metaphase I. At Anaphase numerically unbalanced segregation was frequent. In some of the cells of the hybrid and H. sphondylium 33, which had 50% separation difficulties at Anaphase and a correspondingly lower pollen fertility 60%, one heteromorphic bivalent could be discerned.

A number of meiotic irregularities were recorded in the following species by Garde and Garde (1949):

Thapsia garganica
Opopanax chironium
Torilis neglecta
Seseli tortuosum
Peucedanum hispanicum
Kundmannia sicula

They are noted here because Owens (1974) thought they might be of hybrid origin. In the hybrid between diploid and tetraploid *Eryngium campestre* L. 35-40% of pollen mother cells showed univalents, multivalents and abnormalities such as lagging chromosomes (Reese 1969 in Moore 1971). On the other hand, hybrids which have been examined in *Apium* (Beuzenberg & Hair 1963) and *Sanicula* (Bell 1955) had normal meiosis.

Of the 840 species of Umbelliferae for which counts are available, almost all show regular bivalent pairing (Moore 1971). Exceptions are the chemically induced polyploids (Joshi 1968) and male sterile plants of *Daucus carota* (Zenkteler 1962). The latter had quadrivalents and hexivalents at Diakinesis, and bridge formations at Anaphase I and II. One plant with 70% pollen sterility showed no evidence of meiotic abnormalities and Zenkteler concluded that there are undoubtedly other conditions associated with pollen abortion. Suggestions have been made by Solbrig (1968): non-complementary genes, lethal or semilethal genes, non-functional zygotes or other still poorly understood causes (discussed by Stebbins (1971)).

Chromosome pairing, like fertility, can also be under genetic control and is therefore not always a reflection of the degree of kinship between plants (de Wet & Harlan 1972, Stebbins 1971). In considering the relationship between these two *Heracleum* species it is as well to bear in mind the discovery of B-chromosomes in some populations of *H. sphondylium* sens. lat. (Weimarck 1978). B-chromosomes are thought to be able to affect chiasma formation at meiosis (Rees & Jones 1977).

Overall, the relationship between *H. mantegazzianum* and *H. sphondylium* may be compared with "those genera with an essentially "normal" relationship between the amount of difference between species ... several different types of mechanisms are operating with about equal force". (Stebbins 1960). In more detail Grant (1971) outlined 5 patterns of species relationships of which the following might be said to apply to *Heracleum*:

> "The Geum pattern: Perennial herbs with an outcrossing breeding system and with floral mechanisms having only moderate species to species differences. Species intercompatible within wide limits; but strong incompatibility barriers developed between sections or subgenera. Species belonging to the same species group are interfertile and chromosomally homologous; those belonging to different species groups form hybrids with chromosomal and genic sterility. Related species isolated in nature by ecological and other external factors. *Geum*, *Iris*, *Solanum*, *Silene*".

To appreciate the extent to which *Heracleum* fits the *Geum* pattern and in order to describe the relationship between *H. mantegazzianum* and *H. sphondylium* more exactly, it is necessary to consider the full range of variation in the genus, which has about 70 species in the north temperate regions and North Africa (Clapham et al. 1962). Its distribution is vast: from West Europe to East Asia, north to Scandinavia and south to North Africa, and to North America. At the northern limit there is only one species: *H. sibiricum*, and in North America, *H. lanatum*, (although *H. mantegazzianum* is also naturalized there). The centres of diversity are East Asia, the mountains of south Europe and the Caucasus. According to Mandenova (1950) three basic modifications have taken place within the genus, and these form the basis of her division of *Heracleum* from the USSR into the following sections:

	No. of species
Euheracleum	14
Pubescentia	8
Villosa	5
Wendia	6
Apiifolia	4

A full list of species from "Fl. USSR" (Komarov 1951) is given in Table 6.1 for reference.

Table 6.1. Heracleum in Fl. USSR (Komarov 1951) after Mandenova

Section 1 Euheracleum

Series 1 Sibirica

H. sibiricum

Series 2 Sphondylia

H. cyclocarpum
H. aconitifolium
H. palmatum
H. carpaticum
H. ponticum
H. dulce
H. sphondylium
H. asperum
H. dissectum
H. barbatum
H. colchicum
H. calcareum
H. osseticum

Section 2 Pubescentia

Series 1 Pubescentia

H. pubescens

Series 2 Mantegazziana

H. mantegazzianum
H. grossheimii
H. wilhelmsii
H. sosnowskyi
H. sommieri

Series 3 Trachyloma

H. trachyloma
H. lehmannianum

Section 3 Villosa

H. scabrum
H. stevenii
H. leskovii
H. antasiaticum
H. grandiflorum

Section 4 Wendia

Series 1 Pastinacifolia

H. pastinacifolium
H. chorodanum

Series 2 Transcaucasia

H. transcaucasicum
H. roseum
H. schelkovnikovii
H. albovii

Section 5 Apiifolia

H. apiifolium
H. ligusticifolium
H. olgae
H. transiliense

Heracleum is the most ancient and primitive branch. It has the most species and a vast distribution over most of the area of the genus. It includes H. sphondylium, a polymorphic species with no clear subdivision which grows in subalpine and upper forest zones, forest edges, gorges and ravines of wet woods, tall herb communities and rarely, subalpine meadows. Mandenova considers that these are the fragments of an ancient morphological type which had a wide distribution in the Pliocene. This view is supported by the hypothesis of Mathias (1965) that species with a distribution in North America and Eastern Asia must have been part of the Arcto-Tertiary Flora of North America. H. sphondylium sens. lat. is found as H. lanatum in North America, and H. moellendorfii in East Asia.

The section Pubescentia is characterised by giant size, monocarpic habit, and large vittae. These species are concentrated principally in the forest regions of the Caucasus, in mountain zone woods, with H. lehmannianum outside the range in Turkestan. H. sosnowskyi is widely distributed, but H. mantegazzianum, H. grossheimii and H. wilhelmsii are more localized. H. trachyloma grows in the forests of Armenia, and H. persicum on the slopes of the Elburz. H. wilhemsii and H. trachyloma form considerable thickets, sometimes pure, along rivers.

Section Villosa inhabits more mesophytic places, such as screes and mountain woods to 2200 m. It is characterized by increased pubescence and large dorsal vittae. Often there is accelerated development of the life cycles: H. antasiaticum near Tbilisi starts flowering in May and is finished by late June. These mesophytic forms have evolved in the Eastern Mediterranean.

Section Apiifolia are separated on account of the similarity of their fruit with Pastinaca.

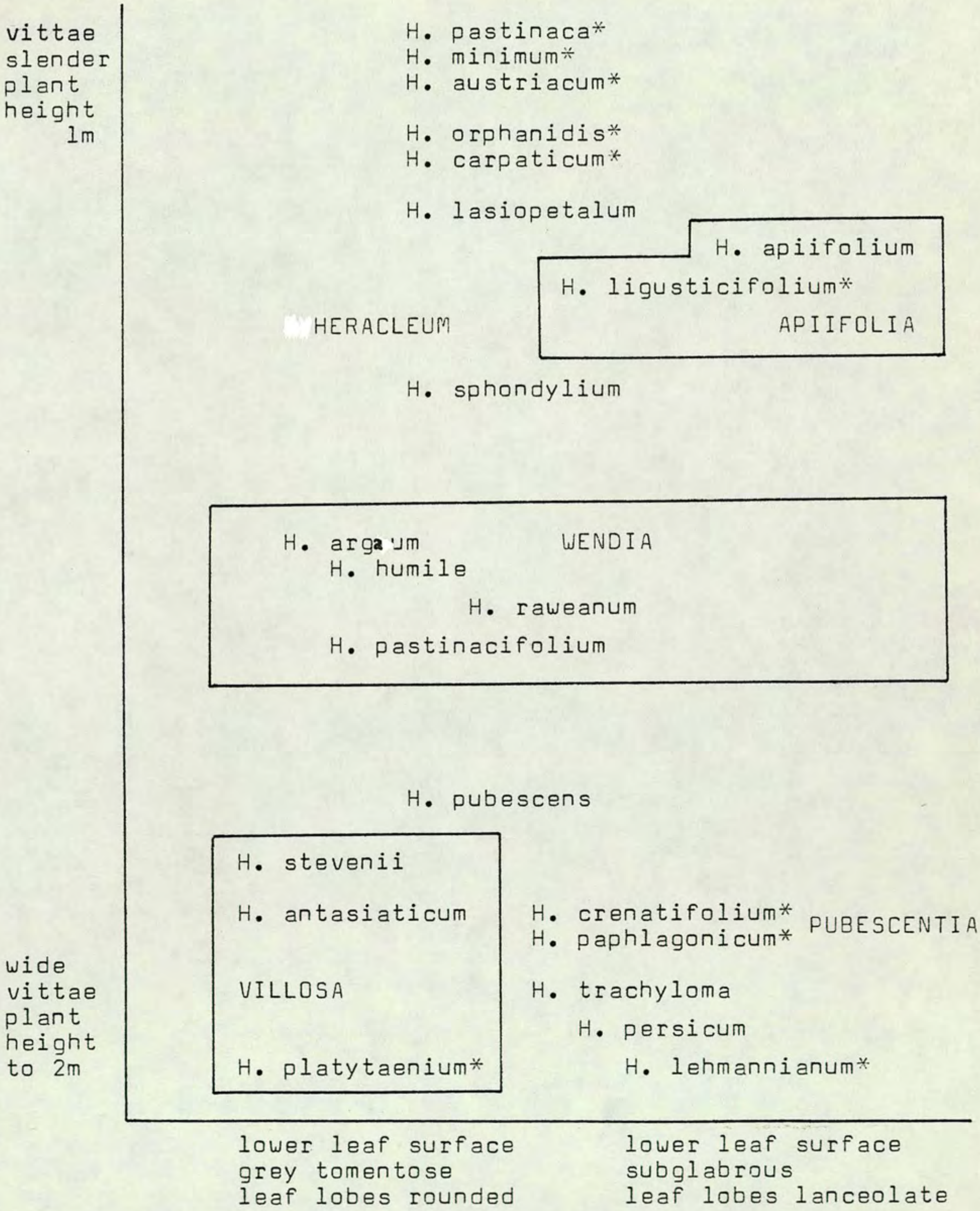
Wendia Mandenova considers to be the most advanced and are characterized by reduced vittae. The most progressive forms grow in subalpine zones and rocky places, and frequently have isolated distribution. It is within this section that, in terms of phylogeny, Mandenova considers the genus to be advancing.

In this respect Heracleum conforms with the recognized general trend in the Umbelliferae. Cerceau (1971) maintains that differentiation and expansion of the family is taking place in the mediterranean as a result of progressively drier conditions. Here are found the genera Echinophora, Orlaya, Lisaea and Turgenia which are annuals with short vegetative cycles, restricted distribution and the most evolved pollen types. Similarly, in North America, Mathias (1965) considers the differentiation of the Umbelliferae to be in response to progressively drier environments in grasslands and desert borders, with genera such as Lomatium which are perennial and become dormant before the summer dry season and Eryngium with species adapted to salt water marshes and vernal pools. In Anatolia, where there are 14 recorded species of Heracleum, Davis (1971) considers the flora to be in an active state of evolution, with aridity and geographical isolation both stimulating rapid diversification.

Heracleum species from the centres of diversity in East Asia and South Europe are arranged along two axes for plant size and leaf pubescence in Table 6.2. The habitat, distribution and diversity of these species are described in "Flora Europaea" (Brummitt 1968) and "Flora of Turkey" (Davis 1972) and are summarized below. Neither Davis (1972) nor Brummitt (1968) divided the genus into sections. Grossheim (1967) in "Flora of the Caucasus" reduced the number of sections to three: Wendia, Apiifolia and Heracleum (the latter containing Pubescentia, Euheracleum and Villosa). In Table 6.2 Mandenova's sections for "Fl. USSR" (Table 6.1) are included for comparison with European and East Asian species of Heracleum.

The small group H. minimum (S.E. France, calcareous screes), H. austriacum (E. Alps), H. pastinaca (E. Medit.), H. orphanidis (Macedonia), H. carpaticum (E. Carpathians), H. ligusticifolium (S. Crimea) are all endemic species of the mountainous regions of the Mediterranean and the Black Sea. H. apiifolium which Davis (1972) says resembles H. austriacum grows in moist meadows, rocky gullies and by streams at 1400-2600 m. in North East Anatolia and West Caucasia. H. sphondylium is given a central position in Table 6.2 but is more variable than this implies, reaching two extremes in Turkey: subsp. cyclocarpum which grows to 2 m in Georgia, and subsp. artivense with grey

Table 6.2. Heracleum species from "Flora Europaea" (Brummitt 1968) and "Flora of Turkey" (Davis 1972) arranged according to Mandenova's Sections



* endemic

pubescent leaves, an endemic of North East Anatolia.

Also in North East Anatolia in a similar habitat, grows the slightly larger *H. pastinacifolium* subsp. *transcaucasicum*, which is weakly differentiated from two allopatric sub-species, *pastinacifolium* in the south-east, and *incanum* which grows in North and East Anatolia but at higher altitudes, 1800 - 3500 m, and in drier places, "rocky slopes, gullies, screes and summits". *H. pastinacifolium* subsp. *incanum* is morphologically similar to *H. humile*, itself a variable species with a wide distribution from north through central to south Anatolia, Lebanon and Anti-Lebanon, which in turn resembles *H. argaeum*, an endemic of central Anatolian limestone woodlands and alpine regions, 1600-2000 m, and *H. raweanum*, an alpine element of the Iraquian flora which grows at 3100 - 3300 m in South East Anatolia. In this very mountainous region of South East Turkey is also found *H. lasiopetalum* " a very distinct species, remarkable for its densely hairy petals and pubescent styles", and the genus *Trignosciadum*, which Davis (1972) considers a possible xerophytic derivative of *Heracleum*.

From the forest edges and streamsides of North East Anatolia in a westerly direction to the low-lying land nearer to the Mediterranean the two grey tomentose-leaf species of *Villosa* are distributed. These are *H. antasiaticum* of North East and East Anatolia, apparently related to *H. stevenii* of the Crimea and *H. leskovii* of Caucasia (formerly *H. villosum* Fischer ex Sprengel), and

H. platytaenium, endemic to Turkey. *H. platytaenium* has a very variable morphology and is found in a wide variety of habitats from mixed forest slopes to streamside banks, all at low altitudes 1-1500 m, in North West and Central Anatolia.

Finally the group of large endemics, *H. pubescens* (S. Crimea), *H. lehmannianum* (Central Asia), *H. crenatifolium* (N.E. and East Anatolia) *H. paphlagonicum* (N. Anatolia) are plants of montane forest, meadows and streams. The distribution of their Caucasian relatives is given in Chapter II. Two of this group, *H. trachyloma* and *H. persicum*, which have apparently achieved a wider distribution, cross the political boundaries of Eastern Anatolia, the South Transcaucasia and Iran.

There are two points to be made from this general survey of the genus:

(1) The existence of widespread and variable species:

e.g. *H. sphondylium*
H. platytaenium and *H. antasiaticum*
H. pastinacifolium

which roughly coincide with Mandenova's division into sections. These occupy a wide range of habitats from forest edge to streamside and rocky mountain slopes, and may resemble the "ecospecies" of Valentine (1978a).

(2) A number of more clearly defined species of restricted distribution, sometimes specialized habitats:

e.g. *H. minimum*, *H. paphlagonicum*, *H. argaeum*

Often these are endemics, closely associated with a more widely distributed species, *H. humile* and *H. argaeum*, *H. sosnowskyi* and *H. mantegazzianum*.

Thus the formation of partly sterile hybrids between *H. sphondylium* and *H. mantegazzianum* means that there are partial barriers to gene flow between Mandenova's sections, while more closely related species, such as *H. platytaenium* and *H. antasiaticum* appear to intergrade and may be interfertile, as in the *Geum* example. The possibly one-way nature of the cross indicates that it is the endemic monocarpic species *H. mantegazzianum* which is isolated from the perennial polymorphic species *H. sphondylium*.

These conclusions on the degree of isolation of *Heracleum* species are supported by additional reports of hybridization in the genus. By itself, the result of the *H. mantegazzianum* x *H. sphondylium* cross in Scotland should not be extrapolated to other populations without reservation. There may be an intraspecific variation in fertility which enables the Scottish *H. mantegazzianum* to cross with *H. sphondylium* with more facility than populations of the same species in the Caucasus, especially as Giant Hogweed was introduced through cultivation. This topic is mentioned in Chapter IV and examples are given by Baker (1951) Stebbins (1960) and Valentine (1978a). In fact, Mme. Satsyperova (pers. comm.) has produced hybrids between *H. ponticum* (*Euheracleum* see Table 6.1 and

Fig. 2.2) and *H. sosnowskyi*, *H. trachyloma* and *H. lehmannianum* (*Pubescentia*) in cultivation in Leningrad. Also she reports seeing spontaneous hybrids between *H. mantegazzianum* and *H. leskovii* (Section *Villosa*, related to *H. antasiaticum* and *H. stevenii*) in the Caucasus. In North Turkey a collection of *Heracleum* from Gümüşane suggests that *H. apiifolium* may be hybridizing locally with *H. pastinacifolium* subsp. *incanum* (Davis 1972). The fertility of these interspecific hybrids was not mentioned, but even very low fertility would be sufficient to account for an exchange of variation between populations and may account for the traditional "critical" nature of the genus.

It is not possible from these observations on interspecific sterility to draw conclusions on the phylogeny of the genus and say that *H. mantegazzianum* was derived by selection for isolation from *H. sphondylium* or vice versa. Valentine (1970) has elsewhere argued the case that selection for incompatibility between species is not possible and that therefore the evolution of sterility will be fortuitous. Natural selection for breeding barriers such as those proposed by Grant (1971) works only on factors such as flowering time and ecological specialization which increase the reproductive output of the population. Therefore it is not possible to use the results of the experimental crosses in support of Mandenova's thesis that *Euheracleum* is the primitive section of the genus from which *Pubescentia* is derived. The only evidence on Phylogeny is that until the nineteenth century the section Pubescentia was, in historical times, confined to Asia and has therefore presumably been separated from West European species of Heracleum for at least that time and probably since the last glaciation. From extensive palynological and morphological studies, Cerceau (1971) has concluded that the general evolutionary pattern in the Umbelliferae has been from a small perennial with simple entire leaves to a taller annual plant with divided, 1-5 pinnate leaves. Within this pattern of development she considers H. mantegazzianum to be at the end of an evolutionary series (Cerceau 1971). When this palynological evidence is combined with the evidence from chemical analysis there is a strong case for the evolution of H. mantegazzianum from the more widespread H. sosnowskyi (Molho et al. 1971). How Euheracleum and Pubescentia are interrelated in their area of common distribution in Asia is not possible to say. The presence of H. paphlagonicum which Davis says resembles H. pubescens (Pubescentia) in that part of the flora of Turkey which contains many relicts of the Boreal Tertiary Flora of temperate Eurasia (Davis 1971) suggests that Pubescentia could equally well have evolved from Euheracleum before the Quartenary glaciation, or both species could have derived from a single proto-Heracleum stock.

The direct effect of hybridization on Heracleum in Britain may be to increase the variation in the genus either by hybrid speciation or introgression. Hybrid speciation generally refers to the various ways by which the F1 progeny of a hybrid cross may become established as a reproductively isolated breeding population. These are summarized by Grant (1971) as:

(1) Vegetative propagation
(2) Agamospermy
(3) Permanent translocation heterozygosity
(4) Permanent odd polyploidy
(5) Amphiploidy
(6) Recombinational speciation
(7) Segregation by isolated external barriers

While vegetative propagation and agamospermy have not yet been encountered in Heracleum, polyploidy has been recorded in 3 of 6 Heracleum species endemic in south India: H. sprengelianum (2n=44 +4B), H. ceylanicum (2n=44), H. ceylanicum (n=22), and one from Nepal: H. nepalense (n=24) (Mandenova et al. 1978). These species now have a restricted distribution in the mountains of South India, but it is thought that their ancestors were once more widespread, had greater ecological tolerance and were related to the progenitors of the Himilayan group. Polyploidy and aneuploidy are widespread in the Umbelliferae (Moore 1971). However, hybrids between H. mantegazzianum and H. sphondylium which were examined by Weimarck were all diploid (2n=22). There was some evidence from field observation of the segregation of hybrids by external isolation; hybrids flowered early at Kale Water. On the 1st July, 5 of 9 hybrids were receptive, but none of the H. sphondylium labelled plants had commenced flowering, and only 12 of the 18 labelled H. mantegazzianum were in the first male phase. Isolation in flowering times is not complete, and at some sites, Warriston and Fairmilehead, hybrids were observed which flowered late. Internal sterility barriers against fertilization by H. mantegazzianum are quite likely to form by recombinational speciation but none of the hybrids gave more than a 0-3% seed set, and would therefore fail to reproduce successfully unless they also regained fertility. At present Heracleum hybrids show no sign of speciation, although the possibility cannot be discounted, particularly on account of the genetic system of H. sphondylium and the existence of polyploidy in related taxa.

The effect of hybridization is more likely to be felt though introgression. The one experimental backcross using hybrid pollen on H. sphondylium stigmas set 14% seed which gave 77% germination. On 3 of the 9 hybrids at Kale Water no fruit was set at all, but 3 of the remainder from which seed was harvested produced about 30 - 40 seedlings per plant from the primary umbel alone. This at least equals the reproductive output from the primary umbel of 4 of the H. sphondylium plants from Kale Water. Only 4 of the H. sphondylium produced as many as 100 to 200 germinating seedlings per primary umbel. Hybrids may therefore compete in numbers of seedlings per plant within populations of H. sphondylium but both are very much less fecund than *H. mantegazzianum* plants for which about 4,500 seedlings may be expected from a single primary umbel. The low numbers of hybrid plants does not exclude the possibility of introgression. Hybrid fertility does not have to be very high (c. 1%) for gene flow between related species (Stace 1975). Weimarck (to be published) found that the chemotographic spot pattern of H6a resembled that of *H. sphondylium* plants at Kale Water, and this plant (Fig.3.2) resembles *H. sphondylium* in all morphological characters but fruit length, dorsal vittae width, hair and pollen length, for which it must be classed as intermediate between parent populations. Although in the general survey of morphometric variation there is no evidence of increased diversity in populations of mixed *H. mantegazzianum* and *H. sphondylium*, this did not include the two very variable sites at Warriston and Fairmilehead, and it is quite probable that in some disturbed habitats there may be extensive backcrossing, if not yet introgression.

Hybridization in *Heracleum* is therefore not unlike the pattern of interspecific contact between other introduced and indigeneous species. Examples of hybrids in the British flora between alien and native plants are listed in Table 6.3. Few are successfully established. *Symphytum* and *Mimulus* hybrids are heteroploid, the latter being sterile and established by clones (McArthur 1974). There are, in fact, only two examples of hybrid speciation in the endemic British flora (Walters 1978), not including those formed by autogamy and apomixis.

Table 6.3. Examples of hybrids in the British Flora between native and alien species (a) introduced through cultivation and (b) as weeds

from Stace (1975) and Clapham et al. (1962).

(a) Species introduced through cultivation:

Raphanus raphanistrum x R. sativus (radish)	50-70% pollen and seed fertile interbreed freely
Tragopogon pratensis x T. porrifolius (salsify)	2-3% seed fertile, do not persist
Endymion non-scriptus x E. hispanicus (N. spain forms hybrid swarms & Portugal)	forms hybrid swarms
Linaria repens x L. purpurea (C. & S. Italy)	1 record only
Pulmonaria longifolia x P. officinalis L. (C. & N. Europe, Caucasus)	disputed - gardens only
Medicago falcata x M. sativa (lucerne)	Pollen and seed set low, naturalized on waste ground E. Anglia and Midlands
Senecio cinerea x S. jacobea	locally recorded, part. fertile
Symphytum officinale L. x S. asperum Lepech.	Hybrid widespread in Europe
Solanum nigrum x S. sarrachoides	(Leslie 1978) local. 0-2% pollen fertile
Mimulus guttatus x M. luteus (N. America)	sterile hybrids selected for horticulture widespread as clones

(b) As weeds:

Calystegia sepium x C. silvatica (S. Europe Caucasus)	fully fertile hybrids common S.E. England
Conyza canadiensis (N. American) x Erigeron acer	rare and irregular associated with parents
Malva neglecta x M. parviflora (medit. and W. Asia casual)	95% fertile 1 record only
Capsella bursa-pastoris x C. rubella (Medit. casual in Surrey & Bucks)	Sterile and rare
Amaranthus hybridus x A. retroflexus (N. American casuals)	Sporadic sterile hybrids

They are *Saxifraga hartii* D.A. Webb., the relict of a hybrid population, and *Senecio cambrensis*, the successful allopolyploid derivative of the recently introduced *S. squalidus* and of *S. vulgaris*. Other endemic species are variants of widespread species or polyploid derivatives often restricted to specialized habitats such as *Cerastium edmondstonii* on serpentine rocks in Shetland (*C. articum*) and *Linum anglicum*, an endemic of calcareous grasslands (*L. perenne*). This pattern of eco-geographical specialization is common throughout Europe and is characteristic of those regions of the world which have a relatively stable flora (Richardson 1978). The partly sterile hybrids formed by introduced *Heracleum*, *Senecio*, *Solanum* and *Tragopogon* may contribute to the variation of parent populations by backcrossing but do not radically change the species limits in the same way as hybrid swarms between introduced and indigenous *Endymion*, *Raphanus* and *Calystegia*. As Stebbins (1960) has commented, hybrid speciation rarely leads to "progressive" evolution.

Compared with the other umbellifer genera, *Heracleum* does appear to be unusual. It is the only easily recognised spontaneous hybrid recorded in Britain - apart from *Apium* x *moorei* (Syme) Druce which does not involve an introduced species. There are in fact 18 introduced species within the family in Britain. Of these, four are the only representatives of their genus; *Astrantia major* L., *Coriandrum sativum* L. (coriander), *Ammi majus* L. (Bishops weed), and *Falcaria vulgaris* Bernh. and a further eight are rare; *Bupleurum fruticosum* L., *B. fontanesii*

Guss. ex Caruel., B. lancifolium Hornem., Caucalis platycarpos L., C. latifolia L., Smyrnium perfoliatum L. (and S. olustatrum L. which is widespread) and Levisticum officinale Koch. There are only three species from three genera which are introduced, widespread, and do not form hybrids. Peucedanum ostruthium (L.) Koch (2n=22) appears to have a northern distribution in Britain while the native P. palustre (L.) Moench (2n=22) is found in fens and ditches in the south. A third species P. officinale L. (2n=c.66) is of local distribution on banks near the sea and rare. Anthriscus cerefolium (L.) Hoffm. (Chervil, 2n=18) might be expected to hybridize with either A. sylvestris (L.) Hoffm. (2n=16) or A. caucalis Bieb. (2n=18) but these three species have different types of stigmas, stout and erect, slender spreading, and subsessile. For Petroselinum crispum (Mill.) Nyman (Parsley) (2n=22) and P. segetum (L.) Koch (2n=18) the only obvious differences between the introduced and native species are flower colour and chromosome number. Non-hybridizing Umbelliferae which are native to Britain are Torilis japonica (Houtt.) DC. (2n=16) and T. nodosa (L.) Gaertn. (2n=22,24)four species of Bupleurum which occupy different habitats, and seven species of Oenanthe all 2n=22, which grow in wet places. Attempts to cross T. nodosa subsp. praecox (n=11) and subsp. nodosa (n=12) failed, probably on account of the different chromosome number (Jury 1978).

The apparent rarity of Umbelliferae hybrids, at least in Britain, can probably be explained by their well defined habitat preferences, and the large number of small genera. Heywood (1971) once made the suggestion that Umbelliferae in the Old World have evolved a limited number of successful character combinations - the large genera - while the small genera are in part relict, even ancestral, groups and in part recently evolved variations on the basic themes of large genera. It would provide interesting evidence for the evolution of incongruity systems to experiment with the large genera of well defined ecospecies such as _Oenanthe_ and _Bupleurum_ to see if they possess the inter-specific sterility Owens (1974) found in _Daucus_, or if, like _Heracleum_, they can hybridize. As the _Apium_ hybrids already suggest, _Heracleum_ would probably not prove to be an exception in the Umbelliferae.

APPENDIX I

List of contributors to the survey on the introduction and distribution of Giant Hogweed in Scotland

List of contributors to the survey on the introduction and distribution of Giant Hogweed in Scotland

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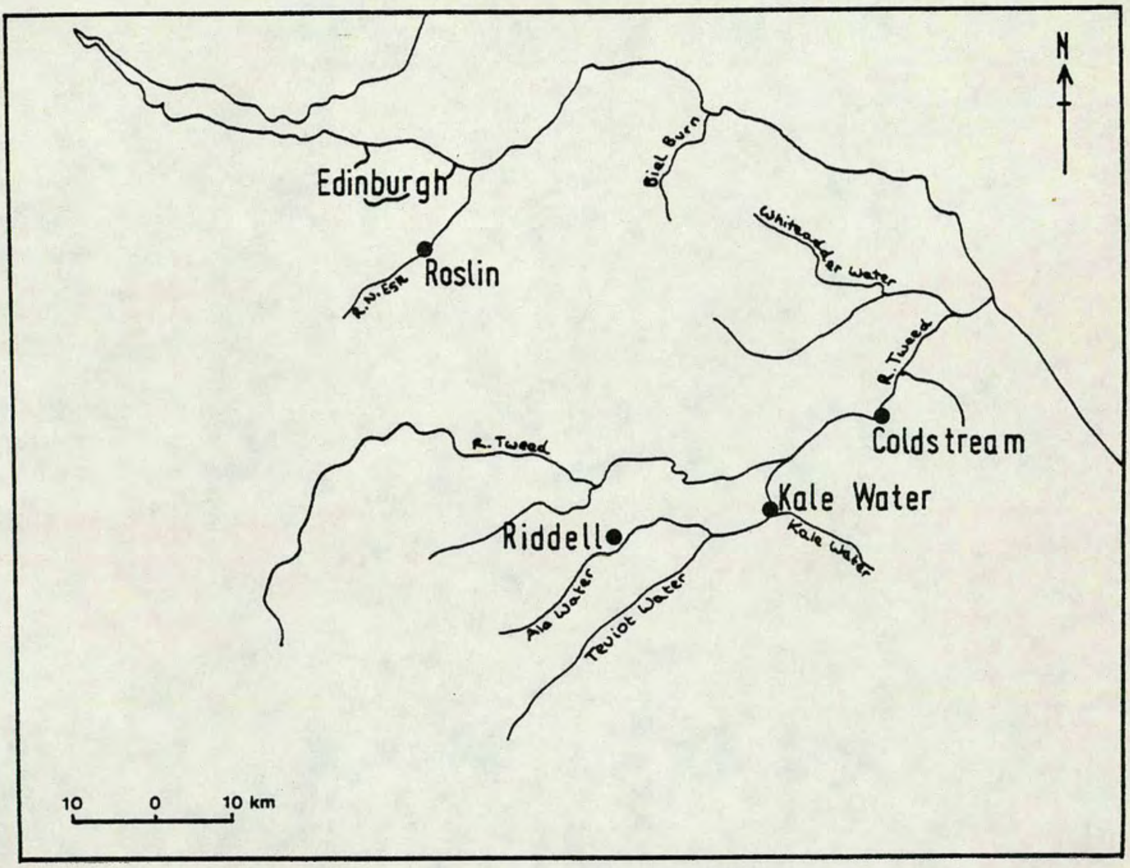
APPENDIX II

Site names and national grid references

Site names and national grid references

Site name	Grid reference	Notes
Abbey St.Bathans	36/763619	Naturalized in the saw mill yard
Biel Water	36/646776	Riverside, below Al road bridge
Coldstream	36/848400	Riverside, waste ground on the right bank of the River Tweed
Currie	36/188679	Overgrown garden of Kinleith Mill House
Fairmilehead	36/244689	Urban waste ground and parkland
Farfield	36/262632	Open field site
Hopetoun	36/093788	Spread from garden of Hopetoun House to adjacent coniferous woodland
Kale Water	36/707278	Backwater of Teviot Water
Laverockdale	36/219684	Previously cultivated, naturalized downstream beside Braid Burn
Park Burn	36/308678	Ruined cottage garden opposite Burndale beside Park Burn
Riddell	36/519247	Overgrown wild garden in woodland beside former Riddell House
Roslin	36/270627	Woodland and waste ground by sewage works between road and River North Esk
Slitrig	36/506100	Woodland and waste ground beside the entrance to Stobs Castle
Southfield	36/444749	Cultivated, naturalized downstream by Longniddry
Warriston	36/254755	Spread from banks of Water of Leith into cemetary grounds



Survey Sites. Roslin, Riddell, Kale Water and Coldstream, in relation to south-east Scotland.

APPENDIX III

Characters measured on field surveys in 1976 and 1977

Character abbreviations are explained in Section 3.2

Characters measured on field surveys in 1976 and 1977

Character	Kale Water 1977	Kale Water 1976	Riddell 1976	Roslin 1976	Coldstream 1976
1. HEIGHT	+	+	+	+	+
2. TSD	+	+	+	+	+
3. BSD	+	+	+	+	+
4. 1^{o} DIAM	+	+	+	+	+
5. NO. RAYS	+	+	+	+	+
6. 1^{o} & 2^{o}	+				
7. No. 2^{o}	+	+	+	+	+
8. BRACTS	+	+	+	+	+
9. LEAF L.	+	+	+	+	+
10. W1	+	+	+	+	+
11. W2	+	+	+	+	+
12. R1	+	+	+	+	+
13. R2	+				
14. d1	+	+	+	+	+
15. d2	+	+	+	+	+
16. b	+	+	+	+	+
17. n.s.	+	+	+	+	+
18. a	+				
19. ax	+	+	+	+	+
20. bsl	+	+	+	+	+
21. bsb	+	+	+	+	+
22. %pf	+				
23. %ss	+				
24. STYLE L	+				
25. POLLEN L	+				
26. MERICARP WEIGHT	+				
27. L	+	+	+	+	+
28. W	+	+	+	+	+
29. dvl	+	+	+	+	+
30. cvl	+	+	+	+	+
31. dvb	+	+	+	+	+
32. cvb	+	+	+	+	+
33. stl	+				
34. stb	+				
35. HAIR L	+				
36. W	+				

APPENDIX IV

MORPHOLOGICAL MEASUREMENTS

Values for individual plants at Kale Water 1977, 1976,
Coldstream, Roslin and Riddell

Character abbreviations are explained in Section 3.2.

KALE WATER 1977 - Characters measured in the field

	Height (m)	TSD (mm)	BSD (mm)	1^{o}diam (mm)	No. of rays	angle 1^{o}&2^{o}	No.of 2^{o}	No.of bracts
H. sphondylium								
1	1.65	5	19	90	20	40	1	0
2	1.50	8	17	140	25	35	2	1
3	1.85	6	14	140	21	35	2	0
4	1.55	3	11	190	15	40	1	0
6	1.70	8	19	130	22	45	2	0
13	2.00	7	13	170	19	45	2	0
18	1.70	6	13	130	18	55	3	0
24	1.30	4	10	110	13	35	1	0
25	1.65	7	15	180	16	45	2	0
26	1.55	5	12	130	18	28	2	0
28	1.40	6	14	140	23	40	2	0
29	1.35	6	12	120	21	42	3	0
30	1.25	5	19	120	14	45	2	0
32	1.25	8	14	140	19	40	2	0
33	1.30	7	14	170	18	35	1	0
H. mantegazzianum								
5	3.20	26	70	600	144	55	6	9
7	3.00	20	70	480	116	70	3	7
8	2.90	21	65	500	95	45	3	7
9	3.20	23	65	600	89	65	3	8
10	2.75	25	60	480	86	50	4	11
11	4.30	25	70	560	115	65	3	11
12	3.40	13	70	550	105	63	3	9
14	3.50	25	80	550	137	65	3	13
15	3.20	25	75	500	96	60	3	10
16	3.00	24	60	550	99	65	4	13
17	2.95	25	55	500	106	60	3	5
19	4.00	28	85	620	120	90	3	10
20	3.30	30	70	700	108	90	3	10
21	3.25	25	80	550	95	85	3	12
22	2.70	23	65	580	79	60	3	10
23	3.35	28	75	550	124	60	4	10
27	2.60	22	70	480	101	60	4	15
31	3.10	24	80	600	105	75	3	12
H. mantegazzianum x H. sphondylium								
1H	2.10	9	34	200	32	57	2	12
2H	1.50	7	18	160	25	32	2	0
3H	2.20	10	25	270	32	58	1	3
4H	2.60	10	34	180	32	48	3	0
5H	2.35	10	30	340	31	31	3	4
6H	2.30	10	23	220	27	27	2	1
6AH	1.55	7	18	160	25	50	1	0
7H	2.40	14	49	380	54	45	3	3
8H	1.80	10	30	200	39	55	2	5

KALE WATER 1977 - Leaf characters

	length (mm)	W1 (mm)	W2 (mm)	R1 (mm)	R2 (mm)	d1 (mm)	d2 (mm)	b (mm)	ns.	a (°)	ax (°)	bsl (mm)	bsb (mm)
H. sphondylium													
1	300	280	230	100	60	70	95	25	2	30	50	40	10
2	300	300	290	90	65	125	115	25	2	45	60	50	45
3	340	300	250	105	75	120	85	35	2	35	45	45	15
4	250	260	200	105	40	55	75	20	1	40	65	30	10
6	390	380	250	140	90	130	90	50	2	50	50	35	25
13	260	280	225	85	60	45	55	15	2	45	65	40	35
18	290	290	200	125	60	55	35	20	2	30	45	40	10
24	180	195	140	85	35	65	40	20	1	60	50	30	25
25	270	275	275	95	60	90	60	35	1	40	65	40	30
26	185	210	160	65	35	65	60	15	2	40	60	30	25
28	220	255	225	70	50	70	80	25	2	50	70	35	25
29	160	190	160	60	30	40	55	15	1	40	60	50	20
30	350	335	250	125	70	85	100	30	2	50	65	35	15
32	205	290	215	80	40	55	65	15	1	25	70	45	25
33	220	330	190	100	35	65	90	35	2	55	55	40	15
H. mantegazzianum													
5	650	1070	730	140	140	310	390	70	1	16	55	70	100
7	750	1090	780	170	145	410	450	60	1	10	85	110	120
8	520	720	480	100	120	170	220	50	1	17	55	75	100
9	600	1040	750	145	140	355	390	70	1	18	57	90	90
10	550	790	660	95	120	235	295	50	1	17	64	90	95
11	530	820	720	110	115	270	320	55	1	17	64	75	100
12	750	1200	1000	200	140	400	450	80	1	18	75	120	120
14	630	920	840	100	125	240	290	60	1	15	67	65	85
15	730	1120	810	195	130	300	390	100	1	18	50	100	100
16	720	980	900	190	120	300	330	80	1	17	75	100	100
17	490	650	550	100	100	220	250	60	1	18	72	100	95
19	640	860	780	155	120	240	280	70	1	18	73	150	100
20	750	1150	930	200	155	350	400	80	1	17	75	140	120
21	660	920	770	170	140	370	420	90	1	18	78	180	100
22	500	780	630	100	100	270	305	65	1	16	78	100	100
23	640	1070	650	165	120	370	400	95	1	14	85	90	90
24	680	1120	900	180	140	340	390	80	1	16	60	95	100
31	530	830	670	120	120	265	310	70	1	16	70	80	100
H. mantegazzianum x H. sphondylium													
1H	450	560	400	145	90	170	170	40	2	22	60	75	65
2H	360	310	220	155	80	90	135	40	1	40	40	40	30
3H	390	470	390	115	85	135	180	55	1	30	55	80	20
4H	470	610	480	140	105	180	215	45	1	28	50	70	55
5H	490	750	500	165	100	225	265	50	1	25	45	65	50
6H	350	480	350	130	70	185	150	60	1	33	50	70	70
6AH	320	260	210	120	70	80	95	25	2	28	55	50	25
7H	550	770	550	160	100	295	295	50	2	30	65	100	65
8H	400	470	410	160	75	100	150	60	2	35	60	60	25

KALE WATER 1977 - Leaf characters - Hair length and breadth

	Length (µm)	Breadth (µm)
H. sphondylium		
1	556	36
2	638	32
3	587	32
4	523	31
6	526	27
13	531	30
18	519	32
24	507	37
25	506	37
26	613	36
28	589	30
29	572	40
30	532	27
32	551	37
33	521	36
H. mantegazzianum		
5	100	17
7	112	27
8	99	20
9	96	19
10	116	22
11	116	31
12	106	27
14	106	21
15	107	22
16	111	21
17	119	23
19	101	20
20	116	22
21	120	22
22	120	22
23	120	23
27	104	19
31	123	18
H. mantegazzianum x H. sphondylium		
1H	261	27
2H	295	27
3H	279	31
4H	202	25
5H	261	27
6H	385	33
6H	308	27
7H	244	31
8H	235	31

KALE WATER 1977 - Fruit characters

	Weight (mg)	Length (mm)	width (mm)	dvl (mm)	cvl (mm)	dvw (mm)	cvw (mm)	st.l (mm)	st.b (mm)	w.b. (mm)	no. vittae
H. sphondylium											
1	10.5	8.30	6.30	4.80	4.05	0.31	0.34	1.10	1.25	0.79	3.45
2	5.6	8.10	5.50	4.70	3.70	0.26	0.28	0.81	1.14	0.65	4.00
3	10.5	9.55	7.25	5.50	4.35	0.31	0.37	0.96	1.10	0.88	4.00
4	6.8	7.60	6.00	4.40	3.30	0.28	0.32	0.87	1.00	0.63	3.95
6	12.3	8.80	6.30	5.70	3.90	0.30	0.28	1.03	1.27	0.78	4.21
13	8.7	8.40	5.80	5.45	4.10	0.28	0.39	0.33	1.13	0.73	3.83
18	18.7	11.00	7.25	6.25	3.75	0.25	0.50	0.88	1.13	0.50	4.00
24	11.8	7.00	5.55	4.40	3.30	0.29	0.41	1.00	1.18	0.75	4.00
25	14.7	8.95	7.15	5.05	4.65	0.26	0.26	0.85	1.08	0.93	4.00
26	12.5	6.90	6.30	3.95	3.10	0.25	0.50	0.78	0.83	0.63	3.95
28	12.0	7.75	6.85	5.00	4.10	0.26	0.41	0.98	1.00	0.58	3.91
29	9.8	9.05	6.10	5.45	4.10	0.43	0.45	0.95	1.20	0.75	3.75
30	11.5	10.30	6.95	5.10	4.10	0.27	0.44	1.05	1.23	0.83	4.00
32	9.0	8.45	6.70	5.00	3.80	0.29	0.49	1.00	1.23	0.83	4.00
33	8.2	7.95	6.20	4.10	3.00	0.25	0.27	0.95	1.23	0.73	3.95
H. mantegazzianum											
5	18.3	12.65	7.50	8.85	6.55	1.13	0.98	1.03	1.68	1.18	4.00
7	17.4	11.85	7.60	7.45	5.30	1.16	1.23	0.95	1.53	1.13	4.00
8	20.2	12.00	8.35	7.60	5.30	1.20	0.95	0.80	1.58	1.28	3.90
9	18.1	10.70	8.05	7.20	5.45	1.23	1.08	1.00	1.80	1.15	3.85
10	21.2	12.65	7.85	7.80	5.70	1.30	1.08	0.88	1.45	1.13	4.00
11	19.5	12.80	7.95	8.50	6.05	1.26	1.03	1.00	1.25	1.10	4.00
12	24.9	12.65	8.30	8.00	6.05	1.28	1.20	0.98	1.40	1.15	4.00
14	23.1	18.50	9.35	8.90	6.00	1.50	1.28	0.98	1.50	1.50	3.95
15	22.1	12.70	8.65	8.45	6.25	1.33	1.10	1.05	1.68	1.25	3.90
16	20.7	11.35	7.70	7.90	5.85	1.23	1.01	1.00	1.55	1.20	4.00
17	17.9	10.05	7.50	6.80	5.35	1.15	1.05	1.10	1.58	1.28	3.55
19	27.2	14.00	8.50	8.45	6.00	1.33	1.03	1.00	1.55	1.35	4.00
20	23.4	13.35	8.65	7.85	6.05	1.20	0.98	1.03	1.68	1.30	3.90
21	25.8	13.40	8.55	8.60	5.90	1.23	0.85	1.03	1.53	1.23	3.85
22	23.0	12.70	8.40	8.45	5.45	1.32	1.03	1.08	1.53	1.23	3.90
23	21.1	12.20	7.75	7.75	5.35	1.18	1.05	1.05	1.83	1.30	4.00
27	21.6	12.75	7.70	8.80	6.25	1.10	0.93	1.13	1.75	1.25	4.00
31	20.3	11.85	7.85	7.75	5.30	1.30	1.25	1.00	1.63	1.28	4.00
H. mantegazzianum x H. sphondylium											
1H	14.4	12.58	8.08	7.25	4.00	0.50	0.50	0.88	1.00	0.83	4.00
2H	29.2	11.25	8.00	7.13	5.38	0.75	0.75	1.00	1.22	1.00	4.00
3H	25.8	11.90	8.35	7.50	6.05	0.60	0.70	0.93	1.13	0.95	3.90
4H	5.4	9.05	6.90	5.30	3.95	0.44	0.57	1.15	0.73	0.63	3.96
5H	23.5	13.60	8.65	7.95	5.50	0.85	0.54	1.20	1.25	1.03	3.90
6H	8.0	12.40	8.35	7.90	5.50	0.62	0.66	1.23	1.25	0.88	4.01
6AH	15.7	10.25	6.90	6.05	4.20	0.46	0.40	1.10	1.15	1.10	4.00
7H	23.0	11.10	7.80	6.40	4.75	0.98	0.81	0.98	1.23	0.98	3.95
8H	19.1	12.90	7.95	7.20	4.75	0.55	0.51	0.95	1.05	0.93	4.00

KALE WATER 1977 - Floral characters

H. sphondylium	%pf	%ss	Style length (mm)	pollen length (mm)
1	81	1	1.50	47.1
2	83	33	1.50	42.5
3	89	33	1.25	44.8
4	91	28	1.50	42.9
6	55	51	1.50	45.0
13	87	20	2.00	44.8
18	89	0	1.75	45.8
24	88	23	1.50	44.6
25	90	40	1.75	44.8
26	85	19	1.50	45.4
28	40	13	1.75	45.0
29	70	8	1.50	45.6
30	87	30	2.00	41.7
32	94	37	1.50	45.4
33	60	34	1.25	44.4
H. mantegazzianum				
5	94	80	3.00	60.4
7	75	87	2.25	65.0
8	97	86	2.25	65.0
9	82	94	2.00	63.1
10	92	92	1.75	66.5
11	92	85	1.50	63.7
12	94	62	2.75	68.7
14	92	87	1.75	65.6
15	93	93	3.00	70.0
16	90	89	1.75	69.2
17	96	84	2.75	68.1
19	97	85	2.00	65.2
20	92	83	2.00	64.0
21	81	71	2.00	65.4
22	95	78	1.50	64.8
23	91	84	2.25	62.7
27	94	87	2.00	67.1
31	96	90	1.50	65.6
H. mantegazzianum x H. sphondylium				
1H	1	0	2.25	52.5
2H	0	1	3.00	55.6
3H	4	2	2.50	54.8
4H	7	0	1.50	56.1
5H	2	3	3.25	53.8
6H	0	0	1.50	52.5
6AH	7	1	1.25	56.5
7H	1	1	2.25	57.3
8H	6	2	2.50	55.0

KALE WATER 1976 - Characters measured in the field

	Height(m)	TSD(mm)	BSD(mm)	1°diam. (mm)	No.of rays	No.of 2°	No.of bracts
H. sphondylium							
1	1.25	4	10	120	15	3	0
2	1.85	6	20	180	23	2	0
3	1.50	6	14	170	16	1	1
15	1.60	5	14	140	14	2	0
16	1.65	4	15	160	17	2	0
18	1.70	5	18	180	14	3	0
19	1.80	6	15	160	20	3	0
23	1.55	5	13	120	17	4	4
24	1.95	5	12	120	19	2	0
26	1.70	5	15	120	18	2	0
28	1.40	3	10	100	13	2	0
29	1.45	4	10	135	18	2	0
H. mantegazzianum							
4	3.35	12	85	600	108	4	8
6	2.65	20	65	570	75	4	7
8	2.80	22	60	640	64	3	18
9	3.20	22	75	610	74	4	14
10	3.35	20	80	620	74	4	12
11	3.05	18	75	560	66	3	9
12	3.25	20	60	580	58	4	11
13	4.00	30	110	740	122	5	23
17	2.75	16	55	440	98	5	12
20	3.20	22	65	570	100	3	6
27	3.15	30	95	620	155	6	11
31	2.90	16	50	500	119	5	11
32	3.50	22	90	640	129	7	11
H. mantegazzianum x H. sphondylium							
5	2.35	12	45	330	44	2	3
7	1.90	10	28	230	33	2	4
14	2.50	13	40	440	46	2	5
21	2.45	10	45	320	29	2	1
25	2.25	12	35	370	35	2	2
30	2.20	13	40	280	44	3	2

KALE WATER 1976 - Leaf characters

	length (m)	W1 (mm)	W2 (mm)	R1 (mm)	d1 (mm)	d2 (mm)	b (mm)	ns	ax	bsb (mm)	bsl (mm)
H. sphondylium											
1	170	190	70	50	22	35	20	1	50	12	28
2	190	160	140	60	60	70	35	2	88	38	60
3	170	250	100	65	32	50	25	1	60	20	30
15	200	260	150	110	85	90	20	1	75	30	40
16	250	340	160	135	30	48	20	2	50	10	30
18	270	400	160	100	95	115	30	2	70	20	45
19	300	380	220	95	35	60	30	2	60	20	50
23	240	240	160	85	50	80	25	1	60	20	35
24	220	220	160	70	69	70	20	2	70	23	30
26	270	250	175	105	75	85	25	1	55	20	25
28	180	200	105	55	35	55	15	1	50	12	25
29	280	320	170	110	55	90	25	1	40	20	40
H. mantegazzianum											
4	680	1300	460	200	250	340	130	1	65	60	85
6	840	1400	620	170	310	400	180	1	55	70	100
8	730	1220	660	190	260	340	160	1	55	60	80
9	750	1020	720	180	310	360	100	1	65	85	110
10	720	1040	480	200	160	230	65	1	70	70	100
11	670	880	380	140	200	260	70	1	60	60	100
12	600	900	360	140	310	430	110	1	70	60	100
13	850	1240	540	230	190	260	70	1	55	65	90
17	470	700	340	135	180	220	50	1	65	80	75
20	730	1280	620	220	260	340	90	1	65	60	110
27	670	1120	480	180	250	350	70	1	50	110	110
31	500	680	320	115	160	230	40	1	40	80	95
32	770	1240	680	230	280	360	55	1	45	80	130
H. mantegazzianum x H. sphondylium											
5	620	760	360	170	140	195	70	1	50	70	120
7	380	580	200	125	120	150	50	1	55	35	70
14	490	700	360	160	105	145	50	1	60	45	80
21	510	700	250	140	180	230	50	1	60	50	110
25	400	560	260	115	120	180	70	2	55	80	80
30	360	500	240	105	120	140	50	1	65	70	90

KALE WATER 1976 - Fruit characters

Mericarp length(mm)	width (mm)	dvl (mm)	cvl (mm)	dvb (mm)	cvb (mm)
H. sphondylium					
8.70	5.75	5.05	4.35	0.26	0.29
8.55	5.60	5.00	4.40	0.25	0.29
8.80	6.10	5.40	3.80	0.30	0.38
7.70	5.55	4.50	3.30	0.26	0.23
8.10	5.90	4.90	3.95	0.25	0.28
H. mantegazzianum					
11.50	7.25	8.00	5.75	1.08	1.00
12.55	7.70	8.55	6.30	1.05	1.00
12.45	7.25	8.50	5.95	1.02	1.00
11.75	7.15	7.85	5.25	1.05	1.00
12.25	6.95	8.70	6.45	1.20	1.00
H. mantegazzianum x H. sphondylium					
11.93	7.05	7.50	5.50	0.52	0.68
12.65	8.45	7.50	5.85	0.78	0.70
11.20	7.95	8.40	7.05	0.73	0.60
12.80	7.35	8.65	6.40	0.80	0.70
12.85	7.60	8.15	6.55	0.66	0.68

COLDSTREAM 1976 - Characters measured in the field

	Height (m)	TSD (mm)	BSD (mm)	1^{o}diam. (mm)	No.of rays	No.of 2^{o}	No.of bracts
H. sphondylium							
2	1.50	5	15	130	19	4	0
10	1.50	5	14	100	18	2	0
11	1.70	6	20	90	14	2	0
12	1.10	5	15	110	18	1	3
13	1.00	5	10	80	17	1	0
14	1.55	7	17	150	16	2	0
15	1.50	6	15	160	14	2	0
16	1.10	5	13	65	14	3	0
17	1.65	8	20	200	23	3	0
18	1.55	7	20	200	23	3	0
19	1.60	7	20	120	19	3	0
20	1.30	6	16	135	19	3	0
21	1.55	8	19	190	21	1	0
22	0.95	5	15	80	12	2	0
23	1.20	9	16	150	18	3	0
24	1.35	6	15	120	37	2	0
25	1.25	6	18	110	34	2	0
26	1.20	5	17	140	42	3	0
27	1.20	6	18	120	32	5	0
28	0.90	6	15	110	28	3	0
H. mantegazzianum							
3	2.70	20	55	520	52	3	6
4	2.60	15	40	440	52	3	6
6	2.80	20	60	520	68	5	6
7	3.45	15	65	520	68	3	13
8	2.80	15	60	420	64	2	6
9	3.70	25	70	620	81	4	10
29	4.02	24	100	700	60	6	0
30	3.85	28	90	700	92	5	0
31	3.50	22	75	560	89	4	0
H. mantegazzianum x H. sphondylium							
1	2.45	11	35	320	34	2	2
5	2.35	10	25	250	42	2	2

COLDSTREAM 1976 - Leaf characters

	length (mm)	W1 (mm)	W2 (mm)	R1 (mm)	d1 (mm)	d2 (mm)	b (mm)	ns	ax (°)	bsb (mm)	bsl (mm)
H. sphondylium											
2	190	220	190	80	20	45	20	1	50	23	50
10	130	140	100	50	15	40	15	1	40	30	40
11	320	300	200	120	25	70	20	2	45	30	30
12	220	200	130	100	25	45	20	2	40	20	30
13	180	200	180	80	25	60	20	1	30	25	40
14	300	400	270	70	60	100	35	2	45	40	65
15	330	260	180	140	35	70	35	2	50	35	55
16	230	210	190	85	30	55	20	1	45	35	50
17	340	300	200	140	40	80	35	1	50	45	75
18	380	320	150	120	50	80	40	2	60	25	60
19	350	400	240	130	45	70	25	2	50	35	40
20	190	300	240	65	45	70	30	1	50	40	45
21	240	300	200	100	40	65	30	2	60	30	70
22	270	150	130	115	10	20	5	2	50	40	55
23	340	260	200	155	50	65	25	2	70	45	75
24	330	300	220	120	30	70	25	2	45	30	60
25	250	250	160	85	25	40	20	2	40	35	50
26	240	300	160	80	40	70	30	2	50	35	50
27	210	300	170	70	40	55	20	2	60	30	55
28	220	240	120	80	35	50	25	2	80	25	50
H. mantegazzianum											
3	320	600	450	80	120	170	40	1	40	90	100
4	500	890	600	140	180	250	50	1	45	90	100
6	810	1300	720	260	320	420	100	1	50	90	100
7	750	1250	820	230	240	370	110	1	45	90	100
8	760	1350	810	210	310	440	130	1	50	100	100
9	1000	1250	800	220	300	390	100	1	45	110	110
29	550	800	720	120	130	190	50	1	60	130	150
30	820	1250	140	200	300	380	100	1	60	110	190
31	600	800	500	120	100	190	50	1	40	130	170
H. mantegazzianum x H. sphondylium											
1	300	400	290	90	110	120	50	1	50	70	90
5	440	510	380	160	140	160	30	1	50	50	175

RIDDELL AND ROSLIN 1976 - Characters measured in the field

	Height (m)	TSD (mm)	BSD (mm)	1°diam. (mm)	No.of rays	No.2°	No.of bracts
RIDDELL - *H. mantegazzianum*							
1	2.7	20	60	540	107	6	9
2	2.7	18	60	460	112	4	12
3	3.1	24	75	590	137	7	8
4	3.1	19	55	530	111	7	8
5	3.3	18	55	550	123	6	12
6	3.2	19	55	530	149	6	7
7	3.3	21	65	570	138	8	6
8	3.4	20	70	520	135	7	8
9	3.7	21	90	500	169	5	4
10	3.1	17	60	470	140	6	5
11	2.4	14	42	420	96	4	10
12	2.6	19	70	420	135	6	8
13	3.1	23	90	530	140	7	20
14	3.4	26	80	580	125	6	12
15	3.5	21	65	510	140	5	10
16	3.0	20	50	500	128	7	13
17	3.7	28	85	550	135	8	10
18	3.3	20	55	560	117	5	6
19	3.0	20	65	600	150	9	8
20	3.2	21	70	500	148	9	8
ROSLIN - *H. sphondylium*							
1	1.50	6	18	140	15	1	0
2	1.80	6	15	140	17	2	0
3	1.35	4	11	105	16	2	0
4	1.80	7	20	220	23	3	0
5	1.40	4	13	110	21	2	0
6	1.50	3	12	100	20	2	0
7	1.25	3	10	80	13	2	0
8	1.65	7	18	250	20	2	0
9	2.05	7	22	150	20	3	0
10	1.40	5	15	120	20	2	0
11	1.75	6	18	240	27	3	0
12	1.20	5	17	120	18	2	1
13	1.15	6	17	210	20	2	0
14	1.50	6	18	175	19	3	0
15	1.40	3	10	90	10	2	0
16	1.90	9	25	220	18	2	0

ROSLIN AND RIDDELL 1976 - Leaf characters

	length (mm)	W1 (mm)	W2 (mm)	R1 (mm)	d1 (mm)	d2 (mm)	b (mm)	ns	ax	bsl (mm)	bsb (mm)
RIDDELL - *H. mantegazzianum*											
1	1100	2240	1200	320	220	380	90	1	40	140	70
2	890	1500	1120	240	300	440	90	1	45	130	55
3	950	1640	1550	220	270	430	80	1	40	170	120
4	840	1360	1160	230	240	360	80	1	40	140	50
5	970	1520	1040	280	260	390	60	1	40	140	90
6	850	1400	1100	240	220	320	60	1	35	150	100
7	1250	2000	1500	340	450	560	100	1	50	140	80
8	1000	1600	1200	240	280	390	80	1	40	145	50
9	1000	1680	1360	160	350	390	90	1	40	170	100
10	850	1640	1180	240	290	410	65	1	40	120	90
11	650	840	700	190	170	270	50	1	35	90	50
12	700	1040	960	170	230	300	60	1	55	140	90
13	1120	1660	1260	290	360	530	100	1	30	140	90
14	1100	2000	810	300	420	580	110	1	45	160	120
15	900	1300	1200	230	200	380	80	1	35	130	100
16	1120	1600	1250	300	340	480	80	1	50	130	90
17	700	1200	1060	140	220	320	60	1	45	190	120
18	800	1320	900	260	210	360	90	1	40	130	60
19	820	1340	940	250	240	360	100	1	40	130	90
20	1000	1300	1160	300	260	370	70	1	40	130	70
ROSLIN - *H. sphondylium*											
1	320	310	185	130	70	110	20	1	50	50	20
2	280	280	220	90	40	75	45	2	50	55	45
3	180	165	125	55	20	55	15	1	40	35	15
4	280	250	180	115	50	70	20	2	60	60	20
5	250	230	170	80	60	70	20	2	75	40	20
6	260	280	170	90	45	70	20	2	55	30	20
7	110	135	70	40	25	40	25	1	80	30	25
8	180	300	180	65	80	100	20	2	60	50	20
9	220	230	140	90	60	70	20	1	70	45	20
10	300	260	180	105	55	75	20	2	70	35	20
11	370	330	180	135	80	110	20	1	55	45	20
12	220	250	130	90	80	85	30	1	70	35	30
13	350	350	195	105	70	110	20	2	45	45	20
14	360	360	200	120	55	75	25	2	65	40	25
15	310	205	140	65	45	70	10	2	45	35	25
16	250	290	150	95	70	80	35	1	60	45	35

ROSLIN AND RIDDELL 1976 - Fruit characters

Mericarp length(mm)	width (mm)	dvl (mm)	cvl (mm)	dvb (mm)	cvb (mm)
H. sphondylium - ROSLIN					
8.90	6.15	5.00	4.00	0.29	0.29
7.90	5.85	4.75	4.00	0.34	0.32
9.05	5.90	7.00	5.55	0.35	0.45
6.90	5.40	4.50	3.40	0.27	0.30
7.25	5.45	4.80	4.10	0.29	0.28
H. mantegazzianum - RIDDELL					
9.80	5.50	7.50	5.10	0.75	0.58
9.65	5.95	7.00	5.00	0.75	0.70
12.70	6.30	9.45	6.40	0.83	0.75
11.95	6.00	8.60	5.35	0.78	0.71
10.50	5.85	7.50	5.01	0.74	0.65

APPENDIX V

MORPHOLOGICAL MEASUREMENTS

Mean, range, S.D., coefficient of variation (S.D. as % of mean) for groups of *H. sphondylium*, *H. mantegazzianum* and *H. mantegazzianum* x *H. sphondylium* at Kale Water 1977 and 1976, Coldstream, Roslin and Riddell.
Character abbreviations are explained in Section 3.2.

KALE WATER 1977 - Characters measured in the field

	H. sphondylium				*H. mantegazzianum* x *H. sphondylium*				*H. mantegazzianum*			
	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
HEIGHT (m)	1.53	(1.25-2.00)	0.22	15%	2.09	(1.50-2.60)	0.39	19%	3.21	(2.60-4.30)	0.43	13%
TSD (mm)	6	(3-8)	2	25%	10	(7-14)	2	21%	24	(13-30)	4	15%
BSD (mm)	14	(10-19)	3	20%	29	(18-49)	10	33%	70	(55-85)	8	11%
1^oDIAM (mm)	140	(90-190)	27	20%	234	(160-380)	79	34%	553	(480-700)	58	11%
NO. RAYS	19	(13-25)	3	18%	33	(25-54)	9	27%	107	(79-144)	17	16%
ANGLE 1^o & 2^o	40	(28-55)			45	(27-58)			66	(45-90)		
NO. 2^o	1.9	(1-3)			2.1	(1-3)			3.4	(3-6)		
NO. BRACTS	1.1	(0-1)			3.1	(0-12)			10.1	(5-15)		

KALE WATER 1977 - Leaf characters

		H. sphondylium				*H. mantegazzianum* x *H. sphondylium*				*H. mantegazzianum*			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
LEAF L	(mm)	261	(160-390)	68	26%	420	(320-550)	75	18%	629	(490-750)	91	15%
W1	(mm)	278	(190-380)	52	19%	520	(260-770)	174	34%	952	(650-1200)	164	17%
W2	(mm)	217	(140-290)	43	20%	390	(210-550)	117	30%	753	(480-1000)	134	18%
R1	(mm)	95	(60-140)	23	24%	143	(115-165)	18	13%	146	(95-200)	39	27%
R2	(mm)	54	(30-90)	18	33%	86	(70-105)	13	16%	127	(100-155)	15	12%
d1	(mm)	65	(35-115)	29	38%	158	(80-295)	69	44%	300	(170-410)	67	22%
d2	(mm)	84	(55-130)	23	31%	188	(95-295)	63	33%	349	(220-450)	68	20%
b	(mm)	25	(15-50)	10	40%	47	(25-60)	11	24%	71	(50-100)	15	21%
ns		1.7	(1-2)			1.4	(1-2)			1.0	(1-1)		
a	(°)	42	(25-60)			30	(22-40)			16	(10-18)		
ax	(°)	58	(45-70)			53	(40-65)			69	(50-85)		
bsl	(mm)	39	(30-50)	7	17%	68	(40-100)	17	26%	102	(65-180)	30	29%
bsb	(mm)	22	(10-45)	10	45%	45	(20-70)	20	44%	101	(85-120)	10	10%

KALE WATER 1977 - Fruit characters

		H. sphondylium				*H. mantegazzianum* *H. sphondylium*				*H. mantegazzianum*			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
MERICARP WEIGHT	(mg)	10.8	(5.6-18.7)	3.2	30%	18.2	(5.4-29.2)	8.1	44%	21.4	(17.4-27.2)	2.8	13%
L	(mm)	8.58	(6.90-11.00)	1.08	13%	11.67	(9.05-13.60)	1.42	12%	12.40	(10.05-14.00)	0.99	8%
W	(mm)	6.41	(5.50-7.25)	0.59	9%	7.89	(6.90-8.65)	0.62	8%	8.12	(7.50-9.35)	0.50	6%
dvl	(mm)	4.99	(3.95-6.25)	0.63	13%	6.96	(5.30-7.95)	0.88	13%	8.06	(6.80-8.90)	0.60	7%
cvl	(mm)	3.82	(3.00-4.65)	0.47	12%	4.90	(3.95-6.05)	0.75	15%	5.79	(5.30-6.55)	0.40	7%
dvw	(mm)	0.29	(0.25-0.43)	0.05	16%	0.64	(0.44-0.98)	0.19	29%	1.25	(1.10-1.50)	0.10	8%
cvw	(mm)	0.38	(0.26-0.50)	0.09	23%	0.60	(0.40-0.81)	0.13	22%	1.06	(0.85-1.28)	0.12	11%
NO. VITTAE		3.93	(3.45-4.21)			3.97	(3.90-4.01)			3.93	(3.55-4.00)		
St.l	(mm)	0.94	(0.78-1.10)	0.09	10%	1.05	(0.88-1.23)	0.13	12%	1.01	(0.80-1.13)	0.08	8%
St.b	(mm)	1.13	(0.83-1.27)	0.12	11%	1.11	(0.73-1.25)	0.17	15%	1.58	(1.25-1.83)	0.14	9%
wb	(mm)	0.75	(0.50-0.93)	0.12	15%	0.93	(0.63-1.10)	0.14	15%	1.24	(1.10-1.50)	0.10	8%

KALE WATER 1977 - Floral characters, hair length and breadth

	H. sphondylium				H. mantegazzianum H. sphondylium				H. mantegazzianum			
	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
% seed set	25	(0-51)			1	(0-3)			84	(62-94)		
% pollen fertility	79	(40-94)			3	(0-7)			91	(75-97)		
pollen length (μm)	44.7	(41.7-47.1)	1.4	3%	54.9	(52.5-57.3)	1.7	3%	65.3	(60.4-70.0)	2.4	4%
style length (mm)	1.58	(1.25-2.00)	0.23	14%	2.22	(1.25-3.25)	0.69	31%	2.11	(1.50-3.00)	0.49	23%
hair length (μm)	551	(506-637)	40	9%	274	(202-385)	52	19%	110	(96-123)	8	8%
breadth (μm	33	(27-37)	4	11%	29	(25-33)	3	10%	22	(17-31)	3	15%

KALE WATER 1976 - Characters measured in the field

		H. sphondylium				*H. mantegazzianum* *H. sphondylium*				*H. mantegazzianum*			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
HEIGHT	(m)	1.62	(1.25-1.95)	0.20	12%	2.28	(1.90-2.50)	0.22	10%	3.17	(2.65-4.00)	0.36	11%
TSD	(mm)	5	(3-6)	1	19%	12	(10-13)	1	12%	21	(12-30)	5	24%
BSD	(mm)	14	(10-20)	3	23%	39	(28-45)	7	17%	74	(50-110)	17	23%
1^{o} DIAM	(mm)	142	(100-180)	27	19%	328	(230-440)	73	22%	592	(440-740)	72	12%
NO. RAYS		17	(13-23)	3	17%	39	(29-46)	7	18%	96	(58-155)	30	31%
NO. 2^{o}		2.3	(1-4)			2.2	(2-3)			4.4	(3-7)		
NO. BRACTS		0.4	(0-4)			2.8	(1-5)			11.8	(6-23)		

KALE WATER 1976 - Leaf characters

		H. sphondylium				*H. mantegazzianum* *H. sphondylium*				*H. mantegazzianum*			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
LEAF	L (mm)	228	(170-300)	46	20%	452	(360-620)	98	22%	690	(470-850)	114	16%
	W1 (mm)	266	(160-400)	78	29%	633	(500-760)	101	16%	1050	(340-1400)	294	28%
	W2 (mm)	148	(70-220)	40	27%	278	(200-360)	67	24%	494	(100-720)	175	35%
	R1 (mm)	82	(50-110)	22	27%	136	(105-170)	26	19%	179	(115-230)	38	21%
	d1 (mm)	54	(22-95)	24	44%	131	(105-180)	27	20%	230	(160-310)	54	24%
	d2 (mm)	71	(35-115)	23	32%	173	(140-230)	35	20%	317	(220-430)	69	22%
	b (mm)	24	(15-35)	6	23%	57	(50-70)	52	9%	102	(40-310)	71	70%
	ns	1.4	(1-2)			1.2	(1-2)			1	(1-1)		
	ax (^{o})	61	(40-88)			57	(50-65)			58	(40-70)		
	bsl(mm)	37	(25-60)	10	28%	92	(70-120)	19	21%	98	(75-130)	15	15%
	bsb(mm)	20	(10-38)	8	38%	58	(35-80)	18	30%	72	(60-110)	15	20%

KALE WATER 1976 - Fruit characters

		H. sphondylium				H.mantegazzianum H. sphondylium				H. mantegazzianum			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
MERICARP L	(mm)	8.37	(7.70-8.80)	0.46	6%	12.29	(11.20-12.85)	0.71	6%	12.10	(11.50-12.55)	0.46	4%
W	(mm)	5.78	(5.55-6.10)	0.23	4%	7.68	(7.05-8.45)	0.54	7%	7.26	(6.95-7.70)	0.28	4%
dvl	(mm)	4.97	(4.50-5.40)	0.32	7%	8.04	(7.50-8.65)	0.52	7%	8.32	(7.85-8.70)	0.37	5%
cvl	(mm)	3.96	(3.30-4.40)	0.45	11%	6.27	(5.50-7.05)	0.61	10%	5.94	(5.25-6.45)	0.48	8%
dvb	(mm)	0.26	(0.25-0.30)	0.02	8%	0.70	(0.52-0.80)	0.11	16%	1.08	(1.02-1.20)	0.07	7%
wb	(mm)	0.29	(0.23-0.38)	0.05	18%	0.67	(0.60-0.70)	0.04	6%	1.00	(1.00-1.00)		

COLDSTREAM 1976 - Characters measured in the field

	H. sphondylium				H. mantegazzianum x H. sphondylium		H. mantegazzianum			
	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	mean	(min-max)	S.D.	Coeff. var.%
HEIGHT (m)	1.33	(0.90-1.70)	2.46	18%	2.40	(2.35-2.45)	3.27	(2.60-4.02)	0.55	17%
TSD (mm)	6	(5-9)	1	19%	11	(10-11)	20	(15-28)	5	23%
BSD (mm)	17	(11-20)	3	16%	30	(25-35)	68	(40-100)	18	27%
1^{o} DIAM (mm)	128	(65-200)	39	30%	285	(250-320)	556	(420-700)	101	18%
NO.RAYS	22	(12-42)	8	38%	38	(34-42)	70	(52-92)	15	21%
NO. 2^{o}	2.5	(1-5)			2	(2-2)	3.9	(2-6)		
NO. BRACTS	0.2	(0-3)			2	(2-2)	5.2	(0-13)		

COLDSTREAM 1976 - Leaf characters

		H. sphondylium				H. mantegazzianum H. sphondylium		H. mantegazzianum			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	mean	(min-max)	S.D.	Coeff. var.%
LEAF	L (mm)	259	(130-350)	64	25%	370	(300-440)	679	(320-100)	205	30%
	W1 (mm)	267	(140-400)	69	26%	455	(400-510)	1054	(600-1350)	280	27%
	W2 (mm)	182	(100-270)	43	24%	335	(290-380)	718	(450-1040)	181	25%
	R1 (mm)	99	(50-155)	29	29%	125	(90-160)	176	(80-260)	62	35%
	d1 (mm)	34	(10-60)	13	37%	125	(110-140)	222	(100-320)	90	41%
	d2 (mm)	61	(20-100)	18	29%	140	(120-160)	311	(170-440)	109	35%
	b (mm)	25	(10-60)	13	37%	40	(30-50)	81	(40-130)	33	41%
	ns	1.7	(1-2)			1	(1-1)	1	(1-1)		
	ax (°)	50	(30-80)			40	(30-50)	48	(40-60)		
	bsl(mm)	52	(30-75)	13	25%	136	(90-175)	124	(100-190)	36	29%
	bsb(mm)	33	(20-45)	7	22%	60	(50-70)	104	(90-130)	17	16%

ROSLIN AND RIDDELL 1976 - Characters measured in the field

	H. sphondylium ROSLIN				*H. mantegazzianum* RIDDELL			
	mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
HEIGHT (m)	1.54	(1.15-2.05)	0.26	17%	3.15	(2.40-3.70)	0.35	11%
TSD (mm)	5	(3-9)	2	31%	21	(14-28)	3	15%
BSD (mm)	16	(10-25)	4	26%	66	(42-90)	13	20%
1^o DIAM (mm)	154	(80-250)	57	37%	522	(420-600)	51	10%
NO. RAYS	19	(10-27)	4	21%	132	(96-169)	17	13%
NO. 2^o	2.2	(1-3)			6.4	(4-9)		
NO. BRACTS	0.1	(0-1)			9.2	(4-20)		

ROSLIN AND RIDDELL 1976 - Leaf characters

		H. sphondylium ROSLIN				*H. mantegazzianum* RIDDELL			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
LEAF LENGTH	(mm)	265	(110-370)	72	27%	931	(650-1250)	160	17%
W1	(mm)	264	(135-360)	62	24%	1509	(840-2240)	330	22%
W2	(mm)	163	(70-220)	36	22%	1133	(700-1560)	211	19%
R1	(mm)	91	(40-135)	29	32%	247	(140-340)	54	22%
d1	(mm)	57	(20-80)	19	33%	277	(170-450)	74	27%
d2	(mm)	79	(40-110)	20	25%	401	(270-580)	83	21%
b	(mm)	26	(15-40)	7	25%	80	(50-110)	17	21%
ns		1.6	(1-2)			1	(1-1)		
ax	(°)	59	(40-80)			41	(30-55)		
bsl	(mm)	42	(30-60)	9	21%	141	(90-190)	21	15%
bsb	(mm)	23	(10-45)	8	36%	84	(50-120)	23	27%

ROSLIN AND RIDDELL 1976 - Fruit characters

		H. sphondylium ROSLIN				H. mantegazzianum RIDDELL			
		mean	(min-max)	S.D.	Coeff. var.%	mean	(min-max)	S.D.	Coeff. var.%
MERICARP L	(mm)	8.00	(6.90-9.05)	0.96	12%	10.92	(9.65-12.70)	1.35	12%
W	(mm)	5.75	(5.40-6.15)	0.32	6%	5.92	(5.50-6.30)	0.29	5%
dvl	(mm)	5.21	(4.50-7.00)	1.02	20%	8.01	(7.00-9.45)	0.99	12%
cvl	(mm)	4.21	(3.40-5.55)	0.80	19%	5.37	(5.01-6.40)	0.59	11%
dvb	(mm)	0.31	(0.27-0.35)	0.04	11%	0.77	(0.74-0.83)	0.04	5%
cvb	(mm)	0.33	(0.28-0.45)	0.07	21%	0.68	(0.58-0.75)	0.06	10%

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HYBRIDIZATION IN THE GENUS *HERACLEUM* IN THE BRITISH ISLES

by

J. GRACE & F. STEWART

MOTS-CLES: Hybridization *Heracleum* Multivariate analysis

RESUME: Une enquête, sur place, sur les populations d'*Heracleum sphondylium* L. indigène et de "Giant Hogweed", *Heracleum mantegazzianum* Somm. & Levier, introduit, suggère qu'il y a hybridation entre les deux espèces. La grande espèce d'*Heracleum*, cultivée à partir de graines d'origine caucasienne, est naturalisée sur terre inculte sur les bords des fleuves en Grande Bretagne depuis 1800. Des mesures morphologiques des populations pures et mélangées des espèces d'*Heracleum* dans le sud-est de l'Ecosse ont été prises. Les techniques analytiques traditionnelles et numériques confirment que les hybrides forment un groupe intermédiaire entre les parents pour ce qui intéresse la couleur, la taille et la pubescence. Les plantes hybrides peuvent être distinguées de "Giant Hogweed" par leur nature vivace et leurs tiges fleuries qui se groupent en touffes au-dessus d'un système de racines rameux. Ils diffèrent de *H. sphondylium* par leur taille et la longueur de leur période de croissance. Un programme complémentaire d'hybridation expérimentale est actuellement en cours.

INTRODUCTION

There are two species of *Heracleum* in the British Isles, the indigenous *Heracleum sphondylium* L. (Hogweed) and the introduced *Heracleum mantegazzianum* Somm. & Levier (Giant Hogweed). A hybrid between giant and common Hogweed, *H. mantegazzianum* Somm. & Levier x *H. sphondylium* L. was first recorded in Ireland in 1951, and has since been noted at individual sites in North East Scotland, South East Scotland, Kent and Middlesex (McCLINTOCK 1975, 270). Voucher specimens of hybrids from central Edinburgh, Coldstream on the River Tweed, and the Black Isle have been deposited in the Edinburgh Herbarium. The hybrid forms have been described by McCLINTOCK (1975) as "Intermediate in size of stem, leaf and umbel, in leaf-outline, in the shape and length of the fruit and vittae, in the hairiness of the stem and sheath, and in the smell when bruised".

Giant Hogweed was first introduced to Britain in the early 1800s as a garden plant. By 1862 a giant *Heracleum* species was known to be naturalised around the Great Western Railway (WHITE 1962). The large flat *Heracleum* seeds are readily dispersed by water, so that where the plant has been cultivated in water gardens Hogweed colonies may become established on suitable sites downstream. In this way large populations have grown up along several lowland rivers in Britain (Fig. 1). In Scotland, along the Tweed and its tributaries the Whiteadder and the Teviot in the South East, and on the Rivers Findhorn, Lossie and Deveron in the North, Giant Hogweed has spread from a few plants introduced c. 1900. At this time seed of the type *H. mantegazzianum* was available from the firm of H. CORREVON in Geneva where, in 1893, plants were grown from seed collected by M. SOMMIER and M. LEVIER on the banks of the River Sekon in Abkhasia. In addition to cultivation seed is dispersed by man to waste ground alongside roads or in urban areas.

The work presented forms part of a larger study concerned with the ecological relationships of *H. mantegazzianum* - an attempt to analyse the new ecological system in which the introduced species has to find a place for itself. This work is not yet complete, but we have decided to present some of our results here in preliminary form. The paper describes a survey of several populations of mixed and pure species in the field, in which multivariate statistics have been used as a means of summarising the pattern of morphometric variation.

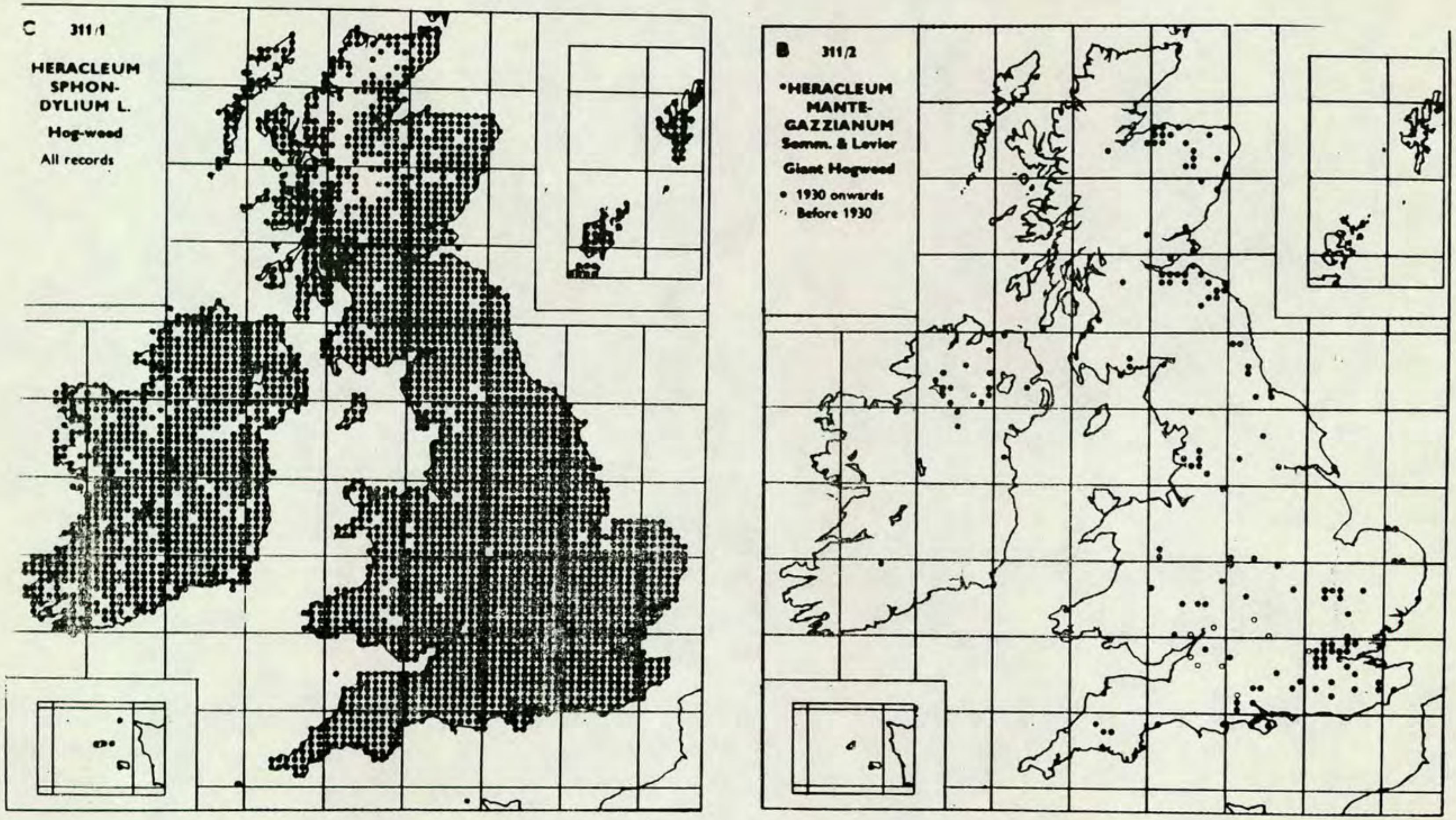

Fig. 1. The distribution of *Heracleum* in the British Isles (Perring & Walters 1976)

MATERIALS AND METHODS

The location of sites used for the survey is given in Table 1.

Table 1. Site names, grid references and sample sizes for stands containing *H. mantegazzianum* (*M*), *H. sphondylium* (*S*) and presumed hybrids (hybrid).

Site name	Site description	National Grid Reference	Sample size		Hybrid
			M	*S*	
Coldstream	riverside	36/848400	9	20	2
Currie	waste ground	36/188679			1
Farfield	field	36/262632		1	
Hopetoun	woodland	36/093788	1		
Jed	field	36/661240		1	
Kale	riverside	36/706278	13	12	6
Muckle Burn	riverside	38/015606	1	1	1
Riddell	woodland	36/519247	20		
Roslin	woodland	36/270627		16	
Park Burn	riverside	36/308678	1		
Selkirk	riverside	36/473293		1	1

Riddell and Hopetoun are both woodland sites where Giant Hogweed was cultivated and now grows wild, and where very few *H. sphondylium* can be found. Roslin, Jed and Farfield are Hogweed sites not yet invaded by *H. mantegazzianum*. The remaining sites are of mixed populations.

At four sites the population was sampled by selecting plants at one metre intervals along a straight line transect. The position of the line was made to pass through as many "intermediates" as possible. Single plants were also examined at other sites. A total of 108 plants were included in the survey.

For each plant the characters listed in Table 2. were measured in the field during July 1976. Only quantitative characters were used. The characters chosen for this preliminary survey were those which could be easily measured in the field, and would be acceptable for the method of analysis.

Voucher specimens taken for the single plants and mass collections made for the larger samples are preserved in the Department of Forestry and Natural Resources, University of Edinburgh.

Table 2. Characters measured in the Field.

1. Diameter of stem at ground level.
2. Number of flowering stems/plant.
3. Height of plant.
4. Number of subumbels below terminal umbel of main stem.
5. Number of bracts below terminal umbel.
6. Diameter of terminal umbel.
7. Number of rays in terminal umbel.

Leaf characters: (leaf selected from mid-point of stem)

8. Maximum leaf width.
9. Length of leaf, not including petiole.
10. Width of petiole at proximal leaflets.
11. Length of rachis from proximal leaflets to second pair of leaflets, or leaf segments.
12. Number of leaflets.

Leaf incision: (proximal segment of outer leaf edge)

13. Length of segment from apex to midrib of leaflet.
14. Depth of incision from apex of segment.
15. Maximum width of segment.
16. Angle of segment midrib to midrib of leaflet.

Bud sheath of terminal inflorescence:

17. Length.
18. Breadth.

The data for 18 characters and 108 plants were analysed by the method of principal components using the Genstat computer program available from Rothamsted Experimental Station, Harpenden, Herts.

RESULTS

When all 108 plants were compared by a principal components analysis using 18 variables a graph of the loadings on the first and second components showed three more or less distinct groups. Plants labelled as possible hybrids in the field were intermediate in the analysis between the two parent types. The first two components together accounted for 74% of the variation. The first component could be attributed to a general size vector, the second to the leaf length variable.

In order to eliminate the general attributes of plant size from the analysis, the dataset was rerun without the character "height", but with all variables transformed by dividing throughout by plant height. An analysis of such transformed data may be regarded as a more accurate assessment of differences due to "plant form". The graph of the first and second component loadings is shown in Fig. 2. The orientation of the groups is similar to the original analysis except that the majority of hybrids lie closer to the

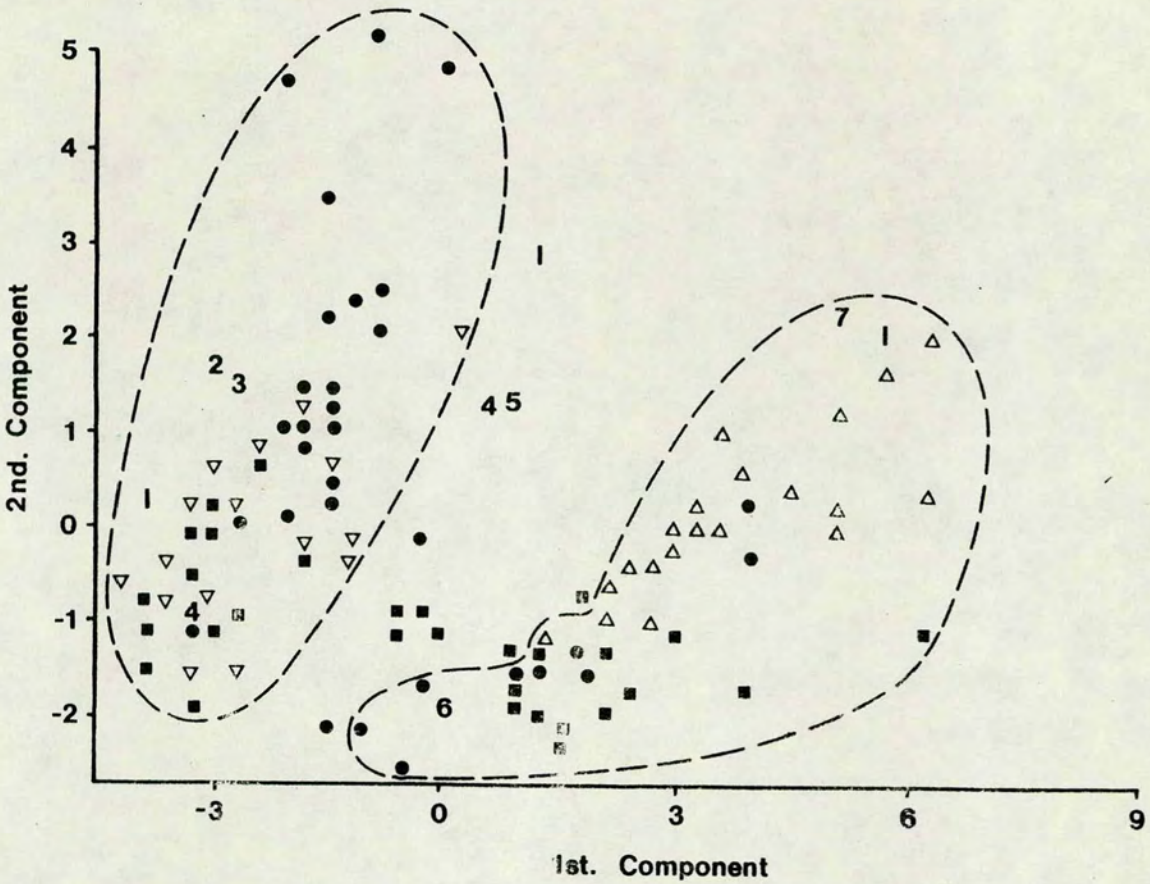

Fig. 2. Principal component analysis of the morphometric data from *Heracleum* at the following populations: 1, Muckle Burn; 2, Jed; 3, Farfield; 4, Selkirk; 5, Currie; 6, Hopetoun; ▽, Roslin; △, Riddell; ●, Coldstream; ■, Kale Water.

H. sphondylium parent, while two Kale Water intermediates have grouped with *H. mantegazzianum*. These two components account for only 62% of the variation and may be attributed to leaf characters: the length of the lobe from tip to main vein of segment and the length of the rachis.

In the field presumed hybrids may be distinguished from *H. mantegazzianum* by their perennial habit, in which several flowering stems grow from the same root system. They have two or three secondary umbels, unlike the large compound umbel of Giant Hogweed, and a smaller number of rays in a form similar to *H. sphondylium*. The range for these characters is summarised in Table 3. and the mean and coefficient of variation is listed for size characters.

Table 3. Characters measured on 45 individuals of *H. mantegazzianum*, 52 of *H. sphondylium* and 11 *H. mantegazzianum* x *H. sphondylium*.

Character	*H. sphondylium*	*H. mantegazzianum* x *H. sphondylium*	*H. mantegazzianum*
		RANGE (min-max)	
No. of 2° umbels	1 - 5	2 - 4	2 - 9
No. of stems/plant	0 - 5	0 - 6	0
No. rays	10 - 42	29 - 47	52 - 169
No. segments	1 - 2	1 - 2	1
No. bracts	0 - 4	1 - 5	0 - 23
		MEAN AND COEFFICIENT OF VARIATION	
Height m	1.47 10%	2.26 10%	3.15 14%
Basal stem diameter mm	16 22%	48 66%	73 36%
Umbel diameter m	0.14 31%	0.32 19%	0.55 14%
Petiole width mm	5 47%	9 30%	19 29%
Rachis length mm	90 30%	15 28%	21 29%
Leaf width m	0.27 27%	0.65 25%	1.26 28%
Lobe length mm	70 20%	170 30%	350 26%
Lobe breadth mm	30 28%	60 32%	90 49%
Lobe incision mm	50 44%	130 17%	250 29%
Angle of lobe to segment	57 22%	56 9%	47 22%
Bud sheath length mm	50 29%	110 44%	120 22%
Bud sheath breadth mm	30 97%	70 30%	90 31%

DISCUSSION

Multivariate analysis of characters measured in the field supports the view that intermediate forms such as those described by McCLINTOCK can be found. Natural interspecific hybridisation is relatively uncommon in the Umbelliferae, the only known cases in Britain being in the genera *Heracleum* and *Apium* (Stace 1975, 268, 270). In *Heracleum* we have found that crosses between the two species are possible. This work is still in progress and will be described in full elsewhere. Both species have 2n = 22, the chromosome number reported in all species of *Heracleum* so far investigated (MAUDE 1939, 1940; HAKANSSON 1943; BELL & CONSTANCE 1966; CAGNIDZE & CHKHEIDZE 1974, 1975). Moreover, other isolating mechanisms are weak, as is often the case where aliens are concerned. *H. mantegazzinaum* is found on the fertile alluvial soils along rivers and as a weed on cultivated land. As a biennial it requires bare soil areas on which to germinate. *H. sphondylium* is widespread along hedgerows and in neglected pastures, and being perennial it survives in a closed sward. Nevertheless there is considerable overlap in their distribution, and the majority of *H. mantegazzianum* sites are close to individuals of *H. sphondylium*. The flowering periods of the species overlap: at the Kale Water site in 1977 both species flowered for three weeks, *H. mantegazzianum* beginning on July 1st and *H. sphondylium* following a week later. Synchrony in flowering is more exact when *H. mantegazzianum* has been chopped down in an attempt at eradication. A second growth occurs and the retarded flowering period coincides with that of *H. sphondylium*. The indigenous *H. sphondylium* attracts many insect visitors - DRABBLE & DRABBLE (1927) recorded 80 Diptera and there are numerous visitors from other insect orders (PROCTOR & YEO 1973, 62). *H. mantegazzianum* is visited less by the smaller insects, but strong fliers such as honey bees and the larger dipterans visit both species and presumably are effective at transporting the pollen.

The hybrid plants are found as occasional individuals where parental types occur together. They do not seem to be well adapted: often they are mechanically unstable and flowering stems fall over. All individual hybrids that we have so far examined show reduced fertility as measured by pollen stainability and seed set, though we have germinated and raised to seedling stage the seeds collected from hybrids in the field. The low fertility of hybrids is offset by their longevity: as they are perennial they may be long-lived and produce large quantities of good pollen and seed. At most sites the hybrids are distinct from the parents suggesting that the plants are the F1 hybrid. However at sites which have been disturbed by cutting, the variation is wider suggesting that back-crossing may have occurred.

Further interpretation of the variation is difficult, as different forms of *H. mantegazzianum* may have been sown in different gardens when the original introductions were made, thus confusing the pattern of variation in the naturalised progeny. Furthermore, *Heracleum* sites are often quite heterogeneous, and variation in soil and microclimate may generate much phenotypic variation. For example, even the number of rays - the most useful character for identification in the field - may vary with the environment: studies on *Daucus* have shown that at higher temperatures more umbels with a greater number of rays are produced on smaller flowering stems (QUAGLIOTTI 1967). To overcome these difficulties, further work has begun in collaboration with Dr. Weimarck of the University of Lund, using cytogenetic analysis at a hybrid site where much morphometric data has been collected and from which herbarium specimens have been taken. In addition, artificial hybrids of known parentage will be raised to compare with field material.

ACKNOWLEDGEMENTS

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TRANSLATIONS TO BE KEPT WITH THESIS

Morphologie générale des fruits d'Heracleum.

Le fruit du genre Heracleum est un noyau constitué de deux mericarpes accolés.Le fruit entier possedr la forme approximative d'une lentille apla tie.Les mericarpes ressemblent à une lentille lens plate-convexe ou même faibl ment concave-convexe (tabl.I-VIII fig.c)et se touchent ± par les surfaces ventrales ± plates (comissures).

L'axe de la fleur (le carpophorum) est fine,séparée en deux jusqu'à la base,elle peut être reconnue sur des mericarpes sous forme d'un enfonceme étroit,souvent très peut visible,qui s'étend de la base jusqu'à ± la moitié de la hauteur du dusque, en se terminant comme un pistil.Cette termina son tubulaire de carpophore reste d'habitude sur le mericarpe (tabl.I-VII fig.b).

Le sommet du fruit est pourvu d'une rondelle à miel (le disque),separée en deux moitiés appartenant aux mericarpes.Cette rondelle se trouve dans l'enfoncement sur le sommet du fruit ou peut aussi ± dépasser le bord des ailes du fruit. En plus,la rondelle est séparée du reste de fruit par un enfoncement annulaire.Il est rare qu'un tel enfoncement manque et dans ce cas le fruit devient progressivement la rondelle.La rondelle mielleuse,vu du coté dorsal des mericarpes,possède une forme ± irrégulièrement conique souvent ± plissée et au-dessus de l'enfoncement annulaire d'habitude élar gie et relevée en collerette. La rondelle mielleuse se transforme progressivement en style qui se termine par le stygmate lentilliforme lent shaped ou sphérique.

Les mericarpes sont nettement différenciées en coté dorsal et ventral. Le coté dorsal est dans sa partie médiane légerement convexe,la partie marginale forme les ailes.

La partie médiane du coté dorsal des mericarpes possède 5 côtes (tabl.I-VIII,fig.a) rarement plus (tabl.VIII,fig.21a), allant de l'enfoncement annulaire sous le disque jusque la base. Trois côtes sont placés dans la partie médiane du coté dorsal,peu éloignés l'une de l'autre; deux autres côtes se trouvent plus éloignés dans la proximité des ailes marginales, ce qui donne une partie intérieure étroite et une partie extérieure ± 3 fois plus large. Toutes les côtes du coté dorsal de mericarpe sont peu saillants mais suffisamment bien indiqués.

Entre les côtes du coté dorsal se trouvent des bandelettes ± bien prononcées.Le plus souvent elles sont quatre,mais on rencontre des fruits avec 3 et 5 chez la même espèce,c'est pourqoi il faut considerer le nombre autre que 4 comme une anomalie (tabl.VIII,fig.21a). Ces bandelettes peuvent avoir partout la même largeur, elles peuvent s'élargir progressivement vers la base des mericarpes,ou s'élargir considérablement dans leu partie inférieure.Leur plus grande largeur varie entre au-dessous de 0,25

T.Koval:Etudes morphologiques des fruits de certaines espèces du genre
Heracleum.
Monographiae Botanicae,vol.XLIX,p.79-109,1975.

Introduction: Le genre Heracleum L. comprend environ 70 espèces répandues
de préférence dans la zone tempérée du Nord et surtout dans les montagnes
d'Europe,d'Asie et d'Amerique.Au sud les espèces d'Heracleum s'étendent
à travers les Indes jusqu'au Ceylan et en Afrique à l'Ethiopie montagneuse.
Mais les espèces les plus nombreuses d'Heracleum se trouvent au sud-ouest
de l'Europe,en Asie mineure,ainsi que en Sibérie et dans les montagnes
de l'Inde orientale; en Amerique du Nord une seule espèce est connue (H.
lanatum) toutes les autres sont des importations.

Dans notre flore le genre Heracleum est représenté par trois espèces, à
l'interieur desquelles ils existent quelques variations.(Koczwara dans le
"Flore polonaise"1960).H.carpaticum indiqué dans les "Plantes de Pologne"
(1953,1969) ne se trouve pas dans les Carpates polonaises.

Le systematique du genre Heracleum n'est pas encore tout à fait établi et
les auteurs unanimement soulignent les difficultés considérables de la
classification de ces plantes à cause de leur variabilité élevée. De la
proviennent aussi les grandes divergences dans la compréhension systéma-
tique de divers auteurs non seulement dans l'attribution à une section
~~déterminée à l'interieur~~ de ce genre,mais ~~de certaines~~ espèces et leurs
variations,de façon que la question du systematique du genre Heracleum
doit être considerée encore comme ouverte.

Dans la diagnose systématique les caractères carpologiques jouent un rôle
important,c'est pourquoi l'étude détaillé de morphologie et d'anatomie des
fruits est indispensable pour une meilleure connaissance du systématique
de ce genre.De même du point de vue pratique l'étude du systématique car-
pologique est une chose utile puisque ces fruits contiennent 0,23 à 1,75
des huiles volatiles ainsi que d'autres substances de reserve,entre autres
de telles qui produisent des brulures (Mandenova 195[illegible]).

Le present travail comprend des recherches sur la morphologie des fruits
de 21 espèces représentant aussi bien la flore europeen que asiatique et
americain.La plupart des plantes étudiées provenait des jardins botaniques
surtout des pays etrangers et les plantes d'etalonnage,en mesure de pos-
sible,ont été ramassé dans les prairies ou dans les pépinières du Jardin
Botanique UAM et du Jardin Pharmaceutique AM de Poznan. L'auteur a utilisé
pour les études de fruits les méthodes classiques utilisées dans les tra-
vaux carpologiques([illegible]
et [illegible]

à 1,25 mm et plus.

La determination de la longueur des bandelettes est difficile parce q chez diverses espèces elles ne commencent pas au même endroit.Par.exp. chez H.lanatum les bandelettes commencent déja un peu plus haut que la moitié de la hauteur du disque,qui,en plus,ne se sépare pas distinctem du coté dorsal des mericarpes; chez d'autres espèces le commencement s trouve sous l'enfoncement annulaire ou même nettement plus bas. Pour c raison la determination la plus exacte de la longueur des bandelettes celle obtenue à partir de l'extrémité d'une bandelette d'une longueur née de la partie médiane de la face dorsale du mericarpe,c'est à dire le disque et l'enfoncement annulaire,ainsi que sans les ailes. Dans no cas nous allons comprendre sous la longueur des bandelettes la distance qu'elles parcourent sur la partie médiane du côté dorsal ou ventral des mericarpes.

Le còté dorsal des méricarpes peut être glabre ou couvert des poils de differente façon. La pilosité épaisse ou scarce (souvent seulement chez fruit jeune)peut consister en poils longs ou courts, doux ou dures.Les poils peuvent être placés en desordre ou de façon bien regulière, dans cas ils sont tous dirigés dans le même sens. Le bord des ailes porte so vent des petits poils dures et pointus,en forme des cônes un peu tordus

Le còté ventral (la comissure) des mericarpes comme règle est glabre e ± brillante et au moins dans sa partie centrale légerement concave ou ± plate (tabl.I-VIII,fig.b). La partie centrale de la commissure,ainsi q le coté dorsal, est bordée par les ailes,qui dans la partie marginale p sèdent un étroit bourrelet dépassant le reste de l'aile.La partie centr de la commissure se trouve un peu au-dessus des ailes ou ± au même nive L'emplacement du carpophore est marqué par un enfoncement étroit ± pron cé, ou il n'est pas marqué du tout ,alors que le sommet du carpophore,d forme pistilaire,est conservé d'habitude sur le mericarpe mure.

La commissure n'a pas de bandelettes ou en possède deux. Dans les cas rares ces bandelettes [illegible] des branchements (H.l[illegible] et H.trachy ma,tabl.III,fig.8b,et tabl.VIII,fig.21 b). Les bandelettes commencent a si au-dessous du disque à une distance ± grande,c'est pourquoi nous det mineront leur longueur de la même facon que pour le coté dorsal des me carpes. Ces bandelettes atteignent le plus souvent ± la moitié de la lo gueur de la commissure,plus rarement elles descendent plus bas ou n'att ent pas la moitié. Elles peuvent avoir la même largeur que celles du cô dorsal ou elles peuvent être un peu plus étroites ou plus [illegible] tion transversale du mericarpe représente une lentille concave-convexe les bandelettes se distinguent en forme des boucles colorées ± elliptique vers l'intérieur du mericarpe.(tabl.I-VIII,fig.c).

L'intérieur du fruit est rempli par l'albumen ayant la forme d'une dem ellipse étroite avec les enfoncements plat~~t~~es pour les bandelettes du côt dorsal des mericarpes et ± reguliérement aplatie ou un peu concave sur la commissure. L'albumen ne remplit pas d'une façon homogène tout l'espace du mericarpe, les coins formés par les ailes restent vides. Un autre espace v de se trouve d'habitude entre l'albumen et le pericarpe sur la commissure au-dessous de l'endroit ou sur le pericarpe commence la trace du caprophо

La couleur des fruits est variable suivant le degrès de leur maturité (Bondarcew 1954) mais en principe elle est la même pour toutes les espèce Elle varie pour le coté dorsal des mericarpes de "flavido-griseus" ou "viridulo-griseus" à travers "fumosus" jusqu'au "saturate-fumosus" ou même "atrobrunneus."

Comme règle la commissure est plus claire que le coté dorsal. Sa couleur varie de pallidus à travers "fumosus" jusqu'au "flavido-griseus". Les bandelettes ± distinctement visibles à travers les teguments recouvrant les mericarpes, possèdent les différents tons de la couleur brun-rouge.

En tenant compte de la dépendance de la coloration des fruits du degrès de leur maturité et ± égalité de la couleur de toutes les espèces, ce carctère n'est pas retenu pour le tableau des caractères, puisqu'il ne peut pa servir pour la diagnose.

Caractères morphologiques des fruits des espèces examinées de Heracle présentés sous formede clé.

1. Commissure sans vittae.
   XVI H.schelkownikovii Woron.
1. Sur la commissure vittae ± distinctes mais toujours présentes.
  2. Sur la commissure vittae visibles immédiatement sous le point d'insertion de carpophore.
    3. Le coté dorsal des mericarpes glabre.
       - XVIII H.sphondylium L.
    3. Le coté dorsal des mericarpes avec les poils.
      4. Vittae sur le côté dorsal des mericarpes à contour ± linéaire ou s'élargissant faiblement vers le bas.
         IV H.granatense Boiss.
      4. Vittae sur le coté dorsal des mericarpes à contour batonne considerablement élargi vers le bas.
  2. XXI H. trachyloma Fisch et Me
  2. Sur la commissure vittae visibles nettement plus bas que le point d'attachement de carpophore.
    3. Vittae sur le coté dorsal des mericarpes visibles déja sur le disque.
       VI.H.lanatum Michx.
    3. Vittae sur le coté dorsal des mericarpes visibles au-dessous

de la depression annulaire sous le disque.

4. Còté dorsal des mericarpes glabre.

5. Vittae sur le côté dorsal des mericarpes au sommet ± aigu.

6. La longueur des mericarpes 8-12 mm.

I H.alpinum L.

6. La longueur des mericarpes pas plus de 7 mm.

7. Le contour des mericarpes couchés sur la commissure ± large elliptique ou ± ~~étroit~~ large anti-ovoïde; la plus grande largeur des vittae sur le còté dorsal des mericarpes ± 0,55 mm.

III. H.elegans Jacq.

7. Le contour des mericarpes couchés sur la commissur ± elliptique ou ± étroit anti-ovoide; la plus grande largeur des vittae sur le còté dorsal des mericarpes ± 0,25 mm.

XVII H.sibiricum L.

5. Vittae sur le côté dorsal des mericarpes au sommet obtu ou arrondi.

6. Le contour des mericarpes couchés sur la commissur ± large elliptique .

XV H.pyrenaicum Lam.

6. Le contour des mericarpes couchés sur la commissur ± large anti-ovoïde.

7. La longueur des mericarpes 6-8 mm.

II H.austriacum L.

7. La longeur des mericarpes 9-11 mm.

4. X H.palmatum Baumg.

4. Coté dorsal des mericarpes avec des poils.

5. Vittae sur le coté dorsal des mericarpes ± aigus

XIII. H.ponticum (Lipsky)Schischk.

5. Vittae sur le coté dorsal des mericarpes au sommet ± obtus ou arrondi.

6. La plus grande largeur des vittae sur le còté dorsal des mericarpes ± 0,5 mm.

VII. H.lehmanianum Bunge.

+6. La plus grande largeur des vittae sur le coté dorsal des mericarpes ± 0,75 mm.

7. Le contour des mericarpes posés sur la commissure ± large fusiformo-elliptique.

\+ V.H.laciniatum Hornem.

+7. Le contour des mericarpes posés sur la commissure ± large anti-ovoide.

H.lescovii

~~++7. Le con~~tour VII H.lescovii Ac.Grossh.

++7. Le contour des mericarpes posés sur la commissure ± étroit anti-ovoïde.

XI H.persicum Desf.

++6. La plus grande largeur des vittae sur le côté dorsal des mericarpes ± 1 mm.

7. Vittae sur le côté dorsal des mericarpes à contou lineaire ou s'élargissant progressivement un peu vers le bas.

XX.H.stevenii Manden.

7. Vittae sur le côté dorsal des mericarpes à contou batonnet, élargi considérablement vers le bas.

8. Le rapport de la longeur des vittae sur le coté dorsal des mericarpes à la longeur de la partie médiane (comprise entre les ailes du même côté ± 3/5.

XII H.platytaenium Boiss.

8. le rapport de la **longueur** des vittae sur le côté dorsal des mericarpes à la longeur de la partie médiane (comprise entre les ailes du même coté ± 4/5.

IX H.mantegazzianum Som.et Lev.

+++6. La plus grande largeur des vittae sur le coté dorsal des mericarpes ± 1,25 mm.

7. Vittae sur le coté dorsal des mericarpes à contou ± lineaire ou s'élargissant un peu vers le bas.

XIV H.pubescens M.B.

7. Vittae sur le coté dorsal des mericarpes à contour batonnet considerablement élargi vers le bas

XIX H.sosnowskii Manden.

Resultats et conclusions.

Les caractères morphologiques des fruits jouent dans le systématique du genre Heracleum le rôle principel, aussi bien comme caractères complém mentaires que uniques sur lesquels est basé la division en sections et autres taxons. Mandenowa dans le Flore de l'URSS, divise le genre Heracleum en 5 sections. A l'interieur de certaines d'entre elles on distingue encore quelques taxons du rang des ~~rangées~~ lignées.

Les espèces étudiées dans ce travail appartiennent d'après Mandenova aux taxons suivants: x)

Section 1. Euheracleum DC.
  Lignée 1. Sibirica Manden
    (XVII.H.sibiricum L.)
  Lignée 2. Sphondylia Manden
    (X.H.palmatum Baumg., XIII.H.ponticum (Lipsky).Schiscl
    XVIII.H.sphondylium L.)
Section 2. Pubescentia Manden
  Lignée 1. Pubescentia Manden
    (XIV.H.pubescens M.B.)
  Lignée 2. Mantegazziana Manden
    (IX.H.mantegazzianum Som.et Lev., XIX.H.sosnowskii Manden)
  Lignée 3. Trachyloma Manden
    (XXI.H.trachyloma Fisch.et Mey., VII.H.lehmannianum Bunge)
Section 3. Villosa Manden
    (VIII.H.lescovii A.Grossh., XX.H.stevenii Manden)
Section 4. Wendia (Hoffm.) Manden
  Lignée 2. Transcaucasica Manden
    (XVI.H.schelkovnikovii Woron.)

Le systématique plus ancien des espèces d'Heracleum de l'Europe Centra (Hegi) ne forme pas de sections, mais à leur place on ~~comme dans~~ l'espèce H.sphondylium une lignée des taxons au rang des sous-espèces, considérées actuellement comme espèces. Si on tient compte ~~des résultats obtenus~~ [illegible] dans ce travail, le systématique de l'espèce H.sphondylium ~~pourrait être~~ [illegible] présenté de façon suivante :

H.sphondylium L.
  sous-espèce 1. sibiricum
    (XVII.H.sibiricum L.)
  sous-espèce 2. australe (Hartman) Neuman
    (XVIII.H.sphondylium L.)
  sous-espèce 3. montanum (Schleicher) Briquet

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x) [illegible]

(III. H. elegans Jacq.)

sous-espèce 4. granatense (Boiss.)Briquet
(IV.H.granatense Boiss.)
sous-espèce 5.pyrenaicum (Lam.)Bonnier
(XV.H.pyrenaicum Lam.)
sous-espèce 6. juranum (Genty.)Thellung
(I.H.alpinum L.)

L'auteur de ce travail appuit ses déductions systématiques sur les résultats d'études réalisés par la méthode dendytique,élaborée par lui entre 1965 et1974.

Comme il ressort du dendrite et des diagrammes ~~construits~~ calculés par l'auteur le systématique du genre Heracleum , basé sur les caractères morphologiques des fruits,ne concorde pas entiérement ni avec le système de Mandenova,ni avec celui de Hegi. Dans le dendrite on trouve trois groupements possédant le rang de sections. Le premier est formé des espèces autour de X.H.palmatum,le second autour de XI.H.persicum et la troisième contient une seule espèce XVI.H.schelkovnikovii. La première section se divise ensuite en deux taxons du rang de série,la seconde en quatre également du rang de série. Cette repartition se présente ensuite de façon suivante:

Section 1.
Serie A :(I.H.alpinum L.,II.H.austriacum L.,III.H.elegans Jacq., VI.H.lanatum Michx.,X.H.palmatum Baumg.,XV.H.pyrenaicum Lam.)
Serie B :(XVII.H.sibiricum L.,XVIII.H.sphondylium L.)
Section 2.
Serie A :(IV.H.granatense Boiss.,V.H.laciniatum Hornem, VII.H.lehmanianum Bunge,VIII.H.leskovii A.Grossh.,IX.H.mantegazzianum Som.et Lev.,XI.H.persicum Desf.,XII.H.platytaenium Boiss.,XIV.H.pubescens M.B.,XX.H.stevenii Manden)
Serie B: (XIII.H.ponticum (Lipsky)Schischk.)
Serie C: (XIX.H.sosnowskii Manden)
Serie D: (XXI.H.trachyloma Fisch.et Mey.)
Section 3.
(XVI.H.schelkovnikovii Woron.)

L'espèce type (centrale) pour tout l'ensemble (c'est à dire accusant la plus petite difference systematique avec toutes les autres) est le XI.H.persicum Desf.Le diagramme montre la relation existant entre lui et les autres espèces.La même espèce est centrale pour la ~~se~~section 2. Pour la section 1.l'espèce centrale est X.H.palmatumBaumg.Dans cette section les taxons groupés en serie A sont par rapport au X.H.palmatum des unités inferieures; au maximum ils peuvent atteindre le rang des variations. Dans la série B les taxons XVII.H.sibiricum et XVIII.H.sphondylium sont aussi des variations.Dans la section 2.série A,la plus gran partie de taxons n'atteint non plus le rang des espèces par rapport au XI.H.persicum.Ce sont:IV.H.granatense,V.H.laciniatum,VII.H.lehmanianum, VIII.H.leskovii,XIV.H.pubescens,XX.H.stevenii. Les autres c'està dire IX.H.mantegazzianum et XII.H.platypaenium sont par rapport au XI.H.persicum les espèces de la même série.

En se basant sur les caractères morphologiques des friuts le rang de nombreuses espècez du genre Heracleum devrait être abaissé, tandis que le contenu des sections 1. 2. et 3. établiés par Mandenova devrait subi des changements considérables.

On trouve des divergences encore plus grandes en comparant le dendri avec la classification de Hegi concernant H.sphondylium. Le diagramme B montre que dans le cas d'acceptation de XVIII.H.sphondyliumcomme taxon type,la comparaison avec lui dessous-espèces de Hegi, ces dernières (à l'exception de XVII.H.sibiricum)s'élèvent au rang des espèces et même dans deux cas des espèces d'une autre section(IV.H.granatense et XV.H.pyrenacium). On voit donc qu'~~en~~, se basant sur la différence systématique des caractères morphologiques des fruits, la classification de l'espèce H.sphondylium ~~en~~ sous-espèces ne pourra non plus être conservée. En consequence, il faut repéter encore une fois, que le systématique du genre Heracleum, établi d'après les caractères morphologiques des friuts, diffère considérablement de ceux existant auparavant, et que les fruits du point de vue morphologique sont si bien differenciés qu'ils permetter une bonne reconnaissance de taxons existants et que la methode de dendrite, exprimant les differences systématiques remet en question le rang systématique de beaucoup de ces taxons.

Gawlowska (1961)a étudié les caractères des fruits d'après la méthodc biometrique de Szaferowa dans le but d'attribution du rang systématiqu à H.sphondylium et H.sibiricum.Comme résultat de ces études elle a reconnu les deux taxons comme espèces. A la lumière de recherches par la methode dendritique et par l'interprétation de la grandeur des differences systématiques (Kowal 1965) le rang de ces taxons devrait être abaissé jusque celui des variations.

The Caucasian species of the genus Heracleum

I. P. Mandenova

The genus Heracleum is one of the least studied of the members of the umbellate family. With the exception of the treatment by de-Kandolk in his 'Prodromus' there is not a single summary in which the material collected over the two centuries since the publication of the species H. sphondylium by Linné has been systematized. The variety of morphological types, the lack of clear boundaries between many of the species and the confused nomenclature give considerable interest to the study of the taxonomy of this ~~species~~genus, especially if we consider the possible economic uses of its species. In the Caucasus the various types of cow-parsnip (the Georgian diki, the Armenian bokh, the Azerbadzhanian baldyrgan) are widely used by the population, who employ the young parts of the plants in cooking. The presence of considerable quantities of essential oils in the leaves and fruit deserves undoubted attention. The Caucasian species of the genus have frequently been the subject of chemical research, but the published facts need verification, since in the vast majority of cases the species involved were not exactly defined. A complete monograph of the genus Heracleum remains a subject for future research, Our researches aimed to fill in the gaps only as regards those species native to the Caucasus. There can be no doubt of the significance of the Caucasus in the development of the genus H. Out of the total number of species, which according to our calculations is 65, it turns out as a result of our researches that 26 grow in the Caucasus, and that with few exceptions these must be accepted as endemic to the Caucasian peninsula. The specific character of the genus is such that many of the confused questions about its taxonomy can be decided successfully only by observing the plants in natural surroundings. The gigantic size typical of the majority of the Caucasian species has usually proved an obstacle to the collection of a sufficiently full collection in a herbarium. We have succeeded in observing many species of this interesting genus in natural surroundings over a number of years and in gathering sufficient herbarium material on each of them. We have also cultivated some species from seed, The comparison of the Caucasian species with the others, available to us as herbarium specimens, has allowed us to come to some conclusions and to work out a taxonomy of the genus, if only in broad outline.

The present work is a first attempt at a critical revision of the Caucasian cow-parsnips, based on observation of the species in natural surroundings, studies of specialist literature and collections kept in the fundamental Botanical Institutes of the USSR.

Mandenova I.P. 1950, The Caucasian species of the genus Heracleum.
Transl. L. McGowan

Nepal, we shall remove the species with the structure of the fruit we have described into a separate genus Tordyliopsis. We note here that the genus Tordyliopsis was described by De Candolle on the basis of an example collected in a non-fruiting condition, for which reason the generic independence of Tordyliopsis was rather doubted by the author himself, and he published the genus with a question mark (DC Prodromus, 1830). We recall that De Candolle placed related species from the Himalayas and Hindustan into various sections of the genus Heracleum. Thus, in establishing the genus Tordyliopsis DC. we supplement his description. We include in this genus as a synonym Semenovia Rgl. et Herd. In the philogenetic series the genera Tordyliopsis and Heracleum occupy different positions. The species included in the genus Tordyliopsis have signs of more ancient organisation, among which we include: the long channels, reaching usually to the base of the fruit; the not always constant number of channels in the grooves and on the commissura of the fruit, and finally, the septate nature of the channels themselves. These features allow us to consider this group to be more archaic. The contemporary centre of specific variation of the genus Tordyliopsis lies in the area of the Himalayas, where from Kashmir to Butan are known approximately 14, with rare exceptions, endemic species. These species grow here, from 1600-2000 up to 5,000 metres above sea level, and are members of the class of vegetation of the moderate type. Comparatively few species are known from the mountain forests of South-west China, from the mountains of Khazi (?) and Burma. A small group of endemic species grows in the mountains of southern India and Ceylon, and single species are found in north-west Tibet, in Pamiro-Alay and Tian-shian. To the west the area of distribution reaches to the mountain ranges of Afghanistan. The areas of distribution of the two species Tordyliopsis and Heracleum are more or less well distinguished geographically, but overlap in part in south-west China. A comparison of the morphological features characteristic of the two genera allows us to consider that Tordyliopsis is a more ancient [illegible] remaining closer to its ancestral forms, than the [illegible] specialised genus Heracleum.

According to their geographical situation, the species we have brought together into the genus Tordyliopsis fall into several groups. The part of the area of distribution in southern India includes the western seaboard of Hindustan - Konkan, and also the mountain area of Nilgiri and Ceylon. Related types are concentrated in the Sino-Himalayan centre, and in the Himalayas they are represented at the present time by a polymorphic cycle of species, philogenetically close, and sometimes even identical to species growing in the forests of Yunan and Sichuan. The ststematic study of this group is as yet far from complete. We note, however, that within the limits of this ancient group some species show progressive traits. Among such traits we include a noticeable tendency towards a certain reduction in the secretory apparatus. In some Himalayan species, such as T. Wallichii, T. Brunonis, the channels on the back of the fruit are significantly shortened, and in T. Wallichii the channels on the commissura are sometimes obliterated. The species T. candicans, common to the forests of Yunan and the Himalayas, is very reminiscent of some species of Heracleum from the section Euheracleum in its appearance (habit?). It is a tall plant with large leaf segments, very enlarged petsl of the marginal flowers, and its channels, while still of the type characteristic of the genus Tordyliopsis, do not reach to the base of the fruit on its back, and are significantly shortened on the commissura, while in T. candicans, as a rule, supplementary channels do not develop.

Only a study of separate species can give a key to the division of the genus or sub-genus into sections. Therefore at the present time we do not have a sufficient basis for the division of the genus Tordyliopsis into its component sections. We place a supplementary description of the genus Tordyliopsis below.

Tordyliopsis DC. I. Manden. em.

Para 1 -refs.

The teeth of the calyx are developed. The petals are reverse ovate or heart-shaped, the external petals of the marginal flowers usually enlarged, deeply bilobular. The fruit is elliptical or reverse ovate, strongly compressed from the back, the ribs narrow, the 3 middle ribs usually narrowly carinal, the 2 marginal ones moved away from the middle ones, adjoining the pteroid peristome of the half-fruit, the channels tapering towards the lower end, septate along their whole length, often reaching almost to the base of the fruit, the channels in the grooves single, occasionally supplementary channels can be observed in the grooves, 2-4-(6) channels on the commissura, occasionally the commissural channels shortened or unclear, the disc cone-shaped.

Para 3 - Latin (P. 15)

Now that we have defined more precisely the size of the genus Heracleum, we turn to the exposition of our ideas about the division of the genus Heracleum s. propr. into sections. We have divided this wide-ranging genus into the following sections: Euheracleum, Pubescentia, Villosa, Wendia, Vocontia, Apiifolia.

The size of the section Wendia, as we understand it, is very different from the size given to it by De Candolle, and a whole series of others following him. As we have already noted, the genus brought forward by Hoffmann was reduced to a section. The ~~genus~~ species named by Hoffmann W. chorodanum (H. chorodanum) collected in the Northern Caucasus in the region of Mineral Waters served as a type of the genus. The absence of channels on the commissura of the fruit was the feature utilised by Hoffmann in diagnosing the genus Wendia, and this led European authors to place in the section Wendia on a purely formal basis species with scarcely visible or obliterated commissural channels such as H. alpinum, H. austriacum, H. minimum, species which were genetically very distant from the plants described by Hoffmann. Lebedour included in the section Wendia, as well as H. chorodanum and H. pastinacifolium, species of quite different kinship such as H intermedium = H. apiifolium, H. grandiflorum. The fruit of both these latter species was unknown to Lebedour. At the same time, the obliteration of the commissural channels did not seem a reliable feature to Lebedour. Thus the species H brevivittatum (= H. pastinacifolium C.Koch) described by Lebedour, which has no channels on the commissura of the fruit, was nonethless included by him in the section Euheracleum with the following comment: "vittis comissuralibus obsoletis ad sect. 2 (Wendia) accedit propter habitum vero his (Euheracleum) enumeravi". Boissier placed species with no channels on the commissura in the section Euheracleum, but nevertheless united these species in a single group, giving them the following characterisation: "vittae comissurales nullae, dorsales clavatae. Folia pinnatum vel bipinnatim secta". A. A. Grossheim (1932) in his work "Flora of the Caucasus", accepted Wendia as an independent genus, and included in it 5 species growing in the Caucasus. In our earlier work (1944) we observed that the Caucasian species included in Wendia should be regarded as members of the genus Heracleum. Indeed the morphological features on which a case could be based are essentially only a certain reduction of the secretory apparatus, expressed in the shortening of the channels on the back of the fruit and their obliteration on the commissura. A tendency towards obliteration of the commissural channels appears in groups of varying origins. In the Caucasian species of the group Wendia we have in individual cases observed the development on the commissura of unclear channels, but apart from all we have already said, the presence in this group of the species H. pastinacifolium, in its habitus still strongly reminiscent of the species of the section Euheracleum, points to the close genetic interrelationships linking the species of the group Wendia with the remaining species of the genus Heracleum. At the same time we cannot share the views of Briquet, who allowed the group Wendia no taxonomic significance at all. Briquet reached his conclusions, not after a complete study of the species he was interested in, but based them solely on the anatomical structure of the fruit, with no reference to the morphology and the taxonomy of the entire genus as a whole. Despite the thoroughness of his research, he nevertheless clearly arrived at the wrong conclusions.

The section Wendia as seen by De Candolle and Lebedour is indeed a completely artificial union of species belonging to different spheres of kinship, but at the same time, species close to H. chorodanum, growing in the Caucasus and Near Asia, represent a definite stage of development of the genus Heracleum, and undoubtedly deserve to be separated into a special section for which, according to the law of priority, we keep the name Wendia.

Below we give a division of the genus Heracleum into sections, in which we have included, as far as we can, all the species of the genus which have been described up to this time.

List Pp 16-18

Note: We decided not to take into account a series of species described Wolf and F.... (H. Wolf, 1934) from China, mainly from the province Yunan, since the diagnosis published by them is very incomplete, the plants were collected without ripe fruit, and the authors produced no comparisons with related species of the genus.

PART 1

1. History of research into the genus Heracleum

The area of distribution of the genus Heracleum is a broad circle taking in Eurasia and North America. In Eurasia the northern boundary is latitude 60 North, rising in places to 70 North, while in the South it takes in North-west Africa, Asia Minor, Iran, Central and East Asia. In N. America the genus is represented by one species only - H. lanatum, which grows from Labrador and Newfoundland to Alaska, and from North Carolina westwards to New Mexico and California.

When we talk of the genus Heracleum we think of tall herb-like plants corresponding to the mezophyllic types of vegetation - mountain forests, sub-alpine meadows. However the genus also includes oreophite species, small plants growing in the upper alpine belt on cliffs and areas of stony scree.

The name Heracleum belongs to the Roman botanist Pliny, and was given to a plant, which has remained obscure, in honour of the legendary hero Hercules. The Greek contemporaries of Pliny, Theophrastes and Dioscorides, used the name as an adjective - Panax Heracleon - and according to Thellung (1925-6) Dioscorides may have used it to refer to Opopanax hispidum. Caesalpinus, Tabernemontanus and a number of other authors used the name Panax Heracleon to refer to various European members of the genus such as Heracleum montanum, Heracleum Pollinianum. It is equally unclear to which plant the name Sphondylium, first used by Dioscorides, was originally applied. According to Thellung the plant depicted by Dioscorides is most likely Pastinaca sativa. Gessner, Mattioli, Bauhin, Morison and Tournefort all used the name Sphondylium in the contemporary meaning of Heracleum, and the latter used the form Spondylium. It was Linnéwho preferred to give the genus the name Heracleum. In 1735, in the first edition of 'Systema Naturae' Linne first inserted the species ~~genus~~ he called Heracleum sphondylium, a species ~~genus~~ growing in Western Europe. Later, in 1753, in his 'Species Plantarum', Linne produced 5 species related to the genus - H. Sphondylium, H. sibiricum, H. Panaces, H. austriacum and H. alpinum. Hoffmann (1814) limited the genus Heracleum to H. sibiricum, a species characterised by its greenish-yellow flowers and the almost ? unenlarged petals of its marginal flowers. The species H. sphondylium has white flowers and significantly enlarged petals, and he transferred it to a separate genus Sphondylium, renaming the H. sphondylium discussed above Sphondylium Branca Ursina. He also included in the genus Sphondylium a number of species cultivated in the Gorenkov gardens and originating from the Crimea and the Caucasus. In order to distinguish the two genera by something other than the colour of their flowers he produced other distinguishing features: in particular the shape of the small oily channels "vittae" in the walls of the fruit. Thus the genus Heracleum (in Hoffmann's sense) is characterised by narrow channels on the back of the fruit, with an insignificant degree of widening into a claviform shape at the lower end only, whereas in the species he allocates to the genus Sphondylium the channels are usually wider, occasionally the whole width of the grooves. We should mention here that the species H. asperum, which has white flowers, was included in the genus Sphondylium by Hoffmann, although it characteristically has narrow channels. Later research also did not support the presence of a correlation between the colour of the flowers and the shape of the channels. From a formal point of view and according to the laws of priority, the species H. Sphondylium is typical of the genus Heracleum* and cannot be removed from membership of that genus.

Linne was familiar with very few species of cow-parsnip, and mainly the European ones. Botanical research in previously little-known areas, especially the Himalayas, near Asia and the Caucasus, brought to light numerous new species. As well as plants which were undoubtedly members of the genus Heracleum, species were found which did not fit the original morphological concept of the genus. Some forms were classified as separate genera, closely related to Heracleum. However these genera were not always recognized later, and often merely complicated the synonymy of the genus Heracleum with new names.

The first such genus to be described was Hoffmann's Wendia. There is still considerable divergence of opinion among taxonomists about the generic independence of Wendia. In our work we give the group of Caucasian- near Asian species, united in the genus Wendia, only sectional significance. The reasons for this decision are laid out in chapter 4. De-Candolle (1830) isolated the genus Tordyliopsis on the basis of a herbarium specimen collected in flower in Nepal. Bentham and Hooker (1867) having studied the fruit of this plant, included the genus Tordyliopsis in the genus Heracleum and later scientists have followed their example. In 1839 Bunge published a description of a new genus - Barysoma. Because of the disagreements in print about the diagnosis of the genus Barysoma (cf. C. F. Ledebour, 1844-6; G. Bentham & J. D. Hooker, 1867; E. Boissier, 1872; A. Takhtadzhan, 1940) we produce here a literal diagnosis of the genus. "Valleculae 4 - vittatae, vittae lineares ad basin mericarpii fere productae. Commissura 6 - vittata, vittis utrinque 3 clavatis contiguis, inaequalibus abbreviatis. Caetera Heraclei"

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*Species lectotypicae generum Linnaei. International Rules of Botanical Nomenclature, p. 141, 1935.

Bunge suggested the species H. villosum Hoffm. as a possible synonym. The origin of the plant described by Bunge as Barysoma villosum is unknown to us. In later works the genus Barysoma was not accepted, but treated as a synonym of the genus Heracleum. Regel and Herder (1866) described the genus Semenovia, a new genus based on herbarium specimens collected by P. P. Semenov in the Zailisky Altai. The authors compared the genus Semenovia with the genera Pastinaca and Orlaya. Perhaps this unsuccessful comparison is the reason why this genus is not mentioned at all in the large summaries such as Bentham & Hooker, Genera Plant., 1867; A. Engler und K. Prantl, Die Natul.Pflanzenfam., 1898. Dalla-Torre (C. G. Dalla-Torre et H. Harms, Genera siphonogamarum, 1900-07) includes the genus Semenovia in 'genera incerta'. Later O. and B. Fedtchenko (1911) included the plant described by Regel and Herder in the genus Heracleum.

Bentham and Hooker, following a tendency to enlarge the genera, amalgamated in the genus Heracleum not only Tordyliopsis DC, but also the genera Wendia Hoffm., Trigonoscadium Boiss., Stenotaenia Boiss., and Symphyoloma C. A. Meyer. Drude (1898) included in the taxonymy of the genus Heracleum Tordyliopsis DC, Wendia Hoffm., and Barysoma Bge. Calestani (1905)based his division of the umbellate family into genera on the anatomical structure of the fruit, thus significantly enlarging the genera. As a result the genus Pastinaca, as visualised by Calestani, includes a whole group of undoubtedly independent, though closely related genera, such as Pastinaca s.str., Malabaila, Heracleum, Zosima, Tordylium. The views of Calestani were later developed by Kozo-Poljansky (1915) and he accepts the genus Pastinaca as described in the work of Calestani.

As a result of our researches we have included Wendia Hoffm. and Barysoma Bge. in the taxonymy of the genus Heracleum.

2. Characteristic morphological features of the genus Heracleum

The majority of the species in the genus are biennial, often with a tendency to perennialise, grasses, with a clearly expressed monocarpic cycle of development, and a root of the rachis type, usually significantly thickened below the root collar. Our researches have shown that it is not always possible to draw a clear boundary between the biennial and perennialising forms. Plants, grown from one and the same seeds behave variously. If they find a favourable environment, they develop a strong rosette of leaves in the first year, and in the second year throw up a stem, flower and fruit, whereas weaker examples may remain at the rosette stage for two, even three years. Once it has blossomed the plant dies off, frequently the umbels are bearing fruit which is not yet quite ripe at the same time as the leaves have turned yellow and begum to wither; more rarely the plants are perennial with long creeping root-stocks (rhizomes). The developmental cycle of many of the high mountain oreophite species is slightly different. Growing in the upper alpine belt, in clefts in rock faces or on scree and stony ground, they often form a many-headed root stock, taking shape in this way rather like loose turf. Of the species we have studied we mention H. ossethicum, H. Schelkovnikovii.

There is usually a single stem, sometimes attaining gigantic proportions, 150-200-(3oo)cm. in height, 2-5 cm. in diameter. The stem branches towards the top and the side branches are often gathered corymbiformly or even umbrella-shaped. But there are also species with thin twig-like stems, not usually more than 40-60 cm. in height. To the latter group belong mainly the oreophite species of the genus. The leaves are very varied in shape and degree od dissection of the blade. It is comparatively rare for the leaves to be simple, usually they are pinnately compound, and the leaf segments are deeply incised or even dissected. The leaflets of the spathe quickly fade and fall off, often they do not appear at all and sometimes they do not appear on the main umbel but do develop on the lateral ones. The leaflets of the indusium are well developed. The [illegible] often polygamous, those in the main umbel nearly all bisexual, [illegible] the weaker lateral umbels are mainly staminate and sterile. The [illegible] of the calyx is quinqedentate, the teeth are leaf-shaped and uneven, occasionally the teeth of the calyx do not develop at all. The petals are conversely ovate, or heart-shaped, deeply, in some species almost to the base, bipartite, in a notch with a small, solitary, ligulate, inward-turning terminal lobule. The outer petals of the flower are usually significantly enlarged. Zygomorphia appears particularly sharply in the flowers situated on the periphery of the umbels. In the umbel as a whole, as well as in its constituent umbellets, zygomorphia gradually weakens from the periphery to the centre. However the genus includes species with almost unenlarged petals, for example H. sibiricum. The petals of the majority of species are pure white, more rarely yellowish-green, or even bright pink. The disc in the flower is broadly cone-shaped and smooth, iccasionally slightly torulose (as in the majority of Caucasian species in the section Pubescentia.) In the latter case, shining droplets of sugary liquid are exuded on the tips of the tubercles. The fruit are strongly compressed from the back, in outline they are reversely ovate, ovate, elliptical or almost rounded. The column is bipartite. The half-fruits are slightly domed from the back, on the commissure in the middle part there is a narrow, longitudinal, carinate projection. The three middle ridges along the back of the half-fruit are approximate to one another and narrowly filiform, while the two lateral ridges are at a significant diatance from the others and are contiguous with the slightly swollen, pteroid peristome of the half-fruit. The small channels in the groove are solitary, but sometimes additional channels can be observed. On the back of the half-fruit the channels are shortened, usually extending from one-half to two-thirds the length of the half-fruit, but in some species they extend almost to the base of the half-fruit. On the commissure of the channels two channels, sometimes commissural ones, may be just discernible or obliterated. They vary in length also; usually the commissural channels are slightly shorter than the dorsal ones. Clavate channels are quite characteristic of the genus Heracleum - "vittae clavatae are a fixed characteristic of the section Pastinaca of Heracleum, although their development (ontogeny) leaves no doubt of their homology with typical vittae" (Kozo-Poljansky, 1914, P. 37). "The secretory channels formed in the young fruit along almost its whole length cease lengthwise growth at one stage of development, becoming similar to sacs growing down from the apex, moved aside by the upward growing base part of the fruit." (B. G. Alexandrov & L. B. Klimochkina, 1947, P. 55). The shape of the channels is very varied. The following variations occur: the dorsal channels can be narrow, broadening towards the lower end in an even and slightly claviform fashion; sometimes comparatively [illegible] channels suddenly broaden in a saccate way towards the lower end [illegible] finally there are broad channels which almost fill the middle groove and gradually and insignificantly widen lower down. The commissural channels can be narrow or wide. Very rarely the channels on the back of the half-fruit taper towards the bottom. The disc in all species of Heracleum near the fruit (at fruiting) is narrowly or broadly cone-shaped, sometimes almost hemispherical; the peristome of the disc is wavy, the surface of the disc is smooth, sometimes with longitudinal radially diverging narrow projections; occasionally the surface of the disc is torulously wrinkled, the styles are upright or only very slightly bent back, though sometimes the styles are bent downwards; the stigma is cut somewhat obliquely, slightly expanded.

2. Characteristic morphological features of the genus Heracleum (cont.)

The anatomical structure of the pericarp

The pericarp can be divided into two clearly differentiated layers; the outer parenchymic layer with the epidermis and the inner sclerenchymic layer, enveloping te seed like a sort of thick case. This latter mechanical layer consists of several rows of thick-walled fibrous cells passing in various directions; in the outer zone they are more or less parallel to the axis of the mericarp, while in the inner zone they are more or less diametric to the axis. A mechanical tissue consisting of few layers and made up only of more or less diametrically positioned fibrous cells stretches right up to the lateral vascular bundles, thus linking the mechanical case with the lateral ribs. The pteroid peristome of the half-fruit is formed from air-bearing parenchyma "aeroform". A cross-section of the half-fruit shows the fibrous-vascular bundles corresponding to the three middle ridges to be rounded or triangular, while the fibrous-vascular bundles corresponding to the lateral ribs are more robust and elliptical, elongated in a radial direction. The small channels pass to the exterior from the belt of mechanical tissue, and this tissue sort of lies under them. (occasionally the commissural channels can be situated to the inside of the mechanical tissue.) Sometimes the unbroken belt of mechanical tissue is interrupted at the point of passage of the commissural channels. Usually the channels have no partitions along their entire length, only occasionally in single channels can one or two partitions be observed, very rarely are the channels septate. Cross-sections of the half-fruit indicate in addition to the usual channels on the back and commissura of the half-fruit, poorly developed rib channels. The seed is closely adjacent to the endosperm at the back, but at the sides and commissura there is a free cavity between the seed and the mechanical case.

V. G. Aleksandrov and L. V. Klimochkina (1947) studied the development of the fruit of Heracleum and its related genus Pastinaca. They concluded that in these genera, as opposed to typical Orthospermae (Aegopodium, Angelica) the pericarp grows quickly and unevenly parallel to the commissural plane and in its development significantly outdistances the endosperm. Only later does the endosperm fill the cavity formed as a consequence of the speedy growth of the pericarp. As a result the endosperm acquires a very compressed shape. The authors suggest the name Platyspermae for this group of genera of the sub-family Apioideae, in contrast to the typical Orthospermae where the growth of the pericarp is even and the cross-section of the endosperm is rounded. Another characteristic peculiar to Heracleum and its related genera is the position of the lateral fibrous-vascular bundles. As the fruit develops these begin to move away from the middle bundles. This change in the original structure, according to the data supplied by Aleksandrov and Klimochkina, is connected with the growth of the sclerenchymic layer, from which arise pteroid excrescences which, coming up against the lateral fibrous-vascular bundles, move them to the side from their original position.

3. A critical analysis of the morphological features

The genus Heracleum has become notorious as one of the most difficult genera of all Eurasian flora. Indeed, considerable difficulties are placed in the path of systematic study of the genus by the absence of clear morphological differences between many of the species, and the presence of intermediate forms. We have found difficulty in enumerating the the features to which priority should be given in differentiating separate species, because any feature, however trivial it may appear, can often acquire considerable taxonomic significance. J. Briquet (1924-6) carried out a detailed anatomical study of the fruits of most European and many near-Asian species of Heracleum. One of the purposes of his research was to allow possible further use of natomical the data acquired for a taxonomy of Heracleum. However, this attempt was unsuccessful because it turned out that all the species studied by Briquet had a more or less homogenous structure of the pericarp. We mention here also that many anatomical features are reflected in the external morphology of the half-fruit.

Thus the shape and dimensions of the mechanical case takes shape clearly against the background of the comparatively few layers of mechanical tissue connecting the case with the lateral fibrous-vascular bundles (ribs). These features can be successfully used for some species. As an example we point to the comparatively small mechanical case enveloping the seed in the species H. chorodanum. Because the case is small the gap between it and the lateral ribs is fairly broad. But in species from the same section Wendia, such as H. roseum, H. Schelkovnikovii, the bulky mechanical case reaches practically right up to the lateral ribs. The shape and dimensions of the fruit itself are features which are, as a rule, subject to considerable variation. We may repeat here in part the words of Marshal Biberstein: "fructuum in Heracleis formam atque magnitudinem non ita esse constantes ut leviores momenti discrimina distinguendis speciebus sufficere queant" (M.B. 1819, p. 226)
However, for related species from the section Villosa the dimensions of the fruit have considerable diagnostic ~~significance~~ value. Among the features which should be given most constant attention we name the shape of the disc and

3. A critical analysis of the morphological features (cont)

the character of its surface. For the whole family Umbelliferae the shape of the disc is a feature of unquestionable significance. (Aug. Pyr. De Candolle, 1829; B. Kozo-Poljansky, 1915; E. Korovin, 1940). We cannot agree with S. G. Tamamshan (1945) that in the diagnosis of the genus the shape of the disc can be taken into account only during flowering, since during fruiting the shape changes or is even completely deformed. The shape of the disc during fruiting is not only exceptionally important in the delimitation of close genera, but also in some cases is of considerable interest in establishing the differences between separate species. We note the narrowly cone-shaped disc with its narrow, linear, radially diverging projections in the Crimean species H. pubescens, and the broadly cone-shaped, almost hemispherical, finely torulously-wrinkled disc in the Caucasian species H. Sosnowskyi. Often closely related species are distinguished from one another by very slight but sufficiently stable features: such as the segmentation of the leaf, for example the species H. cyclocarpum has simple leaves, while the related species H. ponticum has ternate leaves; or the colour of the flowers - bright pink in H. roseum as opposed to H. transcaucasicum, which has white flowers; and so on. The words of B. L. Komarov are applicable to these species; "The degree of deviation is a bad criterion, the main thing is the independent place in the economic structure of nature which is held by a true species, but not by one which has been falsely established." (Komarov, 1940, p. 194).

4. A division of the genus Heracleum into sections.

The first attempt at classification of the species of the genus Heracleum was undertaken by W. D. J. Koch (1825), who used some features indicated by Hoffmann for the genera Heracleum, Sphondylium and Wendia to produce an intra-generic grouping of the European species.

Koch divided the 8 species known to him into the following groups:
(cf p. 9-10)

J. E. Duby (1828) was the first to reduce the genus Wendia into the section Wendia, and following Koch he included in this section the species H. alpinum, growing in the Alps.

Duby also regarded the genus Sphondylium Hoffm. as only a section - sect. Sphondylium (Hoffm.) Duby, and he included in it the species H. minimum Lam. The first classification of the genus Heracleum as a whole belongs to de Candolle (1830), who divided the 26 species of the genus known at that time into 6 sections:

4. A division of the genus Heracleum into sections (cont)

into 6 sections: sect. Tetrataenium, sect. Euheracleum, sect. Sphondylium, sect. Carmelia, sect. Wendia,* sect. Trichogonium. De Candolle gave paramount significance to the colour of the flowers and the number of channels on the commissura of the fruit, and created a very artificial system of the genus, in which close species were often separated and, contrariwise, species with no closely related ties were brought together. For example the species H. Wallichii, which grows in Nepal. Thanks to the presnece of channels on the commissura which were not clearly visible, De Candolle included this species in a special section Trichogonium, although in the totality of its features H. Wallichii is close to the species H. nepalense and H. obtusifolium, also growing in Nepal. These latter species have four channels on the commissura and were included in the section Tetrataenium. The species H. radicans, which in the structure of its fruit is close to other species of the section Tetrataenium, was placed by De Candolle in the section Sphondylium because of its white flowers and enlarged petals.

De Candolle's division into sections was later used by W. D. J. Koch (1837) H. G. Reichenbach (1867) and partly by C. F. Lebedour (1844-46). In the work cited, Koch broadened the section Euheracleum, including in it also the section Sphondylium. Later Lebedour followed him in this. Species growing in the territory included by "Flora rossica" were distributed into 2 sections by Lebedour: sect. Euheracleum and sect. Wendia, However, as the number of known species of Heracleum increased, scientists were faced with the increasingly obvious artificiality of the sectional division of the genus proposed by De Candolle. In his "Flora Orientalis" Boissier, producing 27 species known to him in the Orient, did not accept De Candolle's division. Boissier divided the species of the genus Heracleum into 2 sections: "Sect. 1 Euheracleum, Umbellae involucellatae" and "sect 2 Pseudotragium, Involucra et involucella nulla". In the section Euheracleum Boissier included ~~flowers~~ Species with yellow and white flowers, and species with well developed channels on the commissura as well as those with obliterated channels. The section Pseudotragium was created for a single species - H. pastinaca, growing in the Taurus mountains. The species H. Carmeli; which De Candolle had placed in a special section Carmelia, was separated by Boissier into a monotypic genus Synelcosciadium. Boissier grouped the species within sect. Euheracleum on the basis of the segmentation of the leaf blade. The divisions established by Boissier: simple leaves, ~~compound~~ ternate leaves, compound leaves or doubly pinnately dissected, often bring together species of different kinship. Also, as we have explained, it is not always possible to draw a sharp division between ternate and pinnately compound leaves. It is very often possible to observe within the same species ternate leaves, leaves with one pair of lateral segments, and pinnate leaves with 2 pairs of lateral segments.

* Footnote on name Wendia v Wendtia.

4. A division of the genus Heracleum into sections (cont)

The formation of the second pair of segments often results from the separation and later movement aside of the lateral parts of the terminal segment. Thus the character of the segmentation of the leaf blade, while it can be a valuable diagnostic feature for a species, can in no wise serve as the single criterion for establishing kinship relations between species. C. B. Clarke (1879) did not divide Heracleum into sections, and artificially grouped the Indo-Himalayan species known to him on the basis of the colour of the fruit and its pubescence. Drude (1898) observed that he did not have as yet sufficient information for the division of Heracleum into sections, and he too avoided any sectional division of the genus. He placed all the sections established by De Candolle in the synonymy of the genus Heracleum.*

Kozo-Poljansky (1915) has the following division: Branca Ursina K. Pol. (=Heracleum s. l.) separated into Heracleum Calest., Tordylium Calest. and Condylocarpus K. Pol. In its turn Heracleum Calest. is sub-divided into 2 groups: A. Sphondylium K.-Pol. (Sphondylium Hoffm., Trigonoscadium Boiss.) B. Wendia K.-Pol. (Wendia Hoffm., Wendia auct.). Briquet (1924) on the basis of anatomical study of the fruit of the various species of the genus Heracleum, came to the conclusion that the obliteration of the channels on the commissura of the fruit had no taxonomic significance, and that therefore Wendia could not be separated, not only as an independent genus, but even as a special section. The species H. Pastinaca, which Boissier had separated into the section Pseudotragium, was included in the genus Pastinaca by Briquet. Finally Thellung (1925-6) divides Heracleum into 3 sections: 1.
1. sect. Euheracleum (DC) Boiss., 2. sect. Vocontia (Calest.) Thellung-Pastinaca sect. Vocontia Calest., including one species - H. minimum,
3. sect. Pseudotragium Boiss. with the single species H. Pastinaca.
This strictly concludes our summary of the existing attempts at division of the genus Heracleum into sections. We did not have the opportunity of studying the fruit of Heracleum Pastinaca, since the single example of that species available to us, kept in the herbarium BIN AN USSR, has no ripe fruit. It is quite possible that the species Heracleum Pastinaca belongs [illegible] genus Platytaenium.

* Note. There is a certain inexactitude in Drude. He includes sect. Carmelia among the other sections in the synonymy of the genus Heracleum. At the same time he brings forward as an independent genus on P. 240 the genus Synelcosciadium Boiss., based on the single species in the section Carmelia.

Part 2

A survey of the taxonomy of the Caucasian species of the genus Heracleum

Para1 Pp. 18-19 ~~xxx~~ References.

Type of the genus Heracleum = H. sphondylium L.

The flowers in the main umbel are bisexual, in the lateral umbels often staminate, sterile; the peristome of the calyx is quinqedentate; the teeth uneven, occasionally teeth do not develop, the peristome of the calyx is smooth-edged. The petals are reverse ovate or heart-shaped, at the apex more or less deeply emarginated or bilobular, in a notch with an inward-turning lobule, white, occasionally greenish-yellow or even bright pink, the marginal petals usually strongly enlarged; the disc is broadly cone-shaped, the stigma slightly broadened, and cut slightly obliquely. The fruit are strongly flattened from the back, varying from ovate or reverse ovate to rounded or elliptical, the stem is bipartite, the three middle ribs on the back of the half-fruit are fairly approximate to one another, and narrowly filiform, the two marginal ribs are separated from the middle ones and contiguous with the slightly swollen pteroid peristome of the half-fruit, the small channels in the grooves are solitary, occasionally additional channels have been observed, on the commissural side there are usually two channels, more rarely more than two, or else they do not develop at all, the channels are more or less claviformly broadened towards the lower end, usuallly they do not have partitions, and on both the back of the half-fruit and its commissura the channels are significantly shortened. The endosperm is surrounded by a sort of thick case (made up of mechanical tissue), the cavity between the the case and the lateral ribs is thinner and translucent (made up of few layers of mechanical tissue), the disc at fruiting is narrowly or broadly cone-shaped, wavy round the edge. Biennial herbs with a thickened root, often perennialising; the cycle of development is monocarpic, more rarely perennial herbs.

Distribution. The genus includes about 65 species, growing in the temperate zone of the northern hemisphere, one species is widely distributed in North America.

Key to the determination of species

1. Channels septate along whole length - narrow on back of the half-fruit, narrowing further and coming to a point towards the lower end, reaching ¾ of the way down the half-fruit. Small plants with thin stems and pinnately compound leaves ....H. apiifolium Boiss.

\+ Channels with no partitions on the back of the half-fruit, narrow or broad, broadening to a greater or less extent to the lower end......2

Key to the determination of species (cont)

2. Channels on the back of the half-fruit narrow, towards the lower end more or less suddenly and strongly broadening saccately, those on the commissura clavate, broad. Plants with ternate or pinnately compound leaves.......................... 3

\+ Channels on the back of the half-fruit narrow or broad, gradually and broadening clavately towards the lower end, plants with simple, ternate or pinnately compound leaves.............. 8

3. Small plants up to 50 cm. in height, leaves glabrous, ternate, segments broadly ovate, more or less deeply pinnately cleft into ovate-oblong parts, at the edges more or less evenly large-crenate-toothed. The umbels have 12-15 rays, the rays of the umbel and umbellets have thick squarrose downiness, the external petals of the marginal flowers in the umbellets little enlarged.................13 H. Sommieri I. Manden.

\+ Large plants 1.5 - 2 (3) metres in height. Multi-rayed umbels (40-50), the external petals of the marginal flowers in the umbellets significantly enlarged.................... 4

4. The segments of the ternate or pinnately compound leaves (out of 2 pairs of segments) are not deeply incised, usually 3-lobed, more rarely 5-lobed. Fruit reverse ovate or elliptical, 10-12 mm long, 6-8 mm wide, disc broadly cone-shaped, slightly torulously-wrinkled, the styles slightly longer than the disc.........9..H. Sosnowskyi I. Manden.

\+ Leaf segments deeply pinnately incised into oblong or lanceolate parts...5

5. Leaves pinnately compound of 2-3 pairs of lateral segments, the segments retusely-pinnately-incised into ovate or ovately-oblong lacinules. Fruit 7-11 mm. in length, 5-11 mm broad, reverse ovate, disc broadly cone-shaped with narrow, more or less radially diverging projections, styles the same size as the disc or slightly longer...4. H. trachyloma Fisch et Mey.

\+ Leaves ternate or pinnately compound, their segments deeply incised into oblong or lanceolate lacinules, usually severely elongated and sharpened at the apex. Disc at fruiting slightly torulously-wrinkled.

6. The whole plant covered in thick down, the rays of the umbel and umbellets slightly scabrously-downy..................11 H. Wilhelmsii Fisch et Lall.

\+ The whole plant almost bare or faintly downy, the rays of the umbel and umbellets softly squarrosely downy............ 7

7. Fruit elliptical, 10-11 mm long, 6-7 mm. broad, with practically no tapering towards the base, the channels on the back of the half-fruit running along $\frac{3}{4}$ of its length, on the commissura along half or slightly more than half its length, the disc cone-shaped, the styles 3 times as long as the disc...........................12. H. Mantegazzianum Somm. et Lev.

Key to the determination of species (cont)

7\. ....H. Mantegazzianum Somm. et Lev.

\+ Fruit oblong-reverse-ovate, 12-14 mm. long, 5-6 mm. broad, tapering acutely in wedge-shaped fashion towards the base, the channels shorter, reaching to two-thirds the length of the half-fruit on its back, half its length on the commissura, the disc narrowly cone-shaped, the styles 3-4 times bigger than the disc...............H. Grossheimii I. Manden

8\. The channels on the back of the half-fruit narrow..........................9

\+ The channels on the back of the half-fruit broad, sometimes filling the whole width of the middle groove.... 16

9\. Root-stock multi-headed, releasing sterile rosettes of leaves, the leaves concentrated primarily at the base of the stem, the external petals of the marginal flowers in the umbellets almost unenlarged. The channels on the back of the half-fruit reaching half its length, on the commissura reaching one-third its length, sometimes barely visible...7. H. ossethicum I. Manden.

The totality of features quite different.......... 10

10\. Flowers greenish-yellow, external petals of the marginal flowers in the umbellets almost unenlarged . . . . 8. H. sibiricum L.

\+ Flowers white, external petals of marginal flowers in umbellets usually significantly enlarged 11

11\. Leaves simple, more or less deeply pinnately or palmately incised or even dissected 12

\+ Leaves compound, ternate or pinnate, leaves of the upper stem sometimes simple 13

12\. Leaves palmately dissected, sometimes right to the base, into large segments, broadly reverse ovate with a wedge-shaped base or almost rhomb-shaped, the segments in their turn more or less deeply pinnately incised . . . . .1..H..aconitifolium G. Woron.

\+ Leaves more or less deeply pinnately incised, their parts oblong or ovate, in their turn more or less deeply pinnately incised..

13\. Leaves ternate, from time to time pinnately compound, shallowly pinnately incised 14

\+ Leaves pinnately compound of 2-3 pairs of lateral segments, from time to time the very lowest leaves ternate, the leaf segments deeply, sometimes almost right to the rachis, pinnately dissected into oblong or lanceolate parts 15

14\.

Key to the determination of species (cont)

14\. Leaves ternate, thin, bare on both sides, occasionally with fine down in places on the lower side, the lateral segments, on long petioles, in outline broadly ovate or almost rounded, are usually shallowly lobularly incised. The fruit range from broadly reverse ovate to almost rounded, 7-9 mm. long, 6-7 mm. broad, glabrous, shining, occasionally covered with very small nipple-shaped hairs, the channels on the back of the half-fruit usually reach half its length. .3. H. Ponticum (Lipsky) I. Manden

\+ The plant significantly more thickly downed, leaves ternate, more rarely pinnately compound, the lateral segments on short petioles, usually less than 1 cm. long, the segments in outline ovate or oblong-ovate, more or less deeply incised into ovate acuminate parts. Fruit reverse ovate or oval, 6-10 mm. long, 5-6 mm. broad, covered with small nipple-shaped hairs, the channels on the back of the half-fruit usually reaching $\frac{3}{4}$ of its length . . . . , 4, H. asperum M. B.

15\. The plant bare or slightly downy. The leaf segments pinnately dissected to the rachis into oblong-lanceolate parts, the latter in their turn with shallow and straggly pinnate incisions. Umbel with 8-10 rays. Fruit oblon-reverse-ovate, channels on the back of the half-fruit usually not more than half its length, on the commissura reach one-third or one-quarter the length of the half-fruit . . . . . 6. H. calcareum N. Alb.

\+ Plant more or less thickly covered in usually silvery down, leaf segments more or less deeply pinnately incised into broader, lanceolate, parts, irregularly toothed along the edges. Umbel with 12-15 rays. Fruit reverse ovate or reverse ovately rounded, channels on the back of the half-fruit reaching $\frac{3}{4}$ of its length, on the commissura, half the length of the half-fruit . . . , , . . . 5. H. Colchicum Lipsky

16\. Leaves usually simple, more rarely ternate or pinnately compound, the channels on the back of the half-fruit reaching $\frac{3}{4}$, more rarely half its length, the channels on the commissura clearly visible

\+ Leaves always pinnately compound, channels on the back of the half-fruit never more than half its length, channels on the commissura do not develop . . . .

17\. Leaves always ternate or pinnately compound of 2 pairs of lateral segments, compact, covered with hairs along the large-toothed edges and on the underside along the veins, otherwise bare, the sheathes of the cauline leaves oblong. Umbel with 8-12-(20) rays. . . 15. H. scabrum N Alb

\+ Leaves on the upper side slightly downy, more rarely bare, on the underside more or less thickly downy, even white - tomentose, the sheathes of the cauline leaves markedly broadened, sometimes toothed along the edge. Multi-rayed umbel 30-40-(60) . . . . 18.

18. Plants 20-40 (60) cm. in height, leaves simple, occasionally ternate or pinnately compound, external petals of the marginal flowers very strongly enlarged, up to 10 mm. long . . . . 19 H. grandiflorum Stev.

\+ Plants larger, up to 1 metre in height, leaves always simple, external petals of marginal flowers not strongly enlarged 19

19. Fruit large, 13-15 mm. long, 10-13 mm. broad, broadly reverse ovate, channels on the back of the half-fruit up to two-thirds of its length, channels on the commissura narrow, usually not more than one-third its length . . . . 18. H. antasiaticum I. Manden

\+ Fruit smaller, 7-10 (13) mm. long, 6-9 mm broad, channels on the commissura longer and broader (almost the same width as those on the back of the half-fruit 20

20. Fruit oval, ovate, occasionally reverse ovate, covered with tiny appressed hairs, occasionally long hairs, the channels on the back very broad, filling the middle grooves, reaching to two-thirds - three-quarters the length of the half-fruit, to half its length on the commissura . . . . 16. H. Steveni I. Manden

\+ Fruit almost rounded, more rarely oval, usually covered with a down of tiny prickly hairs, occasionally on the back covered with long entangled hairs, on the peristome with prickly hairs, the channels on the back usually slightly narrower than the grooves, reaching ¾ of the length of the half-fruit, on the commissura half its length . . . . 17. H. Leskovii A. Grossh.

21. The lower part of the stem thickly covered with long,bristly, turned back, appressed hairs, the external petals of the marginal flowers in the umbellets strongly enlarged up to 12 mm. in length, deeply 2-lobed; the lobes oblong . . . . 21. H. chorodanum (Hoffm.) DC.

\+ The lower parts of the stem bare or with short squarrose down, petals of the marginal flowers almost unenlarged,and if enlarged, their lobes broad, almost rounded 22

22. The stem thinly grooved, in cross-section rounded, the sheathes of the cauline leaves usually oblong, slightly broadened, the external petals of the marginal flowers in the umbellets almost unenlarged . . . 20. H. pastinacifolium C. Koch

\+ The stem more or less deeply grooved-ribbed, in cross-section more or less , the sheaths of the cauline leaves strongly broadened, the external petals of the marginal flowers in the umbellets enlarged. 23

23. Plant (40)-60-100cm. in height. Large umbels of 15-20 rays. . . . . 22. H. transcaucasicum I. Manden.

\+ Lower plants 10-25-(40) cm. high. Umbels with 3-12 rays 24

Key to the determination of species (cont)

24. Flowers bright pink. Umbels with 8-12-(5) rays. Channels on the back of the half-fruit reaching one-third, occasionally half, its length. . . . . 23 H. Roseum Stev.

\+ Flowers white. Umbels with 3-5-(8) rays. Channels on back of half-fruit reaching half its length 25

25. Leaflets of the indusium 5-6, uneven, 2-3 of them sometimes equal to or greater than the umbels in height in the flowering state. Fruit reverse ovate, 7-9 mm. long, 4-5 mm. broad, channels slightly narrower than the middle grooves . . . . . . 24 H. Schelkovnikovii G. Woron.

\+ Leaflets of the indusium 2-3. lanceolate, small. Fruit broadly reverse ovate or elliptical, 8 mm. long, 6 mm. broad, channels broad, filling the middle grooves . . . . 5 H. Albovii I. Manden.

12. Heracleum Mantegazzianum Somm. et Lev. (pp 49-51)

Plant up to 3 metres high, stem rounded, grooved, sparsely downy, leaves bare or sparsely downy on the underside, radical and lower cauline leaves on long stalks, usually ternate, the pair of lateral segments on stalks, the segments in outline oblong-ovate, deeply pinnately incised into triangular lanceolate, usually elongated and acuminate towards the tip, parts, the terminal segment separated from the lateral ones, deeply (sometimes almost to the base) pinnately dissected into oblong, elongated and acuminate parts, in their turn pinnately incised, upper leaves comparatively diminished with shorter stalks and strongly extended sheaths, the leaves unevenly sharp-toothed along the edge. Umbellets very strong, multi-rayed (more than 50 rays) the rays of the umbel and umbellets softly and sparsely downy with scarious hairs, the leaflets of the indusium at the main umbel usually do not develop, the leaflets of the indusium are numerous (up to 8), linearly awl-shaped, flowers white, ovary more or less thickly sparsely downy, the teeth of the calyx large, ovate-triangular, acuminate, the external petals of the marginal flowers in the umbellets strongly enlarged, deeply bilobular, the anthers of a pale olive colour, the disc slightly torulose. Half-fruit 10-11 mm. long, elliptical, with practically no tapering towards the base, slightly emarginate at the tip, the back bare or covered with occasional scarious hairs, the peristome with a few prickly hairs or bare, channels on the back reaching three-quarters the length of the half-fruit, those on the commissura reaching half its length or a little less, disc cone-shaped, torulose, styles three times longer than the disc.

12. Heracleum Mantegazzianum Somm et Lev (cont)

Distribution. Western Pre-Caucasus, the southern slope of the western part of the Main Caucasian mountain range. In the upper forest belt on the edges of the forest and clearings in the high grass, occasionally found in the middle forest belt. Endemic.

Classical habitat cf. para. 3 p. 50

Refernces Pp. 50-51

Footnote P. 51

As far as we can judge by very incomplete herbarium examples, in the northern part of the natural habitat, for instance in the Maicop region, a form can be found which is distinguishable from the typical H. Mantegazzianum by its less deeply dissected leaf segments with the terminal parts less elongated. This form requires investigation. In the Stavropol collection in the Herbarium of the BIN AN USSR there are 2 examples close to the species H. Mantegazzianum, one gathered by Gefft -"Stavropol 1837", the other by Akinfie ? in 1889 on the mountain Temnolesky. Unfortunately the collected examples are insufficiently complete for us to include the plant in the species H. Mantegazzianum with any assurance. An idea of the plant growing in Stavropol can be formed by studying the photograph in the work of I. V. Novopokrovsky (1927). At the same time the possibility of finding a colchide (?) species in an extremely distant northerly outpost of Caucasian forest flora, as the Stavropol collection seems to be, is of considerable interest and deserves examination.

The description of H. Mantegazzianum was first compiled by Sommier et Levier from examples grown in Switzerland in the alpine garden of Correvon from seeds they had brought from Abkhazia, and later they cultivated it also in Italy, in Bormio. This species began to be cultivated in Western Europe, and is widely used in gardens and parks, not infrequently growing wild. From examples cultivated in gardens, European authors isolated the variants f. rosocalyx Schwerin and var. immaculatum Vilcz. According to Thellung, the first of these is characterised by a slightly pink calyx and flower buds with a slightly pink colouring which disappears on blossoming. The second variant is characterised by the absence of red flecks on the stem and stalks and has no scent. We give no taxonomic significance to these cultivated forms.

Sect. 2. Pubescentia I. Manden.

Para. 1 (Latin)

Flowers white. Channels on the back of the half-fruit narrow, more or less suddenly and strongly widening saccately towards the lower end, reaching two-thirds, more rarely three-quarters the length of the half-fruit; channels on the commissura more or less uniformly broad, usually reaching half the length of the half-fruit.

Para 3 (Latin)

9. Heracleum Sosnowskyi I. Manden.

Para. 1 (Latin)

Plant 100-150 cm. in height, the stem deeply grooved and ribbed, thinly downed, the leaves bare on the upper side, on the under side slightly squarrosely downed; the radical and lower cauline leaves ternate or pinnately compound, consisting of 2 pairs of lateral segments, the first pair on short petioles, the second sessile; the segments broadly ovate or oblique ovate-oblong, with comparatively shallow lobed or pinnate incisions into 3 broadly ovate parts, the final segment rounded in outline and deeply, sometimes right to the base, incised into 3 ovate parts, in their turn slightly pinnately incised. The umbels large, multi-rayed, the rays of the umbel and umbellets slightly scabrously downed, the leaflets of the indusium numerous, from a slightly broadened base linearly awl-shaped, flowers white, the ovary thickly covered with long down, the teeth of the calyx large and ovately-triangular, the external petals of the marginal flowers in the umbellets enlarged, 9-10 mm. long, and deeply bilobular, the anthers dark purple, the disc slightly torulose. The half-fruits 9-12 mm. long, 6-8 mm. broad, reverse ovate or elliptical, when immature thickly downed, the ripe half-fruits have occasional prickly hairs on the peristome, and occasional scarious hairs on the back, the channels on the back of the half-fruit reach to three-quarters of its length, on the commissura to half its length, the disc hemispherical, torulously wrinkled, the styles twice, occasionally three times, as long as the disc.

Distribution. The Eastern part of the Main Caucasian range, south-west Transcaucasia, east Transcaucasia. Endemic. In the middle and upper forest belt, on the edges of the forest and in glades.

Classical location. (Latin)

References (Pp 43-44)

Remarks. The area of distribution of the species H. Sosnowskyi takes in the systems of the Great and Small Caucasus. It is quite possible that this species may be found in Anatolia. In the south-west of its area of distribution it probably passes into the regions of Armenia bordering on Georgia. However, the imperfect herbarium specimens collected on the Lorisky plateau do not permit us to include them in this species. Throughout its large area of distribution the species varies, principally in the shape of its leaves. In the specimens collected by us in Meskhetia and serving as a model for the description of the species the leaves are ternate with broadly ovate, slightly lobed lateral segments. The considerable herbarium material studied by us and the observations made of living plants allow us to include in the species H. Sosnowskyi also plants with pinnately compound leaves and slightly more lengthened and deeply incised segments, and the latter form, perhaps, is more broadly spread.

Apart from the shape of the channels the following features of the species H. Sosnowskyi must be recognized as characteristic and sufficiently constant; the fine scabrous downiness of the rays of the umbel and umbellets, the less enlarged petals of the marginal flowers compared with the species H. Mantegazzianum and H. Wilhelmsii, and, finally, the broad, torulously wrinkled disc. At one time the ternate segmentation of the leaves served as a starting point for an erroneous comparison of H. Sosnowskyi with the species H. spathiphyllum C. Koch (sect. Villosa I. Manden.). Only after systematic critical analysis of the genus did it become completely clear that, in spite of the system of the genus adopted by Boissier, the shape of the leaves was unsuitable for fixing the interrelationships between species. The species H. Sosnowskyi, thanks to its widespread distribution, has more than once been collected, defined and usually included in various "Florae" under the name H. pubescens M. B. (the form with pinnately compound leaves). The history of the description of H. pubescens is fairly confused, but its main points are as follows. In 1814 Hoffmann in his Gen. Umbelliferarum included a short description of the fruit of one of the cow-parsnips, growing in the Gorenkovsky Botanical gardens and gave to the species the name Sphondylium pubescens, and included under that name the species H. speciosum, which had been cultivated in the Deritsky Botanical gardens. A completely clear and accurate description of H. pubescens was first compiled by Marshall Biberstein from specimens growing in the southern Crimea sent by Steven. Apart from the Crimea, Marshall Biberstein also found H. pubescens to grow in the eastern Caucasus -"Habitat in Tauria maxime meridionali locis inumbratis roscidis, circa Nikitam haud rarum nec non in agris pagi subalpini Chiulug Caucasi orientalis". In the herbarium of Marshall Biberstein is preserved an authentic

authentic example of the species, with the following label "H. pubescens Nikita com. Steven 1812" and there are also a few examples of the same species labelled H. tauricum, H. verrucosum; these latter names belong to the nomina nuda, and we paid them no attention. One of the named herbarium examples has two labels, one stating "H. verrucosum sp. Nk.", the other "Heracleum verrucosum. In Cauc. Orient, Steven 1812", the very defective herbarium material on this page belongs, apparently, also to different plants. The plant, growing in the Crimea, for which we retain the name H. pubescens M. B. senso proprio, is well differentiated from the Caucasian species H. Sosnowskyi by its few-rayed umbel, by the soft squarrose downiness of the rays of the umbel and umbellets, and lastly by the narrow cone-shaped and non-torulous disc. Since cow-parsnips from the cycle H. pubescens have been cultivated for a long time, we cannot, of course, exclude the possibility that the species we have called H. Sosnowskyi has an older name. Marshall Biberstein placed the species Sph. pubescens as a synonym of H. pubescens, however, we being unable to establish the origin of the plant growing in the Gorenkovsky gardens, refrain from such synonymisation. Similarly we can express no views about the species H. speciosum Weinm. and H. gummiferum Willd., the former cultivated in the Derptsky Botanical gardens, the latter in the Berlin Botanical gardens. The shape of the channels noted by Hoffmann for the species H. speciosum hort. dorpath. "vittae oblongae turgidae, incrassatae basi, mediae longiores, commissurales fere aequali latitudine, dimidiam partem seminis attingentes" (Hoffm. l.c.) and by De Candolle for the species H. gummiferum Willd. "vittis dorsalibus gracilibus ultra medium productis apice subito in clavam dilatatis" (DC Prodr. p. 193), allows us only to establish that the plants derived from the section Pubescentia I. Manden. Thus the attempt by Thellung (1925-6) to rename H. pubescens M.B. as H. speciosum Weinm. with a division into 3 variants: var. pubescens (M.B.) Thell., var. Wilhelmsii (Fisch. et Lall.) Thell. and var. trachyloma (Fisch. et Mey.) Thell - seems to us a purely formal and unsuccessful solution to the question.

10. Heracleum Wilhelmsii Fisch. et Lallem.

Para 1 (Latin)

Plant 100-150 cm. in height, the stem deeply grooved and ribbed, thickly covered in shaggy down, the leaves bright green and bare on the upper side, on the under side paler and thickly squarrosely downed with small hairs, the radical and lower cauline leaves ternate or pinnately compound, consisting of 2 pairs of lateral segments; the first pair on short petioles, the second sessile, the segments ovate in outline, oblique, pinnately incised into lance-shaped, sharply acuminate parts, the final segment almost rounded in outline

outline, deeply pinnately incised into ovate-oblong parts, in their turn deeply pinnately incised into sharply acuminate lance-shaped lacinules, the upper leaves diminished, on short petioles or sessile with a strongly extended sheath. The umbels large, up to 40-50 cm. in diameter, multi-rayed, the rays of the umbel and umbellets slightly scabrously downed, the leaflets of the spathe and indusium numerous, linearly awl-shaped from a slightly broadened base, the flowers white, the ovary thickly downed, the teeth of the calyx ovate-triangular, the external petals of the marginal flowers in the umbellets strongly enlarged, 10-12 mm. long, deeply bilobular, the anthers dark purple, the disc slightly torulose. The half-fruits 10-13 mm. long, 7-9 mm. broad, reverse ovate, thickly covered with prickly, appressed, upward-growing, curved hairs, sometimes with an admixture of long scarious hairs, alternatively prickly hairs are found only on the peristome and at the base of the half-fruit, the back being covered only with long entangled scarious hairs, the channels on the back of the half-fruit reaching three-quarters of its length, those on the commissura half its length, the disc cone-shaped, torulously wrinkled, the styles 2-3 times longer than the disc.

Distribution. In the upper forest and subalpine belts of the western part of the Trialetsky range. Endemic.

Classical location. (Latin).

References. (P. 47)

Remarks. This species, which was described by Fischer and Lalleman from the collections of Williams and (in?) Kodiani (Kadiani), was grown by them in the large Peterburg Botanocal gardens. Herbarium specimens of H. Wilhelmsii with the note "Planta valde aromatica odore suavi" are kept in the Herbarium of the Library of the Academy of Sciences of the USSR, and Fischer and Lalleman noted the closeness of this Caucasian species to H. persicum, which grows in northern Iran. Boissier considered H. Wilhelmsii to be a variant of H. pubescens M.B. He considered the most significant feature of variation to be the character of down on the fruit, "Fructus toto disco aculeolatus, aculeis plurimis in setulam adpressam productis" (Boiss. l.c.). This diagnosis repeats almost word for word the description of the fruit by Fischer and Lalleman "fructibus oblongo obovatis toto disco aculeolatis; aculeis plurimis in setulam adpressam productis". We studied the species H. Wilhelmsii in the vicinity of Bakuriani. Our observations showed that, indeed, the half-fruit is sometimes covered thickly with prickly hairs, such hairs being particularly well expressed on the peristome of the fruit, while in the middle part the hairs are longer, and more regularly pointed, frequently the hairs on the back are softer, long scarious hairs, slightly entangled. Thus the character of the down on the fruits varies considerably. The closest species to H. Wilhelmsii are the species H. Mantegazzianum and H. Grossheimii, and H. Wilhelmsii is differentiated from them above all by the much more abundant downiness on all parts of the plant and the thin prickly down on the rays of the umbel and umbellets.

11. Heracleum Grossheimii Г. Manden.

Plant 100-150 cm. in height, the stem deeply grooved and ribbed, thinly downed, the leaves yellowish green and bare on the upper side, the under side paler with thin occasional down or bare, the radical and lower cauline leaves ternate or pinnately compound, consisting of 2 pairs of lateral segments; the first pair on short petioles, the others sessile, the segments ovate in outline, deeply pinnately incised into lance-shaped, elongated and acuminate parts, the final segment almost rounded in outline, deeply pinnately incised into ovate-oblong parts, pinnately incised in their turn, the upper cauline leaves diminished, ternate, with a shorter petiole and a strongly enlarged thinly downed sheath, the topmost leaves sometimes consist of a sheath and a small, simple, pinnately dissected blade, the leaves irregularly sharp-toothed along the edges. The umbels large, multi-rayed, the leaflets of the spathe and the indusium linearly awl-shaped, uneven, the rays of the umbel and umbellets softly squarrosely downed with scarious and stalky glandular hairs, flowers white, the ovary thickly squarrosely downed, the teeth of the calyx large, ovately triangular, the petals of the marginal flowers in the umbellets strongly enlarged, deeply bilobular, the anthers purple, the disc slightly torulose. The half-fruit 12-14 mm. long, 5-6 mm. broad, oblongly reverse ovate, strongly tapered towards the base, slightly emarginate towards the tip, the back bare or with the occasional scarious hair, the peristome of the half-fruit at the tip and the base has a few straight, prickly hairs, the middle channels on the back of the half-fruit reach two-thirds its length, the lateral channels sometimes half its length, the channels on the commissura are not more than half the length of the half-fruit, the disc narrowly cone-shaped, torulously wrinkled, the styles 3-4 times bigger than the disc.

Distribution. Grows in Imeretia and Guria in the upper forest belt, in forest glades and on the edges of forest roads. Endemic.

Classical location. The Adzharo-Imeretinsky range, near Bakhmaro, 2200 m. above sea level.

References (P. 48)

Para. 2 (Latin)

11. Heracleum Grossheimii I. Manden. (cont)

Remarks. Apart from the listed locations this species was observed by us in Guria, on the road to Bakhmaro in the forest behind the village of Chkhakaura. The species H. Grossheimii is close to H. Mantegazzianum, but well differentiated from it by the fruit, which are larger and strongly cuneately tapered towards the base, and have shorter channels. H. Grossheimii is differentiated from H. Wilhelmsii Fisch. et Lallem. by the significantly less downiness of all parts of the plant, by the soft, squarrose stalky-glandular down on the rays of the umbel and umbellets, by the shorter channels on the fruit, and by the significantly more elongated disc with its longer styles.

13. Heracleum Sommieri I. Manden.

Para 1. (Latin)

Plant up to 50 cm. in height, stem deeply grooved, ribbed, in the lower parts almost bare, in the upper parts -thickly squarrosely downed, radical and lower cauline leaves ternate, the lateral segments on short petioles, ovate in outline, oblique, more or less deeply pinnately incised into ovate acuminate parts, the final segment significantly apart from the lateral segments, broadly ovate or almost rounded, more or less deeply pinnately incised into ovate or ovate-oblong parts, in their turn sometimes with shallow pinnate incisions, the few upper cauline leaves with extended downed sheaths and a small pinnately dissected blade, all leaves bare on both sides, more or less regularly crenate-toothed along the edges, slightly ciliate. The umbels with 12-14 rays, the rays of the umbel and umbellets thickly squarrosely downed, the leaflets of the spathe few, deciduous, the leaflets of the indusium narrowly lance-shaped, uneven, the flowers white, the ovary thickly squarrosely downed, the teeth of the calyx very noticeable, the external petals of the marginal flowers in the umbellets comparatively little enlarged (they are twice as big as the ovary), bilobular up to the middle, the anthers olive-coloured. The half-fruits with diffuse cobwebby down.

Distribution. The subalpine meadows of Svanethia. Endemic.

Classical location. (Latin)

References P. 52

Remarks. The plant was first collected in Svanethia by Sommier and Levier near the village of Enashi, and described by them as a variant of H. pubescens M.B. This is their description "...... (Latin) Pp 52-3."

13. Heracleum Sommieri I. Manden. (cont)

We had only one single specimen of this species at our disposal, collected by D. I. Sosnowsky in flower at the classical location near Latali (Enashi). The complex of morphological features typical of this form are its somewhat low height; the bare leaves and thickly squarrosely downed rays of the umbel and umbellets, the few rays of the umbel; the lack of enlargement of the petals, giving this plant a distinctive appearance, - these allow us to see it as an independent species. We have named it after the botanist Sommier, who was the first to draw attention to it. The leaves of H. Sommieri are similar in shape to the leaves of H. pubescens, with which Sommier and Levier related it, or more accurately, to the leaves of the species H. Sosnowskyi, found vicariously in the Transcaucasus. The character of the downiness of H. Sommieri is identical to that of H. Mantegazzianum. We are inclined to think that, in spite of the apparently sharp difference between the gigantic H. Mantegazzianum and H. Sommieri, which scarcely reaches 50 cm. in height, that these two species are genetically closely linked to one another. The area of distribution of H. Sommieri is very small, at the present time we know of only one single habitat for it: the subalpine meadows of the Latali region in Svanethia, 1300-1400 m. above sea level, to the south-east of the Bechoysky pass. Further collection of this rare plant may allow us to be more exact in defining its relationship with the other species of the section Pubescentia.

14. Heracleum trachyloma Fisch. et Meyer

Para 1 (Latin)

Plant 100-150 cm. in height, the stem deeply grooved, ribbed, fairly thickly downed, the leaves bare on the upper side, the lower side slightly squarrosely downed, the radical and lower cauline leaves pinnately compound, consisting of 2-3 pairs of lateral segments; the first pair on short petioles, the others sessile, the segments ovate or ovate-oblong, oblique, retusely pinnately incised into ovate or ovate-oblong parts, the final segment rounded in outline, deeply pinnately incised into ovately oblong parts, in their turn pinnately incised. The umbels large, multi-rayed, the rays of the umbel and umbellets softly squarrosely downed with scarious hairs, the leaflets of the indusium numerous, linearly awl-shaped from a slightly extended base, the flowers white, the ovary covered thickly with long down, the teeth of the calyx large, ovately-triangular, the external petals of the marginal flowers in the umbellets enlarged, deeply bilobular, the anthers olive-coloured. The half-fruits 7-11 mm. long, 5-7 mm. broad, reverse ovate or elliptical, the back usually thickly downed with long scarious hairs, the peristome with thin, upward-growing prickly hairs, the channels on the back reaching three-quarters the length of the half-fruit, those on the commissura half its length, the disc hemispherical, the styles the same length as the disc, never more than twice its length.

Distribution. The southern Transcaucasus and Talysh, in deep ravines on the banks of mountain streams and waterfalls, where it sometimes forms thick undergrowth. Endemic.

Classical location. (Latin)

It appears that the name Shikar on the 5-verst map of the Caucasus corresponds to Shukyar, in the Daralagezsky region of the Armenian SSR (it was attributed to Karabakh by previous researchers). Shovits' remark that Shikar is near Nakhichevan-chay is not quite accurate - the plant was collected by Shovits on June 8th, 1829, and judging by his itinerary, placed in the Flora of the Caucasus by Lipsky, it was not until June 10th that Shovits, having crossed what was in all probability the Bichenagsky pass, entered the valley of Nakhichevan-chay.

References. Pp. 54-55

Remarks. This species is close to H. Sosnowsyki, but differentiated from it by small features such as: the shape of the leaf segments, the more significantly enlarged petals of the marginal flowers, the longer and more squarrose down on the rays of the umbel and umbellets, the more richly downed fruits, the disc without tubercles, and the narrow longitudinal projections on the disc at fruiting. Boissier placed the species H. trachyloma among the variants of H. pubescens M.B., differentiating it from the typical only in the downiness of the fruit "Fructus toto disco papillis longis setosus margine muriculatus" (Boissier, l.c.). The fruit of H. trachyloma, as in many species of the section Pubescentia, has its peristome covered with prickly hairs, these hairs consisting of a strongly enlarged base, changing into short, slightly bent, sharp points; the tips of the hairs often break off, and as a consequence the surface of the half-fruit becomes torulous. Fischer and Meyer, when describing the species H. trachyloma, noted in their diagnosis that the leaves were downy on both sides, however, in spite of their diagmosis, in the authentic specimens collected by Shovits, the leaves are bare on the upper side; Karl Koch, who collected this species in Armenia, drew attention to this discrepancy in his day also.

Espèces Caucasiennes du genre Heracleum 1950
p. 90-101 I. P. MANDENOVA

TROISIEME PARTIE

PRINCIPALES VOIES DE L'EVOLUTION DU GENRE HERACLEUM

Les représentants du genre Heracleum sont très caractéristiques des provinces boisées de l'Eurasie tempérée et de l'Amériqu Nord. En Eurasie la limite septentrionale de l'aire du genre s'étend depuis la presqu'île scandinave jusqu'au Kamtchatka, et en Amérique Nord, depuis l'Alaska jusqu'au Labrador et New-faundlend, alors que la limite méridionale comprend l'Afrique Nord, l'Asie Antérieure et Orientale ; en Amérique Nord elle s'étend depuis la Californie et le Mexique méridional jusqu'à la Caroline septentrionale.

Plusieurs grands centres de développement du genre apparaissent nettement sur le fond général de cette vaste aire : l'Asi Orientale, les régions montagneuses de l'Europe Méridionale et le Caucase. Sans parler déjà des vastes régions désertiques du Paléartique inaccessibles pour les représentants de ce genre mésophylle, les immenses étendues forestières au Nord de l'Eurasie sont pauvres en espèces du genre Heracleum. A proprement parler, à la limite septentrionale du genre en Europe on rencontre une seule espèce : H. sibiricum L., largement répandue dans la partie européenne de l'U.R.S.S. et en Sibérie Occidentale. Il faut noter également le rôle extrêmement modeste qu'a joué l'Amérique du Nord dans le développement du genre, puisqu'aussi bien pour la partie de l'aire de l'Océan Pacifique que de l'Océan Atlantique on ne connaît qu'une seule et unique espèce : H. lanatum Mich.

Si la question concernant les centres de la diversité spécifique du genre peut actuellement être résolue avec une précision suffisante, les questions de l'origine du genre se présentent, par contre, comme extrêmement complexes.

Transl. J. Carbonnier

En voulant éclairer, dans la mesure du possible, l'origine du genre *Heracleum*, nous nous fondons sur les données de l'analyse systématique de ce genre.

Mettre en évidence les principaux stades de développemen d'un tel ou tel genre n'est pas un problème facile, surtout parce que nous avons à faire ici à un groupe pour lequel les données paléontologiques n'existent pas. Dans les travaux concernant le genre *Heracleum* les difficultés inévitables que les chercheurs rencontrent lors de l'approche des questions de phylogenèse, se compliquent encore par le fait que nos recherches n'ont embrassé au fond que les espèces, habitant le Caucase, c'est-à-dire pas plus de la moitié de tous les représentants du genre. La connaissance des espèces restantes ne pouvait être réalisées qu'à la base de l'étude de la bibliographie spécialisée et du matériel d'herbier relativement importat. Les conclusions auxquelles nous sommes arrivées actuellement subiront peut être certaines modifications dans l'avenir, lors de l'étude approfondie des espèces, croissant au-delà des limites du Caucase, espèces, dont à l'heure présente nous ne pouvons nous faire qu'une idée tout à fait générale. Néanmoins, nous nous considérons en droit d'examiner tout le matériel étudié avec une appréciation phylogénétique~~s~~, en partant de là, d'essayer d'observer les principales lignes de développement du genre dans son ensemble.

Dans le genre *Heracleum* aussi bien que dans les genres proches, tels que : *Tordyliopsis*, *Pastinaca*, *Malabaila*, *Zosima*, *Stenotaemia*, *Platytaenia*, *Tordylium* et autres que nous réunissons dans une tribu commune *Pastinaceae*, le phénomène de l'hétérochronie des indices (KOZO - POLIANSKII, 1940) est assez nettement exprimé.

Dans le péricarpe des genres énumérés on observe le tissu sclérenchimateux indiquant les caractères archaïques propres de leur structure et qui reflètent, peut être, les relations phylogénétiques de ce groupe de genres avec la branche très ancienne de la famille *Umbelliferae*, la sous-famille *Hydrocotyloideae* ; ou bien nous conduisent-ils peut être plus encore en profondeur aux ancêtres probables des Ombellifères, c'est-à-dire vers les Araliales. De plus, la forme des méricarpes, fortement aplatis parallèlement à la commissure et avec un rebord aliforme bien exprimé, forment ce que l'on appelle un parenchyme aérifère ("aerofor" d'après la terminologie de KOZO-POLIANSKII), caractérise le fruit anémochore idéal et ne peut être considérée autrement que comme un indice d'une haute spécialisation. Tout ce groupe de genres dans la sous-famille *Apioideae* se trouve quelque peu isolé et il nous est impossible de joindre actuellement les fils rompus qui nous conduiraient aux sources de l'origine de ce groupe et auraient de cette façon mis en évidence l'aire géographique de sa provenance. L'analyse systématique du genre *Heracleum* reste la clé unique à la connaissance de l'origine et à son évolution ultérieure. En ligne générale nous avons tracé plus haut l'aire de ce genre.

L'étude des différents cycles sur le fond de leur répartition géographique déroule devant nous le tableau suivant :

La section *Euheracleum* doit être reconnue comme la branche ancienne la plus primitive du genre.

Cette section, occupant en quelque sorte une position principale, est la plus riche en espèces et embrasse une vaste aire, coïncidant avec la plus grande partie de l'aire générale du genre.

Les espèces de la section *Euheracleum* coïncident avec lesforêts montagneuses de l'Eurasie, de l'Amérique du Nord et de l'Afrique Septentrionale et, apparemment, pour le centre de formation de la section on doit considérer l'Asie Orientale et plus spécialement les régions montagneuses de l'Unnzn et de Sychuan, où la section *Euheracleum* est représentée par un très grand nombre d'espèces et de formes endémiques. M. de BOISSIEU (1903), ayant déjà décrit depuis la Chine, d'après les collections du Museum d'Histoire Naturelle de Paris, une série d'espèces se rapportant à cette section, a noté que les espèces *séparées* par lui n'épuisent de loin toute la diversité de formes présentée dans les collections du Muséum. Cependant, les collectes occasionnelles et incomplètes ne lui ont pas permis de décrire ces formes en tant qu'espèces nouvelles. Au fur et à mesure de l'avance vers le nord-ouest et le nord de l'Asie nous rencontrons un appauvrissemen considérable de composition spécifique. Notons en passant que certaines espèces croissant en Sibérie et au Japon ne sont pas différenciées morphologiquement de manière tranchée et sont liées entre elles par des termes de passage.

A cette section appartient également l'espèce H. lanatum représentant unique du genre Heracleum en Amérique du Nord. Cette dernière espèce si proche du cycle oriental asiatique de formes, que certains auteurs ont estimé possible de rapporter à l'espèce H. lanatum, en qualité de ses synonymes, toute une série d'espèces indépendantes, croissant au Kamtchaïka, en Sibérie et en Chine, telles que H. dulce (Kamtchatka) H. moellendorfii (Chine). L'aire embrassée par les espèces de la section Euheracleum, s'étend loin à l'ouest, attignant l'Espagne (Pyrénées) et le Nord-Ouest de l'Afrique (système de l'Atlas). Dans les Alpes et dans les systèmes montagneux de l'Europe Méridionale de nombreuses espèces des sections Euheracleum ont obtenu le développement.

Le Caucase s'est présenté comme l'un des très important centres de développement pour les espèces de la section Euheracleum. Les très nombreuses espèces endémiques croissant sur les terres, se rapportent aux éléments caractéristiques de la flore forestière mésophylle actuelle du Caucase. Géographiquement, elles coïncident, dans l'essentiel, avec la Transcaucasie Occidentale, la région de la flore kolchidienne relique, mais on les rencontre aussi dans les régions voisines de Kolchida, sur la pente septentrionale de la partie ouest de la crête principale et dans la région de Barjom - Bakuriansk. Il n'y a qu'une seule espèce H. asperum qui est largement répandue dans la région de toute la crête principale et au Daghestan.

Les espèces de la section Euheracleum croissent dans les zones subalpestres et les zones forestières supérieures, sur les lisières des bois, dans les gorges et ravins boisés humides et profondes ; elles rentrent fréquemment dans la composition des herbes hautes et sont plus rarement rencontrées sur les près subalpestres. D'après les données de V. L. KOMAROV (1929) l'espèce H. dulce croît au Kamtchatka sur les orées des bois des côtes ensemble avec Cirsium kamtschaticum et Cilium avenaceum ; cette espèce forme des broussailles herbeuses touffues. Pour les végétations herbeuses de grande taille et boisées de l'Altaï, A. P. SHENNIRON (1938) dans le nombre des plantes caractéristiques, note l'espèce H. dissectum. Certaines espèces apparemment plus jeunes telles que : H. colchicum et H. calcareum, endémiques pour la partie occidentale du Grand Caucase coïncident exclusivement avec la zone alpestre, où elles croissent sur les moraines, sur les éboulements pierreux et les terrains des mines.

Dans la composition de la végétation de haute montagne du Caucase et des Alpes rentrent certaines espèces oréophytes, n'ayant pas de parents proches parmi les autres représentants caucasiens et européens du genre Heracleum. Parmi eux notons avant tout H. osseticum espèce croissant dans la partie centrale de la crête Principale Caucasienne sur le pente du Sud, où on rencontre dans la zone alpestre à une altitude de 2 000 à 3 000 m, sur les éboulements pierreux et rocailleux. L'espèce qui lui est la plus proche, H. austriacum croît dans la zone alpestre des Alpes Bavaroises et Tripolitaines. H. austricum à l'opposé de H. ossethicum, espèce, morphologiquement, suffisamment conservatrice, manifeste une assez grande gamme de variation. Ainsi, la forme typique mise à part, on connaît la variété var. glaberrimum (H. glaberrimum DALLATORRE 1899) A l'est de l'aire en Carinthie, en Styrie Inférieure et en Kraïne, l'espèce H. austriacum est remplacée par H. süpolium, espèce très proche mais qui se distingue de H. austriacum, principalement par une coloration des fleurs rose vif. Ces espèces sont des plantes de taille relativement peu importante, à tige mince et feuilles composées-pennées. Leurs fruits possèdent des canalicules étroites, sur les côtes commissurales du fruit, elles présentent même une certaine tendance à l'oblitération. Apparemment, ce groupe réunit des espèces convergentes relativement jeunes, survenues indépendemment l'une de l'autre au cours du processus d'oréophytisation en état de progression.

Lorsqu'on fait la connaissance très proche d'éspèces de la section Euheracleum, on constate que les espèces séparées en dépit de rupture importante de l'aire, ne se différencient pas morphologiquement d'une manière tranchée, en manifestant un polymorphisme considéralbe. Les espèces de cette section se différencient l'une de l'autre par des indices peu importants, exprimés parfois de manière insuffisamment nette. Aussi, cet état des choses a donné l'occasion à des interprétations les plus divergentes quant à l'étendue de telle ou telle espèce et le genre Heracleum devint ainsi l'un des plus complexes, peuplant la terre de l'Eurasie.

En étudiant les espèces, croissant actuellement dans les régions forestières isolées les unes des autres, se trouvant en Asie Orientale, au Caucase, en Europe, en Afrique du Nord et en Amérique du Nord, nous réunissons, en quelque sorte les maillons séparés, habituellement peu différenciés, d'un rang phylogénitique commun, les fragments d'untype morphologique unifié, ayant obtenu dans le pliocène une large diffusion dans les régions forestières de l'Eurasie et de l'Amérique du Nord. Le type Euheracleum a obtenu sur la périphérie de l'aire la possibilité pour un développement ultérieur. A la suite de ce fait au Caucase, en Crimée, en Asie Antérieure, dans le milieu écologique nouveau, d'autres espèces ont pris naissance, qui ultérieurement se sont transformées en cycles indépendants. Les espèces composant les sections Pubescentia Villosa et Wendia portent des caractères d'une certaine formation nouvelle, d'une spécialisation manifeste, parfois d'une profonde transformation. Dans l'histoire du développement du genre Heracleum elles ouvrent une page nouvelle.

La section Pubescentia constitue le maillon le plus proche de la section Euheracleum. Habituellement les représentants de la section Pubescentia rappellent fortement les espèces de la section Euheracleum. Ce sont également des herbes fréquemment monocarpiques et quelques fois géantes, portant des puissantes ombelles avec des fleurs marginales très agrandies et les feuilles très grandes ; les segments des feuilles sont fendus de manière relativement peu profonde. La transformation s'exprime par un élargissement fort et soudain de canalicules à leur extrémité inférieure.

En raison du fait indiqué, les canalicules du côté dorsal du frui acquièrement un aspect sacciforme très manifeste. Les espèces de cette section sont concentrées principalement dans les provinces forestières du Caucase. En dehors du Caucase elles sont rencontrée en Crimée, en Lasistan ? en Iran du Nord et, enfin, une espèce de ce grope *H. lehmannianum* croit au Pamiro-Alaï, quelque peu séparemment de l'aire générale, occupée par les espèces de la section *Pubescentia*. Au Caucase cette section est représentée par une série de petites espèces vicariantes remplaçant les unes les autres. Il semblerait que dans ce processus général de remplacemen des formes, apparaissent deux séries d'espèces, tendues vers les centres reliques de Caucase : occidental, colchidient et oriental, celui de Hirkansk. Morphologiquement la différenciation s'exprime par le caractère différent de la surface du disque. Cheztoutes les espèces d'origine colchidienne, depuis *H. sosnowskyi*, espèce largement répandue dans la zone boisée moyenne du Grand et Petit Caucase, jusqu'aux espèces aux aires locales étroites, telles que *H. mantegazzianum*, *H. Grossheimii*, *H. wilhelmsii*, *H. sommieri*, le disque des fleurs est finement tuberculeux et celui des fruits est tuberculeux ridé. A Falysh croit l'espèce *H. trackyloma*, dont l'aire embrasse également les massifs forestiers de l'Arménie. L'espèce proche *H. persicum* est propre aux bois qui habillent les pentes de l'Elbrouz. Ces dernières espèces, qui se rapportent au centre de Hirkansk, se caractérisent par un disque de fleur lisse, alors que le disque des fruits a des saillies étroites divergeant de façon radiaire plus ou moins régulière. Les bois de la zone montagneuse moyenne et de la zone supérieure en particulier constituent les lieux habituels d'habitats pour les espèces de la section *Pubescentia*. Certaines espèces, telles que *H. wilhelmsii*, *H. trachyloma* forment le long des cours de rivières des broussailles considérables, parfois pures ; les espèces de cette section rentrent fréquemment dans la composition des végétations des herbes hautes.

La section *villosa*, en présentant une branche phylogénitique spéciale, constitue un des dérivés du type ancien *Euheracleu*

Les espèces composant la section Villosa, morphologiquemen se caractérisent par des fruits ayant des canalicules claviformes, régulièrement épaissies, mais par différenciation du type Euheracleum, leurs canalicules sont beaucoup plus larges ; quelquefois elles sont aussi larges que les mollécules centrales. Les espèces de cette section ont eu leur développement en Asie mineure, au Caucase et en Crimée. Dans leur extension elles sont aussi liées, principalement aux régions boisées, coïncidant avec les zones montagneuses moyenne et supérieure et atteignant dans sa propagation verticale une altitude allant jusqu'à 2200 m. Notons cependant, qu'en règle générale les espèces de la section Villosa croissant dans les conditions bien moins mésophytes que celles qui se rapportent aux deux premières sections. Ainsi, les pentes pierreuses et rocailleuses, les ébaulements, les versants éclairés des gorges forestières sont les lieux habituels d'habitats des représentants de la section Villosa. Parfois on les trouve sur les versants abrupts méridionaux dénudés fortement ensoleillés. Naturellement, un grand nombre de ces espèces sont considérablement xérophytisées : leur xéromorphisme s'exprime par le développement d'une abondante pubescence, recouvrant fréquemment toute la plante d'un duvet tomenteux complet ; ceci est surtout exprimé de manière particulièrement manifeste sur la face inférieure du limbe. La croissance dans des conditions relativement arides accélère considérablement le cycle de développement de certaines espèces de ce groupe. Ainsi par exemple, H. antasiaticum dans les environs de Tbilissi commence à fleurir au milieu du mois de mai et vers la fin de juin la plante achève déjà son cycle. Par leur importance systématique, les espèce de la section Villosa n'ont pas la même valeur entre elles. L'espèce H. scabrum, croissant dans la partie occidentale du Caucase, où elle occupe une aire de peu d'importance, allant de la région de Krasnodarsk (Mont Lysaïa) jusqu'à Psyrtzkha, doit être considérée comme une relique conservatrice. Par la forme de ses feuilles composées pennées H. scabrum rappelle quelque peu les espèces de la section Euheracleum. C'est justement cette raison qui a servi de prétexte à N. AL'BON, qui a décrit H. scabrum, en comparant cette espèce avec H. asperum. Néanmoins, on doit considérer cette comparaison comme étant purement pour la forme. Nous ne pouvons pas rapprocher *H. scabrum* avec aucune des espèces connues de ce genr Nous avons devant nous une sorte de relique qui, par opposition à la majorité des représentants du genre *Heracleum*, se trouva, en quelque sorte, figé dans ses limites morphologiques et qui occupe actuellement une petite aire nettement relique, sur la surf ce de laquelle il n'est rencontré qu"assez rarement. Tout ce groupe polymorphe complexe d'espèces qui a été placé pour le Caucase et la Crimée sous un nom commun d'*H. villosum* constitue un contraste absolu avec cette espèce.

Chez les espèces croissant dans la région du grand Caucase et de ses contreforts septentrionaux, on observe le plus important polymorphisme ; ceci témoigne qu'ici le processus de formation des espèces ne s'est pas encore éteint. AU Petit Cauca ce cycle est représenté par *H. antasiaticum*, espèce plus stable quant à ses caractères. Cette espèce croît essentiellement dans la partie orientale du Petit Caucase ; la crête Konguro-Alangez constitue la limite Est de son extension, aussi bien de toute la section dans son ensemble. Une espèce de la section *Villosa*, *H. steveni* croît en Crimée et les autres en Asie Mineure. Ainsi, depuis Lazistan on connait l'espèce *H. spathyphyllum* croît en Anatolie près de Caïserie et sur l'extrémité occidentale s'Anatolie qui correspond à peu près au territoire de la province antique d Lidie. La dernière espèce de cette section que nous connaissions *H. amanum*, croissant sur le mont Alma-Dag (Amanus) se caractéris par des feuilles composées pennées faiblement duvetées avec de gros segments et présente un type morphologique. Ainsi, la secti *Villosa*, est la branche qui s'est formée dans la Méditerranée orientale et a évolué dans le sens d'une certaine xéromorphie. Le espèces, ayant conservé une structure plus ou moins mésomorphiqu telle que : *H. scabrum*, *H. amanum* sont très conservatrices et occupent actuellement les aires locales étroites.

La section suivante *Wendia* doit être considérée comme une étape plus avancée dans le développement du genre *Heracleum*. Les systèmes montagneux de l'Asie Mineure, du Caucase et de l'Ira du Nord constituaient pour les espèces réunies en section *Wendia*, les lieux de formation spécifique accrue. Les espèces morphologi entrant dans cette section, se caractérisent par la réduction nettement marquée de l'appareil de sécrétion et qui s'exprime par le racourcissement des canalicules dorsales du fruit et par leur oblitération sur la commisure. La tendance à une certaine réduction des canalicules apparaissait aux différents degrés de développemen du genre. Pour le groupe d'espèces très proche, que nous réunisson en section Wendia, la réduction des canalicules est extrêmement caractéristique.

Dans la chaine des espèces proches, composant les sections Wendia, nous pouvons distinguer des maillons anciens, dont les espèces sont rattachées aux sociétés forestières mésophyles. H. choradanum et H. pastinacifolium, et très probablement H. anisactis en font partie. La première d'entre elles possède une aire quelque peu morcelée ; cette espèce croît dans les bois feuillus montagneux de l'Amérique du Nord et se rencontre à nouveau dans le bois qui garnissent les versants de la crête de Zangesur (Congouru Alangez) et dans les forêts de Karabah. Les plantes atteignent un mètre cinquante de hauteur et leurs feuilles sont de type mésophylle avec des segments foliaires de grande taille. Le port habituel général de H. pastinacifolium le rapproche des espèces de la section Euheracleum. La deuxième espèce H. choradanum possède une aire plus vaste englobant le Pré-Caucase et la Transcasie Oriental et Méridionale. Cette espèce croît dans la zone moyenne, quelquefo dans la zone supérieure montagneuse sur les lisières des bois, sur les clairières, le long des routes et chemins forestiers, dans les broussailles, les buissons. L'espèce H. anisactis est proche d'H. pastinacifolium, elle croît en Iran du Nord. Les autres espèces caucasiennes de cette section : H. transcaucasicum, H. albovii et H. schelkovnikovii forment un groupe plus progressif, et apparemment plus jeune. Les prés subalpestres constituent des stations habituelles de certaines d'entre elles, d'autres espèces coïnciden avec la zone alpestre supérieure ou moyenne, où elles croissent dans les crevasses des rochers, sur des terrains pierreux et des éboulements.

Les espèces largement répandues sur des prés subalpins sont aussi fréquemment rencontrées dans la zone subnivale. Dans ce dernier cas on observe habituellement une certaine différenciation, conduisant à la formation de formes nouvelles, qui se sont adaptées aux conditions modifiées du milieu extérieur. Ainsi, l'espèce H. transcaucasicum, croissant sur les prés subalpins du plateau Arménien, dans la zone subnivale des sommets volcaniques d'Agmagan, et d'Aragatz (Tlagez), sur les terrains rocailleux "chingil", est représentée par la forme grandiflore H. transcaucasicum var. grandiflorum. L'espèce H. roseum, largement répandue sur les prés subalpins de l'Ossétie Méridionale et de Mtiuletie, sur les éboulements caillouteux de la zone subnivale est représentée par une variété particulière H. roseum var. schistosum.

Toutes les espèces caucasiennes de la section Wendia sauf H. chorodanum et H. roseum sont rattachées au Petit Caucase Les espèces proches occupent fréquemment les aires isolées, en îlot en quelque sorte dans les systèmes montagneux de l'Asie Mineure et du Nord-Ouest de la Syrie. Ainsi, H. incanum croît sur le plateau d'Anatolie Orientale dans le système de Bingel-Daga, alors qu'en Anatolie intérieure dans la zone alpestre du massif d'Erdjisch croît l'espèce H. argaeum. L'espèce H. humile occupe une aire relativement étendue ; elle est rencontrée aussi bien en Anatolie Nord-Ouest, dans le massif Uen-Dag que dans le Sud surle territoire correspondant aux provinces antiques de Pisidie, de Lycaonie et de Cataonie ; cette dernière espèce est aussi indiquée pour la Livanie. La présence des relations apparentes indubitables entre les espèces oréophytisées, de la section Wendia especes parfois géographiquement fortement séparées, ne peut être expliquée qu par leur origine provenant des types communs à développement inaccoutumé.

Deux espèces vicariantes : H. ligusticifolium, croissant en Crimée et H. Apiifolium au Caucase sont propres à ces pays la première à laCrimée, la deuxième à la Transcaucasie Occidentale et au Lazistan qui, phytogéographiquement, est proche de cette dernière. H. apiifolium, avec toute une série d'autres espèces, caractéristiques pour la Colchiolie pénètre sur le versant nord de la crête principale caucasienne, où elle est rencontrée dans la région de la Réserve Nationale Caucasienne et dans la région de Klukhorsk de la République S. S. Georgienne (Teberday). Au Sud, cette espèce entre dans les limites du Lazistan et du plateau d'Anatolie Orientale les environs de la ville d'Erzeroum. *H. apiifolium* croit dans la zone alpestre sur les prés humides et herbes basses des ruisseaux et des torrents montagneux.

L'espèce endémique de Crimée *H. ligusticifolium* coïncide avec la chaîne principale de Crimée et surtout à ses secteurs les plus élevés (Babougan-iaïla) ; elle croît sur les pentes pierreuses, abruptes, sur les versants rocheux, sur les terrains rocailleux et caillouteux, sur les éboulements. Ces deux espèces proches se caractérisent par des fruits ayant des canalicules ne s'élargissant pas vers l'extrémité inférieure et septées sur toute la longueur, c'est pourquoi elles ressortent, en quelque sorte, du cadre de l'étendue que nous adoptons pour le genre *Heracleum*. Par la structure du fruit elles se rapprochent du genre *Pastinaca* parent proche de *Heracleum*, alors que par la structure de la fleur ce sont des berces typiques. Nous réunissons ces deux espèces : *H. apiifolium* et *H. ligusticifolium* en une section spéciale *Apiifolia*. Il se peut que plus tard,,lorsque la systématique des genres entrant dans la tribu *Pastinaceae* et en premier lieu du genre *Pastinaca* sera étudiée plus en détail ; il serait possible de considérer ce groupe en tant que genre oligotypique.

H. minimum, croissant dans les Alpes Occidentales (Dauphiné) dans la zone alpestre, sur les éboulements mouvants pierreux, constitue l'espèce la plus isolée morphologiquement, d'autres espèces du genre *Heracleum*, propres à l'Europe. Cette espèce se caractérise par les dimensions peu importantes de toute la plante et par des feuilles disséquées d'une manière très caractéristique, en petites lobules triangulaires. Les canalicules dans les fruits sont très étroits, filiformes, de longueur différente et ne sont pas toujours apparentes. Cette espèce oréophyte originale a été, à juste titre isolée en une section spéciale *Vocontia* (Calest) Thell.

II

En faisant apprécier le rôle du centre floristique caucasien, il convient de s'arrêter sur certaines particularités de répartition géographiques des espèces qui reflètent les phénomènes généraux du développement de la flore du Caucase.

L'attraction de la section ancienne *Euheracleum* vers la région relique Colchidienne attire avant tout l'attention. Ce phénomène est observé de manière particulièrement manifeste, apparente au Petit Caucase, où la ligne extrême est de la propagation des espèces de la section *Euheracleum* passe pour la région~~n~~ de Barjoni-Bacouriansk, qui se trouve sous une forte influence de la province floristique Colchidienne. Notons à ce propos qu'au Caucase les espèces de la section *Euheracleum* en aucun cas ne peuvent être rattachées au nombre des endémiques conservateurs en état de disparition car ici elles sont représentées par de petites espèces progressives. Certaines espèces, comme *H. colchicum* et *H. calcareum* coïncident avec les moraines et les éboulements de la zone alpestre. Ce sont des espèces relativement jeunes, dont la formation doit, sans doute, être rapportée ~~de~~ à la période ~~du~~ holocène. Au stade actuel du développement, *H. colchicum* est très polymorphe et la diversité qui apparaît entre les formes, propres aussi bien à la partie occidentale qu'à la partie orientale de l'aire de l'espèce, indique ses caractères progressifs. Ainsi, le genre *Heracleum* multiplie le nombre des exemples cités par A. A. GROSSHEIM d'endémisme progressif jeune, propre aux espèces de la région relique colchidienne. Il faut souligner également la richesse et la diversité des espèces du genre *Heracleum*, croissant en Colchidie et la pauvreté extraordinaire, qui met en évidence le contraste à l'autre centre relique, celui de Talysch, dans la flore duquel nous trouvons une seule espèce de ce genre, *H. trachyloma* appartenant à la section *Pubescentia*. Ainsi le genre *Heracleum* se rapporte au nombre des types tertiaires inhabituels, largement représentés en Colchidie et absents dans la flore relique de Talysch, tels que :

- *Castanea*, *Staphylea*, *Philadelphus*, *Paris*, *Helleboru*

A. L. TAKHTADJIAN (1946) est porté à attribuer ce phénomène aux conditions climatiques arides des périodes *interpluviales*. Cependant selon toute apparence, on doit chercher l'explication dans les causes historiques, c'est-à-dire dans l'isolement des deux centre floristiques qui a lieu au cours de la période tertiaire, centre Colchidien et celui de Hirkansk. Dans ses travaux A. A. GROSSHEIM (1926, 1936, 1948) a, à plusieurs reprises, attiré l'attention sur ce fait.

Les représentatnts des différents grapes, d'après la génèse, se développent dans la zone alpestre aux lieux d'habitat des ébaulements et des rocs, se sont transformés en formes oréophytes, formes parfois possédant les organes végétatifs d'une structure analogue et qui créaient une ressemblance habituelle considérable entre les espèces de parenté lointaine. En tant qu'exemple sepctaculaire d'une telle convergence on peut nommer *H. ossethicum*, manifesttant une ressemblance avec certaines espèces oréophytes de la section *Wendia*, telles que :

- *H. schelkovnikovii*, *H. albovii*, *H. humile*.

III

Le genre *Heracleum*, dans sa répartition, est lié essentiellement avec la végétation latifoliée de la zone tempérée de l'hémisphère boréal. Dans la flore actuelle, il se présente comme une des reliques de la végétation forestière tertiaire et partage ainsi le sort de nombreux genres inhabituels, qui sont arrivés jusqu'à nous dans leurs anciens types, dans les îlots laisés de la végétation latifoliée. L'étude de la systématique du genre montre que le noeud complexe de son évolution s'est noué sur le territoi de l'Asie Orientale? Le rôle remarquable qu'a jué dans la formatio du genre *Heracleum* le centre floristique de l'Asie Orientale n'est nullement le fait du hasard. Ainsi qu'il a été établi en ce qui concerne toute une série de genres, l'Asie Orientale constitue l'un des plus considérables centres de développement de la flore forestière mésophylle, aussi bien dans la partie de ses représentants ligneux que de plantes herbacées cénotiquement liées avec eux. Le rôle de l'Asie Orientale dans le formation des flores tempérées du continent de l'Eurasie a été éclairé par les travaux classiques de V. L. KOMAROV. En relation successive avec les opinions exprimées par KOMAROV, se trouve les travaux de V. P. MALEEV "Reliques tertiaires dans la flore du Caucase Occidental", dans lesquels l'auteur différencie le complexe reliquo-tertiaire du Caucase oriental en groupes de stade différent et en groupes génétiquement différents. Dans la flore forestière mésophylle du type de "Tourgaïsk", qui s'est formée sur le territoire du continent d'ancien Angara, le dit auteur différencie deux branches :

- celle d'Angaride Sud, dont le développement et l'émigration se sont produits dans la partie méridionale de l'Angaride Sud, et la branche d'Angaride Nord, liée avec les parties plus septentrionales de l'Angaride. D'après V. P. MALEEV, les éléments de la flore d'Angaride méridionale ne peuvent fréquemment être délimités avec une netteté suffisante des éléments de la flore subtropicale, alors que la branche nordique manifeste fréquemment les relations génétiques avec la même flore du type indo-malayen. Le genre Heracleum que nous avons étudié peut servir comme un des exemples du genre angaride, ayant de profondes relations avec la flore tropicale. Originaire de cette flore, ce genre a trouvé au début de son existence des conditions plus ou moins favorables pour l'évolution ultérieure sur le territoire du développement de la flore angaridienne. C'est justement ici, dans les forêts de hautes montagnes, dans les broussailles des hautes herbes que pouvait prendre naissance le type morphologique qui s'est transformé en genre Heracleum. Ce genre au cours du processus du développement progressif pendnnt la période tertiaire s'est enrichi d'un grand nombre d'espèces et propagé sur des vastes étendues de l'Eurasie.

Le destin historique de ces deux genres proches : Tordyliopsis, genre plus ancien et Heracleum, genre plus jeune et apparemment plus spécialisé, n'est pas le même. Dans la première partie de ces travaux l'aire générale occupée par le genre Tordyliopsis a été décrit de manière suffisamment détaillée.

Comme on peut le voir, cette aire est quelque peu morcelée. Lors d'une analyse plus proche de l'aire, une concentratio élevée des espèces dans la partie orientale, c'est-à-dire en Indostan et en Hymalaya attire l'attention, a lors que dans la direction de l'Ouest, on constate une brusque diminution du nombre des espèces et la diversité spécifique en état de disparition. Ces données nous font supposer que les espèces du genre Tordyliopsis pénétraient vers l'Ouest par les crêtes des montagnes qui bordent l'Angaride méridionale.

La pénétration du noyau de genre Tordyliopsis vers l'Ouest doit être rapportée vers le début du néogène, car l'assèchement de la partie Est de Tetis dans le miocène, entraînant l'aridisation considérable du climat, devrait interrompre relativement tôt la migration des éléments forestiers mésophylles.

Le genre Heracleum a obtenu la propagation dans des latitudes beaucoup plus élevées. Dans le système des Himalaya où vers le sud de la barrière himalayen, les espèces se rapportant à ce genre ne sont plus du tout rencontrées. Naturellement, il faut chercher pour ce groupe d'espèces une voie plus nordique de migration. Compte tenu du milieu ambiant cénologique, dans lequel pouvait se développer ce genre, on doit supposer que la distribution et toute l'histoire suivante de son développement sont liées au sort des forêts pliocènes de l'Eurasie. Etant devenu l'un des composants de la flore angaridienne, le genre Heracleum a parcouru, un long chemin évolutif, dont la diversité des types morphologiques, qui est manifestée par les espèces arrivées à nos jours, en témoigne. Comme l'a montrée l'étude du matériel réel dans les refuges de la flore relique tertiaire les centres secondaires importants se sont créés. Le rôle des centres floristiques caucasien et de l'Asie Antérieure se présente comme étant particulièrement important. Dans le nouveau milieu ambiant écologique se sont développés ici les types originaux lesquels au cours de processus de l'évolution ultérieur ont abouti à la formation des espèces réunies en sections Pubescentia, Villosa et

Wendia. Ainsi, le développement du genre Heracleum suivait des voies différentes, mais en dehors de la ligne mésophyte principale, les sens de l'évolution xérophyte et criophyte du genre se sont nettement tracées.