

Notes on the taxonomy of *Pseudolysimachion longifolium* complex (Scrophulariaceae)

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ABSTRACT: The taxonomic evaluation of the *Pseudolysimachion longifolium* complex revealed differences between western (i. e., European and W Asian) populations and the other Asian plants. The examination of lectotype specimens of *Veronica longifolia* L. (≡ *Pseudolysimachion longifolium* (L.) OPIZ) and *Veronica maritima* L. (≡ *Pseudolysimachion maritimum* (L.) Á. & D. LÖVE) showed that the former name refers to the eastern populations whilst the latter belongs to the European/W Asian plants. The recognition of two subspecies within *Pseudolysimachion maritimum* is shown to be doubtful. Taxonomic position of *Pseudolysimachion septentrionale* (BORISS.) Á. & D. LÖVE and *P. taigischense* (STEPANOV) HOLUB is discussed.

KEYWORDS: *Pseudolysimachion longifolium* complex, taxonomy, nomenclature, distribution

Introduction

In the course of the study of the taxonomy and distribution of the genus *Pseudolysimachion* (KOCH) OPIZ in the Czech Republic (TRÁVNÍČEK 2000) and Slovakia (TRÁVNÍČEK 1997), a special attention had to be concentrated on the highly variable species *P. longifolium* s. lat. In addition to the investigation of the herbarium material from various parts of the distribution range of the species (main herbaria consulted were BRA, BRNM, BRNU, LIM, LTM, MMI, OL, OLM, OP, PR, PRC, ROZ, SAV, SLO; abbreviations by HOLMGREN et al. 1990), a

relatively detailed field examination of its variation and distribution of the diploid and tetraploid cytotypes in Czechia and Slovakia was carried out (TRÁVNÍČEK & VINTER 1999, TRÁVNÍČEK et al. 2001). Attention was also paid to the nomenclatural problems in the group.

A brief history of the taxonomic treatment

Problems of the taxonomy of the *Pseudolysimachion longifolium* complex were dealt with by a number of authors in the past. LINNAEUS himself (1753: 10) recognized two species of the group, *Veronica maritima* L. and *V. longifolia* L. In the 19th century, a period when taxonomy was based almost purely on morphological grounds, the conspicuous variability of the group of *Pseudolysimachion longifolium* attracted the attention of many botanists (see, for instance, SCHRADER 1803, ROEMER & SCHULTES 1817: 95, 96, OPIZ 1825: 109, 110 and 244, HOST 1827: 3-5, SEIDL in BERCHTOLD & SEIDL 1836: 30, 31, SCHUR 1866: 498, etc.). They introduced a series of species names, many of them, however, must be considered as taxonomic synonyms nowadays (see RÖMPP 1928: 47, 48, HÄRLE 1932: 16, 17, STROH 1942: 390, 391). One of the most remarkable contributions to the understanding of the taxonomy of the group is found in PRINTZ (1921: 380-384, t. X, XI), where *Veronica pseudolongifolia* PRINTZ was described, and an important fact was pointed out that the Siberian populations of the group were noticeably different from the European ones. Until recently, nevertheless, the latter work has remained neglected. It was the conspicuous morphological diversity of the European plants, and the relatively early discovery of the karyological variation within the group that absorbed an effort of recent students (HÄRLE 1932: 14-22, GRAZE 1933: 519-521, 1935, LEHMANN 1940: 480-487, SKALICKÝ 1956, HARTL 1966: 150-153, BORSOS 1967: 7-10, RAITANEN 1967, M. A. FISCHER 1969: 437-439, KUKKONEN 1986). A problem of the correlation between morphological traits of European plants and the ploidy level was addressed several times. Moreover, BORISSOVA (1955a: 341-343) proposed a separate, specific status for slightly aberrant northern populations of the group (see also HÄRLE 1932: 21) under the name *Veronica septentrionalis* BORISS. (= *Pseudolysimachion septentrionale* (BORISS.) Á. & D. LÖVE). On the other hand, a more separate position of the eastern, Siberian populations of the *Pseudolysimachion longifolium* group was generally considered as unjustified, or the problem was avoided (cf. MONJUSCHKO 1924: 117, 118, HÄRLE 1932: 20, BORISSOVA 1955b: 368 (see the synonymy), SKALICKÝ 1956: 128, ELENEVSKIJ 1968, STEPANOV 1997: 93). Only in the last decades, a certain distinctiveness of the Asiatic populations and their more or less separate status has been accepted again (BELJAEVA & SIPLIVINSKIJ 1975: 869, VOROSCHILOV 1982 sec. STEPANOV 1997: 93, IVANINA 1991: 313, TRÁVNÍČEK 1997: 270, HOLUB 1998: 109).

***Pseudolysimachion longifolium* s. lat. in Europe – one or two species ?**

The central, principal problem of the taxonomic investigation of the *Pseudolysimachion longifolium* group in Europe in the 20th century is represented by the above question. LINNAEUS (1753: 10) distinguished his two species *Veronica maritima* and *V. longifolia* primarily on the basis of the number of leaves per node and the character of indentation of leaf margins:

V. maritima: „spicis terminalibus, foliis ternis inaequaliter serratis“,

V. longifolia: „spicis terminalibus, foliis oppositis lanceolatis serratis acuminatis“.

The most remarkable gross morphological variability of the European *Pseudolysimachion longifolium* s. lat. is indeed exhibited by the arrangement of leaves along the stem and by the leaf shape, and it is therefore not possible to disregard the differences emphasized by LINNAEUS. The main difficulty in the taxonomic application of these characters consists in the fact that the two forms do not differ significantly in their ecological requirements nor they do form distinct populations. It is a well know fact, moreover, that they are linked by a series of intermediate morphotypes (HÄRLE 1932: 15, SKALICKÝ 1956: 125, 130, BORSOS 1967: 7, RAITANEN 1967: 483, 484). On the other hand, there have been two major arguments preventing botanists to treat the two forms as taxonomically identical. First, the morphotype 'maritima' predominates in northern Europe (and particularly on coastal habitats in Scandinavia) and hence there is a certain geographical (and, maybe, also ecological?) preference (LEHMANN 1940: 485, 486). It is, however, rather weak because the 'maritima' morphotype is found, relatively less frequently, in other parts of the European range of the species (HÄRLE 1932: 14, 15, LEHMANN 1940: 485, SKALICKÝ 1956: 125) where it forms mixed populations with the 'longifolia' form. In addition, even in the regions dominated by the 'maritima' morphotype the other form is not rare, either (RAITANEN 1967, KUKKONEN 1986; the author's herbarium findings). The difference merely consists in the relative frequency of the two forms in different regions.

The other circumstance supporting the apparent separate status of the two morphotypes is the absolute prevalence of diploids in the regions with the 'maritima' morphotype predominating (RAITANEN 1967: 471, KUKKONEN 1986: 41, TRÁVNÍČEK et al. 2000). Also the first chromosome counts made on plants more exactly characterized morphologically (HÄRLE 1932, GRAZE 1933: 519-521, 1935) pointed to a certain correlation between the ploidy level and the morphology of the samples analysed. As a consequence, the 'maritima' morphotype has repeatedly been characterized as diploid, and the 'longifolia' form as tetraploid in the literature (GRAZE 1935, LEHMANN 1940: 481, 482, HARTL 1966: 152, 153, M. A. FISCHER 1969: 438, ROTHMALER et al. 1982: 465). However, results of detailed studies of RAITANEN (1967) and KUKKONEN (1986) in Finland cast serious doubts on the above generalization. The Finnish plants were found (with a single exception) diploid but the ploidy level was recorded in the 'longifolia' morphotype, too.

A thorough evaluation of the distribution of the two cytotypes in Czechia and Slovakia yielded the following results (TRÁVNÍČEK et al. 2001, TRÁVNÍČEK & VINTER 1999):

- Tetraploid plants largely prevail; among 45 populations, only four proved to be diploid (in two geographically remote couples of populations). This situation substantially differ from that found in Finland.
- No population was comprised of both cytotypes.
- No clear correlation was ascertained between the ploidy level and the basic two morphotypes. Plants with 3(4) leaves per whorl were found either diploid or tetraploid, and the same applies to the opposite-leaved plants. The absolute majority of populations contained various morphotypes, not only the typical 'maritima' and 'longifolia' but also diverse intermediates. It turns out that the variation of leaf arrangement and shape cannot be classified as two main types, and that the character of variation is more complex (see also BORSOS 1967: 7-9).
- Certain differences were found between the two cytotypes in quantitative characters but the differences are manifested in the average population values and need not concern all individuals. Individual variation within populations is considerable, and some diploid plants may show values typical of tetraploids and *vice versa*. The determination of ploidy levels according to the quantitative morphological traits is therefore very unreliable.
- No differences have been observed in the ecological requirements of the two forms.

The above facts combined with further information from the literature make it possible to draw the following conclusions:

1. In spite of a certain difference in the geographical distribution between the two main morphotypes within the European populations of *Pseudolysimachion longifolium* s. lat., and although there is a weak correlation between the morphology and the ploidy level, the differentiation does not suffice to distinguish two separate taxa at the level of species or subspecies. The absence of features of qualitative nature may suggest that the tetraploids represent an autopoloid derivative of diploids. It is possible that the occurrence of certain prevailing character combinations in some regions (for instance, in Scandinavia) is a result of the partial ecological and geographical isolation. The isolation appears to be too incomplete and short, however, to lead to the formation of distinctly differentiated population structures that might be evaluated as subspecies.
2. Despite the fact that the coexistence of the two ploidy levels within populations has not been ascertained in Czechia and Slovakia, it cannot be excluded elsewhere in view of the sympatric overall distribution ranges and the indistinct differences in their ecology (see TRÁVNÍČEK et al. 2001). As shown by HÄRLE (1932) and GRAZE (1933, 1935), the gene flow between different ploidy levels in the genus *Pseudolysimachion* is not impossible. Crossing between a diploid (as a maternal plant, in particular) and a tetraploid may give rise to a fertile tetraploid hybrid (GRAZE 1933: 556, 1935:

658, 659). This process was also proven in the case of the two cytotypes of the European *P. longifolium* s. lat. (GRAZE 1935: 636, 654). It is likely that a tetraploid hybrid may easily backcross with its tetraploid parent. In mixed populations, this process may lead to a gradual elimination of diploids, and a change towards a purely tetraploid population may be expected. If a usual higher competitive ability of established polyploids (upon comparison with their diploid ancestors) is taken into account, the above process may be a very plausible scenario accounting for the prevalence of tetraploid populations in the area studied. Provided that such a process really takes place, the diploid populations might represent relict groups of individuals not yet absorbed by the gradually expanding tetraploid populations.

In this connection, it may be useful to mention that, in S Scandinavia, a hybridization was observed between the diploid *Pseudolysimachion longifolium* s. lat. and the tetraploid *P. spicatum* (L.) OPIZ subsp. *spicatum* (RAITANEN 1967, and the author's herbarium observations). These hybrids probably are tetraploid and, in all likelihood, frequent backcrosses with the tetraploid *P. spicatum* occur. Most of the hybrids are closer to *P. spicatum*, and it is impossible to draw a line between them and the 'true' *P. spicatum* (RAITANEN 1967: 483). In this case, a total disappearance of the diploid *P. longifolium* (s. lat.) is prevented by the substantially different ecological requirements of the two species.

By all accounts, the above picture of the relationships between the diploid and the tetraploid cytotypes within *P. longifolium* s. lat. in Europe gives arguments in favour of accepting a single, morphologically and karyologically variable species (see also TRÁVNÍČEK et al. 2001).

***Pseudolysimachion longifolium* s. lat. in Euroasia: one or two species ?**

In a broader circumscription, *Pseudolysimachion longifolium* occupies an extensive, Euroasian geographical range (cf. WALTERS & WEBB 1972: 251, BORISSOVA 1955b: 368-369, ELENEVSKIJ 1968: 66, YAMAZAKI 1957: 135, 1968: 409 etc.). In Europe, it occurs from France, Belgium, Holland and NW Germany to Denmark, Scandinavian countries (reaching Lapland, and the Pechora River basin up to Kolguev Island in the north). Its southern limit is found in S Italy, the former Yugoslavia, and from Bulgaria to Turkey (M. A. FISCHER 1978: 688). From Ukraine and European Russia it extends to the North Caucasus but does not reach Crimea in the south. The Asian part of its range includes Siberia from the Urals to the basins of rivers Khatanga, Lena and Kolyma. In the south, it occupies a territory from Aralo-Caspian region to the Tien-Shan, Balkhash Lake, the Altai, N Mongolia, and eastwards through the Baikal Lake area to the Okhotsk Sea, Amur basin, Mandshuria and North Korea. It is reported from Sakhalin (IVANINA 1991: 313, 315). Records from Japan probably refer to other, closely related taxa (cf. YAMAZAKI l. c.).

In 1921, PRINTZ (1921: 380-384, t. X, XI) published a description of a new species, *Veronica pseudolongifolia*. The description was based on plants from

southern Krasnoyarsk region (upper Yenisei River basin). PRINTZ gave a detailed comparison of his new species with the European *V. „longifolia”* and with *Veronica spuria* L. (= *Pseudolysimachion spurium* (L.) RAUSCHERT). *Veronica pseudolongifolia* is reported to differ from the European *V. „longifolia”* primarily by remarkably shorter petioles (only 1-2 mm long), always rounded or slightly cordate (not cuneate) leaf blade base, usually almost entirely glabrous leaves (if hairy then trichomes confined to veins beneath), short pedicels (c. 1 mm long), shorter bracts, shorter, ovate, usually obtuse (not lanceolate, distinctly acute) calyx teeth, tooth margins with short glandular hairs. In addition to the region mentioned, PRINTZ reports his new species from more northerly regions in the Yenisei valley, at about 60°N. On the basis of his study of the herbarium material at Botanical Gardens, St. Peterburg (LE nowadays), PRINTZ suggested that *V. pseudolongifolia* extended throughout Siberia, westwards approximately to the Tomsk region. PRINTZ also supposed that *V. pseudolongifolia* substituted the related species, “*V. longifolia*” and *V. spuria* in that territory.

MONJUSCHKO (1924: 117, 118) discussed the question of the separate status of *Veronica pseudolongifolia* when describing a new species *V. komarovii* MONJUSCHKO from the Far East (Amur, Mandshuria, Korea). Based on a herbarium study at LE, he did not accept *V. pseudolongifolia* as a separate species. The main support for his conclusions is the fact that the Siberian population almost always have pedicels (and often petioles) longer than the measurements given by PRINTZ. This was confirmed by HÄRLE (1932: 20) who studied Siberian material in the Moscow University herbarium (MW). On the other hand, he pointed out the fact that the eastern plants have exclusively opposite leaves, in contrast to the European populations with common, or even dominating plants with leaves in 3(-4)-leaved whorls. Specimens of the typical ‘three-leaved’ plants were reported by HÄRLE as far to the east as the Tobolsk vicinity (the westernmost Siberia). The separate specific status of the PRINTZ taxon has not been accepted by most of the later authors (BORISSOVA 1955b: 368, SKALICKÝ 1956: 128, ELENEVSKIJ 1968, 1977: 151, POLOZHIIJ 1996). STEPANOV (1997: 93) again refers to the MONJUSCHKO’s arguments, and confirms their validity. Recently, some botanists working in Siberia and the Far East have accepted *V. pseudolongifolia* (BELJAEVA & SIPLIVINSKIJ 1975: 869, VOROSCHILOV 1982 sec. STEPANOV 1997: 93). IVANINA (1991: 313) acknowledged the existence of *V. pseudolongifolia* but did not include the Far East populations in it.

After a detailed study of the herbarium material of *Pseudolysimachion longifolium* s. lat., I have arrived at the conclusion that the taxon described by PRINTZ represents the most distinct aberrant within *P. longifolium* s. lat. It is therefore justified to evaluate it at least as a subspecies, or more probably as a separate species. However, its variation range is wider than that reported by PRINTZ, which also concerns the characters commonly discussed in the literature, i. e. the length of pedicels and petioles. Plants more or less corresponding to the description given by PRINTZ were seen from the Urals, West Siberian Lowlands, the Altai, the West Sayan, Baikal Lake vicinity, N Mongolia,

the Nerczynsk, Blagoveshchensk and Vladivostok regions (see the list of localities below). On the contrary, no similar plants were observed in a relatively rich herbarium material from various regions of Europe. Tab. 1 summarizes main differences between the European and Asian plants of *P. longifolium* complex.

Important differences between the two taxa consist in the character of indumentum of individual parts of the inflorescence. While the European form has calyx tooth margin with eglandular, usually longer trichomes (Figs. 1, 2), the Asian plants possess calyx teeth with margins covered with very short, mostly glandular hairs (Figs. 3, 4). This character is illustrated also in the original work by PRINTZ (1921: 381); the original figure also very clearly shows the prevailing shape of calyx in the Asian taxon. Another figure with a detail of flower, pedicel and the bract (MONJUSCHKO 1924: 123, under the name *Veronica longifolia*) also seems to correspond to the features of the Asian *Pseudolysimachion longifolium* plants discussed. As regards the indumentum of the remaining parts of the inflorescence (axis, bracts, pedicels), it is generally sparser in the Asian plants.

Further differences given in the Tab. 1 are less constant but, when used as a character complex, may represent a useful aid in the correct identification of the two taxa.

With the exception of two plants on a single herbarium sheet from Mongolia (where leaves were in 3-leaved whorls in the uppermost nodes), all the other specimens studied had exclusively opposite leaves. PRINTZ (1921: 380) admits that the Asian taxon may include 'three-leaved' specimens but HÄRLE (1932: 20) did not observe such plants. Also ELENEVSKIJ (1968: 66) mentioned the fact that opposite-leaved plants clearly predominate in the area to the east of the Urals, and in E Siberia they represent the sole form of *Pseudolysimachion longifolium* s. lat. Z. KAPLAN (pers. comm.) studied two medium sized populations of *P. longifolium* s. lat. in the Baikal region; all the plants studied were found opposite-leaved.

On the contrary, in the populations of the European form, individuals with leaves in three-leaved whorls almost always prevail (in the northern coastal populations this dominance is even more pronounced), sometimes plants with 4-leaved whorls are found.

The length of petioles is a frequently discussed character (MONJUSCHKO 1924: 118, HÄRLE 1932: 20, 21, SKALICKÝ 1956: 128, ELENEVSKIJ 1968: 66, STEPANOV 1997: 93). In the Asian type, the most common range is 3-4 mm according to my measurements (PRINTZ, 1921: 382, gives 1-2 mm) but rare aberrants with petioles to 1 cm long can be found. In the European plants, the petiole length seems to decrease from the south to the north (see also ELENEVSKIJ, l. c.). Central European plants often have petioles 8-10 (15) mm long, north European specimens the petioles are often shorter, sometimes only 4-5 mm. Nevertheless, plants with petioles only (1) 2-3 mm long, not rare in the Asian populations, were not found in the European material.

Tab. 1. – Differences between the western (mostly European) and eastern (Asian) plants of the group of *P. longifolium*

	Western type (Europe and W Asia)	Eastern type (Asia)
Stem	glabrous in lower part, covered with eglandular, arcuate, recurved (or often irregularly arranged, flexuose and partially intertwined) hairs below inflorescence; in the inflorescence ± densely covered with curved, relatively long eglandular hairs	glabrous in lower part, covered with eglandular, arcuate, recurved hairs below inflorescence; in the inflorescence (sometimes also just below it) with short, ± straight or curved eglandular hairs, often also with scattered glandular trichomes
Leaves	often in 3(-4)-leaved whorls, rarely opposite (two per node)	two per node, opposite, exceptionally in 3-leaved whorls in upper part of stem
Leaf blade base	cuneate, truncate or cordate	truncate or shallowly cordate, rarely cuneate
Petioles	(4) 6-10 (15) mm long	(2) 3-4 (10) mm long
Indumentum of upper stem leaves	sparsely or densely (also among veins on both sides) covered with longer eglandular hairs, adaxial surface sometimes also with scattered very short glandular hairs or sessile glands, rarely leaves glabrous or only with scattered short glandular hairs	glabrous on both sides, or adaxial surface exclusively with very short glandular hairs and abaxial surface with very sparse (usually confined to veins) eglandular and/or glandular hairs
Bracts	usually narrow, linear to linear-subulate, gradually narrowing in a long apex, reaching at least 1/3 of calyx but frequently exceeding it	narrowly oblong-lanceolate to narrowly linear, often subabruptly contracted in a relatively shorter apex, usually ± equalling pedicels or shorter, sometimes as long as calyx
Pedicels	(1) 1.5-3 (5) mm long, often densely covered with relatively long slightly curved eglandular hairs	(1) 1.5-2.5 (3.5) mm long, with scattered short ± straight eglandular and sometimes also glandular hairs
Calyx	(1.5) 2-3 (4) mm long, often dissected to 3/4 or more	usually 1.-1.5 mm, rarely to 3 mm, dissected usually to 2/3

Tab. 1. - continued

	Western type (Europe and W Asia)	Eastern type (Asia)
Calyx teeth	acute, narrowly triangular to broadly lanceolate, rarely ovate-lanceolate (Fig. 1)	most often obtuse to rounded, broadly ovate to ovate, less often ovate-lanceolate to lanceolate (and then \pm acute) (Fig. 3)
Calyx indumentum	calyx margins with eglandular, longer (usually many-celled) straight or curved hairs (Fig. 1, 2), sometimes hairs also on the tooth surface, rarely calyx almost glabrous	calyx margins with very short (usually one-celled) straight, mostly glandular hairs (Fig. 3, 4), tooth surface glabrous, rarely with scattered very short glandular trichomes
Capsule	glabrous	glabrous or rarely with solitary glandular hairs on the top

In the European plants, upper cauline leaves often possess a \pm continuous both-side indumentum of longer eglandular hairs, whilst this type of hairs either is completely absent from the leaves of the Asian type or is confined to veins underneath upper leaves. Exceptionally, however, plants with leaves lacking the longer eglandular hairs can be found in populations of the European type, too.

While bracts of the European type most often exceed lower half of calyx during flowering time (and frequently even exceed the whole length of calyx), the Asian taxon possesses bracts usually \pm reach calyx base. Not seldom the bracts of Asian plants are even shorter than pedicels (a character shared with *Pseudolysimachion spurium*). The opposite extreme, i. e. bracts reaching 1/2 or even the top of calyx, is much less frequent (in particular, such plants are found in the vicinity of Nerczynsk).

Another important character is the shape and size of calyx. About 95 % of the European plants have calyx teeth distinctly acute, usually lanceolate to triangular-lanceolate. Only c. 10 % of Asian plants were found to have calyx teeth acute, approaching the shape teeth of the European plants. Similar situation is found in the case of calyx size.

No distinct differences were observed between the two taxa in the length of pedicels. Pedicels c. 1 mm long reported by PRINTZ (1921: 380, 383) represent a marginal condition, not a rule, in the Asian plants.

The Asian taxon in question resembles *Pseudolysimachion spurium* in the character of calyx indumentum. Asiatic plants also \pm match *P. spurium* in the shape of calyx teeth and in the tendency to develop shorter bracts and petioles. The Asian type of *P. longifolium* has leaf blades widest in their proximal part and the blade base usually is rounded to shallowly cordate; *P. spurium* is

characterized by leaf blades having the widest dimension in the middle, the blade base being always cuneate. Further differences between the two taxa can be observed in the density and the shape of inflorescence. Plants of *P. spurium* have, as a rule, racemes less dense but the whole inflorescence is more densely branched than that of *P. longifolium* s. lat. (irrespective of the origin of plants). While *P. spurium* has stems most often hairy throughout, plants of *P. longifolium* s. lat. are characterized by stems glabrous near base. Finally, *P. spurium* is a species of drier habitats, confined to dry steppe or sparsely wooded steppe stands; the Asian *P. longifolium* is ecologically close to the European type, and prefers moist (or even swampy) habitats.

In conclusion, it is obvious that the typical representatives of the Asian taxon of the *Pseudolysimachion longifolium* complex differ from the European ones in a whole set of characters. In the extensive territory from the Altai to the region of Lake Baikal and N Mongolia (from where a satisfactory material was available) the Asian taxon is very distinctive, with a relatively restricted variation. Much less satisfactory material was studied from regions farther to the east. In a preliminary way, it is possible to suggest that the variation increases towards the east, the situation will require additional study. The most eastern plants, however, are generally closer to the Asian taxon than to the European plants.

The territory of West Siberian Lowlands and the Urals, only a limited material was studied by me (about 15 specimens). A part of the plants corresponded to the Asian type, another part was intermediate between the two types, and the rest was referable to the European taxon. Generally speaking, it is obvious that both types occur in the W Asian areas, and their hybridization there is very likely.

If we accept that each of the two types should be considered as a separate taxon, a question arises, what rank should be assigned to them. In view of the fact that the two taxa differ in several characters that are usually accorded higher importance in the genus *Pseudolysimachion*, I prefer the treatment at the rank of species. On the other hand, I admit that the taxa might be evaluated as distinctly differentiated subspecies of a single species, mainly because of the existence of intermediate populations. Taxonomic evaluation at the rank lower than subspecies (or even full synonymization) should be considered as inappropriate, however. The whole problem requires a more profound study of the material from various parts of the Asian part of the geographical range of the whole group.

Correct names for the European and Asian species

The search for correct names applicable to the European and Asian species of the *Pseudolysimachion longifolium* complex inevitably must start (and, as shown below, also end) with LINNAEUS. A fact was mentioned above that LINNAEUS (1753: 10) used the number of leaves per node and leaf margin indentation as diagnostic characters for distinguishing his two species, *Veronica maritima* and *V. longifolia*. Although the latter name has generally been used to cover both Linnaean taxa (KOCH 1837: 527, 528), KERNER (1874: 22) proposed

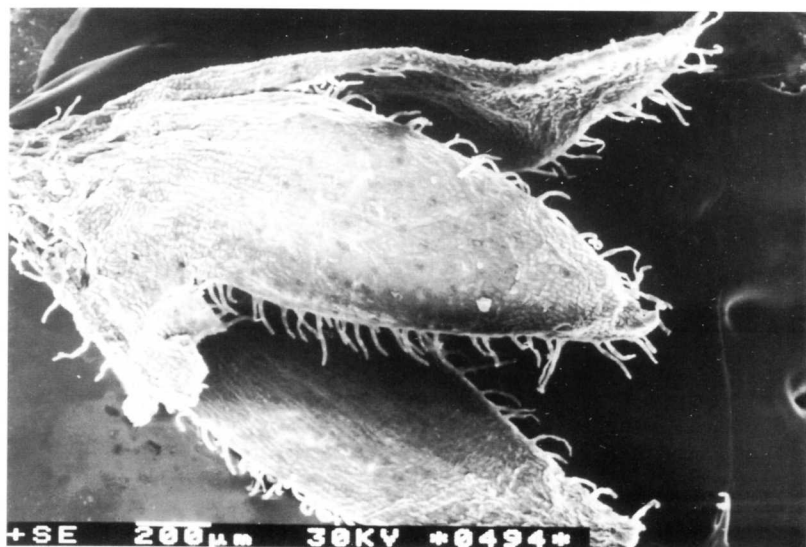


Fig. 1: *Pseudolysimachion maritimum* (L.) Á. & D. LÖVE: calyx tooth with indumentum (locality: the Czech Republic, S Bohemia, Lužnice R. basin, Dráčov near Soběslav).

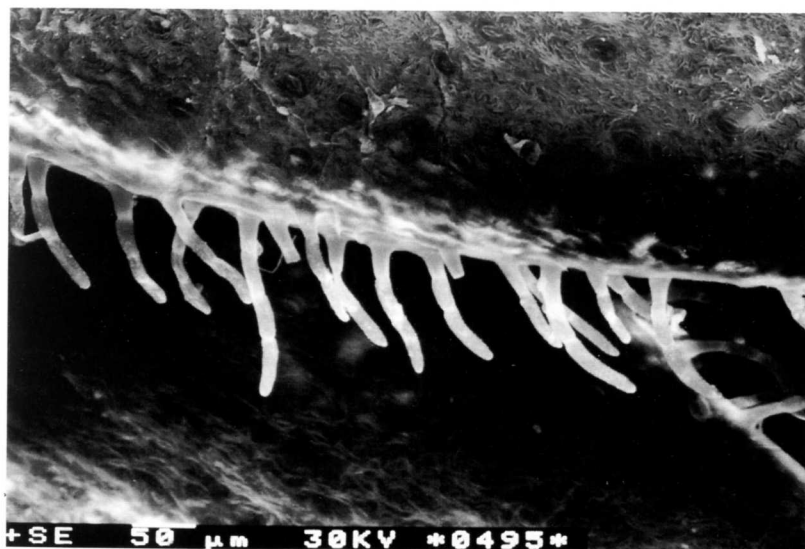


Fig. 2: *Pseudolysimachion maritimum* (L.) Á. & D. LÖVE: detail of indumentum of the calyx tooth margin (locality: the Czech Republic, S Bohemia, Lužnice R. basin, Dráčov near Soběslav).

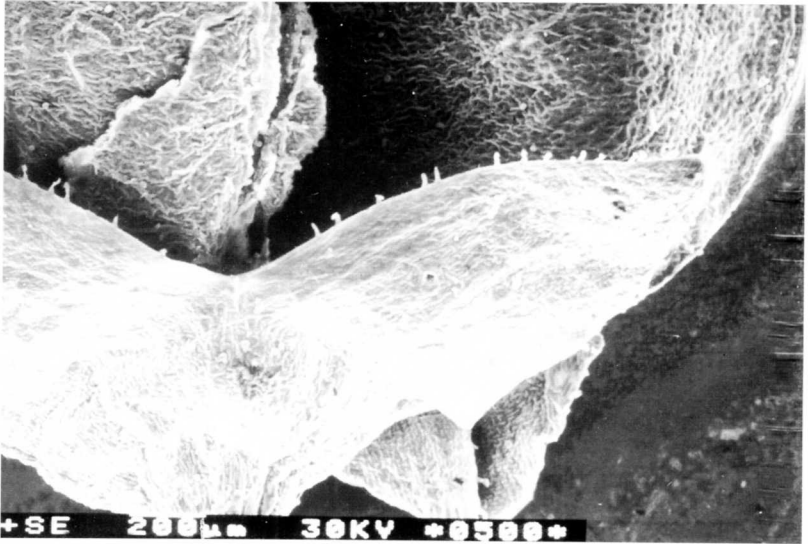


Fig. 3: *Pseudolysimachion longifolium* (L.) OPIZ s. str.: calyx tooth with indumentum (locality: Russian Federation, the Altai, Chuya R. valley, NW of Chilit).

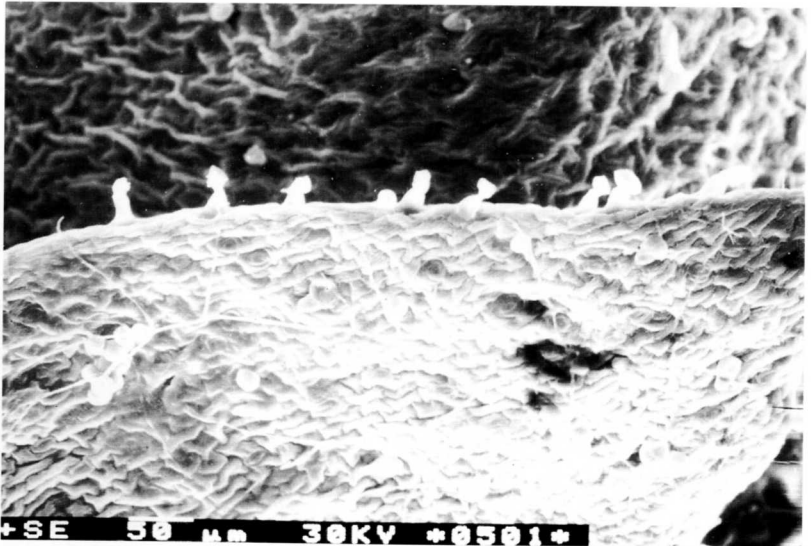


Fig. 4: *Pseudolysimachion longifolium* (L.) OPIZ s. str.: detail of indumentum of the calyx tooth margin (locality: Russian Federation, the Altai, Chuya R. valley, NW of Chilit).

to prefer the name *V. maritima*. His main argument was the fact that LINNAEUS (1753: 10) cited, as one of the original elements of *V. longifolia*, an image published by CLUSIUS („*Veronica* l erectior latifolia. *Clus. hist. l. p. 346*”). The image represents a taxon of the vicinity of *Pseudolysimachion spicatum*, most probably *P. orchideum* (CRANTZ) WRABER (see HÄRLE 1932: 7). At the same time, there is a specimen in LINN under no. 26.6, evidently a syntype, with a plant undoubtedly belonging to the group of *P. longifolium* as understood nowadays. Before the typification, the interpretation of the name *Veronica longifolia* L. was not unequivocal, and the name used to be considered as a „*nomen ambiguum*”. The name *V. maritima* L. was regarded as unproblematic by KERNER, and thus more suitable for the taxonomic complex of *V. longifolia*.

E. FISCHER (1997: 113, 114) has recently typified both Linnaean names; both types come from LINN. The specimen no. 26.4 was selected as the type of the name *V. maritima* L. It contains a plant (see also HÄRLE 1932: Fig. 8) with narrower, acutely and deeply dentate leaves in four-leaved whorls, leaf blade base is cuneate, and petioles are conspicuously long, calyx teeth very sharply acute, their margins with eglandular hairs, bracts distinctly exceeding calyx. The plant very well corresponds to the ‘maritima’ morphotype of the group of *Pseudolysimachion longifolium* (see also the Tab. 1).

The type of *Veronica longifolia* L., the plant on the specimen 26.6 in LINN (see HÄRLE 1932: Abb. 9, TURRILL 1928: 20), was found very surprising upon closer examination: it has opposite leaves, petioles conspicuously short, bracts shorter than, or equalling pedicels, calyx teeth \pm ovate, subacute, with margins covered with very short glandular trichomes. The above characters clearly indicate that the type plant does not belong to the European taxon of the *Pseudolysimachion longifolium* group; it represents the Asian one (see the Tab. 1). The name *Veronica maritima* L. (\equiv *Pseudolysimachion maritimum* (L.) Á. & D. LÖVE) thus refers to the western, European-West Asian species, and the name *Veronica longifolia* L. (\equiv *Pseudolysimachion longifolium* (L.) OPIZ) to the eastern, Asian one. LINNAEUS (1753: 10) probably did not observe the difference between the two taxa; the original material and distribution data („Habitat in Tataria, Austria, Suecia”) show that he united opposite-leaved individuals of the European species with the Asian taxon (the term ‘Tataria’ also covered the region of Middle Asia in the Linnaean times). Later on, the same treatment was adopted by most authors. It was PRINTZ (1921) who first correctly distinguished the two taxa and recognized the Asian plants as a separate species. Paradoxically, according to the recent typification, the Linnaean name becomes correct for the Asian species, and the name published by PRINTZ is to be relegated to its synonymy. In the following text, the name *Pseudolysimachion longifolium* s. str. is used in the sense of the recent typification; *P. longifolium* s. lat. comprises both the Asian and the European taxon.

What is *Veronica septentrionalis* BORISS. ?

In 1955, when preparing an account of the genus *Veronica* for Flora of the USSR (BORISSOVA 1955b), BORISSOVA (1955a: 341) described a new species, *V. septentrionalis* BORISS. It follows from the original description that *V. septentrionalis* is characterized by opposite, almost sessile, sparsely hairy to subglabrous leaves with 3-5 mm long petioles, lanceolate glabrous bracts scarcely equalling pedicels, almost glabrous, c. 1.5 mm long calyx with ovate, obtuse teeth. BORISSOVA (1955a: 341, 342; see also BORISSOVA 1955b: 348) emphasized the following characters as diagnostic: inflorescence is a single, dense, short, only 1-5 (10) cm long and 2 cm wide raceme, capsules (in comparison with *V. „longifolia”*) larger, to 4-5 mm long and ovoid (in *V. „longifolia”* the capsules should be subglobose, c. 3 mm in diameter). BORISSOVA did not distinguish Asian plants of the *Pseudolysimachion longifolium* group from the European ones, nor did she mention the character of calyx hairs (not even in Flora of the USSR - BORISSOVA 1955b: 369). The geographical range of *Veronica septentrionalis* was reported to occupy northern territories of NE Europe and Siberia, reaching Kanin Peninsula and North Dvina R. basin in the west and the Kolyma R. basin in the east. In Flora of the USSR (BORISSOVA 1955b: 369) the species is recorded as far to the west as the Karelia-Lapland region.

Subsequently, various treatments of *Veronica septentrionalis* have appeared in the literature. LÖVE & LÖVE (1976: 518) accept its separate status, HOLUB (in HOLUB & POUZAR 1967: 425), KUVAEV (in KUVAEV & LAZAREV 1981: 953), TRÁVNÍČEK (1997: 270) regard it as a subspecies of *P. longifolium* s. lat. ELENEVSKIJ (1968) and MALYSHEV & PESCHKOVA (1979: 769) treat it as a mere variety (as *Veronica longifolia* var. *borealis* TRAUTV. ex MIDDEND.). WALTERS & WEBB (1972), ELENEVSKIJ (1977: 151), and most recently POLOZHII (1996: 32), for instance, relegate *V. septentrionalis* to the synonymy of *V. longifolia*. RAITANEN (1967: 485) mentioned that tetraploid plants from Kuusamo in SE Finland correspond to the description of *V. septentrionalis* but did not judge the taxonomic value of that form. It is not surprising that most authors deny the specific status of *V. septentrionalis*. BORISSOVA (1955a: 342, 1955b: 369) gives tundra and sparsely wooded tundra as a habitat of her species; it is therefore quite plausible that *V. septentrionalis* represents a mere northern ecotype (or only an ecomorph) of *Pseudolysimachion longifolium* s. lat.

Because two species, *Pseudolysimachion maritimum* and *P. longifolium* s. str., are recognized within *P. longifolium* s. lat., a question arises which of the two species should include the BORISSOVA's form. The type specimen of *Veronica septentrionalis* was not studied by the present author, and it is therefore necessary base our conclusions on the protologue of *V. septentrionalis*, and on the geographical origin of the type in particular. According to most of the characters given by BORISSOVA, i.e., the opposite leaves, length of petioles, size and shape of calyx, and the sparse indumentum of inflorescence, it may be supposed that *V. septentrionalis* is closely related to, or even identical with

Pseudolysimachion longifolium s. str. However, one of the important characters, the indumentum of calyx teeth margins, was not examined by BORISSOVA.

The nomenclatural type of the name comes from Nachodka promontory (NW Siberia, gulf of Tazov). I have studied a single herbarium specimen (with three plants at the stage of early flowering) from a relatively close region, Nachodka Bay in the gulf of Ob. The plants matched the description of *Veronica septentrionalis* very well. With the exception of the general habit (plants low, with a short, unbranched inflorescence), the plants shared all the diagnostic characters, including the glandulose indumentum of calyx, with the typical *Pseudolysimachion longifolium* s. str. (see the Tab. 1). If we accept the assumption that *Veronica septentrionalis* represents a derivative of *Pseudolysimachion longifolium* s. str., we have to deal with the problem of taxonomic identity of populations from northwestern Arctic Europe identified as *Veronica septentrionalis* by BORISSOVA, too (see BORISSOVA 1955a: 342, 343, 1955b: 369). Under the above conditions, there are two alternatives:

- Populations from NE Europe form a northern ecotype (or an ecomorph) of *Pseudolysimachion maritimum*, and BORISSOVA included them in her *Veronica septentrionalis* on the basis of a superficial similarity in their general habit.
- Populations from NE Europe do not belong to *Pseudolysimachion maritimum* and are referable to the N Siberian *Veronica septentrionalis* (i. e. to *Pseudolysimachion longifolium* s. str.) which thus reaches NE Europe and the N Urals.

The above questions may be answered, and the taxonomic value and relationships of *Veronica septentrionalis* assessed only after a thorough study of the type specimen of the name, together with an examination of a representative herbarium material from the northern regions, and field investigation of populations. The above facts, however, make it clear that the main line within the *Pseudolysimachion longifolium* complex is to be drawn between eastern and western populations, not between northern and southern ones.

1. *Pseudolysimachion maritimum* (L.) Á. & D. LÖVE

(Figs. 1, 2)

Pseudolysimachion maritimum (L.) Á. & D. LÖVE, Bot. Not. 128: 518, 1976.

Basionym: *Veronica maritima* L. Sp. Pl. 10, 1753.

Typus: specimen no. 26.4 in LINN (lectotypus E. FISCHER 1997: 114).

Selected synonyms:

- ≡ *Veronica longifolia* var. *maritima* (L.) W.D.J. KOCH Syn. Fl. Germ., ed. 2, 606, 1844.
- ≡ *Pseudolysimachion longifolium* subsp. *maritimum* (L.) HARTL in HEGI III. Fl. Mitteleur., ed. 2, 6/1: 152, 1966.

- ≡ *Veronica longifolia* subsp. *maritima* (L.) SOÓ & BORSOS in BORSOS Acta Bot. Acad. Sci. Hung. 13: 9, 1967.
- = *V. ruthenica* ROEM. & SCHULT. Syst. Veg. 1: 96, 1817.
- = *V. ticinensis* POLLINI Fl. Veron. 3: 768, 1824.
- = *V. brachtii* OPIZ Naturalientausch 9: 110, 1825.
- = *V. bracteata* OPIZ Naturalientausch 10: 244, 1825.
- = *V. jungbaueri* OPIZ Naturalientausch 9: 110, 1825.
- = *V. kosteleckii* OPIZ Naturalientausch 9: 109, 1825.
 - ≡ *Pseudolysimachion kosteleckii* (OPIZ) OPIZ Seznam 80, 1852.
- = *V. nenningii* OPIZ Naturalientausch 9: 110, 1825.
 - ≡ *Pseudolysimachion nenningii* (OPIZ) OPIZ Seznam 80, 1852.
- = *V. pettersii* OPIZ Naturalientausch 9: 109, 1825.
 - ≡ *Pseudolysimachion pettersii* (OPIZ) OPIZ Seznam 80, 1852.
- = *V. elata* HOST Fl. Austr. 1: 3, 1827.
- = *V. geniculata* HOST Fl. Austr. 1: 5, 1827.
- = *V. commutata* SEIDL in BERCHT. & SEIDL Oekon.-Techn. Fl. Böhm. 1/1: 31, 1836.
 - ≡ *Pseudolysimachion commutatum* (SEIDL) OPIZ Seznam 80, 1852.
- = *V. riparia* SEIDL in BERCHT. & SEIDL Ökon.-Techn. Fl. Böhm. 1/1: 30, 1836.
 - ≡ *Pseudolysimachion riparium* (SEIDL) OPIZ Seznam 1852.
- = ? *V. taigischensis* STEPANOV, Bot. Zhurn. 82/9: 93-94, 1997 incl.
 - ≡ *Pseudolysimachion taigischense* (STEPANOV) HOLUB, Preslia 70: 109, 1998.
- *V. longifolia* auct., non L. Sp. Pl. 10, 1753: auct. europ., e. g. WALTERS & WEBB in TUTIN et al. Fl. Eur. 3: 251, 1972.
- *Pseudolysimachion longifolium* auct., non (L.) OPIZ Seznam 80, 1852: auct. europ., e. g. HARTL in HEGI III. Fl. Mitteleur., ed. 2, 6/1: 150, 1966.
- *Veronica spuria* auct., non L. Sp. Pl. 10, 1753: CRANTZ Stirp. Austr., ed. 2, 335, 1769.

Description

Perennial herbs with a short, tightly many-headed rhizome and often with lateral subterraneous stolons. Basal leaf rosettes not developed. Stem 60-150 (-200) cm high, branched in the upper part or, more rarely, unbranched, glabrous at base, hairy in the middle and in the inflorescence, covered with eglandular, ± appressed, arcuate, mostly recurved (or often irregularly arranged, flexuose and partially intertwined) hairs. The lowermost cauline leaves sometimes reduced, scale-like, the others with a distinctly developed petiole and blade, in 3 (4)-leaved whorls or opposite. Upper leaves (bracts subtending the inflorescence branches) not reduced, leaf-like. Leaf blades not divided, in middle leaves 5-15 (-20) cm long, 1-3 (-4) cm wide, narrowly to broadly lanceolate, with a cuneate, truncate or cordate base, usually with an elongated apex, margins usually acutely dentate to serrate, sometimes deeply doubly serrate. Petioles of middle cauline leaves (4-) 6-10 (-15) mm long, those of upper leaves shorter. Lower cauline leaves glabrous, withering in flower, upper ones most often covered with scattered to dense ± appressed (on adaxial surface) or arcuate (beneath) eglandular trichomes, more rarely ± glabrous. Racemes quite dense, as a rule, slender (narrow), (1-) 3-7 (-9) per stem, their axes covered with eglandular, usually curved hairs. Terminal raceme frequently over 15 cm long, often two times as long as the others. Pedicels of lateral racemes usually indistinctly bent to almost straight, spreading at an angle 15-25°. Bracts subulate to linear-lanceolate, (2-)

3-4 (-8) mm long, conspicuously longer than young (green) flower buds, longer than flower and fruit pedicels, covered with eglandular trichomes. Flowers without smell, their pedicels (1-) 1.5-3 (-5) mm long, covered with eglandular trichomes. Calyx (1.5-) 2-3 (-4) mm long, frequently over 3/4 divided, calyx teeth most often lanceolate to triangular, acute, lower two longer than the upper ones, with scattered eglandular hairs or glabrous on outside surface, margins usually with eglandular, straight or arcuate trichomes. Corolla usually pale violetish blue. All corolla lobes of similar shape (upper ones mostly the broadest, lower ones narrowest), relatively broad, broadly ovate to rounded (the upper one sometimes broader than its length), 2.5-3.5 mm long, 2.0-3.5 mm wide. Filaments c. 5-6 mm long, anthers c. 1.8-2.0 mm long, 0.8 mm wide. Ovary broadly ovoid, glabrous. Style (5-) 6-7 (-8) mm long. Capsule laterally slightly compressed, ovoid, broadly ovoid to globose, about 2.5-3.5 mm long, 2.5-3.0 mm wide, slightly emarginate at apex and carinate, usually slightly exceeding the calyx, glabrous. Seeds minute, c. 0.9 x 0.7 x 0.3 mm, light brown to yellow-brown.

Variation and relationships

The species, as understood in the present paper (see above), exhibits a conspicuous variability in the arrangement of leaves along the stem and in the leaf shape. There are usually three, rarely two and exceptionally four leaves per node. The opposite leaves, at the same time, are relatively broad while leaves in whorls, as a rule, are narrower. Broader leaves most often have cordate to truncate blade base while narrow leaves are characterized by cuneate blade base. A certain correlation between the arrangement of leaves along the stem and their width and shape, however, does not seem to be significant taxonomically. It is very likely that it only represents a result of morphogenetic mechanisms of leaf development. The mechanism apparently does not give any great chance for leaves in whorls to reach the same width as the opposite leaves. The fact that plants with whorled leaves prevail in populations in a certain part of the species' range (e.g., in coastal regions of Scandinavia) is of some taxonomic importance but the geographical or ecological distinctiveness of the latter morphotype is too weak to serve as basis for the taxonomic treatment at a level higher than variety.

The species varies in a number of additional characters: the size and shape of calyx and corolla, length of pedicels and bracts, and length of petioles. The nature of this variation, however, is more or less an individual fluctuation within limits typical of this species. The variation in the indumentum mostly concerns its density: the most common plants have scattered to dense eglandular upper leaf indumentum but plants with \pm glabrous leaves can be found, too. The qualitative characters of indumentum are less liable to variation. For instance, plants with admixed glandular hairs on the calyx tooth margins were quite exceptional in the ample herbarium material studied. The exception is represented by some plants from the White Carpathians, E Moravia (the Czech Republic) where, nevertheless, this character probably appears as a result of introgressive hybridization with *Pseudolysimachion spurium*, formerly common in the area

(TRÁVNÍČEK et al. 2001). Similarly, the presence of glandular hairs on calyx teeth in some plants of *P. maritimum* in Ahvenanmaa province, Finland, might have originated through an introgression from *P. spicatum* (subsp. *spicatum*), cf. RAITANEN (1967: 478).

Higher taxonomic weight should be accorded to the ploidy variation in *Pseudolysimachion maritimum*. The investigations carried out hitherto have shown, however, that there is no significant correlation between the ploidy level and morphological characters and/or geographical distribution of the cytotypes (TRÁVNÍČEK et al. 2001, TRÁVNÍČEK & VINTER 1999). Moreover, if the fact is taken into consideration that fertile hybrids between diploids and tetraploids may originate (GRAZE 1935: 658, etc.), there is little support for the recognition of subspecies or even species within *P. maritimum* (e.g., HARTL 1966: 152, 153, M. A. FISCHER 1969: 438, ROTHMALER et al. 1982: 465, E. FISCHER 1997: 113, 114, etc.).

A problem that remains unsolved is the taxonomic treatment of populations from the NE limit of Europe, and their relationships to the Siberian populations of the „taxon” called *Veronica septentrionalis* (for details, see above). All the other species (not hybrids) described of the *Pseudolysimachion longifolium* complex from Europe whose names appear in the above synonymy are to be considered as a part of the variability range of *P. maritimum*. Thus, in the section *Longifolia* (T. YAMAZ.) TRÁVNÍČEK* in Europe only *P. bachofenii* (HEUFF.) HOLUB and *P. spurium* should be regarded as separate species (TRÁVNÍČEK 1998: 195).

A special problem is represented by *Pseudolysimachion taigischense* (STEPANOV) HOLUB, recently described as *Veronica taigischensis* STEPANOV from a single locality in the Taigisch River basin in the West Sayan, S Siberia, i.e. from the core region of the range of *Pseudolysimachion longifolium* s. str. According to the original description and the drawing (STEPANOV 1997: 93-94), the taxon is characterized by a low growth, the plants are 40-60 cm high, with opposite leaves, long petioles (10-15 mm), leaf blade broadly cuneate at base. Bracts are linear to acicular, up to 10-15 mm long in lower flowers, i.e., distinctly exceeding calyx teeth, calyx 3.5-4.0 mm long, teeth oblong-lanceolate, acute. STEPANOV regards the following features as diagnostic for *P. taigischense*: a much branched upper part of stem, stems decumbent, the leaf shape and relative large seeds (0.9-1.2 mm long). Unfortunately, the plant indumentum is not mentioned in the protologue. In spite of the absence of the most important character (inflorescence indumentum), it is evident from the above description that *P. taigischense* is closer to the European *P. maritimum* than to the Asian *P.*

* TRÁVNÍČEK (1998) proposed a combination *Pseudolysimachion* sect. *Longifolia*, with a direct reference to a name (considered a basionym) *Pseudolysimachion* ser. *Longifoliae* HOLUB in HOLUB & POUZAR, Folia Geobot. Phytotax. 2: 423, 1967. However, there is an older, validly published name based on the same type: *Veronica* sect. *Pseudolysimachium* ser. *Longifoliae* BORISS. ex T. YAMAZ., J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot., 7: 134, 1957. The above nomenclatural combination in *Pseudolysimachion* thus should be cited as *Pseudolysimachion* sect. *Longifolia* (T. YAMAZ.) TRÁVNÍČEK (cf. Art 33 of ICBN – GREUTER et al. 1994).

longifolium s. str. It is understandable that in the region with *P. longifolium* s. str. predominating, such a population represents a remarkable, distinct entity. Only an examination of the type specimen of the name and a field study might elucidate the taxonomic position of *P. taigischense*. It cannot be excluded, however, that it represents an isolated, and maybe relatively aberrant population of *P. maritimum* (see also Distribution).

Chromosome number

Chromosome number of the species: $2n = 34$, $2n = 68$.

Other counts have seldom been reported (see TRÁVNÍČEK et al. 2001 for more detailed comments). Diploids mainly prevail in N Europe but their occurrence is known in C and S Europe (N Italy); C Europe is dominated by tetraploid populations.

Ecology

Moist, vernaly floody meadows in the floodplain areas along rivers, meadow ditches, river and oxbow bank shrubby vegetation, margins of reed stands and alluvial scrub, rarely wet meadows outside river basins. In N and NE Europe, the species occurs in hygrophilous coastal vegetation and (?) the tundra zone vegetation. It grows on water-soaked soils sometimes drying in summer, rich in nutrients, of neutral to basic reaction, in floodplain situations. It is a heliophilous to semisciaphilous species, it avoids permanently shady sites.

Distribution

The geographical range of *Pseudolysimachion maritimum* occupies most of Europe, the species occurs in the following regions (abbreviations according to TUTIN et al. 1964): Au, Be, Bu, Cz (the Czech Republic and Slovakia), Da, Fe, Ga, Ge, He (probably only a garden escape), Ho, Hu, It, Ju (Slovenia, Croatia, Bosnia and Serbia), No, Po, Rm, RS (N, B, C, W, E), Su, Tu. The exact position of the eastern limit is uncertain. The easternmost locality documented by a specimen seen is situated c. 200 km W of Novosibirsk (Baraba, between Ubinski and Borisoglebski, leg. Krylov 1912 BRNU). One of the two plants on this herbarium sheet represents a typical 'three-leaved' *P. maritimum*, the other has opposite leaves, and also further characters belong to a morphotype closer to *P. longifolium* s. str. Also HÄRLE (1932: 20) studied a specimen of the typical *P. maritimum* from the West Siberian Lowlands: „Noch aus dem Gouv. Tobolsk sah ich eine ziemlich normale *V. maritima* L. mit zu 3 in einem Wirtel stehenden, ca. 6-7 mm lang gestielten Blättern". In addition, it will be necessary to pay attention to plants from the Aralo-Caspian part of the range of *P. longifolium* complex. No material has been examined from that area. A question of the occurrence of *P. maritimum* in the West Sayan (Taigisch River) is closely connected with the taxonomic treatment of the population recently described as *Veronica taigischensis* (see above).

2. *Pseudolysimachion longifolium* (L.) OPIZ

(Figs. 3, 4)

Pseudolysimachion longifolium (L.) OPIZ Seznam 80, 1852.

Basionym: *Veronica longifolia* L. Sp. Pl. 10, 1753.

Typus: specimen no. 26.6 in LINN (lectotypus E. FISCHER 1997: 114).

Synonyms:

- = *Veronica pseudolongifolia* PRINTZ Veg. Sibir. Mongol. Front. 380, 1921.
 - ≡ *Pseudolysimachion longifolium* subsp. *pseudolongifolium* (PRINTZ) HOLUB, Preslia 70: 109, 1998.
- = *V. septentrionalis* BORISS., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R 17: 341, 1955 incl.
 - ≡ *Pseudolysimachion septentrionale* (BORISS.) Á. & D. LÖVE, Bot. Not. 128: 518, 1976.
 - ≡ *P. longifolium* subsp. *septentrionale* (BORISS.) HOLUB in HOLUB et POUZAR, Folia Geobot. Phytotax. 2: 425, 1967.
- = ? *V. exortiva* KITAG., J. Jap. Bot. 26: 17, 1951.
 - ≡ *V. longifolia* subsp. *exortiva* (KITAG.) KITAG. Neo-Lineam. Fl. Manshur. 573, 1979.

Differences between *Pseudolysimachion longifolium* s. str. and *P. maritimum* are summarized in Tab. 1 and annotated above.

Variation and relationships

The variability of the species is, to a great extent, shown in Tab. 1 and in the above comments but it requires further examination on the basis of a more extensive herbarium and live material. However, some general features of the variation can be inferred now. In contrast to the European *Pseudolysimachion maritimum*, *P. longifolium* s. str. exhibits a less conspicuous variation in leaf arrangement and shape. Of about 80 herbarium specimens studied, only two plants possessed a few three-leaved whorls in upper part of stem, all the others were opposite-leaved. Expectably, the opposite arrangement of leaves is followed by a narrower variation range of the leaf width and the shape of leaf blade base. Again, only very few individuals were observed having narrower leaves and cuneate blade base. Generally, the other morphological traits may be characterized, to a great extent, in the same way as those in *P. maritimum*.

The variability in chromosome number has not been explored satisfactorily, and no clear taxonomic conclusions can be drawn (see comment in the relevant chapter). With respect to the quite extensive range, a certain geographical variation cannot be excluded. Provided that the northern populations, probably described as *Veronica septentrionalis*, prove to be sufficiently distinct taxonomically, they perhaps might represent a subspecies of *Pseudolysimachion longifolium* (subsp. *septentrionale* (BORISS.) HOLUB).

Relationships between *Pseudolysimachion longifolium* s. str. and some other E Asian species of the sect. *Longifolia* remain unclear. It particularly concerns *P.*

oligense (KOMAROV) HOLUB (the Far East – Ussuri region), *P. kiusianum* (FURUMI) HOLUB s. lat. (Korea, Mandshuria, Japan), *P. ovatum* (NAKAI) T. YAMAZ. (Korea), *P. sachalinense* (T. YAMAZ.) T. YAMAZ. (Sakhalin) (= *Veronica subsessilis* sensu BORISS., Fl. SSSR 22: 371, 1955), and *P. subsessile* (MIQ.) HOLUB (Japan).

Chromosome number

Chromosome number of the species: $2n = (? 64-) 68, ? 2n = 34$.

The tetraploid chromosome number should be regarded as well documented in *Pseudolysimachion longifolium* s. str. From the Baikal Lake region BELJAEVA & SIPLIVINSKIJ (1975: 869) gave a count $2n = 64$ under the name *Veronica pseudolongifolia* PRINTZ*. Records of $2n = 68$ from the following regions probably refer to *P. longifolium* s. str.: the West Sayan (loc.: Kashkereta R., MALAKHOVA 1971 sec. KROGULEVICH & ROSTOVTSEVA 1984: 227), from the Amur region (loc.: Dzheltulakskiy Rayon, Tynda R., PROBATOVA & SOKOLOVSKAJA 1989: 123) and from the Khabarovsk Region (Ul'skiy Rayon, Udyl Lake, PROBATOVA & SOKOLOVSKAJA 1989: 123). A question of the taxonomic position of plants analysed from the Putoran Range ($2n = 68$, loc.: Talnach, KROGULEVICH 1976 sec. KROGULEVICH & ROSTOVTSEVA 1984: 227) and from Yakutia ($2n = 64$, loc.: Mogdy R., KROGULEVICH in KROGULEVICH & ROSTOVTSEVA 1984: 227) requires further study. There is a doubtful record of $2n = c. 90$ from Yakutia (loc.: Arga-Salaa R., KROGULEVICH in KROGULEVICH & ROSTOVTSEVA 1984: 227). Diploid chromosome numbers ($2n = 34$) for plants that, from the geographic viewpoint, might belong to *P. longifolium* s. str. are reported from the West Sayan (KRASNOBOROV 1976 sec. KROGULEVICH & ROSTOVTSEVA 1984: 227) and from Tuva (loc.: Tes-Khems'kiy Rayon, Shurmak R., KRASNIKOVA et al. 1983: 830).

If we suppose that all the above counts really refer to *Pseudolysimachion longifolium* s. str., taxonomic relationships among diploids, tetraploids and perhaps pentaploid (?) populations are to be studied.

Ecology

PRINTZ (1921: 383-384) reports the occurrence of his *Veronica pseudolongifolia* from scrub and other vegetation of little islands in rivers and on river banks. Z. KAPLAN (pers. comm.) observed the species at wet sites in the vicinity of Lake Baikal. POLOZHIJ (1996: 32) reports Siberian plants of the *Pseudolysimachion longifolium* complex from woodland meadows and open wet meadows, from sparse *Betula* woodlands and grassy pine woods, from river bank shrubby vegetation, seldom from semi-steppe meadows. Because the northern populations (referred to as *Veronica septentrionalis*) probably also belong to *Pseudolysimachion longifolium* s. str., we can conclude that it also grows in the tundra vegetation and sparsely wooded tundra. Herbarium labels most often mention wet floodplain sites.

* All the other authors give their counts under the name *Veronica longifolia* (or *Pseudolysimachion longifolium*).

Although the basic ecological nature of the species seems to be close to that of the European *Pseudolysimachion maritimum*, it is inevitable to study the ecological requirements of *P. longifolium* s. str. in more detail. In contrary to the situation found in *P. maritimum*, the Asian *P. longifolium* s. str. not rarely reaches the subalpine belt (cf. ELENEVSKIJ 1968: 66, POLOZHIJ 1996: 32). It is not quite impossible that certain ecological differences will be ascertained between the two species. Together with the geographical vicariance, they may have contributed to the taxonomic differentiation of these two closely related taxa.

Distribution

According to the material revised (see below), the following regions should be listed as parts of the range: The Ural, West Siberian Lowlands, the Altai, the Sayan Mts., N Mongolia, Lake Baikal region, Transbaikalia, the Amur R. region and the vicinity of Vladivostok. PRINTZ (1921: 383) reports its occurrence (as *Veronica pseudolongifolia*) as far to the west as the Tomsk area and the Yenisey basin (up to 60°N), and supposes that „this new species is rather widely distributed in northern and middle Asia”. Also records of YAMAZAKI (1957: 135, 1968: 409) may refer to *Pseudolysimachion longifolium* s. str.: he gave it from Manshuria and North Korea. IVANINA (1991) reported plants under that name from Sakhalin. It is important to determine the western limit of the species. The Urals and W Siberia are territories where the ranges of *P. maritimum* and *P. longifolium* s. str. probably overlap. The northern limit of *P. longifolium* s. str. depends on the solution of the *Veronica septentrionalis* problem (see above).

Specimens studied

Russian Federation

The Ural ("Exped. Uralensis") (Branth 1847 PR, PRC). – **W Siberian lowlands:** Nakhodka Bay, Ob R. mouth (Míša 1919 BRNU); Tomsk, between Basakdayka and Kalarovo (Chinina 1965 BRNU). – **The Altai:** distr. Ust-Koksu, Korgonski khrebet, Sauzar, c. 1100-1600 m (Vašák 1972 BRA, PR); distr. Ust-Koksu, Korgonski khrebet, Vasilyevka, c. 1000-1300 m (Vašák 1972 BRA, PR); distr. Ust-Koksu, Terektinski khrebet, Ust-Koksu, c. 1050-1400 m (Vašák 1972 BRA); distr. Ongudai, Teldekpen, by Katun R., c. 500 m (Vašák 1972 PR); distr. Ongudai, Sumulta R. mouth, Katun R., c. 600 m (Vašák 1972 PR); distr. Kosh-Agach, Severochuyski khrebet, locality "Perevalka", between Kurai and Mt. Aktru, c. 1400-1600 m (Vašák 1972 PR); Chuya R. valley, NW of Chilit, c. 1400 m (Kusák 1991, herb. Kusák); distr. Maima, Gornolaitaisk (Ulala), Seremeyka Hill, c. 450-600 m (Vašák 1972 PR); distr. Maima, Rybalka, c. 310-350 m (Vašák 1972 BRA, PR); Maima, an island in R. Katun, c. 300 m (Vašák 1972 BRA, PR); Turochak, Biya R., c. 360-370 m (Vašák 1972 PR); distr. Turochak, Teleckoie Ozero, Artybach, c. 436-500 m (Vašák 1972 BRA, PR); distr. Ulaganski, Teleckoie Ozero, Bele R. mouth, c. 436-450 m (Vašák 1972 PR); distr. Ulaganski, Teleckoie Ozero, at Kokchi Creek, c. 436-450 m (Vašák 1972 PR). – **W Sayan:** Oja R. valley, along road between Abakova and Kyzyl, c. 1400 m (Kusák 1990 herb. Kusák). – **Lake Baikal:** Irkut R. valley, near Irkutsk (Hostička 1961 PR); banks of Angara R. in Irkutsk (Frantík & Stejskalová

1983 PRC); between Glinka and Kulinnoe at the ESE foot of the mountain range of Svjatoj Nos Peninsula, 480 m (Kaplan 1993 OL); the Chentej – Czikoï Mts., Borstschovocznyi Range, sources of Malaja Aschinga (A. Maximov & M. Maximov 1967 BRNU, PRC: Gerb. Fl. SSSR no. 5091, very typical). - **Nerchinsk**: Nerch R. (Karo 1889 BRNM, BRNU, PR: Plantae Dahuricae, no. 197, less typical). - **Blagoveshchensk** (Karo 1906 PR). - **Vladivostok** (Brym 1920 PR).

Mongolia

N Mongolia: 20 km NW of Bulgan, c. 1200-1600 m (Deyl & Soják 1965 PR); 6 km S of Unt (65 km NW of Bulgan), c. 1200-1600 m (Deyl & Soják 1965 PR); 15 km WNW of Bulgan, c. 1200-1700 m (Deyl & Soják 1965 PR); Nuht Valley near Mt Choybalsan, c. 20 km of Ulan-Bator, c. 1200 m (Hostička 1961 PR, Soják 1961 PR); Nuht Valley, Mt Bogdúl, c. 15 km SSW of Ulan-Bator, c. 1500-2000 m (Deyl & Soják 1965 PR); Zaisan Valley, at N slopes of Mt. Bogdúl S of Ulan-Bator, c. 1400-2000 m (Deyl & Soják 1965 PR); Khentei Mts: Terelzh R., near road from Ulan-Bator, 48° 10' N, 107° 12' E, c. 2000 m (Vašák 1966 PR); distr. Khentei, Terelzh, 60-70 km from Ulan-Bator (Soják 1961 PR); distr. Khentei: near the ruins of a monastery 210 km E of Ulan-Bator, c. 1350 m (Deylová 1974 PR); Khentei, 230 km E of Ulan-Bator, c. 1300 m (Deylová 1974 PR).

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