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Morphological diversity and taxonomy of the *Pimpinella tragium* VILL. group (Umbelliferae – Apioideae) in the Mediterranean

With 11 Figures, 3 Maps and 4 Tables

Summary

Variability of morphological characters in *Pimpinella tragium* VILL. group was investigated using herbarium material natural populations field sampling and cultivated plants. As a result of anatomical and morphological research, and by means of Principal Component Analysis and Canonical Variance Analysis, two polymorphic species were distinguished – *P. tragium* VILL. with hairs 0.05–0.2 mm long and *P. polyclada* BOISS. & HELDR. with hairs 0.3–1 mm long. Both polymorphic taxa include forms differing in density of pubescence and leaf dissection. Distribution of pinnatisect and bipinnatisect leaf forms over the range corresponds to the pattern of summer precipitation and duration of the drought period. In *P. tragium* several ecotypes could be distinguished, differing in leaf shape and structure, life history and development rhythm. However, recognition of infraspecific taxa is inexpedient and can misrepresent the complicated pattern of morphological variability within *P. tragium* VILL.

Zusammenfassung

Aufgrund der Untersuchung von Herbarmaterial, der Stichprobenanlyse an natürlichen Populationen und kultivierten Exemplaren wurde die Variabilität morphologischer Merkmale bei *Pimpinella tragium* VILL. erforscht. Auf der Basis anatomischer und morphologischer Studien und unter Verwendung verschiedener Methoden zur Analyse der Variabilität sind zwei polymorphe Arten – *P. tragium* VILL. mit einer Länge der Behaarung von 0,05–0,2 mm und *P. polyclada* BOISS. & HELDR. mit einer solchen von 0,3–1 mm – zu unterscheiden. Die beiden polymorphen Taxa schließen Formen mit verschiedener Behaarungsdichte und Blattgliederung ein. Die Verteilung der Formen mit fiederförmigen und doppeltfiederförmigen Blättern im Areal entspricht der sommerlichen Niederschlagsmenge und der Dauer der Trockenperiode. Bei *P. tragium* sind mehrere Ökotypen zu beobachten, die sich durch Form und Struktur ihrer Blätter und Besonderheiten in Ontogenese und Entwicklungsrhythmus voneinander unterscheiden. Die formelle Ausgliederung von infraspezifischen Taxa ist jedoch noch nicht zweckmäßig, da die morphologische Variabilität von *P. tragium* dadurch verwischt wird.

Introduction

Pimpinella tragium VILL. is a widespread complex of species with great morphological variability and confused taxonomy. It is distributed in the Mediterranean from Spain to Lebanon, in North-West Africa, Asia Minor, the Caucasus, the Central Kopet-Dagh and in the South of the East European Plain.

Most taxonomists (BOISSIER 1872; HALÁCSY 1901; WOLFF 1927) considered *P. tragium* VILL. to be a polymorphic species with several varieties, some widespread over the range of *P. tragium*, and others are restricted in their distribution. Nevertheless some hardly distinguishable races from Russia and neighbouring territories have been treated until now as species (SCHISCHKIN 1950a, b; PIMENOV & TIKHOMIROV 1981, 1995). SCHISCHKIN recognized nine species, differing in leaf blade dissection, umbel ray number, hair density, fruit size and stylodium length, characters used to characterize varieties of *P. tragium* in Europe. He did not take into account variability of the characters and transitional forms, so the species identification has been a great problem.

TUTIN (1968a, b), MATTHEWS (1972) and ENGSTRAND (1987) treated some morphological forms of *P. tragium* as subspecies with partly overlapping distribution areas. They distinguished subsp. *lithophila* (SCHISCHK.) TUTIN from Southern Europe, the Crimea, Turkey and Iran; subsp. *depressa* (SIEBER ex SPRENG.) TUTIN from Crete; subsp. *pseudotragium* (DC.) MATTHEWS from Turkey, Iran, Armenia and Iraq; subsp. *titanophila* (WORONOW) TUTIN from East Europe and subsp. *polyclada* (BOISS. & HELDR.) TUTIN from the Balkans and Asia Minor.

Every taxon described in the *P. tragium* group was characterized by several features, each representing only a small part of general range of values observed in this group. The broad morphological variation of some taxa and transitional forms among them has complicated the taxonomy of this polymorphic group, making the taxonomic rank and relations of the intraspecific taxa uncertain.

The aims of our research were 1) to estimate morphological variability in the *P. tragium* group, 2) to throw light in differentiation trends in *P. tragium* and 3) to make new taxonomic proposals.

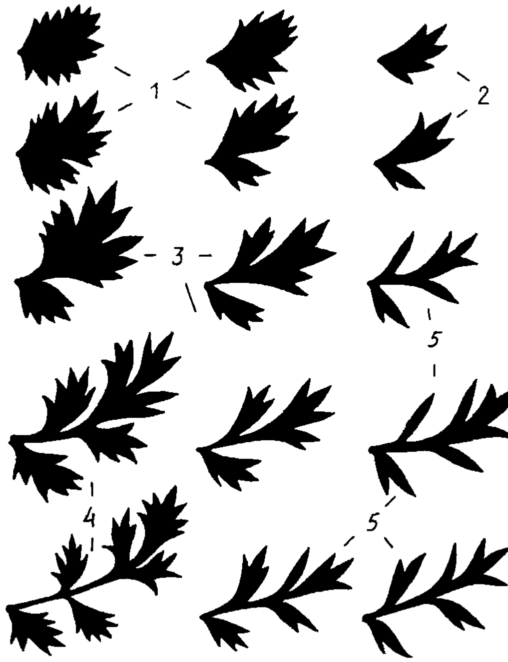


Fig. 1
Segment types of rosette leaves in *P. tragium* group

Material and methods

We studied about 2000 specimens from 20 herbaria (B, BAK, BM, DNZ, E, ERE, G, GAL, K, KW, LE, M, MHA, MPU, MW, SO, SOM, TBI, W, YALT) and more than 1500 specimens from 23 natural populations from Asia, the Caucasus, the Crimea, Bulgaria and the East European Plain.

We determined leaf shape and its degree of dissection using the second lateral segment from the base in a mature rosette leaf. To describe the diversity of segment dissection, we reduced all cases to a few types, ascribing them numbers from 1 to 5 (Fig. 1). The greater the degree of dissection the bigger the number.

For each of the specimens 15 characters previously used as diagnostic have been scored:

1. Segment type of adult rosette leaf:
   1 – unequally serrate-incised segment with numerous teeth in the margin;
   2 – pinnatifid segment with 5–6 lacinulas or teeth;
   3 – pinnatipartite segment with serrate-incised lacinulas and a separate basal lobe;
   4 – pinnatisect segment with numerous serrate lobes or lacinulas;
   5 – deeply pinnatipartite or pinnatisect segment with narrow lacinulas.

2.–5. Hair length (mm) on the lower part of stem (2), on the rosette leaves (3), on the umbel rays (4) and on the fruits (5).

6. – 9. Hair density (in points from 0 to 4) on the lower part of the stem (6), on the rosette leaves (7), on the umbel rays (8) and on the fruits (9):
   0 – absent, 1 – trace, 2 – sparse, 3 – dense, 4 – very dense.

10. Plant height (cm).

11. Average number of umbel rays.

12. Inflorescence branching (from 0 to 3 points): 0 – the main umbel only is present; 1, 2, 3 – paracladia of the 1st, 2nd and 3rd order present, respectively.

13. Fruit length (mm).

14. Fruit width (mm).

15. Stylodium length (mm).

The range of variation and means of most of the characters were analysed in populations and some parts of the range *P. tragium*. To observe variation trends of leaf dissection and hair density over the range, the proportions of plants with particular characteristics were analysed for populations and regions. Distributional patterns of some of the characters were compared with precipitation for three summer months and drought duration (WALTER & LIETH 1966; Reference book on climate of the USSR 1968–1970; WALTER et al. 1975). Multivariate techniques (PCA and CVA) were applied to studies of the character variation in the group using the Biomedical Computer Programs (BMDP 1977) package.

Life history, population diversity and environmental dependence of some of the characters were studied in 10 populations (Table 1) grown in the Botanical Garden of Moscow State University in 1984 to 1986. Leaf form variability was analysed using a sample of 100 specimens. Plant anatomy was studied with the usual techniques at 600×, 900× magnifications. Ultrascopic micrographs were made with the scanning microscopes HSM-2A, HITACHI S-405 a.

Results

Distribution and ecology of the *P. tragium* group

All taxa of the *P. tragium* group are polycarpic perennial herbs with sympodially innovated hemirosette monocarpic shoots, forming many-headed rhizomes.

The preliminary study of herbarium specimens showed that hair length on leaves is the most important diagnostic character, permitting the division of the taxa, whenever recognizable as belonging to the *P. tragium* group, in two subgroups. The first subgroup (*P. tragium* VILL.) comprises the taxa with short, adpressed or squarrose, 1–3-cellular hairs, 0.05–0.2 mm long, on leaves and on the lower part of the stem (Fig. 2a, c; Fig. 3a). The second subgroup (*P. polyclada* BOISS. & HELDR.) includes taxa with 3–5-cellular hairs, 0.3–1 mm long (Fig. 2b, d; Fig. 3c). The races within the subgroups differ in leaf dissection, some having pinnatisect leaves and others bipinnatisect ones.

The shorthaired taxa display various leaf forms. Pinnatisect lowermost leaves are common in the most widespread taxon *P. tragium* var. *tragium* (= *typica* HALÁCSY), which occurs everywhere in the Mediterranean and Asian parts of the *P. tragium* group range. It has also been known as *P. lithophila* SCHISCHK. or *P. tragium* subsp. *lithophila* (SCHISCHK.) TUTIN. Similar plants from Southern France have been known as *P. tragium* var. *canescens* (LOISEL.) POIR.

Table 1
The origin of cultivated samples of *P. tragium* VILL.

No.	Species	Region	Habitat
1	*P. lithophila*	The Crimea, Simferopol, Lekarstvennoye	Sheep's-fescue steppe, northern clay hillsides
2	*P. titanophila*	Donetsk reg. Starobeshevo, Vasyljevka	Sheep's-fescue-thyme steppe on granite
3	*P. titanophila*	Donetsk, Amvrosievka, Blagodatnoye	Grazed feather-grass-sheep's-fescue steppe on limestone
4	*P. titanophila*	Donetsk, Novo-Azov, Khomutovo	Open herb-feather-grass steppe on limestone
5	*P. titanophila*	Saratov	Marl
6	*P. titanophila*	Samara, Zhiguli, Bakhilova Poljana	Limestone talus scree at roadsides
7	*P. titanophila*	Samara, Zhiguli, Strel'naja Gora	In clefts of limestone rocks
8	*P. daghestanica*	Daghestan, Makhachkala, Tarki	In clefts of limestone rocks
9	*P. tomiophylla*	Bashkiria, Ishimbay, m. Tura-Tau	Limestone rocks and screes
10	*P. titanophila*	Lugansk, Melovoje, Streltsovka	Open petrophytic steppe on chalk

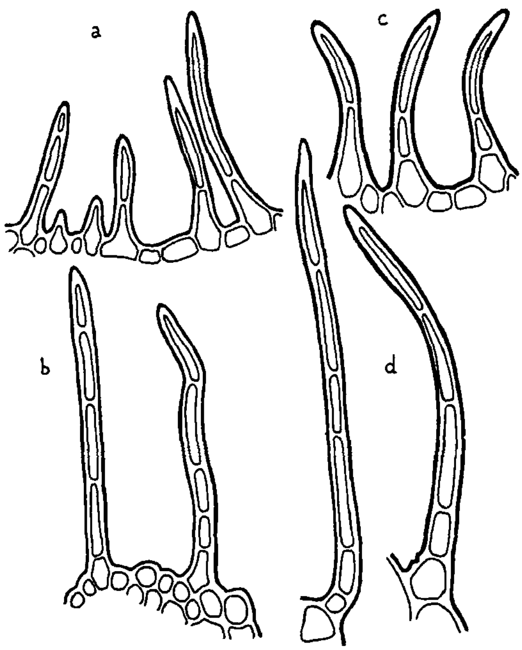


Fig. 2
Hairs on fruits (a, b) and leaves (c, d)
a, c – *P. tragium* VILL.; b, d – *P. polyclada* BOISS. & HELDR.

The shorthaired subgroup includes the largest densely haired *P. tragium* var. *pseudotragium* (DC.) BOISS. from Kurdistan, Iranian Azerbaijan and Armenia, *P. turcomanica* SCHISCHK. and *P. litwinowii* SCHISCHK. from the Kopet-Dagh and similar plants from Algeria and Sicily. It also includes the miniature *P. tragium* var. *depressa* (SIEBER ex SPRENG.) DC. from mountain pastures in Crete and similar plants from the Crimean mountains.

The shorthaired subgroup includes bi-pinnatisect *P. tragium* var. *laciniata* DC., which has been described at species rank under various names: *P. titanophila* WORONOW and *P. tomiophylla* (WORONOW) STANKOV from the East European Plain; *P. idae* TAKHT., *P. daghestanica* SCHISCHK. and *P. grossheimii* SCHISCHK. from the Caucasus. This leaf-form also occurs in the Mediterranean region.

All the above mentioned shorthaired taxa are here included in *P. tragium* VILL., while longhaired plants are treated as *P. polyclada* BOISS. & HELDR. Longhaired plants include *P. tragium* var. *polyclada* (BOISS. & HELDR.) BOISS. and var. *sartorii* (BOISS. & HELDR.) HALÁCSY from the Balkans; *P. tragium* var. *cyprica* (BOISS.) WOLFF from Cyprus; some similar specimens from Asia Minor and Lebanon referred by WOLFF (1927) and MATTHEWS (1972) to *P. tragium* var. *pseudotragium* (DC.) BOISS. All these forms are tall (up to 1 m) with large pinnatisect leaves and serrate-dentate segments. They have bristly-squarrous long hairs on leaves and stems, dense on the lower part of the stem and sparse or absent at the top of the stem. The forms differ mainly in hair density, the Cyprian plants having the highest and var. *sartorii* the lowest.

Shorthaired plants are distributed in the Mediterranean, from Spain and North-East of Africa to Asia Minor, in the Caucasus and the Kopet-Dagh, where they inhabit limestone rocks and screes or open petrophitic steppe and hemishrub communities. In the steppe zone of the East European Plain they grow on exposed and permanently disturbed limestone or chalky hillsides and river banks. Longhaired plants are distributed in the Balkans, Cyprus and Asia Minor on open rocky summits and woody slopes of high mountains (Olympus, Parnassus, Athossus) covered by forests of *Abies nordmaniana, A. cilicica, Cedrus libani, Pinus brutia* and receiving sufficiant precipitation (AKMAN & KETENOGLU 1986; BOTTEMA 1986; GRAZIANSKY 1971; GREBENSHCHIKOV 1957; QUÉZEL 1986).

The distributional areas of both groups overlap in the Eastern Mediterranean, but they prefer different habitats there. Shorthaired plants inhabit permanently disturbed open slopes and limestone rocks at low altitudes or steppe communities in the upper zone of mountain ranges. Longhaired plants on the other hand, grow in more humid conditions under the forest canopy at altitudes from 900 to 1500 (2000) m a. s. l. Correspondingly, they produce different morphological forms there. For example, longhaired plants from wooded slopes in the Pontus and the Taurus ranges in Asia Minor have mesomorphic, densely pubescent, pinnatisect leaves with large segments, 2–6 cm in diameter (Amasya, *J. BORNMÜLLER*, no. *372, 2214;* Kastamonu: Tossia, *P. SINTENIS* no. *4800*; Karaman, Oyklu Dag, *P. DAVIS* no. *16168).* In the same regions shorthaired plants inhabit open rocky summits with steppe or hemi shrub communities and have xeromorphic

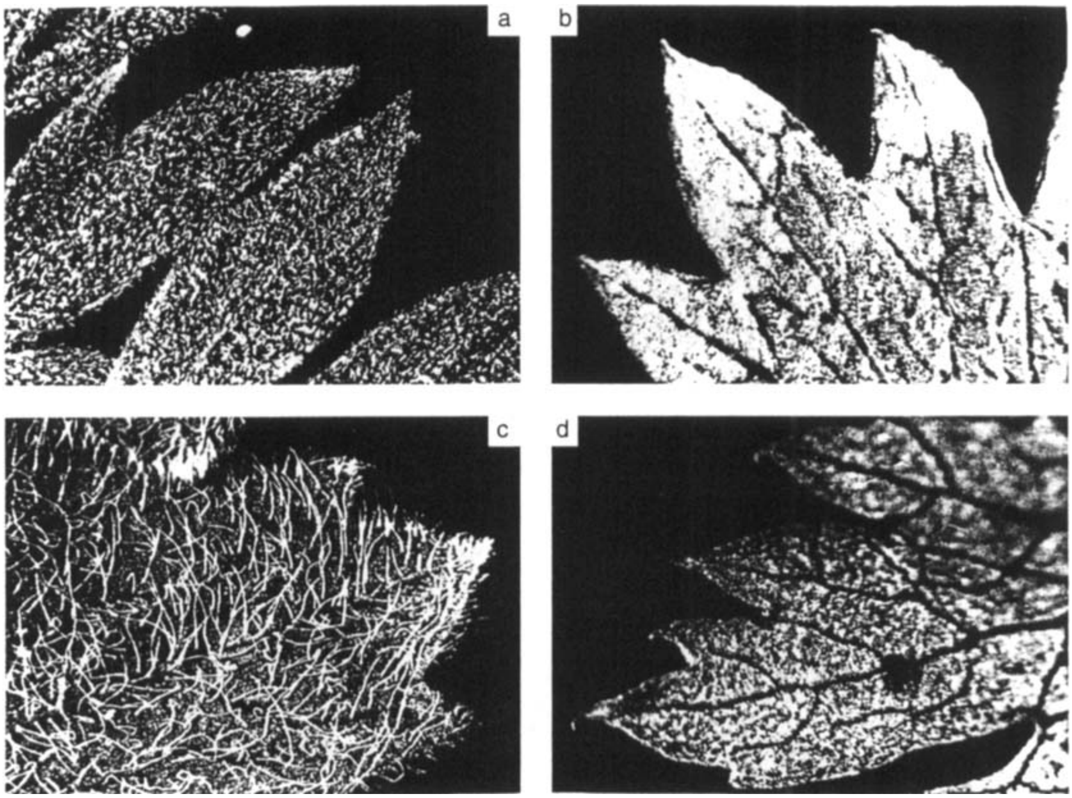


Fig. 3
Pubescence on leaves of *P. tragium* VILL. (a, b) and *P. polyclada* BOISS. & HELDR. (c, d)
a – Russia, Charkov, Volchansk *(P. titanophila)*, b – France, Var, Montrieux *(P. tragium)*; c – Turkey, Amasya, *BORNMÜLLER* no. *2214 (P. polyclada)*;, d – Greece, Parnassus, *SARTORI* no. *67 (P. sartorii)*

bipinnatisect leaves (Kastamonu: Iljas Dag, *P. DAVIS* et al. no. *38398*; Taurus, *TH. KOTSCHY* nos. *196, 212*). In Albania, Macedonia and Serbia shorthaired plants are absent from the upper mountain zone with abundant moisture. The longhaired plants growing there have large thin leaf blades, unusually bipinnatisect and sparsely pubescent. Both groups thus include pinnatisect and bipinnatisect leaf forms, but the longhaired plants look more mesomorphic than *P. tragium*.

Morphology and anatomy of the *P. tragium* group

A comparative study of shorthaired and longhaired plants showed similar structure of the petals, stem, petiole, roots and rhizome, and some diversity in morphology and anatomy of leaf blade and fruits.

Leaf blade anatomy

Shorthaired plants from the Mediterranean, Asian and Caucasian regions with a semiarid Mediterranean climate have rather mesomorphic pinnatisect leaves appearing in spring. The plants of northern shaded slopes have dorsiventral blades with a 1-layered palisade mesophyll and stomata mainly on the lower surface (Fig. 4a), while those of open rocky slopes have isobilateral blades with 1–2 layers of palisade mesophyll and numerous stomata on both surfaces. In more humid regions with a longer growing season (Talysh) the plants possess pinnatisect or bipinnatisect leaves with

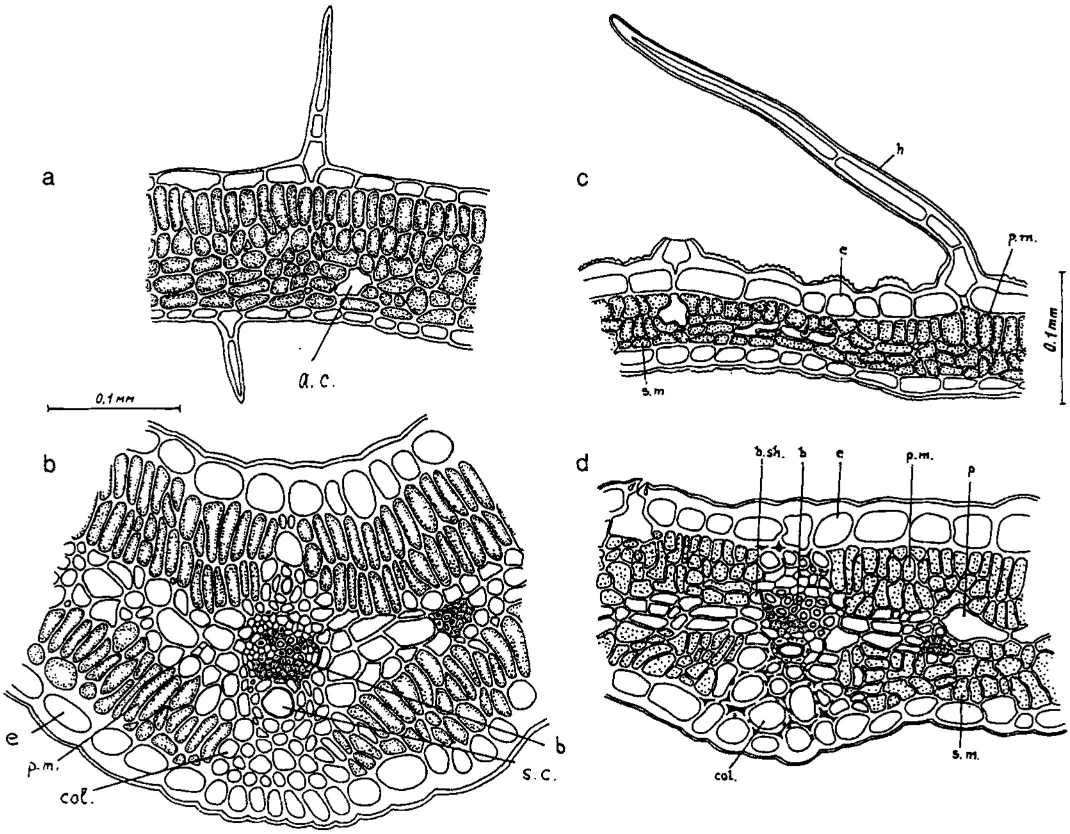


Fig. 4
Leaf anatomical structure of *P. tragium* VILL. (a, b) and *P. polyclada* BOISS. & HELDR. (c, d) in a transverse section

a – *P. turcomanica* SCHISCHK., Turkmenistan, the Kopet-Dagh; b – *P. titanophila* WORONOW, Russia, Lugansk reg., Melovoye distr., Streltsovka; c – Turkey, Amasya, Logman; d – Greece, Olympus
a. c. – air cavity; b – bundle; b. sh. – bundle sheat; col – collenchyma; e – epidermis; h – hair; p – parenchyma carrying water; p. m. – palisade mesophyll; s. m. – spongy mesophyll; s. c. – secretory canal

a 1-layered palisade mesophyll protected by a higher thickwalled epidermis, or with thinwalled and densely pubescent epidermis.

More xeromorphic leaves are common in plants of open limestone and chalk slopes in East Europe and Daghestan with a continental climate. They have bi- or tripinnatisect leaves with the narrowest lacinulae (Fig. 4b), lasting all summer. The thick leaf blade consists of 4–6 compact layers of palisade mesophyll subdivided by parenchyma carrying water and surrounding the vascular bundles. The most thickwalled epidermis has power cuticle, very sparse trichomes and numerous stomata on both surfaces.

Similar variants of leaf structure are found in longhaired plants with pinnatisect leaves. The specimens from wooded slopes have thin dorsiventral blades with 1 layer of palisade mesophyll, 2–3 layers of spongy mesophyll, stomata mainly on the lower surface, thickwalled epidermis and power cuticle (Fig. 4c). Plants from open limestone rocks have thick dorsiventral or nearly isobilateral blades with watercarrying parenchyma between the many layered palisade and the spongy mesophyll. The large epidermal cells have thick outer walls, thick cuticle and stomata on both surfaces (Fig. 4d). Longhaired specimens from alpine meadows in Albania and Serbia have sparsely haired mesomorphic bipinnatisect leaves. So both groups include similar variants of leaf structure corresponding to light and humidity conditions.

Fruits

As some taxa of *P. tragium* did not differ in fruit morphology and anatomy (AKSENOV & TIKHOMIROV 1972) we studied fruits of 35 specimens from the Mediterranean, Asia and East Europe. Both groups have ovate or oblong-ovate mericarps, semicircular with filiform inconspicuous ribs and a flat commissure in transverse section (Fig. 5). Stylopodia are cushion-shaped or semiconical, 0.15–0.40 mm long and 0.2–0.5 mm wide, narrowed into glabrous (rarely pubescent in densely haired fruits) stylodia 0.6–2.5 mm long.

Shorthaired plants *(P. tragium)* have mericarps 1.5–3.5 × 0.9–1.5 mm covered by 3–5-cellular erect or curved hairs 20 – 300 µm long (Fig. 5a, b, c). They contain 3–6 secretory canals in each dorsal vallecula, 2–6 commissural secretory canals and solitary extrafascicular ones in the ribs, the latter sometimes obliterated.

Longhaired plants *(P. polyclada)* have larger mericarps 2.5–3.5 × 1.5–1.7 mm covered by 3–5-cellular hairs 200 – 300 µm long. They contain 6–8 vallecular secretory canals, 2–6 commissural ones and solitary extrafascicular canals, all of them larger than in shorthaired plants (Fig. 5d).

The ultrasculpture of the fruit and hair surface reported before for a single specimen of *P. tragium* (ZIVKOVIC 1982) is the same in four shorthaired specimens from the Crimea, Daghestan, Armenia and Bashkiria and in two longhaired ones from Turkey and Macedonia (Fig. 6a, c, e). The epidermal cuticle has microfolds 3–4 wide alternating with equal furrows. The hairs 20–30 µm in diameter are linear, straight or curved, gradually acuminate, rounded or flattened when dried, with a smooth base and warty free end. Smooth round, oval or

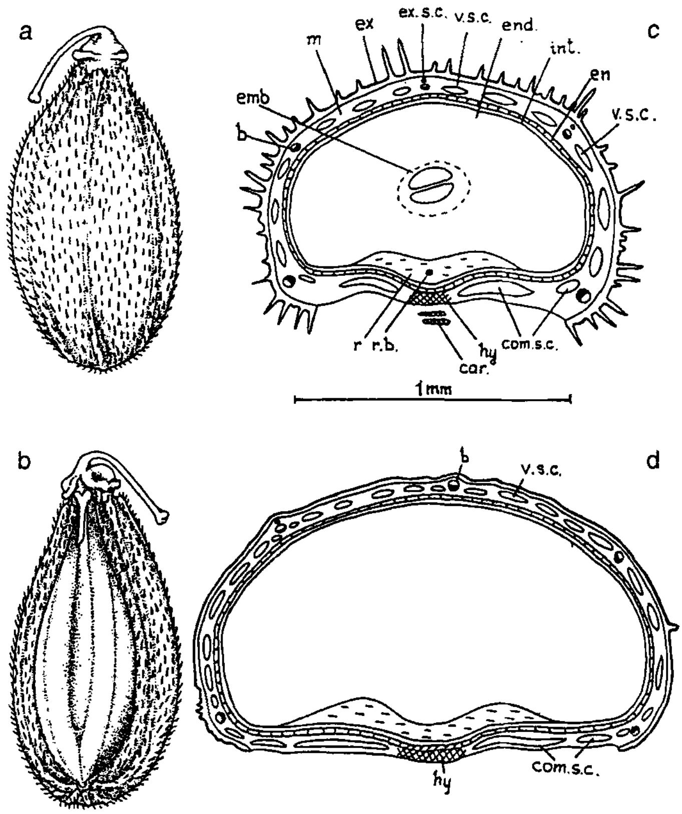


Fig. 5
Fruit and mericarps of *P. tragium* VILL. (a, b, c) and *P. polyclada* BOISS. & HELDR. (d) in a transverse section

b – bundle; com. s.c. – commissural secretory canal; emb – embryo; en – endocarp; end – endosperm; ex – exocarp; ex. s. c. – extrafascicular secretory canal; hy – hydrocytes; int – integumentum; m – mesocarp; r – raphe; r. b. – raphe bundle; v. s. c. – vallecular secretory canal

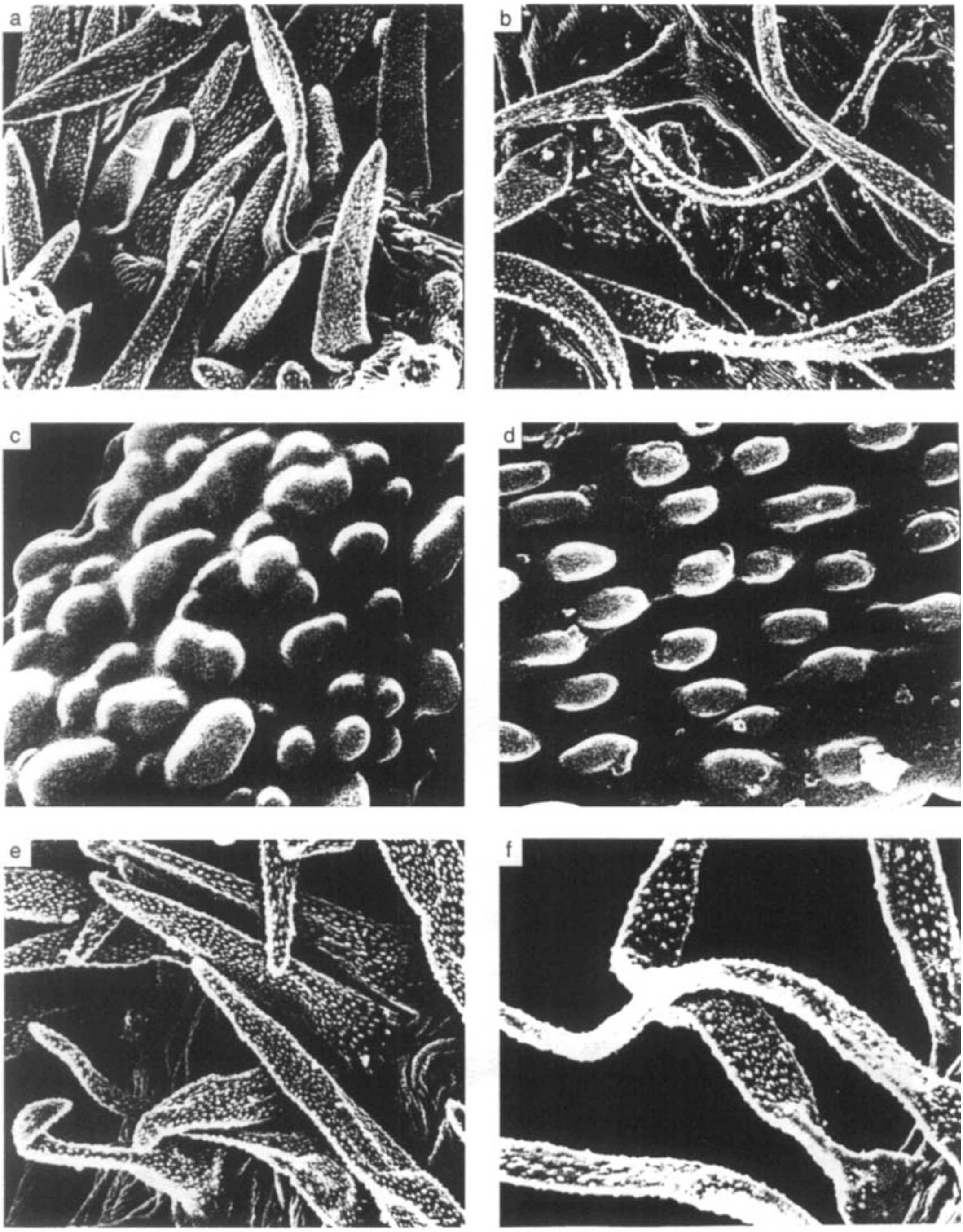


Fig. 6
The ultrasculpture of hairs and epidermal cells on fruits (a, c, e) and leaves (b, d, f)
a, b, c, d, – *P. pseudotragium* DC., Kurdistan, *KOTSCHY* no. *344*; e – *P. polyclada* BOISS. & HELDR., Greece, Athossus, *TH. PICHLER*; f – *P. polyclada* BOISS. & HELDR., Turkey, Amasya, *BORNMÜLLER* no. *2214*. Magn. ×300, ×5000

oblong warts 2–3 × 1.5–2 μm apart from 1–2 diameter distance. A similar structure is observed on leaves of both groups (Fig. 6b, d, f).

Longhaired and shorthaired plants slightly differ in mericarp size, the number of vallecular canals and hair length, but the taxa within each group have very similar fruit morphology and anatomy.

Chromosome numbers

Various chromosome numbers have been reported for shorthaired *P. tragium*: $2n = 18$ from Spain (GARDÉ & M.-GARDÉ 1949) and the Crimea (ROSTOVTSEVA 1982; SZ.-BORSOS 1970), $2n = 22$ from Bulgaria (LÖVE 1978), $2n = 20$ from Italy (GARBARI et al. 1980) and Turkmenia (VASILJEVA 1981). In 24 specimens of *P. tragium* from East Europe, Daghestan and Turkmenia, two somatic chromosome numbers ($2n = 18, 20$) were detected (YURTSEVA 1988). $2n = 20$ has been reported for longhaired race from Greece (LÖVE 1981).

Life history and leaf shape transformation in shorthaired *P. tragium* VILL.

The life history of shorthaired plants was studied in 10 experimental populations in the garden (Table 1) and in nature. The seeds of plants from the Crimea and Daghestan disperse in August–September, from the East European Plain in September–October. The seeds germinate after stratification at the end of April for 12–15 days (southerns races) or 30 days (northern races).

A pronounced heterophylly usual for *Pimpinella* appears clearly in some *P. tragium* races and moderately in others. Growing more dissecting during the life history, the leaves of mature plants are dissected to various degrees, resulting in a great diversity of leaf forms in populations.

Comparing leaf series typical for populations (Fig. 7) we can see the population differences increase with the appearance of new rosette leaves, more dissected in some plants,

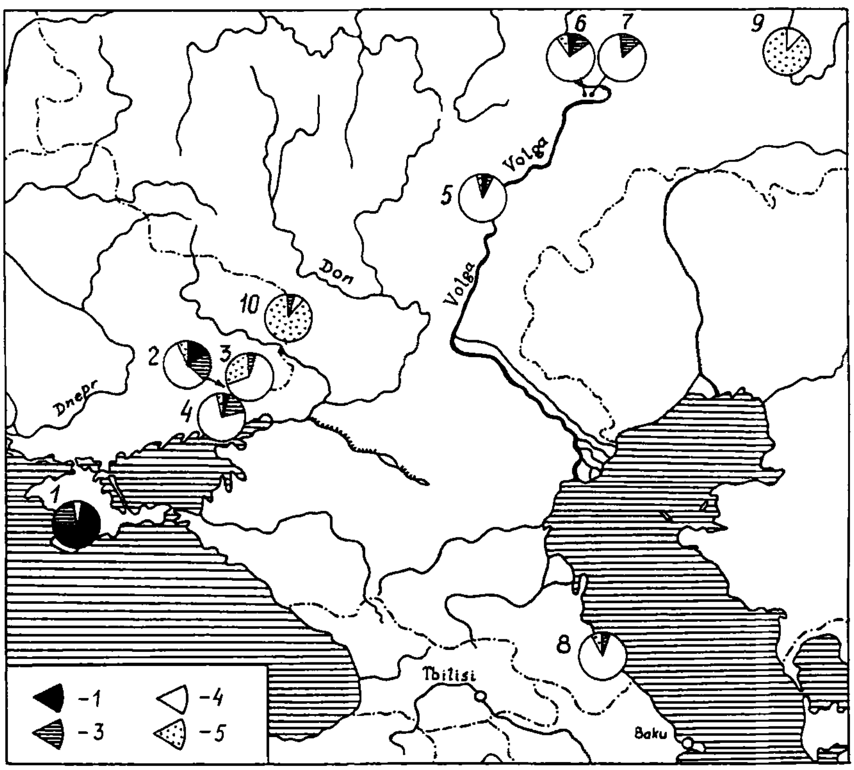
Fig. 7
Leaf series of *P. tragium* VILL.
a – *P. lithophila* SCHISCHK., the Crimea, Simferopol distr., Lekarstvennoye; b – *P. titanophila* WORONOW, Russia, Zhiguli, Bakhilova Poljana; c – *P. titanophila*, Russia, Lugansk reg., Melovoye distr., Streltsovka; d – *P. tomiophylla* (WORONOW) STANKOV, Russia, Bashkiria, Ishimbay distr., Tura-Tau

less in others. The proportion of plants with various segment types in ten populations are shown in Map 1.

The seedlings from the Crimea, Daghestan and the south of the East European Plain had cotyledons 1–1.5 mm width and 4–8 long petiolate leaves with deeply serrate-incised or dissected laminas. The succeeding rosette leaves of the Crimean plants were pinnatisect with 1–4 pairs of serrate-incised segments (Fig. 7a). By the end of the first season most of the Crimean plants had pinnatisect leaves, while a quarter of plants developed bipinnatisect or transitional ones (Map 1: 1).

Ukrainian and Daghestanic plants developed finally bi- or tripinnatisect leaves (Fig. 7b, c; Map 1: 2–8), rarely pinnatisect ones. The plants from northern limestone outcrops of the Eastern European Plain had seedlings with the narrowest seed-lobes, 0.5–0.9 mm width, small first leaves with 3–5-angular laminas followed by 2–3-pinnatisect leaves with narrow linear lacinulae (Fig. 7d). Occurring in many Ukrainian populations, this leaf form predominated in the Central Russian Upland and Bashkiria (Map 1: 9, 10), being more adaptable to strong light and air drought, sharp temperature fluctuations and winds on open chalky and limestone slopes. Leaf xeromorphy increased in hemirosette shoots of shorthaired races, appearing earlier in the life history of northern chalky plants.

Although the Crimean and Bashkirian plants differed significantly in leaf shape, a complete series of transitional populations united the extreme forms. The proportion of plants with xeromorphic leaves and narrow lacinulas rose from the South to the North across the East European Plain. This trend an be explained by the facts that plants from the petrophytic steppe communities in the South had been



Map 1
The proportion of plants with various segment types in 10 populations of *P. tragium* VILL. by the end of the first season of cultivation. The origin of samples see Table 1, segment types see Fig. 1, p. 480

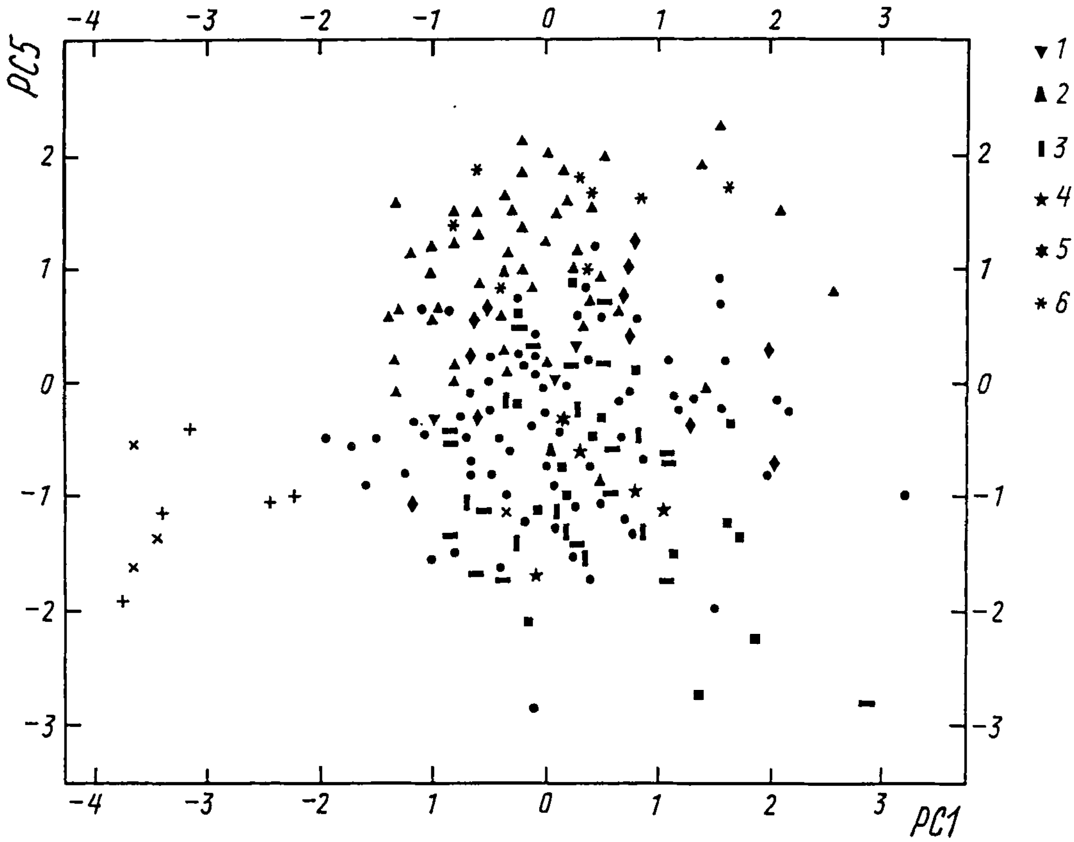


Fig. 8
Principal Component Analysis of *P. tragium* VILL. ($n = 274$)
1 – *P. daghestanica* SCHISCHK.; 2 – *P. idae* TAKHT.; 3 – *P. confusa* WORONOW; 4 – P. *turomanica* SCHISCHK.; 5 – *P. litwinowii* SCHISCHK; 6 – *P. grossheimii* SCHISCHK. The other signs see Fig. 9

forced to migrate to open chalk or limestone outcrops in the North. Appearing already in the seedlings, in mature plants the differences were greater among the populations of southern and northern races.

In cultivation in garden soil all plants passed their life history stages more quickly than on limestone, but preserved the degrees of leaf dissection typical for each race. Innovation shoots appeared from axillary buds of the lowermost leaves in spring or autumn and developed over one or several seasons.

The Crimean plants produced two leaf generations and ceased growth late in the summer. Their spring mesomorphic leaves died off and a new leaf generation appeared in October. In the garden the plants developed as biennials and formed 18–20 reproductive shoots (mono- or dicyclic). In nature they lived 3–5 years and formed 1–3 reproductive shoots. The plants from Armenia and the Kopet-Dagh had a similar developmental rhythm.

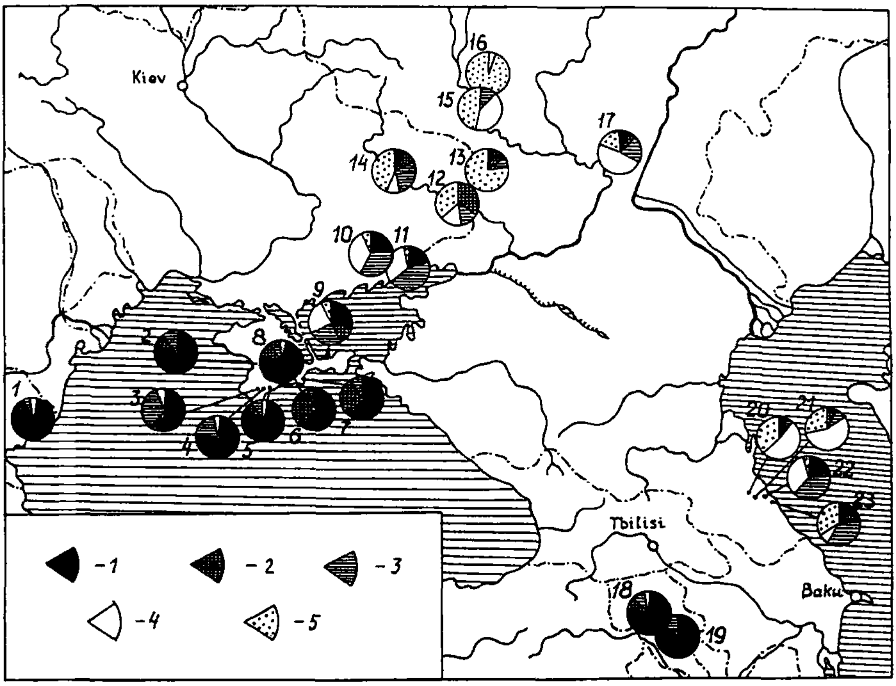
The steppe plants from Southern Ukraine and Daghestan formed di- or tricyclic innovation shoots, rarely monocyclic ones. Most of them started flowering in the second or third year.

Northern plants from limestone outcrops developed more slowly. Their early life history stages lasted many years, the total life time attaining 10–15 or more years. They had di- or polycyclic shoots and some monocyclic ones. They produced annually 1–2 reproductive shoots in nature and 3–10 in culture and many vegetative shoots. Northern races also had two leaf generations, but the xeromorphic leaves lasted throughout the summer.

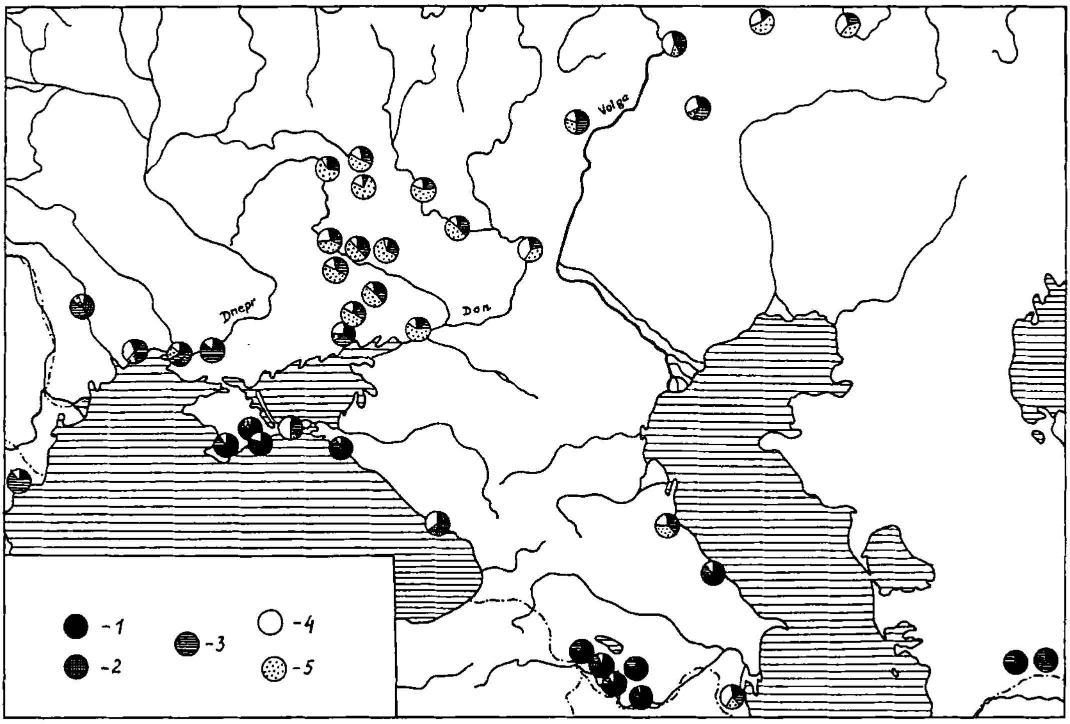
Geographical variations of morphological characters in shorthaired *P. tragium* Vill.

The variability of certain characters has been studied (Yurtseva 1985, 1987) in 23 populations of *P. tragium* from the East European Plain, the Caucasus and the Crimea and in some parts of Russia and neighbouring territories. The reproductive characters such as the number of umbel rays, fruit size and style length varied widely in populations, slightly changing their values over the area. Characters of clear adaptive value such as plant height, degree of leaf dissection, hair length and density varied over the area according to environment.

Leaf dissection. All segment types were found in a majority of populations, but the proportion of each leaf-form varied over the area (Maps 2, 3). Pinnatisect leaves with serrate segments (type 1 in Fig. 1) predominated in the Crimea, Bulgaria, Armenia (Map 2: 1–8, 18, 19), Turkmenistan, Southern Daghestan and occasionally along the Caucasian Black Sea (Map 3). In Northern Daghestan, Abkhasia, Talysh and the East European Plain they did not exceed a quarter or were absent (Map 2: 10–17, 20–23; Map 3). The plant with bipinnatisect leaves (segment types 4 and 5 in Fig. 1) predominated there, increasing in proportion to 90% in chalky hills of the East European Plain (Map 2: 12–17; Map 3). In the Eastern Crimea they rose to a half (Map 2: 9), being rare or absent in the South-West Crimea. The transitional leaf-form (type 3 in Fig. 1)



Map 2
The proportions of plants with various segment types in 23 populations of *P. tragium* Vill.
1 -Bulgaria, Balchik; 2 – The Crimea, Simeferopol distr., Lekarstvennoye; 3 – the Crimea, Sevastopol distr., Baydarskye Vorota; 4 – the Crimea, Yalta distr., Aj-Petri; 5 – the Crimea, Yalta distr., Nikita; 6 – the Crimea, Stary Krym, Agarmysh; 7 – the Crimea, Sudak; 8 – the Crimea, Belogorsk distr., Belaya Skala; 9 – the Crimea, Kazanteep; 10 – Ukraine, Donetsk reg., Volodarskoye distr., Kamenny Mogily; 11 – Ukraine, Donetsk reg., Novo-Azov distr., Khomutovo; 12 – Ukraine, Lugansk reg., Krasny Jar; 13 – Ukraine, Lugansk reg., Melovoye distr., Streltsovka; 14 – Kharkov reg., Jzyum; 15 – Russia, Voronezh reg., Pavlovsk distr., Belogorye; 16 – Russia, Voronezh reg., Bobrov distr., Shestakovo; 17 – Russia, Volgograd reg., Logovsky distr., Syrotinskaya; 18 – Armenia, Ashtarak distr., Lusakert; 19 – Armenia, Abovijan distr., Geghardt; 20 – Daghestan, Bujnaksk distr., Kumtorkali; 21 – Daghestan, Bujnaksk distr., Atly-Bujun; 22 – Daghestan, Makhachkala distr., Tarki; 23 – Daghestan, Bujnaksk distr., Talgi. 1 – 5. The segment types see Fig. 1, p. 480



Map 3
The proportion of plants with various segment types (see Fig. 1) in some parts of *P. tragium* VILL. area

was abundant in Southern Ukraine and on the Black Sea coast (Map 3).

The geographical distribution of plants with variously dissected leaves coincides with the pattern of summer precipitation and duration of summer drought. Plants with dissected leaves predominate in the Mediterranean and Asian parts of the range of *P. tragium* with arid or semiarid Mediterranean climates. Deep and long summer drought during 3–6 months, spring and autumn rains are usual here, while summer precipitation does not exceed 100 mm (AKMAN & KETENOGLU 1986).

Plants with bipinnatisect leaves are common in the East European Plain and in Northern Daghestan which have continental climates. Summer precipitation there reaches 100–200 mm, the drought is not so severe and does not exceed a month, so xeromorphic leaves are still alive in late summer. Similar plants occur also on Mediterranean and Asian regions with subhumid mediterranean climates (AKMAN & KETENOGLU 1986; GROSSHEIM 1948; GULISASCHVILY et al. 1975), where summer drought is anchiorated by humid sea air masses. Such conditions exist on the mountain slopes facing the Mediterranean, Black and Caspian Seas and in Southern France and Northern Spain, Abkhasia, Asia Minor (the Pontus and Taurus), in Talysh and Elburs.

The plants from hot and well-drained limestone and chalky outcrops in the northeast of the *P. tragium* range with a continental climate (the Middle Volga, the Don and Bashkiria) have bipinnatisect leaves, but with the narrowest and the most xeromorphic laniculas.

Pubescence. Hair length and density vary over the *P. tragium* range according to climatic and soil conditions. The most densely long-haired leaves and stems were found in regions with severe summer drought and rather dark soils – in Armenia, Turkmenistan and Southern Ukraine. Hair length and density on leaves was moderate in the Crimea, rose up in Southern Ukraine, then decreased to the North–East across the East European Plain with increasing precipitation. More than a half the plants from the Volga and Bashkiria areas had glabrous leaves. Many plants from the Black Sea coast, Daghestan, Talysh and the Central Kopet-Dagh were glabrous on leaves, uppermost stem and rays. The mean number of hairs in 1 mm² of shade leaves was as 1.5–1.7 times less than in those developed in full sunlight.

Multivariate analysis of *P. tragium* group

Two specimen sets chosen for multivariate analysis included specimens with mature fruits, representing the full range of morphological diversity in the *P. tragium* group over the area. The first set ($n = 274$) comprised shorthaired plants and similar ones with glabrous leaves and stems (Fig. 3a, b). The second set ($n = 325$) included 274 plants of the first set and 51 longhaired and similar glabrescent plants (Fig. 3c, d). All the species were scored for 15 characters (see materials and methods) and were treated by Principal Component Analysis (PCA) and Canonical Variance Analysis (CVA).

Principal Component Analysis

The PCA of the first set ($n = 274$) separated into shorthaired and glabrous specimens (Fig. 8; Table 2) and scattered then along PC 1 and PC 5 according to length and density of hairs and leaf dissection.

The full set ($n = 325$) separated into three groups (Fig. 9). The first comprised plants with hairs 0.1–0.2 mm long and included the taxa of *P. tragium* VILL.: 1 – var. *laciniata* DC. (= *P. titanophila* WORONOW) with bipinnatisect leaves; 2 – var. *tragium* (= *P. lithophila* SCHISCHK.) with pinnatisect leaves; 3 – "intermedia" subgroup transitional between 1 and 2; 4 – var. *depressa* (SIEBER) DC. and 5 – var. *pseudotragium* (DC.) BOISS. non WOLFF (= *P. confusa* SCHISCHK.). The first group looked rather homogeneous. All the "species" of "Flora URSS" (SCHISCHKIN 1950b) fell into it.

The second group included plants with hairs 0.5–1.0 mm long: 7 – var. *polyclada* (BOISS. & HELDR.) BOISS. from the Balkans; 8 – var. *cyprica* (BOISS.) WOLFF from the Cyprus; 9, 10 – the specimens from Lebanon (9) and Asia Minor (10.). The third group included glabrous or glabrescent plants (6) that resemble shorthaired or longhaired ones.

The variables contributing to plant segregation along PC 1 were hair length on leaves, stems and fruits and leaf dissection, along PC 2 – hair density on stems, leaves, umbel rays and hair length on umbel rays (Table 3).

Table 2
Loadings of 15 characters on the first five axes in Principal Component Analysis of *P. tragium* VILL. group. ($n = 274$). The values lower 0.4 are not given. The factors 1–5 accounted for 61.3% of total variation

Characters	Factors				
	PC1	PC2	PC3	PC4	PC5
Hair length on leaves	0.750				
Hair density on leaves	0.697				
Hair length on stems	0.676				
Hair length on rays	0.617				
Hair density on stems	0.607				
Hair density on fruits		0.738			
Hair length on fruits		0.641			
Hair density on rays		0.626			
Rays number			0.809		
Plant height			0.797		
Stylodium length			0.558		
Fruit length				0.877	
Fruit width				0.876	
Leaf dissection					0.687
Branching					0.612
% of total variation	16.82	12.07	12.07	11.66	8.67

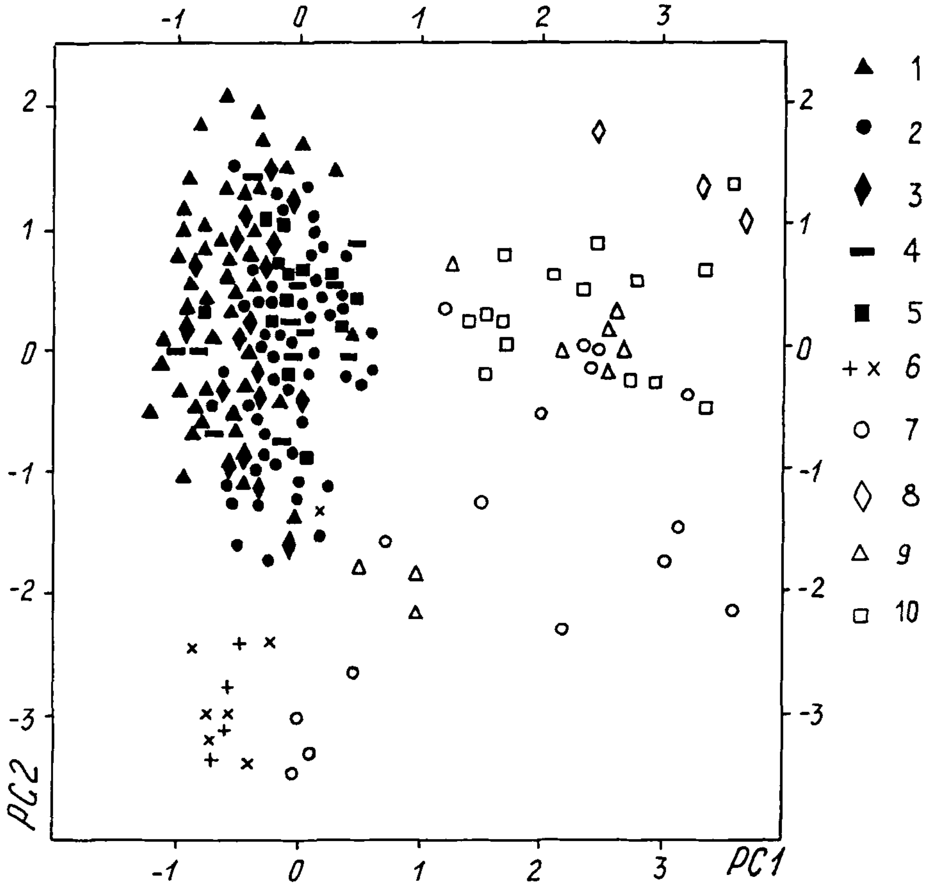


Fig. 9
Principal Component Analysis of *P. tragium* group (n = 325)
1, 5 – shorthaired; 7–10 – longhaired; 6 – glabrous plants
1 – var. *laciniata* DC. (= *P. titanophila* WORONOW); 2 – var. *tragium* (= *P. lithophila* SCHISCHK.); 3 – *"intermedia"* group with transitional leaf dissection degree; 4 – var. *depressa* (SIEBER) BOISS.; 5 – var. *pseudotragium* (DC.) BOISS. non WOLFF; 6 – glabrous plants similar to shorthaired *P. tragium* VILL. (+) and var. *sartorii* (BOISS. & HELDR.) BOISS. (×); 7 – var. *polyclada* (BOISS. & HELDR.) BOISS.; 8 – var. *cyprica* (BOISS.) WOLFF; 9, 10 – the plants from Lebanon (9) and Asia Minor (10), similar to var. *pseudotragium* (DC.) BOISS. sensu WOLFF p. p. (1927)

Correlation between morphological characters and environmental factors in *P. tragium* VILL.

To confirm environmental dependence of morphological characters we used linear correlation coefficients (r). The degree of leaf dissection correlated with summer precipitation (r = +0.44) and duration of summer drought (r = –0.50). The values were not high, first because of the rough estimation of climatic data for each place and second because of the great polymorphism in local populations. Weak correlation between leaf dissection and altitude (r = –0.30) could be explained by the fact that pinnatisect leaf-forms grew mainly in mountain regions with arid climates, while bipinnatisect ones – on plains with more humid climates. Fruit size weakly correlated with drought duration (r = –0.23) and summer precipitation (r = +0.24): the longer the drought, the smaller the fruits.

When ecological characteristics were included in the PCA (n = 274) we found that PC 2

Table 3
Loadings of 15 characters on the first six axes in Principal Component Analysis of *P. tragium* VILL. group. (n = 325). The values lower 0.4 are not given. Factors 1–6 accounted for 70.5% of variation

Characters	Factors					
	PC1	PC2	PC3	PC4	PC5	PC6
Hair length on leaves	0.918					
Hair length on stem	0.903					
Hair length on fruits	0.516				0.617	
Hair density on stem		0.864				
Hair density on leaves		0.799				
Hair density on rays		0.611			0.438	
Fruit length			0.901			
Fruit width			0.881			
Rays number				0.808		
Plant height				0.696		
Stylodium length				0.644		
Hair density on fruits					0.787	
Branching						0.798
Hair length on rays		0.453				–0.423
Leaf dissection	–0.427					0.419
% of total variation	15.81	13.96	11.77	10.92	9.56	8.49

had the highest loadings of segments dissection, summer drought time and summer and year precipitation (Table 4). So leaf dissection showed weak but sound negative correlation with drought duration and positive with summer precipitaion.

Canonical Variance Analysis

The CVA was applied to build a classification based on a full set of characters and to check on the validity of our attribution of samples to 10 subgroups. The CVA of the full data set (n = 325) split it into two large clusters (Fig. 10). The shorthaired plants *(P. tragium)* formed the first general cluster of 1–5 subgroups, differing in degree of leaf dissection (the numbers denote subgroup centers). *P. tragium* var. *pseudotragium* (5) from Northwestern Iran (Kurdistan, Lurestan, Iranian, part of Azerbaijan) hardly differed from *P. tragium* var. *tragium* (2) in the summ of the characters. *P. tragium* var. *depressa* combined the smallest plants from Crete and other parts of the *P. tragium* area and bordered with *P. tragium* var. *tragium* (2). The group of specimens with intermediate characters (3) fell between the forms with extreme variants of leaf dissection, i. e.: (1) – *P. tragium* var. *laciniata (= P. titanophila)* and (2) – *P. tragium* var. *tragium (= P. lithophila)*.The intermediate plants (3) often grew side by side with plants of 1, 2 and 4 subgroup and do not represent a special geographical race.

The longhaired plants *(P. polyclada)* formed another cluster of varieties of *P. tragium* (WOLFF 1927): 7 – var. *polyclada*, 8 – var. *cyprica*, 9, 10 – var. *pseudotragium* WOLFF non (DC.) BOISS. from Lebanon (9) and Asia Minor (10). On the plane of the first and second canonical axes these clusters formed almost a right angle between them, demonstrating distinct correlation of the characters. Glabrous plants were distributed among longhaired and shorthaired ones.

Leaf dissection and hair length on leaves were the best characters for subgroup discriminating. Hair density on stem and leaves, hair length on stems, the number of umbel rays, plant height and stylodia length were also essential for classification.

The CVA split the second set (n = 274) into two specimen clusters – shorthaired and glabrous ones (Fig. 11) The first included subgroups with various segment dissections (1–5), the second comprised glabrescent specimens similar to shorthaired plants (6).

Table 4
Loadings of 15 morphological characters and 4 environmental factors in Principal Component Analysis of *P. tragium* VILL. ($n = 274$). Loading values lower 0.4 are not shown. The first six Factors accounted for 62.8% of total variation.

Characters	Factors					
	PC1	PC2	PC3	PC4	PC5	PC6
Hair density on leaves	0.743					
Hair length on leaves	0.720					
Hair density on stem	0.672					
Hair length on stem	0.632					
Hair length on rays	0.621					
Summer drought time		–0.907				
Summer precipitation		0.905				
Segment dissection		0.614			–0.470	
Plant height			0.817			
Rays number			0.810			
Stylodium length			0.514			
Fruit width				0.865		
Fruit length				0.843		
Altitude					0.709	
Year precipitation		0.408			0.672	
Hair density on fruit						0.718
Hair length on fruit						0.665
Hair density on rays	0.485					0.490
Branching						–0.449
% of total variation	14.05	13.18	9.58	9.04	8.64	8.38

Multivariate methods confirmed, that *P. tragium* could be really segregated into two groups by the set of characters used, firstly by the hair length on leaves and in the lower part of the stem. In the absence of hairs some specimens inevitably fell into a mixed group in the PCA results and were distributed among pubescent plants in CVA results. Glabrous and shorthaired plants grew together in France, Algeria, Italy, Daghestan, East Anatolia, Greece (Korax, Eubaea, Cephalonia) and on the East European Plain. Similarly, both glabrous and longhaired plants were found side by side in Athossus, Olympus, Parnassus in Greece and at Ida in Western Anatolia. These facts should be referred to as cases of population polymorphism. Identification of glabrous plants should take into account examination of pubsecent plants growing in the vicinity.

Discussion

Anatomical and morphological study of the *P. tragium* group have shown a close resemblance between shorthaired and longhaired plants, the two types differing mainly in the hair length on leaves and on the lower part of the stem: 0.05–0.2 mm in *P. tragium* and 0.3 to 1 mm in *P. polyclada*. Both groups have the same mericarp structure, although they are a little larger and with more numeral vallecular secretory canals in longhaired plants. Both groups inhabit mainly limestone substrata. The distributional area of shorthaired plants is larger and includes the area of the longhaired race. But conditions humid enough for the shorthaired race are rather arid for the longhaired, so their requirements do not coincide and they occupy different habitats in adjacent mountain belts. Longhaired plants prefer more humid, often woody habitats, while the shorthaired race inhabits open stony slopes. Both groups include plants with various degrees of leaf dissection and hairy density, demonstrating similar adaptations in leaf morphology and anatomy. In more humid conditions the leaves have more prolonged growth and are more dissected. Glabrous and sparsely haired plants in both groups are concentrated in open light places and regions with sufficient rainfall during the growing period.

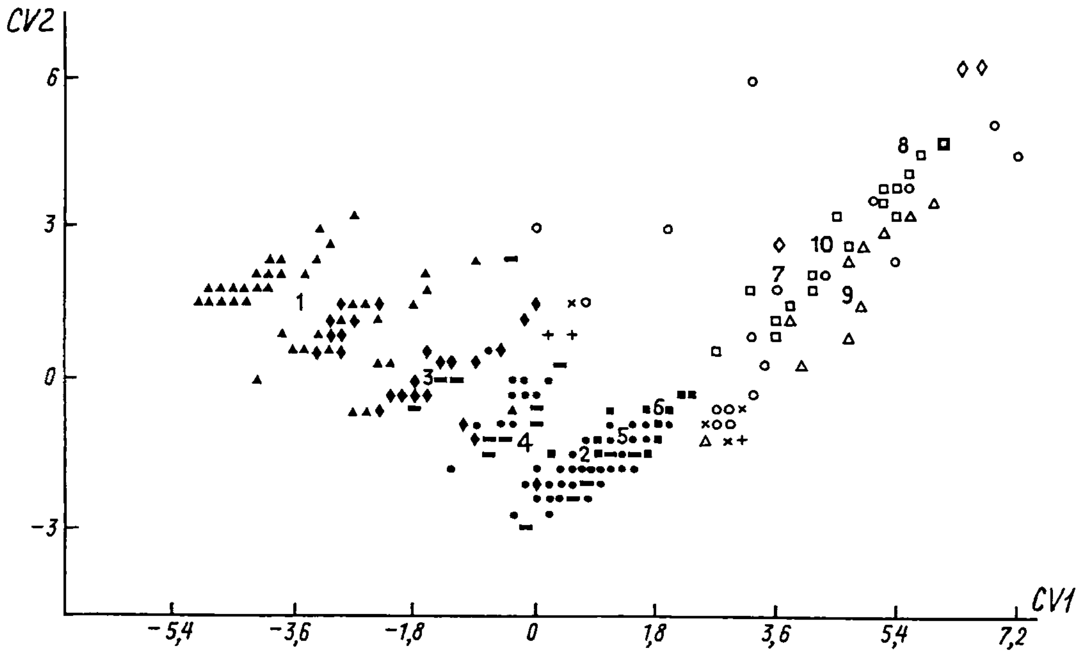


Fig. 10
Canonical Variance Analysis of *P. tragium* group (n = 325). The group numbers see Fig. 9

Longhaired and shorthaired plants can be considered ecological races or subspecies of a single species, formed in neighbouring mountain belts in the East Mediterranean. On the other hand, they may be thought as two related, but distinct species, of independent origin in different parts of the Mediterranean having then extended their areas and formed various ecological and morphological races. Intermediate forms found in Greece (HARTVIG 1986) may confirm the first point of view, but could be regarded as the result of interspecific hybridization.

Studying available herbarium material from Greece and Turkey we did not find any intermediate form or intermixed population, so we assume the second point of view. A more detailed study of these taxa is, however, necessary in the Balkans and Asia Minor for more confident taxonomic interpretation.

The great morphological variability meant that there were no distinguishing taxa within each group, although several ecotypes can be recognized in *P. tragium*. The plants of the Mediterranean and Asian regions with semiarid Mediterranean climates are adaptable to spring and autumn rains and summer drought. They have densely haired mesomorphic pinnatisect rosette leaves, assimilating in spring, and ceasing growth in late summer. They have dior monocyclic innovation shoots and live 3–5 years in nature.

The other ecotype is represented by plants of the steppe zone in the East European Plain with continental climate and some Mediterranean and Asian mountain regions with subhumid Mediterranean climates. Being adapted to semiarid conditions, these plants have also two leaf generations, but these have prolonged growth during the summer. Arid conditions and the edaphic properties of limestone substrata have resulted in the selection of bipinnatisect xeromorphic leaves and slower development. These plants have di- or tricyclic innovation shoots and a longer lifetime.

The plants with the narrowest glabrescent laniculas of bipinnatisect leaves can be regarded as a different ecotype. They predominate on chalk and limestone outcrops of the East European Plain. High light intensity, sharp

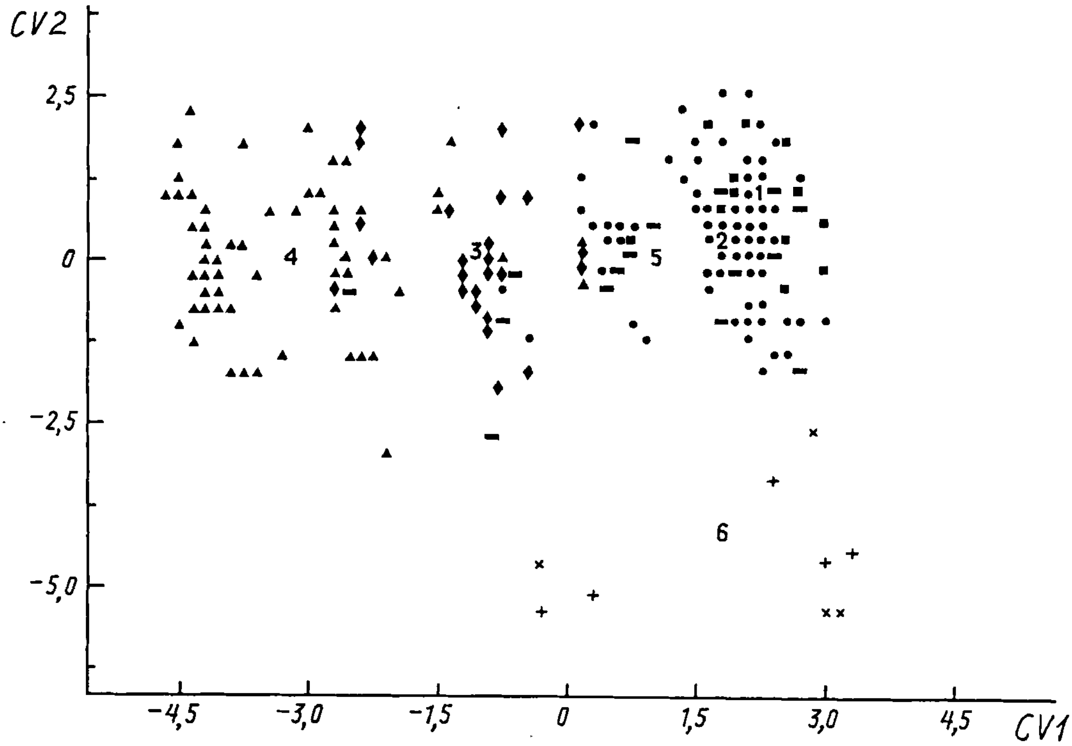


Fig. 11
Canonical Variance Analysis of *P. tragium* group. (n = 274). The group numbers see Fig. 9

temperature fluctuations, air drought and nutrient poor substrata have resulted in the elaboration of the most xeromorphic leaf structure, polycyclic shoots and a lifetime exceeding 15 years.

The geographical distribution of races coincides with a complex pattern of climatic and soil conditions throughout the *P. tragium* VILL. range, but creates problems for its taxonomic treatment. As environment conditions sharply alternate or gradually change across the area, it is difficult to separate races or population groups with unique complexes of characters or to draw borderlines between them. Some local populations possess morphological features no less important than those of large geographical races. Taxonomic segregation would however tend to confuse rather than clarify the variation patterns of the species.

Variation pattern of *P. polyclada* BOISS. & HELDR. gives even less grounds for taxonomical subdivision. In conclusion, therefore we recognize two distinct species, each possessing numerous ecological races, but do not separate any infraspecific taxa in them.

Taxonomy

Pimpinella tragium **VILL.**

Hist. pl. Dauph. 2: 605 (1787); DC., Prodr. 4: 121 (1830); ENGSTRAND in Rech. Fl. Iranica 162: 324 (1987).

≡ *P. tragium* var. *typica* HALÁCSY, Consp. Fl. Graec. 1: 682 (1901). *P. tragium* subsp. *typica* TUTIN, Fl. Europ. 2: 332 (1968).

= *P. canescens* LOISEL., Not. plant ajout. Fl. France: 47, t. 4 (1810).

= *P. tragium* var. *canescens* (LOISEL.) POIR. in LAM. Encycl. Meth. Bot. Suppl. 1: 683 (1810).

= *P. depressa* (SIEBER ex SPRENG.) DC., Prodr. 4: 119 (1830).

= *P. tragium* var. *depressa* (SIEBER ex SPRENG.) BOISS., Fl. Or. 2: 871 (1872).

= *P. tragium* subsp. *depressa* (SIEBER ex SPRENG.) TUTIN, Feddes Repert. 79 (1–2): 62 (1968).

= *P. tragium* var. *laciniata* DC., Prodr. 4: 120 (1830).
= *P. pseudotragium* DC., Prodr. 4: 122 (1830).
= *P. tragium* var. *pseudotragium* (DC.) BOISS., Fl. Or. 2: 871 (1872); WOLFF in ENGLER Pflanzenreich 90 (IV. 228): 251 (1927), p.p.
= *P. tragium* subsp. *pseudotragium* (DC.) MATTHEWS in DAVIS Fl. Turkey 4: 361 (1972), p.p.
= *P. zagrosica* (BOISS. & HAUSSKN.) BOISS., Fl. Or. 6: 253 (1888).
= *P. tragium* var. *sartorii* auct. non (HELDR. ex BOISS.) HALÁCSY: WOLFF in ENGLER Pflanzenreich 90 (IV. 228): 251 (1927), p.p. excl. typo.
= *P. tragium* var. *polyclada* auct. non (BOISS. & HELDR.) BOISS.: WOLFF in ENGLER Pflanzenreich 90 (IV. 228): 250 (1927), pro min. p., excl. typo.
= *P. tragium* subsp. *polyclada* (BOISS. & HELDR.) TUTIN: MATTHEWS in DAVIS Fl. Turkey 4: 361 (1968), quoad specim. *KOTSCHY*, no. *196*!
= *P. titanophila* WORONOW in Fl. South-East Europ. p. URSS 5: 792 (1931).
= *P. tragium* subsp. *titanophila* (WORONOW) TUTIN, Feddes Repert. 79 (1–2): 62 (1968).
= *P. titanophila* var. *tomiophylla* WORONOW in Fl. South-East Europ. p. URSS 5: 793 (1931).
= *P. tomiophylla* (WORONOW) STANKOV in STANKOV & TALIEV Man. high. Pl. Europ. p. USSR: 531 (1949).
= *P. confusa* WORONOW in Acta Inst. Bot. Acad. Sci. USSR, ser. 1 (1): 219 (1933).
= *P. idae* TAKHT., Not. Syst. Geogr. Tphilis. 9: 24 (1940).
= *P. caucasica* SCHISCHK. in GROSSHEIM, Man. Pl. Caucas.: 228 (1949), nom. invalid. (nudum).
= *P. daghestanica* SCHISCHK., Not. Syst. (Leningrad) 12: 203 (1950).
= *P. grossheimii* SCHISCHK., Not. Syst. (Leningrad) 12: 204 (1950).
= *P. lithophila* SCHISCHK., Not. Syst. (Leningrad) 12: 206 (1950).
= *P. tragium* subsp. *lithophila* (SCHISCHK.) TUTIN, Feddes Repert. 79 (1–2): 62 (1968); MATTHEWS in DAVIS Fl. Turkey 4: 361 (1972), pro max. p.
= *P. turcomanica* SCHISCHK., Not. Syst. (Leningrad) 12: 207 (1950).
= *P. litwinowii* SCHISCHK., Not. Syst. (Leningrad) 12: 208 (1950).
= *Tragium columnae* SPRENG., Spec. Umbellif.: 134 (1818).
= *Tragium depressum* SIEBER ex SPRENG. in ROEM. & SCHULT., Syst. Veg. 6: 392 (1820).

Type: Southern France (Dauphine, *VILLARS*, no. *442* – BM!).

Perennial (–5) 10–60 (–100) cm high with woody tap-root, straight or inclined, and one or more striate solid stems innovated and branched sympodially. Basal parts of stems form many-headed rhizome covered by numerous scale-like dead petioles. Plant pubescent with short straight or curved hairs 0.5–0.2 mm long, rarely glabrescent or glabrous at the top. Rosette leaves numerous, long-petiolate 5–20 cm long, with laminae oblong, ovate or broad-ovate in outline, 5–15 cm long and 2–8 cm width, pinnatisect or bipinnatisect (1- or 2-pinnate) with 3–6 pairs of segments, densely or slightly pubescent or almost glabrous. Segments oblong, ovate or broad-ovate with subcordate heart-shaped or cuneate base and acuminate tips, incise, pinnatipartite or pinnatisect into narrow lanceolate, linear or ovate acuminate decurrent lobuli. Cauline leaves vaginate with small sessile or upper reduced laminae. Umbels 2–4 cm in diam. open in flowers and closed in fruits with 5–20 equal rays 2–4 cm long, densely or sparsely pubescent, rare glabrescent. Bracts and bracteoles absent or 1–2, linear. Umbellulae with 10–20 flowers, pedicels haired 0.1 mm long. Petals white, rare pink or pinkish to 1 mm long, obovate with lobules inflexed, hairy on the back. Fruit oblong-ovoid, 2–3.5 mm long, 1.2–1.5 mm width, covered by short straight or adpressed hairs 0.1–0.2 mm, rarely almost glabrous. Mericarps with filiform inconspicuous primary ribs, 3–6 vittae in dorsal vallecular 2–6 in commissura. Stylopodia cushion-shaped, stylodia (1) 1.5–2.5 (3) mm long. $2n = 18, 20, 22$.

Flowers in June–August, fruits in August–September.

Habitats: on exposed limestone outcrops – limestone, chalk and marl, rarely on granite, basalt, sandstone and schist. On cliffs, on disturbed slopes and gravel screes, in rarefied stony mountain meadow steppes, herb-sheep's-fescue steppes and sheep's-fescue-thyme steppes. In mountain regions of the Mediterranean and Asia at altitudes of 1000–2500 m a. s. l., in steppe zone of the East European Plain at altitudes of 100–200 m a. s. l.

Distribution: the Mediterranean from Spain to Lebanon, North-West Africa, Asia Minor, Caucasus, Kopet- Dagh, South of the East European Plain.

Pimpinella polyclada **BOISS. & HELDR.**

in BOISS. Diagn. pl. or., sèr. 2 (2): 75 (1856).
≡ *P. tragium* var. *polyclada* (BOISS. & HELDR.) BOISS., Fl. Or. 2: 872 (1872); WOLFF in ENGLER Pflanzenreich 90 (IV.228): 250 (1927), pro max. p.

≡ *P. tragium* subsp. *polyclada* (BOISS.& HELDR.) TUTIN, Feddes Repert. 79 (1–2): 62 (1968); MATTHEWS in DAVIS Fl. Turkey 4: 361 (1972), excl. spec. *KOTSCHY* no. *196*!
= *P. olenea* BOISS. & HELDR. ex. BOISS. Fl. Or. 2: 75 (1856).
= *P. tragium* var. *olenea* (BOISS. & HELDR. ex BOISS.), HALÁCSY Consp. Fl. Graec. 1: 682 (1901).
= *P. parnassica* BOISS. & HELDR. ex BOISS., Fl. Or. 2: 75 (1856).
= *P. tragium* var. *parnassica* (BOISS. & HELDR. ex BOISS.) HALÁCSY, Consp. Fl. Graec. 1: 682 (1901).
= *P. longiradiata* BOISS. & HELDR. ex BOISS., Fl. Or. 2: 75 (1856).
= *P. polyclada* var. *pauciradiata* BOISS. Fl., Or. 2: 75 (1856).
= *P. sartorii* HELDR. ex BOISS., Fl. Or. 2: 75 (1856).
= *P. tragium* var. *sartorii* (HELDR. ex BOISS.) HALÁCSY, Consp. Fl. Graec. 1: 682 (1901); WOLFF in ENGLER Pflanzenreich 90 (IV.228): 250 (1927), pro p., incl. typo.
= *P. cyprica* BOISS., Fl. Or. 6: 253 (1888).
= *P. tragium* var. *cyprica* (BOISS.) WOLFF in ENGLER, Pflanzenreich 90 (IV. 228): 251 (1927).
= *P. tragium* var. *pseudotragium* auct. non (DC.) BOISS., WOLFF in ENGLER, Pflanzenreich 90 (IV. 228): 251 (1927), quoad pl. ex Amasya (*BORNMÜLLER* no. *2214*!), Egin (*SINTENIS* no. *2663*!).
= *P. tragium* subsp. *pseudotragium* (DC.) MATTHEWS in DAVIS Fl. Turkey 4: 361 (1972), quoad pl. ex Kizilcahaman (*ALPAY* no. *56*!), Amasya (*BORNMÜLLER* nos. *372*!, *2372*!, *2214*!), Egin (*SINTENIS* no. *2663*!), Karaman (*DADLEY* no. *16168*!), Sana-Dagh (*BORNMÜLLER* no. *3726*!).
= *P. tragium* var. *lithophila* auct. non (SCHISCHK.) TUTIN: MATTHEWS in DAVIS Fl. Turkey 4: 361 (1972), quoad pl. ex Eskisĕchir: Mihalliccik (*DUDLEY* no. *37203*!), Kizilcahaman: Alis Da (*KHAN* et al. no. *564*!).

Type: Greece, Thessalien ("In monte Olympi Thessaliae, regione sylvatica, *HELDREICH* no. *2457*" – G-Boiss.!). Isotypi: (*HELDREICH* nos. *2454*, *2457* W!, LE!).

Perennial herb 25–100 cm high with tap root and one or many sympodially innovated stems, forming many-headed rhizomes covered by thick dark-brown bark and scale-lake remains of petioles. Stems solid, terete, sympodially branched, smooth or thin striated, covered by straight or slightly twisted hairs on the lower part, glabrescent or glabrous at the top. Rosette leaves long petiolate, 10–25 cm long with oblong blade 3–5 cm long, 5–15 cm width, pinnatisect, rarely bipinnatisect with 3–6 petiolate or sessile segment pairs, densely or rarely pubescent. Segments oblong, ovate, broad-ovate or rounded with subcordate or cuneate base slightly acuminate tip, incise-serrate, rarely deeply pinnatisect into acute lanceolate or ovate decurrent lobuli. Cauline leaves vaginate with small sessile blades, pinnatisect with 3–5 incise-serrate or 1–3 lanceolate segments. Umbels 3–6 cm in diam. with 5–15 equal glabrous or densely haired rays. Umbellulae with 10–20 flowers, bracts or bracteoles absent. Petals white or cream, obovate, hairy on the back with lobule inflexed. Fruits ovate, 2.5–3.5 mm long, 1.2–1.5 mm width, covered by straight hairs 0.3–0.5 mm long. Stylopodia cushion-shaped, stylodia 2–3 mm long glabrous or hairy. $2n = 20$.

Flowers in June–July, fruits in July–August.

Habitats: In the coniferous forest mountain belt at altitudes of 900–1500 (2000) m. a.s.l., in cliffs of limestone and marble rocks, mainly on northern slopes.

Distribution: The Balkans, the Cyprus, Asia Minor.

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