

## Article

### ***Taeniopetalum* Vis. (Apiaceae), a neglected segregate of *Peucedanum* L., supported as a remarkable genus by morphological and molecular data**

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#### **Abstract**

The genus *Taeniopetalum* Vis., comprising three species and two subspecies, has been traditionally treated within *Peucedanum* L., sometimes segregated as a section or subgenus. Molecular (ITS nrDNA sequences), morphological and especially microcarpological data show that *Taeniopetalum* is distant from the type group of *Peucedanum* (*P. officinale* L. and its allies). According to molecular data, *P. obtusifolium* Sm. belongs to the same clade. This affinity is supported morphologically (by similarities in fruit structure). Thus *P. obtusifolium* can also be placed with *Taeniopetalum*. A taxonomic treatment for the genus *Taeniopetalum* is provided along with an identification key. Three new combinations are published:

*Taeniopetalum arenarium* subsp. *borysthenicum* (Klokov ex Schischk.) Pimenov & Ostr., *T. arenarium* subsp. *neumayeri* (Vis.) Pimenov & Ostr. and *T. obtusifolium* (Sm.) Pimenov.

**Keywords:** Apiaceae, carpology, ITS nrDNA, molecular systematics, morphology, *Peucedanum*, *Taeniopetalum*

#### **Introduction**

*Taeniopetalum* Vis. is a little-known genus of the Apiaceae, usually treated as a part of *Peucedanum* L. s.l. *Taeniopetalum* was described by Visiani (1850) as a monotypic Balkan genus; its nomenclatural type is the concurrently described *Taeniopetalum neumayeri* Vis. A year later Bunge (1852) published a new genus *Taeniopetalum* Bunge and a species, *T. peucedanoides* Bunge without any reference to the earlier publication by Visiani (1850). The name *Taeniopetalum* Bunge became a later homonym of the name *Taeniopetalum* Vis.

*Peucedanum alsaticum* L. was cited as a synonym of *Taeniopetalum peucedanoides* (Bunge, 1851: 127) and this made the latter an illegitimate superfluous name that cannot be used and should be placed into the synonymy of currently accepted name that is homotypic with *P. alsaticum* L. The specimen bearing the name *T. peucedanoides* was collected by A. Lehmann in what is now Orenburg Province and Bashkortostan Republic of Russia (“auf der Linie zwischen Orenburg und Orskaya 540” and “zwischen Ufa und Sterlitamak, VII. 1840 s.n.”). Both sheets from the collection by Lehmann found by us in W and P herbaria

appeared to be identical to *Xanthoselinum alsaticum* (L.) Schur. We accept *Xanthoselinum* Schur as a distinct genus independent from *Peucedanum* (Reduron *et al.*, 1997).

*Taeniopetalum* Bunge is a nomenclatural synonym of *Xanthoselinum*.

*Taeniopetalum* Vis. was reduced to a section of *Peucedanum* L. (*Peucedanum* sect. *Taeniopetalum* (Vis.) Rchb.f. ex Calest. (1905)) and later to a subgenus of *Peucedanum* (*Peucedanum* subgen. *Taeniopetalum* (Vis.) Thell. (Thellung, 1926)).

*Taeniopetalum neumayeri* is closely related to *Peucedanum arenarium* Waldst. & Kit., previously described from the Hungarian Pannonian steppe (puszta). The former was regarded as a subspecies, *P. arenarium* subsp. *neumayeri* (Vis.) Stoj. & Stef., of the latter, (Stojanov & Stefanov, 1948: 857). Two species described independently as *P. macedonicum* Janka (Janka, 1873: 203) and *P. serpentini* Andras. & Jávorka (Jávorka, 1921: 25) later turned out to be synonyms of *T. neumayeri* (Hayek, 1927). According to Calestani (1905), the section *Taeniopetalum* contains two species, *P. neumayeri* (Vis.) Rchb.f. and *P. macedonicum*, although the author noted that the characters of *P. arenarium*, referred by him to the section (*Eu*)*Peucedanum*, corresponded more to *Taeniopetalum*. Tikhomirov (1987) transferred *P. arenarium* to *Taeniopetalum* and published the combination *T. arenarium* (Waldst. & Kit.) V.N.Tikhom. that is omitted from the IPNI database. Following Soó (1965, 1966), he also noted the absence of differences between central and eastern European populations of *T. arenarium* s.str. and separated *P. borysthenticum* Klokov ex Schischk. as an independent species, while relying on the characters listed in its protologue.

Another separate taxon of the section *Taeniopetalum* is *Peucedanum urbani* Freyn & Sint. ex H.Wolff (Wolff, 1924: 68), a narrow endemic species of Kaz Dağları (Mt. Ida) in northwestern Turkey, known only from one locality (circa fontis Scamandri). It was treated by Chamberlain (1972) as a subspecies of *P. arenarium* (*P. arenarium* subsp. *urbani* (Freyn & Sint. ex H.Wolff) D.F.Chamb.).

We added to our comparative analysis one more species, which had never been explicitly treated as a part of the genus *Taeniopetalum*. This is *Peucedanum obtusifolium* Sm. described as early as 1806 (Sibthorp and Smith, 1821: 189) and later transferred to *Ferula* L. (Sprengel, 1818), *Pastinaca* L. (Candolle, 1830), and *Malabaila* Hoffm. (Boissier, 1872; Degen, 1895). Degen (1897) and Halácsy (1901) were the first to note an affinity between *P. obtusifolium* and *P. arenarium*. Like *P. arenarium*, *P. obtusifolium* grows in sands, particularly on dunes near the seashore.

Previous morphological studies of *Taeniopetalum* are scarce. Moreover, none of the existing treatments of *Peucedanum* s.l. of Europe and Southwest Asia placed all the five taxa within *Taeniopetalum*. In each of these treatments (Hayek, 1927; Schischkin, 1951; Tutin, 1968; Chamberlain, 1972; Kuzmanov and Andreev, 1982), only two or three species or subspecies of the genus *Taeniopetalum* have been mentioned. Nevertheless, these publications contain important information about diagnostic characters of *Taeniopetalum* species. The diagnostic morphological fruit characters have been carefully described for *P. arenarium* (Klan, 1947). Particularly in mericarps Klan noted large epidermal cells with strong outer walls. A specific character of exocarp cells was brought out in a rather unusual way in the *Taeniopetalum* protologue (Visiani, 1850: 50): “ab omnibus autem *Peucedaneis* discrepat epicarpio squamuloso etc”. A distinctive morphological character, such as large epicarp cells, is therefore critical in the discussion on the taxonomic placement of the genus *Taeniopetalum*. The following characters were used for delimitation of *Taeniopetalum* taxa: leaf segment shape, umbel ray number and length, and pedicel length.

Until recently, none of the taxa included in *Taeniopetalum* (in the above-circumscribed sense) had ever been a subject of DNA sequencing. The genus was not included in the comparative molecular studies of the *Peucedanum* complex (Shneyer *et al.*, 1995; Spalik *et al.*, 2004; Downie *et al.*, 2010).

To clarify the taxonomic position of *Taeniopetalum* species and their relationships to true *Peucedanum* species (*Peucedanum* sect. *Peucedanum*), we have carried out comparative molecular analyses of nrDNA ITS sequences of all the above-mentioned species supported by detailed morphological and fruit anatomical studies, which are essential for taxonomy in the family Apiaceae.

## Material and Methods

For the morphological and anatomical studies, herbarium material from BM, BP, BR, BUC, CL, CRAI, E, FI, G, GOET, I, K, KW, LD, LE, MW, MHA, OXF, PAD, PR, S, US, W and WU (acronyms follow Thiers 2016+) was used. To clarify variability limits and diagnostic value of taxonomically important characters, we studied herbarium holdings of *Taeniopetalum* in BP (including isolectotypes of *Peucedanum urbani*), LE (including lectotype of *P. borysthenicum*), MHA, MW, PAD (types of *Taeniopetalum neumayeri*), and in PR (lectotype of *P. arenarium*). Our own field collections and observations were made for

*T. arenarium* subsp. *borysthenicum* (Klokov ex Schischk.) Pimenov & Ostr. in Russia and Ukraine and for *T. obtusifolium* (Sm.) Pimenov in Turkey and Bulgaria.

For a detailed morphological study, measurements of fruits, umbels and leaves were taken from herbarium specimens and in the field.

SEM investigations of fruits were made with a CamScan S-2 (accelerating voltage 15 kV and working distance 56 mm) at the magnification of 15–3000x. Dry fruits were placed on aluminium stubs and sputter-coated with gold or gold-palladium to a thickness of ca. 25 nm.

For the anatomical study, fruits were softened in hot water or in a glycerol-alcohol-water mixture; free-hand sections were processed with phloroglucinol and hydrochloric acid, then kept in glycerol.

Fruit and petal morphology was studied with a stereomicroscope Olympus SZ61 (x45). In petal morphology we follow Reduron (1978), Froebe *et al.* (1981) and Jahnke and Froebe (1983).

For molecular phylogenetic analysis, sequences of the nuclear ribosomal DNA internal transcribed spacer (nrDNA ITS1, 2) were generated for 14 accessions of various geographic origins representing all the species and subspecies of the genus *Taeniopetalum*. For *T. arenarium* subsp. *arenarium* from Slovakia, we were able to produce only the ITS1 sequence.

In addition, we used GenBank sequences for the ITS region of nrDNA for 31 taxa of Apiaceae (see Appendix).

Total DNA was extracted from leaf tissue with the *NucleoSpin* plant DNA isolation kit (Macherey-Nagel, Düren, Germany) following the manufacturer's protocol. The strategies for amplification and sequencing of the ITS region (including primer location and characteristics) are provided in Valiejo-Roman *et al.* (2002). Amplification products were purified using the DNA Cleanup Mini kit (Evrogen, Moscow, Russia). Direct sequencing was performed using *ABI PRISM 3100 Genetic Analyzer* (Applied Biosystems, Foster City, CA, USA) and *BigDye Terminator Cycle Sequencing Ready Reaction Kit*. Both forward and reverse DNA strands of all samples were sequenced. Newly obtained sequences were deposited in GenBank.

An initial set of taxa for comparison with *Taeniopetalum* was determined by using the BLAST option of the GenBank database. This search suggested that the following Apiaceae species were most similar: *Peucedanum gallicum* Latour., *Peucedanum officinale* L. and

*Thysselinum palustre* (L.) Hoffm. These taxa belong to Selineae Clade in the currently adopted molecular classification of Apioideae (Downie *et al.*, 2010). After preliminary analyses, the dataset was designed to cover representatives from Selineae Clade with special attention to *Peucedanum*. Members of *Selinum* L. (*S. carvifolia* (L.) L. and *S. broteroi* Hoffmanns. & Link) are used as outgroups based on higher-level molecular studies of Apiaceae (Spalik *et al.*, 2004). The ITS data matrix was analyzed using both maximum parsimony (MP) and the Bayesian inference (BI).

The parsimony analysis involved a heuristic search conducted with PAUP\* (version 4.0b8; Swofford, 2003) using TBR branch swapping and equal weighting of characters, treating gaps as missing data. One thousand replicates with random taxon addition were performed, and all the shortest trees were saved. Bootstrap analysis (Felsenstein, 1985) was performed to assess the degree of support for particular branches on the tree, and bootstrap values were calculated using 1000 replicates with TBR branch swapping and random addition of taxa. One thousand of the most parsimonious trees from each replicate were saved.

Bayesian inference was explored using *MrBayes* version 3.2.5 (Ronquist *et al.*, 2012). The GTR+G model of sequence evolution was selected using the Akaike information criterion from an analysis using the program Modeltest version 3.7 (Posada and Crandall, 1998). A total of 60,000,000 generations were performed, and trees from the first 300,000 generations were discarded. The number of generations to be discarded was determined with cold chain log likelihood observation using Tracer version 1.5 (Rambaut and Drummond, 2007).

## Results

As is evident from our brief essay on the taxonomic history of the genus *Taeniopetalum*, there has been no consensus as far as the ranks of some of the included taxa. For the time being, yet obviating the employment of nomenclature suggested as a result of this work, and for the sake of simplicity, we discuss the characters of all the five taxa under their valid names in *Peucedanum* and in the specific rank.

## Morphological characters

*Leaf ultimate segments.* The leaves vary in presence/absence and size of petiolules at segments of the first and second order as well as size and shape of segments (Table 1). These were only the longer segments that were measured. All the segments are mucronulate.

*Rays of central umbel.* Umbel rays are variable in length in all the taxa studied, the longest ones being 1.5–2 times longer than the shortest. Maximal ray length in the central umbel is presented in Table 1. *Peucedanum urbani* differs from the rest of the species (excluding *P. neumayeri*) in the number of rays and length of the longest rays, all other species having rays no more than 13 cm long.

*Pedicel length* (Table 1). *Peucedanum neumayeri* and *P. urbani* usually have shorter pedicels than the rest of the species.

*Petal morphology* (Fig. 1) in all *Taeniopetalum* taxa is uniform. Petals are small, orbicular, 1–1.5 mm long (the largest in *Peucedanum obtusifolium*), without wings, lobe inflexed, petal bend slightly concave. The inflexed lobe is somewhat variable, though usually

Table 1. Morphological characteristics of fruiting plants in *Peucedanum* taxa

Characters	<i>P. arenarium</i>	<i>P. borystenicum</i>	<i>P. neumayeri</i>	<i>P. obtusifolium</i>	<i>P. urbani</i>
Plant Height, cm	90–150(200)	90–150(200)	20–150(200)	(20)30–60	30–100
General Leaf Outline	3–4-pinnate	3–5-pinnate	2–5-pinnate	bipinnate	3–4-pinnate
1 <sup>st</sup> -Order Petiolule Length, cm	3–9	3–8	3–8	2–3	4–8
2nd-Order Petiolule Length, cm	(0.5)2–4	(0.5)1–4	(0.5)2–4	0–0.5	1–4
Ultimate Segment Morphology	Entire, bifid, (trifid), elliptic, elongate, linear; acute, mucronulate	Entire, bifid, (trifid), elliptic, elongate, linear; acute, mucronulate	Entire, bifid, (trifid), linear; acute, mucronulate	Entire, bifid, trifid, pinnatifid; broadly elliptic, elliptic, ovate-oblong, lanceolate; obtuse (acute, mucronulate)	Linear, acute, mucronulate
Ultimate Segment/Lobe Width, mm	1.5–4	1.5–3(4)	0.8–2	2.5–6	1–1.2
Ultimate Entire Segment/Lobe Length, mm	10–30(40)	12–40(50)	10–18	6–12	9–20
Leaf Reduction within Inflorescence	Leaves reduced to sheaths	Leaves reduced to sheaths	Leaves reduced to sheaths	Leaves with small blades, except uppermost ones	Leaves reduced to sheaths
Central-Umbel Peduncle Length, cm	(5)7–13(17)	(0)6–15(23)	6–13	5–15	12
Number of Rays in Central Umbel	5–10(16)	6–11(14)	4–12	5–7(13)	2–4(6)
Maximal Ray Length in Central Umbel, cm	5–11(13)	5–10(11)	4–9(13)	3–8	15–23
Pedicel Length, mm	(2)3–5(7)	3–5(6)	1–3(4)	(1)2–4	1–2(4)
Petal Colour	Yellow	Greenish	Yellow	Sulfur Yellow	Yellow
Mature Schizocarp Shape	Obovoid, ellipsoid, (pyriform)	Pyriform (obovoid)	Obovoid (ellipsoid)	Broadly ellipsoid, broadly obovoid, obovoid, ellipsoid	
Schizocarp Length, mm	6–9	7–10(11)	7–8	8–15	
Schizocarp Width, mm	4–6	4–6(7)	4–5	7–11	
Apical Notch	Absent	Absent	Absent	Present	
Lateral Rib/Seed Cavity Length Ratio	¼ – ½	½	¼ – ½	½	

crenate and rather broad. Each petal has a keel along the midrib and a small (less than one-half of lobe length) bridge between the petal body and inflexed lobe. Secretory ducts are indistinguishable in the intact petals, visible only on sections: 1–3 ducts in the midrib and 1–2 on each side of the petal blade. The secretion is light yellowish-brown.

*Carpology.* Mericarp morphology and anatomy are illustrated in Figs. 2–4. Immature fruits in all the studied taxa are elliptic to oblong, mature fruits are variable in shape and size (Table 1).

With the exception of fruit shape, all investigated species are very similar in fruit morphology, micromorphology and anatomy. Their fruits consist of two ovoid mericarps, carpophore bifid to base. Beak absent, mericarps homomorphic, glabrous, 7.5–15.0 mm long, 4.5–11.0 mm broad, strongly compressed dorsally. Primary mericarp ribs straight, with entire margin, dorsal ribs filiform or inconspicuous, lateral ribs narrow-winged or thickened; secondary ribs absent. Calyx teeth prominent, short triangular, stylopodia low, conical; styles medium-sized, recurved.

When the mericarp surface is studied with SEM, the cellular structure of the exocarp is always clearly visible (Figs. 2–3). Exocarp cells large, 30–60  $\mu\text{m}$  (in *Peucedanum neumayeri*, up to 70  $\mu\text{m}$  long), isodiametric, and elongated. Cell borders sunken, anticlinal walls straight, outer periclinal walls convex (at borders of lateral ribs cells sometimes with concave outer walls). Cuticle tuberculate, sparse rugose or rugose, smooth, or else sparse striate. Under optical stereomicroscope the fruit surface appears granular.

Mericarp anatomy, as revealed on cross-sections (Fig. 4), is characterized by broad commissure (exocarp interrupted near margins of lateral ribs) and large (25–60  $\mu\text{m}$ ) exocarp cells with non-lignified thick walls. Most of the mesocarp parenchyma is compressed and destroyed, so that there are cavities in mesocarp. Inner fibrous mesocarp is absent. Parenchyma in distal parts of lateral ribs with lignified, pitted cell walls. Vascular bundles compact, situated at primary rib bases. Vallecular vittae, (oil tubes) one in each furrow and two on commissural side; rib vittae, one in each rib, rather large, though smaller than vallecular ones. Endocarp not lignified. Endosperm on commissural side either slightly convex or slightly concave; embryo with two cotyledons. In *Peucedanum obtusifolium* lateral

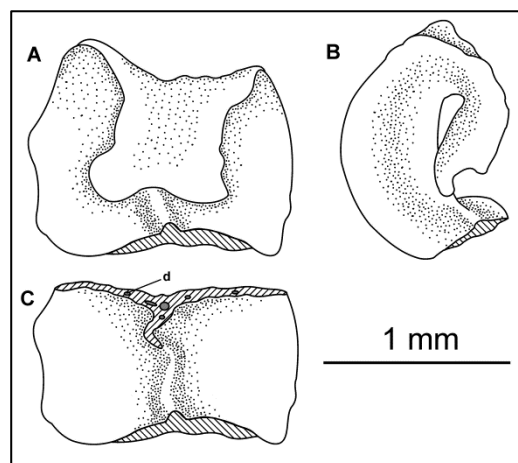


Figure 1. Petals of *Taeniopetalum arenarium* subsp. *arenarium*. A: frontal view, B: side view, C: dissected petal. Abbreviation: d – secretory duct

ribs are broad, approximately half as large as seed cavity, in *P. borysthenicum* – ca.  $\frac{1}{3}$  of seed cavity and in *P. arenarium* and *P. neumayeri* ca.  $\frac{1}{4}$ .

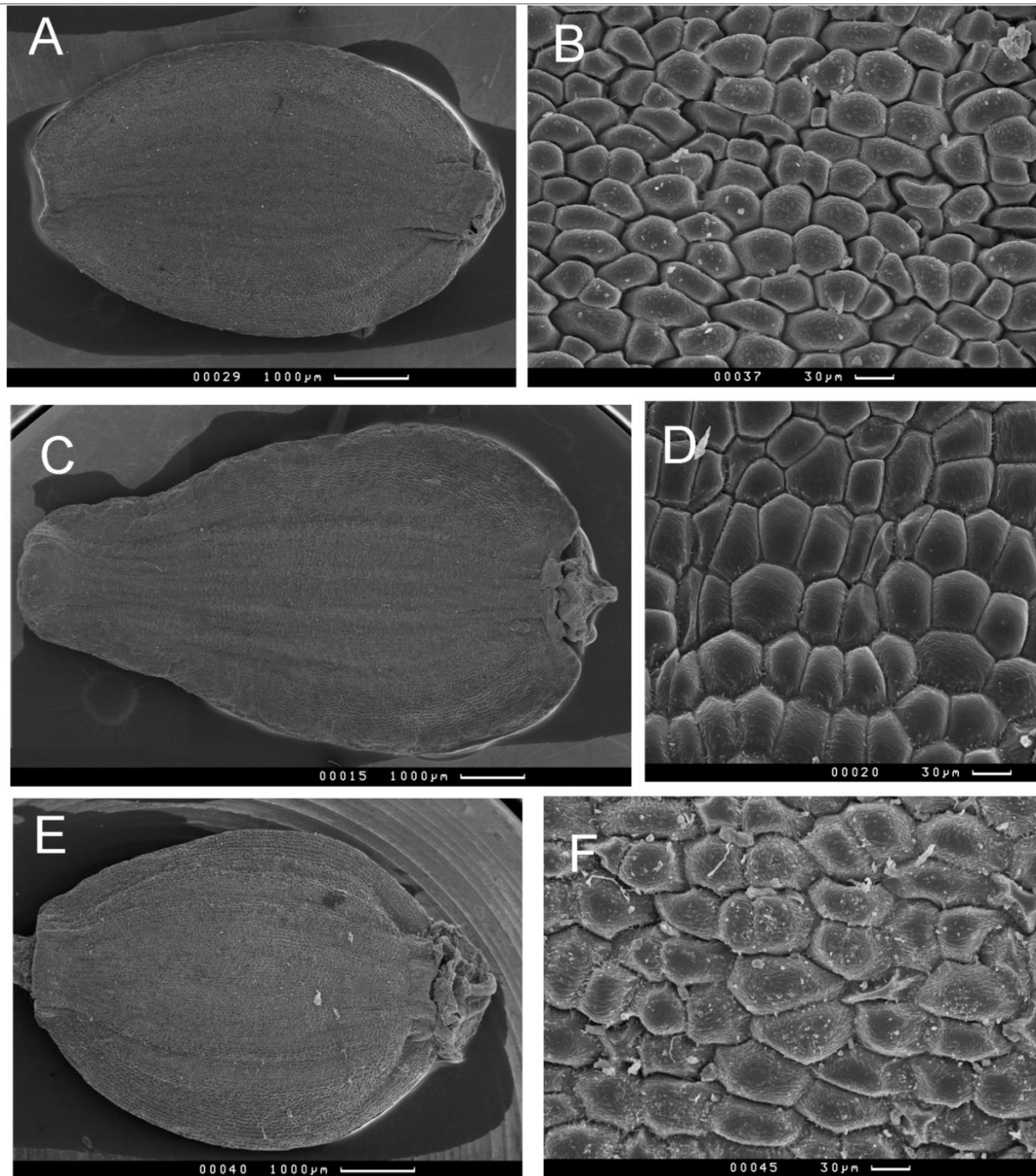


Figure 2. SEM images of fruits in *Taeniopetalum arenarium* subsp. *arenarium* – A, B; *T. arenarium* subsp. *borysthenicum* (Klokov ex Schischk.) Pimenov & Ostr. – C, D; *T. arenarium* subsp. *neumayeri* (Vis.) Pimenov & Ostr. – E, F; A, C, E: mericarps; B, D, F: details of exocarp



### Molecular characters (nrDNA ITS)

Representatives of several different populations were used for each taxon participating in the study of infraspecific variation in ITS sequences. No variation was found in *Peucedanum arenarium*, *P. borysthenicum* or *P. obtusifolium*. Therefore, *P. arenarium*, *P. borysthenicum* and *P. obtusifolium* are represented by single terminals in our trees. *P. urbani* was represented only by a single accession. Three populations of *P. arenarium* subsp. *neumayeri* produced slightly different ITS sequences, all of which were used in the molecular phylogenetic analyses. The majority of the studied samples exhibited identical ITS sequences, which were similar not only within the species or subspecies, but also among different species.

In 14 ITS sequences of *Taeniopetalum*, the length of ITS1 was 218 bp and that of ITS2 – 220 bp. The alignment of 37 ITS sequences resulted in a matrix of 439 nucleotide positions after exclusion of 31 ambiguous positions. Of the remaining sites, 88 characters were potentially parsimony-informative, 71 characters were parsimony-uninformative and 280 were constant.

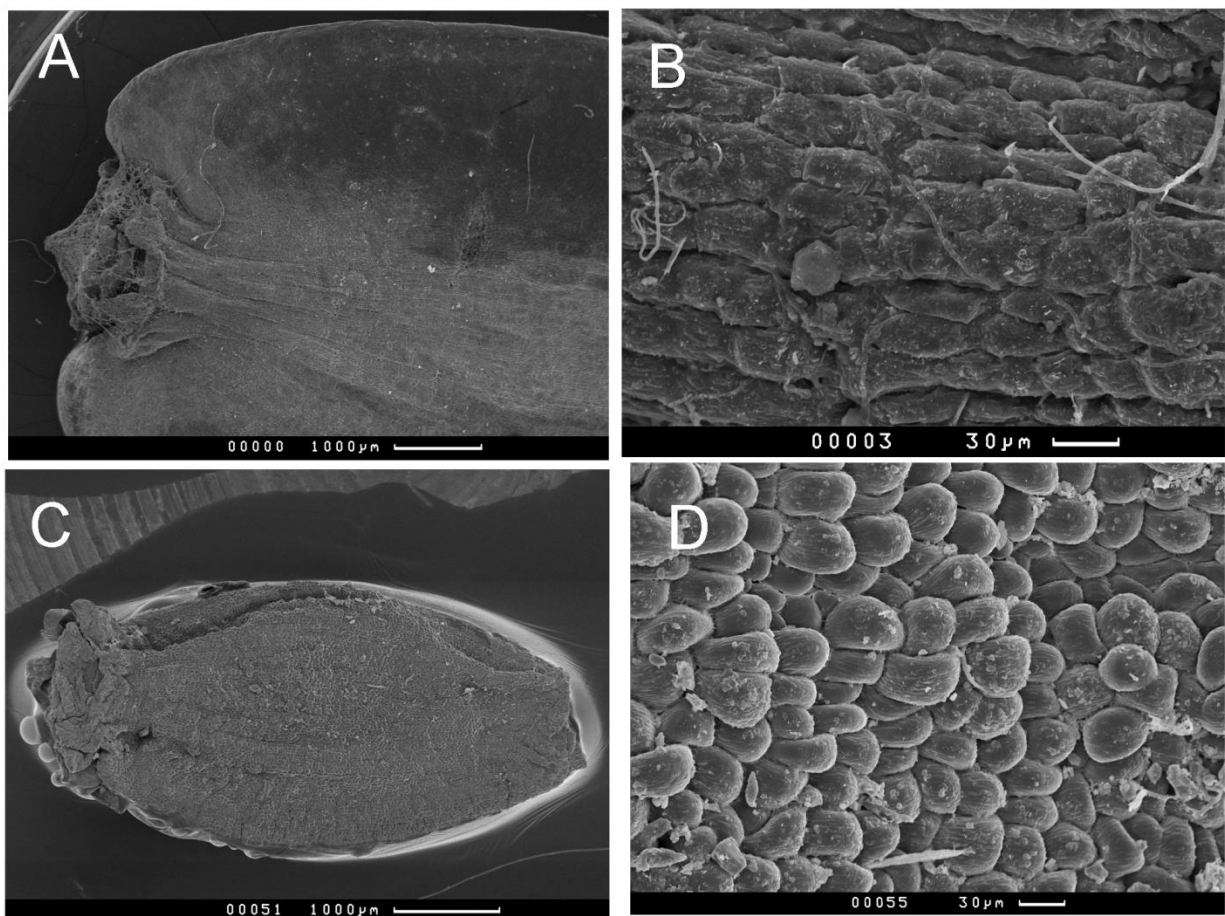


Figure 3. SEM images of fruits in *Taeniopetalum* species. – A, B: *T. obtusifolium* (Sm.) Pimenov; C, D: *T. urbani* (Freyn & Sint. ex H. Wolff) Pimenov. – A, C: mericarps; B, D: details of exocarp

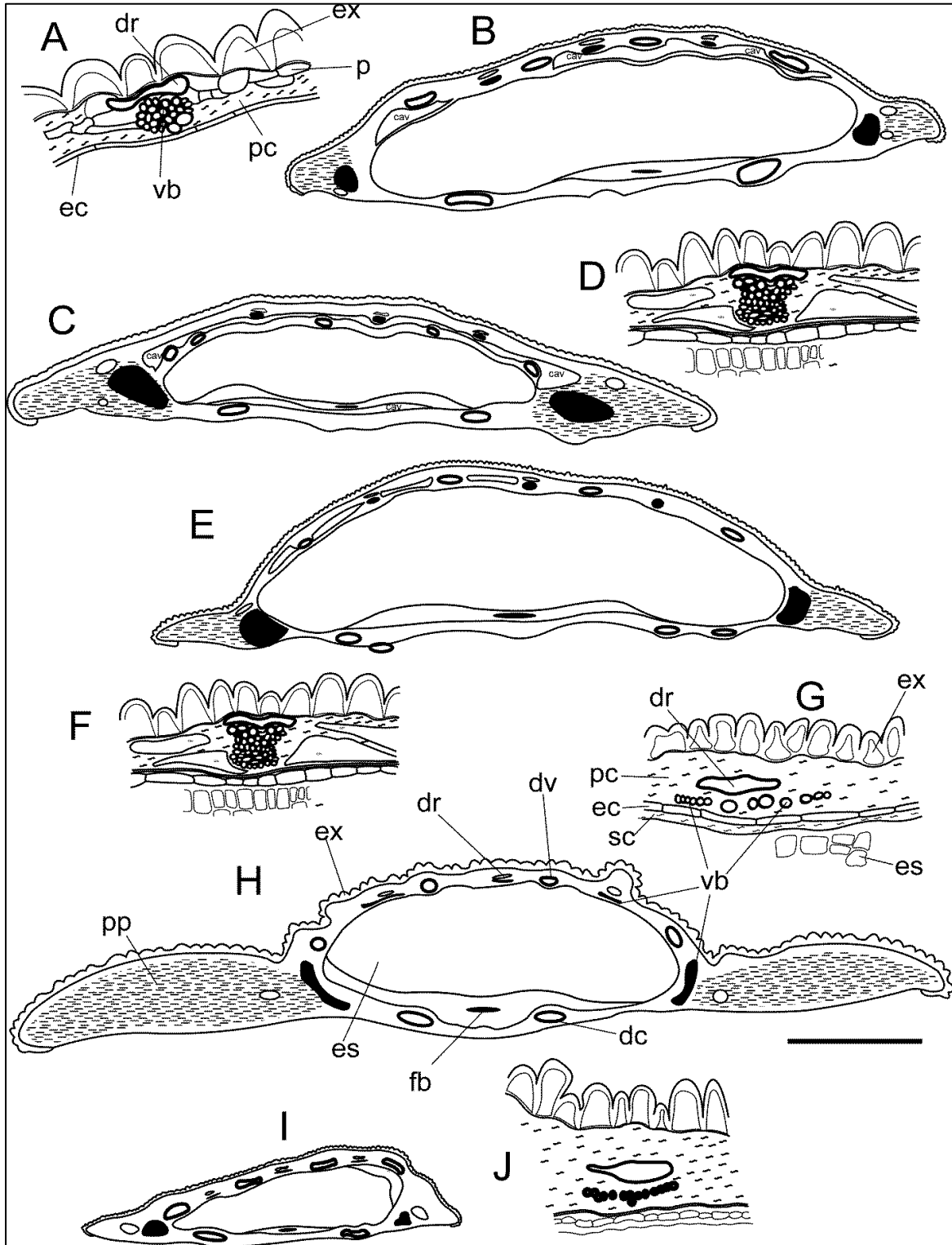


Figure 4. Mericarp cross-sections. – A, B: *Taeniopetalum arenarium* subsp. *arenarium*; C, D: *T. arenarium* subsp. *borysthenticum* (Klokov ex Schischk.) Pimenov & Ostr.; E, F: *T. arenarium* subsp. *neumayeri* (Vis.) Pimenov & Ostr.; G, H: *T. obtusifolium* (Sm.) Pimenov; I, J: *T. urbani* (Freyn & Sint. ex H. Wolff) Pimenov. – A, D, F, G, J: details of dorsal rib; B, C, E, H, I: mericarp cross-sections. Scale bars: B, C, E, H, I, =1 mm; A, D, F, G, J = 0.2 mm. (Abbreviations: cav – cavity, dc – commissural secretory duct, dr – rib secretory duct, dv – vallecular secretory duct, ec – endocarp, es – endosperm, ex – exocarp, fb – funicular bundle, p – parenchyma, pc – collapsed parenchyma, pp – lignified parenchyma with pitted cell walls, sc – seed coat, vb – vascular bundle)

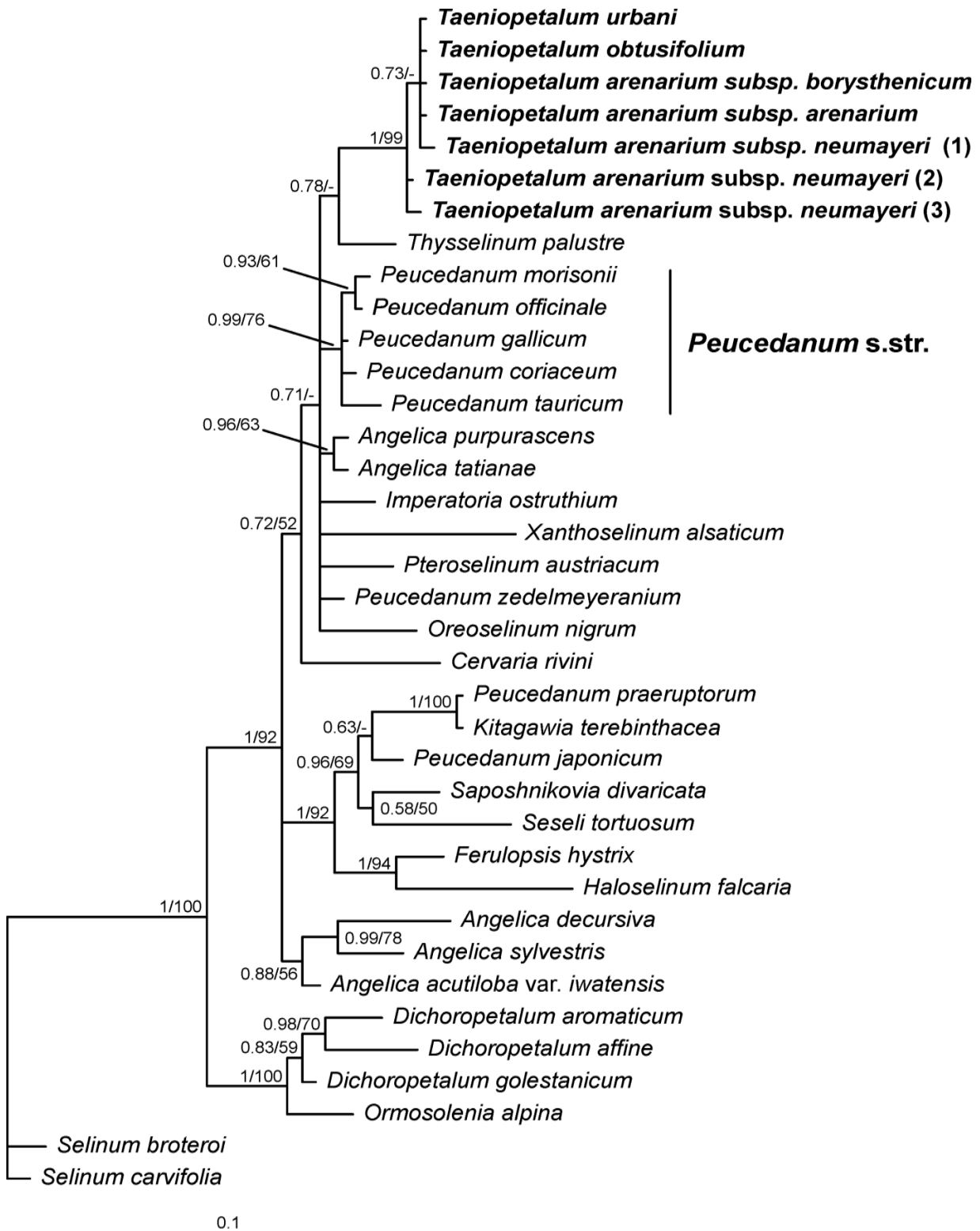


Figure 5. Bayesian tree obtained from analysis of 38 nrITS sequences. Branch lengths are proportional to the number of character changes. Maximum-parsimony bootstrap support and Bayesian posterior probabilities are indicated above nodes. *Peucedanum* s.str. group is indicated. Taxa belonging to *Taeniopetalum* according to newly accepted treatment are shown in bold

In the maximum parsimony analysis, 1368 shortest trees (274 steps) were found, CI (Consistency Index) 0.748 and RI (Retention Index) 0.823. Topologies of trees obtained from

maximum parsimony and Bayesian analyses were generally similar. Thus, only the Bayesian 50%-majority-rule tree with posterior probability values (PP) and parsimony bootstrap percentage (BS) is shown in Fig. 5. Both in maximum parsimony and Bayesian trees, all *Taeniopetalum* taxa group together, and this grouping is strongly supported (PP 1; BS 99%) by possessing seven nucleotide substitutions, five of which are unique. On the Bayesian tree, *Thysselinum* Adans. is moderately (PP 0.87) supported as sister to *Taeniopetalum*, while in the parsimony analysis, the position of *Thysselinum* is unresolved.

## Discussion

In current floristic literature, the genus *Taeniopetalum* is usually treated within *Peucedanum*, being separated sometimes as a section or a subgenus. Our molecular phylogenetic analyses show monophyly of *Taeniopetalum* and its distant placement from the type group of *Peucedanum* (*P. officinale* L. and its allies) in nearly the same manner as some presently accepted segregate genera, such as *Imperatoria* L., *Cervaria* Gaertn., *Haloselinum* Pimenov, *Dichoropetalum* Fenzl, and *Xanthoselinum* Schur. The discovered molecular differences between *Taeniopetalum* and *Peucedanum* attain even more significance when molecular data are compared with morphological. Therefore, we have every reason to treat *Taeniopetalum* as a separate genus. Although, on the one hand, ITS sequences clearly demonstrate a fairly isolated position of *Taeniopetalum* among segregate genera of *Peucedanum*, they are, on the other hand, of little use for species discrimination within the genus.

In the ITS tree, the species *Peucedanum obtusifolium* belongs to the same clade as the species of *Taeniopetalum*. *Peucedanum obtusifolium* and *Taeniopetalum* share fruit structure, especially micromorphological characters (large exocarp cells), but differ in the life form (polycarpic vs. monocarpic), habit (prostrate vs. erect), leaf structure (2–3-pinnate vs. 3–5-pinnate leaves), shape of distal cauline leaves (with small blades vs. without blades and reduced to sheaths) and fruit morphology (either with or without apical notch). Our results confirm *Peucedanum obtusifolium* placement with the other taxa of the genus *Taeniopetalum* and its treatment as a distinct species within that group.

Visiani (1850), while describing the new genus *Taeniopetalum*, mentioned colorless branched secretory ducts in the petals. Our study of petal morphology reveals that in all *Taeniopatalum* taxa petal secretory ducts are multiple, though indistinguishable on the

surface of intact petals. Multiple secretory ducts in petals have been found in other genera of Umbelliferae (Vinogradova, 1991; Zakharova *et al.*, 2012).

In our opinion, *Peucedanum arenarium*, *P. neumayeri* and *P. borysthenicum* are morphologically so similar to each other that it would be pointless to regard them as three separate species. They somewhat differ in petal color, fruit shape, length of pedicels and shape of leaf segments. The two most widely distributed *Peucedanum* species appear to differ from one another in their fruit shape: schizocarps of *P. arenarium* are obovoid to ellipsoid (rarely pyriform), whereas those of *P. borysthenicum* are pyriform (or else both pyriform and obovoid fruits occur on the same plant). We believe the status of subspecies (in the same way as *P. arenarium* subsp. *neumayeri*) is the most suitable for populations from Ukraine and the southern part of European Russia.

The taxonomic status of *Peucedanum urbani* treated by Chamberlain (1972) as a subspecies of *Peucedanum arenarium* constitutes another question. From other subspecies of *P. arenarium* mentioned above *P. urbani* differs in the number (2–4 vs. 5–14) and length (15–23 cm vs. 5–13) of rays in the central umbel and should be maintained as a separate species.

Relying on the results of molecular analyses and a study of the morphology and fruit anatomy, we propose to treat *Taeniopetalum* as a separate genus. With the inclusion of *Peucedanum obtusifolium* into *Taeniopetalum*, the genus contains 3 species, one of which has three subspecies. Below we present a taxonomic conspectus, which includes the new combinations *Taeniopetalum arenarium* subsp. *borysthenicum* (Klokov ex Schischk.) Pimenov & Ostr., *T. arenarium* subsp. *neumayeri* (Vis.) Pimenov & Ostr. and *T. obtusifolium* (Sm.) Pimenov, along with an identification key to the species and subspecies of *Taeniopetalum*.

### **Taxonomy and nomenclature**

*Taeniopetalum* Vis., Fl. Dalm. 3: 49. 1849.

≡ *Peucedanum* L. sect. *Taeniopetalum* (Vis.) Halácsy, Consp. Fl. Graec. 1: 639. 1901.

≡ *Peucedanum* L. subgen. *Taeniopetalum* (Vis.) Thell., Ill. Fl. Mit.-Eur. 5 (2): 1367. 1926.

**Type:** *Taeniopetalum neumayeri* Vis.

Perennial monocarpic or polycarpic herbs with taproot and single stem or with branched rootstock and several stems, with fibrous collar (remnants of leaves) at the base of stem. Stems solid, striate, glabrous. Petioles of basal leaves rounded on cross-section, solid,

with peripheral and central vascular bundles. Basal leaves glabrous, 2–4-pinnate, with straight rachis; primary and often secondary segments with petiolules, ultimate segments entire, linear, lanceolate or pinnatifid. Stomata hemiparacytic. Distal cauline leaves represented by slightly inflated sheaths, sometimes with tiny blades. Umbels corymbose with 2–16 unequal rays, without involucre or with 5–7 short involucre bracts. Umbelets compact with rather short pedicels and with 5–10 short involucel bracts. Calyx teeth triangular, up to 0.5 mm long. Petals greenish-white or yellow. Fruits glabrous, with fine-granular surface, strongly compressed dorsally, with filiform or inconspicuous dorsal ribs and broad, thick marginal wings. Exocarp of large convex cells, commissure broad. Mesocarp mostly of non-lignified parenchymatic cells, in mature fruits partly destroyed, lateral ribs filled with lignified parenchyma with pitted walls. Secretory ducts 1–2 in each vallecule, 2–4 at commissure, rib ducts in mature fruits small or inconspicuous. Endosperm on commissural side flat. Chromosome number  $2n = 22$ .

Three species and two subspecies.

*Peucedanum* s.l. is a polyphyletic group of plants with strongly dorsally compressed fruits, broad commissure and flat ventral side of endosperm. Many species were transferred to the genera *Cervaria*, *Dichoropetalum*, *Kitagawia* Pimenov, *Macroselinum* Schur, *Oreoselinum* Mill., *Rhizomatophora* Pimenov, *Thysselinum*, *Xanthoselinum*, *Imperatoria* L. and *Pteroselinum* Rchb.

*Taeniopetalum* differs from all the members of *Peucedanum* s.l. by large convex exocarp cells. In cladistics, this character is regarded synapomorphic.

*Cervaria* differs from *Taeniopetalum* in grooved petioles, large ovate dentate ultimate leaf segments, numerous umbel rays (11–30), prosenchymatic lignified inner mesocarp; *Dichoropetalum* – in grooved petioles without central bundles, leaves of many species having pinnatisect leaves with pinnatipartite segments, sessile primary segments (additionally, *D. caucasicum* (M.Bieb.) Soldano, Galasso & Banfi differs in large ovate dentate ultimate leaf segments, calyx teeth absent, some species have large rib secretory ducts); *Kitagawia* – in grooved petioles without central bundles, broad dentate or pinnatisect ultimate leaf segments, rather large distal cauline leaves, white petals; *Macroselinum* – in the absence of fibrous collar at the stem base, 1–2-pinnate leaves with sessile segments, entire broad, dentate ultimate segments, numerous (10–30) umbel rays, white petals; *Oreoselinum* – in geniculate leaf rachis, broad, dentate or lobate ultimate leaf segments, numerous (10–30) umbel rays, white petals, solitary vallecular secretory vittae and ducts located proximally of vascular

bundles; *Peucedanum* s.str. in yellow petals, fruits of some species with lignified prosenchyma in inner mesocarp, the chromosome numbers  $2n = 22, 66$ ; *Rhizomatophora* – in the absence of fibrous collar at the stem base, long rhizomes, fistulose petioles without central bundles, large broad dentate ultimate leaf segments, numerous (10–35) umbel rays, white petals, diacytic, paracytic and anomocytic stomata, mesocarp almost entirely of lignified pitted parenchyma; *Thysselinum* – in the absence of fibrous collar at the stem base, alate ribs along the stem, grooved fistulose petioles without central bundles, pinnatipartite leaf segments, numerous (15–40) umbel rays, rather large involucre bracts: *Xanthoselinum* in grooved petioles without central bundles, pinnatifid leaf segments (similar to those of *Selinum carvifolia*), large rib secretory ducts, *Imperatoria* – in the absence of fibrous collar, short rhizomes, unbranched stem, biternate leaves with broad dentate segments, distal cauline leaves with blades, numerous (up to 50) umbel rays, white or pink petals; and *Pteroselinum* – in the absence of fibrous collar, pinnatifid leaf segments (similar to those of *Selinum carvifolia*), rather large involucre bracts, white petals and prosenchymatic hypendocarp.

**Key to *Taeniopetalum***

- 1a.** Polycarpic herbs with branched rootstock; leaves 2–3-pinnate; first-order segments petiolulate, second-order segments sessile or with petiolules up to 5 mm, ultimate segments pinnatifid, bifid or simple, obtuse, elliptic to lanceolate; upper cauline leaves (except uppermost ones) with small blades. Fruits broadly ellipsoid to broadly obovoid, 8–15 mm long, 7–11 mm broad, with apical notch. Plants usually prostrate, up to 60 cm tall . . . . . ***T. obtusifolium***
- 1b.** Monocarpic herbs with taproot; leaves 3–5-pinnate; first- and second-order segments petiolulate, second-order petiolules 5–40 mm long; ultimate leaf segments entire or bifid, linear, oblong or narrowly elliptic, obtuse or acute; all cauline leaves in synflorescence region reduced to sheaths. Fruits ellipsoid, obovoid or pyriform, 5–9(10) mm long, 4–6 mm broad without apical notch. Plants erect, 30–200 cm tall . . . . . **2**
- 2a.** Central umbels with 2–4 rays, longest rays in central umbels 15–23 cm in fruit; pedicels very short, ca. 3–4 times shorter than fruits; leaf segments 1–1.2 mm broad . . . . ***T. urbani***
- 2b.** Central umbels with 5–14 rays, longest rays in central umbels 5–13 cm in fruit; pedicels short or long; leaf segments 0.8–4 mm broad (*T. arenarium*) . . . . . **3**
- 3a.** Petals greenish; fruits pyriform, rarely obovoid; leaf segments 1.5–3 mm broad. . . . .  
 . . . . . ***T. arenarium* subsp. *borysthenticum***

- 3b.** Petals yellow; fruits ellipsoid or obovoid, rarely pyriform; leaf segments 0.8–4 mm broad  
 ..... **4**
- 4a.** Pedicels 3–7 mm long, ca. twice shorter than fruits; leaf segments 1.5–4 mm broad . . . . .  
 ..... ***T. arenarium* subsp. *arenarium***
- 4b.** Pedicels 2–3 mm long, ca. 3–4 times shorter than fruits, leaf segments 0.8–2 mm broad . .  
 ..... ***T. arenarium* subsp. *neumayeri***

***Taeniopetalum arenarium*** (Waldst. & Kit.) V.N.Tikhom., Biol. Nauki (Moscow) 6: 76, 1987, p.p., quoad nomen.

***T. arenarium* subsp. *arenarium*** ≡ *Peucedanum arenarium* Waldst. & Kit., Descr. Icon. Pl. Hung. 1: 18, tab. 20. 1800; Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30, 1: 1036. 1927; Todor, Fl. Republ. Socialist. Roman. 6: 606. 1958; Soó, Magyar Fl. 2: 482. 1966; Tutin, Fl. Eur., ed. 2, 2: 362. 1968; Nikolich, Fl. Srbije 5: 285. 1973; Assyov et al., Consp. Bulg. Vasc. Fl.: 289. 2006. ≡ *Angelica arenaria* (Waldst. & Kit.) M.Hiroe, Umbel. World: 1351. 1979.

**Type:** Hungary: ‘Crescit in clivis arenosis Pestini, ad Gödellő, Száda, Vörös-Egyház.’ (lectotype PR!, designated by Chrtek and Skocdoplova, 1982).

**Distribution** (Fig. 6.): Serbia (Vojevodina and Danube Valley above Belgrade), Romania, Hungary, Slovakia, Ukraine (SW). In Slovakia three regions of distribution known in the past are now reduced to one locality, namely Sandberg Hill (Devínska Kobyla) near Bratislava. The plant is included in the Red List (Šerá *et al.*, 2005). In the Czech Republic the species is considered extinct (Procházka, 2001). In Romania it is also included in the Red List (Dihoru and Dihoru, 1994). The boundary between *T. arenarium* subsp. *arenarium* and *T. arenarium* subsp. *borysthenticum* in eastern Romania is not completely clear to us due to a lack of plants with mature fruits. The studied samples from adjacent Moldova belong to *T. arenarium* subsp. *borysthenticum*.

***T. arenarium* subsp. *borysthenticum*** (Klokov ex Schischk.) Pimenov & Ostr., **comb. nov.** (urn:lsid:ipni.org:names: 77158568-1).

≡ *Peucedanum borysthenticum* Klokov ex Schischk., Fl. URSS 17: 354. 1951.

**Type:** Ukraine: ‘Prope oppidum Dnepropetrovsk [Ekaterinoslav, now Dnepr], in arenosis ad ripam Borysthensis’, 20.VIII.1901, *Akinfiev* (holotype LE!).

**Distribution** (Fig. 6.): Ukraine, South European Russia: Voronezh Region, Rostov Region, Volgograd Region. Sandy steppes.



**Note:** Klokov (1950, 1951; Schischkin, 1951) distinguished the new species, *Peucedanum borysthenicum*, from *P. arenarium* in having more numerous umbel rays (7–10 vs. 5–7 in the latter), which become contracted at fruiting stage. We could not decisively confirm the latter difference; as to the number of umbel rays, it is variable both in Hungary and East Europe, the change being gradual, without a gap. However, we did find the following differences: fruits are ellipsoid to obovoid and petals yellow in *Taeniopetalum arenarium* ssp. *arenarium* s.str. (from Hungary), while fruits are pyriform and petals greenish-yellow in *T. arenarium* ssp. *borysthenicum*. However, these differences are not absolute (Table 1).

***T. arenarium* subsp. *neumayeri* (Vis.) Pimenov & Ostr., comb. nov.**

(urn:lsid:ipni.org:names: 77158569-1).

≡ *Taeniopetalum neumayeri* Vis., Fl. Dalm. 3: 49, 1849. ≡ *Peucedanum neumayeri* (Vis.) Rchb. f., Icon. Fl. Germ. Helv. 21: 63, tab.64. 1865; Calestani, Webbia 1:239. 1905; Hayek, Repert. Spec. Nov. Regni Veg. Beih. 30, 1: 1035. 1927. ≡ *Peucedanum arenarium* Waldst. & Kit. var. *neumayeri* (Vis.) Malý, Glasn. Zemaljsk. Muz. Bosni Hercegovini 30: 79. 1919. ≡ *Peucedanum arenarium* Waldst. & Kit. subsp. *neumayeri* (Vis.) Stoj. & Stefanov, Fl. Bulg., ed. 3: 857. 1948; Tutin, Fl. Eur., ed. 2, 2: 362. 1968.

**Type:** Croatia. ‘In monte Dinara’, *A. Mazzolini* (lectotype PAD!, **designated here** by Pimenov and Ostroumova); ‘In vineis rupestribus insulae Jaklian prope Ragusa’ [Dubrovnik]. *F. Neumayer* (syntype PAD!).

= *Peucedanum macedonicum* Janka, Oesterr. Bot. Z. 23: 203. 1873; Boiss., Fl. Orient., Suppl.: 1018. 1888; Calestani, Webbia 1: 239. 1905.

**Type:** Bulgaria. ‘In Macedonia orientali: in collibus margaceis ad ped. m. Perim-Dagh.’ 20.VIII.1871, *Janka*.

= *Peucedanum serpentini* Andras. & Jávorka, Bot. Közlem. 19: 25. 1921.

**Type:** Albania: ‘In locis ombrosis ad jugum Čafa-Morina inter Djakova et Tropoja’, 31.VII.1917, *Andrasovszky* (lectotype BP; designated by Kováts, 1998: 126; see also Pifkó 2004: 67, fig. 3; isolectotypes BP, K!).

**Distribution** (Fig. 6.): Croatia, Bosnia and Herzegovina, Montenegro, Albania, Macedonia, Bulgaria, northern Greece, Turkey (Muğla – a locality isolated from the rest of the area).

We could not locate any reliable collection from the territory of the modern Macedonia (FYROM). In Greece the species was first reported from the Timfi Mts. (Authier, 1991), then from Konitsa, Kastoria (Konstantinidis and Kamari, 2000), and Mt. Smolikas (Evergetis *et al.*, 2012). Finally, *Peucedanum arenarium* subsp. *neumayeri* was discovered in Northern

Pindos, North Central, and Northeast floristic regions of Greece (Dimopoulos *et al.*, 2013). Stony slopes, screes, serpentines. Lubarda *et al.* (2014) attribute *Taeniopetalum neumayeri* to the Pontic chorological group (this is true for the entire species *T. arenarium*), the Illyrian-Balkan chorological subgroup and the East Illirian-Balkan-Moesian floristic element. In Turkey the species was qualified as vulnerable (Özhatay *et al.*, 2008–09).

***Taeniopetalum obtusifolium*** (Sm.) Pimenov, **comb. nov.**

(urn:lsid:ipni.org:names:77158570-1).

≡ *Peucedanum obtusifolium* Sm., Fl. Graec. Prodr. (J.Sibthorp & J.E.Smith) 1: 189. 1806; Fl. Graec. 3: 70. 1821; Degen, Oesterr. Bot. Z. 47 (2): 52. 1897; Halácsy, Consp. Fl. Graec. 1: 640. 1901; Calest., Webbia 1: 230. 1905; Hayek, Rep. Spec. Nov Regni Veg. Beih. 30(1): 1035. 1927; Webb, Proc. Roy. Irish Acad. 65 (1): 47. 1966; Chamberlain., Fl. Turkey (P.H.Davis, ed.): 477. 1972. ≡ *Ferula obtusifolia* (Sm.) Spreng., Sp. Umbell.: 80. 1818; Spreng., Syst. Veget., ed. 16 (C.P.J.Sprengel) 1: 914. 1824. ≡ *Pastinaca obtusifolia* (Sm.) DC., Prodr. 4: 190. 1830. ≡ *Malabaila obtusifolia* (Sm.) Boiss., Fl. Orient. 2: 1054. 1872; Degen, Oesterr. Bot. Z. 45 (2): 67. 1895.

**Type:** Greece and Turkey: ‘In Boeotia [Greece] et ad Ponti Euxini littora [Turkey]’, *Sibthorp* (lectotype OXF!, **designated here** by Pimenov; isolectotype BM, n.v. indicated by Chamberlain, 1972: 477). There is no herbarium documentation for the species distribution either in Boeotia (a district of Ancient Greece northwest of Athens) or in Greece as a whole. Webb (1966) noted that the species has never been relocated in *locus classicus* (eastern Greece).

**Distribution** (Fig. 6.): Turkey (European: Kirklareli, Istanbul; N (Pontic) Anatolia: Istanbul, Kocaeli, Sakarya, Zongultak); Bulgaria (Black Sea – Ostroumova & Stoyanov (2016)); at maritime sands. The species is not included in the modern checklist of vascular plants of Greece (Dimopoulos *et al.*, 2013). In Turkey the species was qualified as vulnerable (Özhatay *et al.*, 2008-09).

***Taeniopetalum urbani*** (Freyn & Sint. ex H.Wolff) Pimenov, Pl. Biosystems 148(5-6): 1108. 2014. ≡ *Peucedanum urbani* Freyn & Sint. ex H.Wolff, Repert. Spec. Nov.Regni Veg. 20: 68. 1924; Rech.f., 1943, Fl. Aegaea: 413. 1943. ≡ *Peucedanum arenarium* Waldst. & Kit. subsp. *urbani* (Freyn & Sint. ex H.Wolff) Chamberlain, 1972, Fl. Turkey (P.H.Davis, ed.) 4: 478.

**Type:** Turkey: ‘Troas: in monte Ida [Kaz Da.] in decliv. montosis circa fontis Scamandri’, 29.VII.1883. *Sintenis* 494 (lectotype G!, designated by Pimenov and Sutorý, 2014: 1108; isolectotypes BM!, BR, E!, GOET, K!, LD!, LE!, P!, US!, W!). Note: in some herbaria (for

instance, in S) a quite different plant belonging to *Dichoropetalum* (probably, to an undescribed species) is kept with the same label and under the same number 494.

**Distribution** (Fig. 6.): Turkey (W Anatolia: Çanakkale, Balıkesir). Stony slopes. In Turkey the species was qualified as endangered (Özhatay *et al.*, 2008-09).

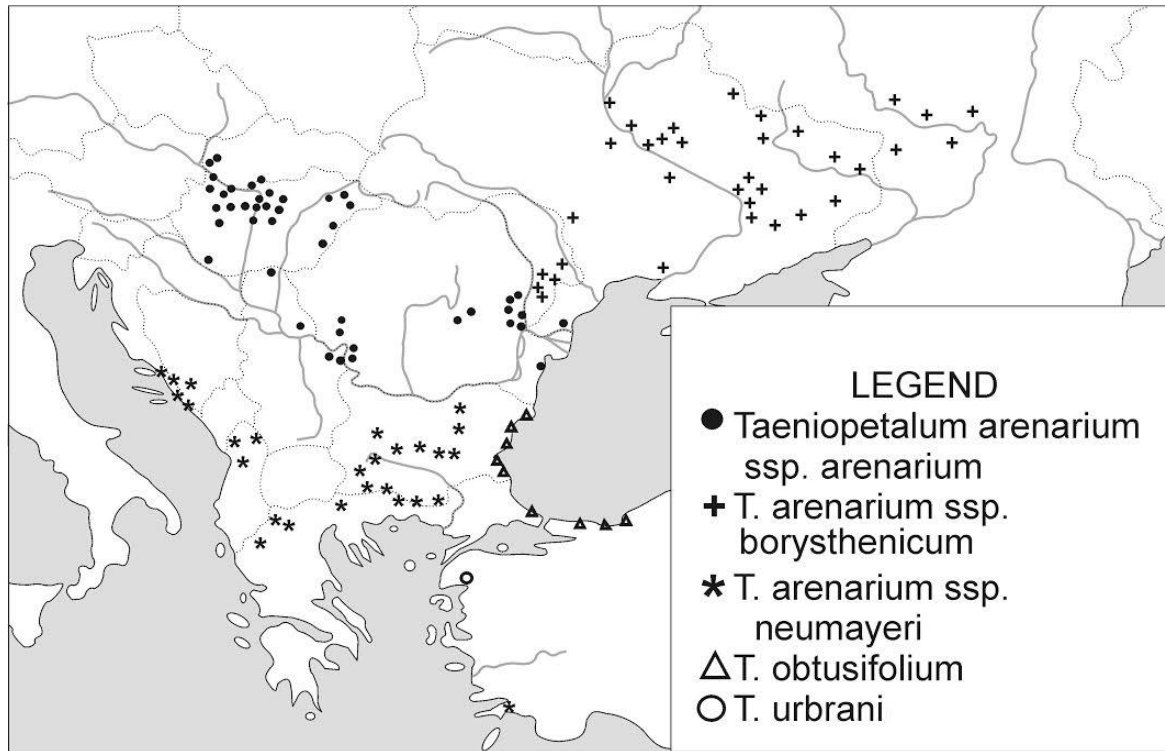


Fig. 6. Distribution of *Taeniopetalum* taxa

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**Appendix.** Voucher information and GenBank accession numbers for plants used in the present study.

New ITS sequence data:

***Taeniopetalum arenarium*** (Waldst. & Kit.) V.N.Tikhom. subsp. ***arenarium***: (1) [= *Taeniopetalum arenarium* (Waldst. & Kit.) V.N.Tikhom.] Hungary, Budapest Comit, 25.VII.1911, *J.B.Kümmeler et al.* 65 (LE), KT282437; (2) [= *Peucedanum arenarium* Waldst. & Kit.] Slovakia, Presburg, Neudorf, 29.IX.1875, *J.Wiesbauer s.n.* (K), KT282439. ***Taeniopetalum arenarium*** (Waldst. & Kit.) V.N.Tikhom. subsp. ***borysthenicum*** (Klokov ex Schischk.) Pimenov & Ostr.: (1) [= *Taeniopetalum arenarium* (Waldst. & Kit.) V.N.Tikhom.] Russia, Volgograd Region, 3 km from Shelekhovo, 11.VI.2005, *M.G.Pimenov et I.A.Schanzer* 60 (MW), KT282441; (2) Ukraine, Kiev, IX.1889, *I.Schmalhausen s.n.* (LE), KU307263; (3) Ukraine, Dnipropetrovsk prov., 26.VIII.1940, *M.Klokov s.n.* (LE), KU307265; 4) Ukraine, Poltava Region, Prokhorovka, 23.VIII.1948, *M.Kotov s.n.* (LE), KU307264. ***Taeniopetalum arenarium*** (Waldst. & Kit.) V.N.Tikhom. subsp. ***neumayeri*** (Vis.) Pimenov & Ostr.: (1) [= *Peucedanum neumayeri* (Vis.) Rchb.f.] *P.Hartvig et P.Strid* 24190 (C), KT282433; (2) [= *Peucedanum neumayeri* (Vis.) Rchb.f.] Herzegovina, in declivibus lapidosis faucibus Narenta prope Grabovica, 07.IX.1907, *K.Maly s.n.* (K), KT282434; (3) [= *Peucedanum neumayeri* (Vis.) Rchb.f.] Dalmatien, Ragusa, 16.XI.1910, *A.Hayek s.n.* (WU), KU307266. ***Taeniopetalum obtusifolium*** (Sm.) Pimenov: (1) Bulgaria, slopes to south from Primorsko village, 07.IX.2015, *T.A.Ostroumova s.n.* (MW), KU307267; (2) [sub *Peucedanum arenarium* Waldst. & Kit.] Bulgaria, locality Arkutino, South Black Sea coast, Bourgas distr., 03.X.2008, *Gussev, Stoeva & Bosseva s.n.*, KT282436; (3) [sub *Peucedanum arenarium* Waldst. & Kit.] Bulgaria, Burgas prov., 33 km NE of Burgas, 42°42'N, 27°42'E, 07.VIII.1988, *S.L.Jury & S.P.Thornton-Wood* 9532 (MHA), KT282438; (4) Turkey, A2(E), Istanbul, Kilyos, 41°14'N, 29°08'E, 18.VII.2007, *M.G.Pimenov & E.V.Kljuykov* 134 (MW), KT282440. ***Taeniopetalum urbani*** (Freyn & Sint. ex H.Wolff) Pimenov: [= *Peucedanum urbani* Freyn & Sint. ex H.Wolff] Turkey, Troas, Kaz Da Mts., 29.VII.1883, *P.Sintenis* 494 (W), KT282435.

Previously published ITS sequence data:

***Angelica acutiloba*** (Siebold & Zucc.) Kitag. var. ***iwatensis*** (Kitag.) Hikino, AB697607. ***Angelica decursiva*** Franch. & Sav., JX022912. ***Angelica purpurascens*** (Avé-Lall.) Gilli, AF008611. ***Angelica sylvestris*** L., HQ256681. ***Angelica tatianae*** Bordz., AF008610, AF009089. ***Cervaria rivini*** Gaertn. [= *Peucedanum cervaria* Cusson ex Lapeyr.], AF009087, AF008608. ***Dichoropetalum affine*** (C.A.Mey.) Pimenov [= *Peucedanum pschawicum* Boiss.], AF008619, AF008690. ***Dichoropetalum aromaticum*** (Rech.f.) Pimenov & Kljuykov [= *Johrenia aromatica* Rech.f.], EU169288. ***Dichoropetalum goletanicum*** (Rech.f.) Pimenov & Kljuykov [= *Johrenia goletanica* Rech.f.], EU169289. ***Ferulopsis hystrix*** (Bunge ex Ledeb.) Pimenov, EU169271. ***Haloselinum falcaria*** (Turcz.) Pimenov [= *Peucedanum falcaria* Turcz.], FJ489365, FJ489366. ***Imperatoria ostruthium*** L., AF077896. ***Kitagawia terebinthacea*** (Fisch. ex Trevir.) Pimenov [= *Peucedanum terebinthaceum* (Fisch. ex Trevir.) Ledeb. JF977820. ***Oreoselinum nigrum*** Delarbre [= *Peucedanum oreoselinum* (L.) Moench], AF495836, AF495837. ***Ormosolenia alpina*** (Sieber ex Schultes) Pimenov, HQ269391. ***Peucedanum coriaceum*** Rchb., AF495824, AF495825. ***Peucedanum gallicum*** Latour., AM408882. ***Peucedanum japonicum*** Thunb., AF495826. ***Peucedanum morisonii*** Besser ex Schult., AF077903. ***Peucedanum officinale*** L., AF495820, AF495821. ***Peucedanum praeruptorum*** Dunn, DQ132871. ***Peucedanum tauricum*** M.Bieb., AM408884; ***Peucedanum zedelmeyerianum*** Manden., AF164834, AF164859. ***Pteroselinum austriacum*** (Jacq.) Rchb. [= *Peucedanum austriacum* (Jacq.) W.D.J.Koch], AF495842, AF495843. ***Saposhnikovia divaricata*** (Turcz.) Schischk., AF495838, AF495839.



*Selinum broteroi* Hoffmanns. & Link, AY179029. *Selinum carvifolia* (L.) L., AY328930, AY179028. *Seseli tortuosum* L., AY179031. *Thysselinum palustre* (L.) Hoffm., AY179035. *Thysselinum lancifolium* (Hoffmanns. & Link) Calest., AY179036. *Xanthoselinum alsaticum* (L.) Schur, AF495834, AF495835.