

Morphological variation of *Rumex longifolius* DC. in the Alps and mountains bordering Bohemia

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Abstract. Neophytic populations of *Rumex longifolius* (northern dock) in the Alps and the mountain ranges bordering Bohemia were investigated to compare the length-width ratio of the basal leaf blades, the shape and size of the valves (fruiting inner perianth segments), and the tendency to develop tubercles on the valves. Five populations from the Czech Republic (Krkonosé mountains and Mount Ještěd), Germany (Bavarian Forest), Austria (Arlberg Pass), and Switzerland (Engadin) were described by quantitative evaluation of specimens collected in 2014–2018 and their offspring cultivated in the Botanical Garden of Frankfurt am Main for 2 growing seasons. Results of this study indicate that the populations probably originated by discrete introduction events. The Engadin population shows features of introgression with *Rumex crispus*. Probably *R. longifolius* is native here, but there is indirect evidence only. The morphology of specimens from the upper Tyrolian Inn valley in the herbarium of the Natural History Museum Vienna suggests their origin from the Engadin, which should be confirmed statistically by further collections. The taxonomical significance of subsp. *sourekii* Kubát, described on the basis of a single character (leaf shape), is questioned because of the polymorphism of the species, and the correlation of leaf width with age and vigour, observed in the cultivation experiments. The morphological variability and ecological preferences of *R. longifolius* suggest its probable hybrid origin from *R. aquaticus* and *R. crispus*.

Key words: Alps, Central Europe, hybrid origin, introgression, morphology, native population, neophyte, *Rumex longifolius*

1. Introduction

The native range of *Rumex longifolius* DC. (northern dock) comprises Iceland, the British Isles, Scandinavia and adjacent Russia, the Pyrenees, Cantabrian Mountains, and the Massif Central in France (Jalas & Suominen 1988). In Scandinavia, the species is a grassland weed requiring control measures (Beachell 2018), while at the southern fringe of its range – in Germany just south of the Danish border – it is considered as rare and endangered (Romahn 2021).

Despite its subruderal preferences, *R. longifolius* has been only sporadically noticed as an alien outside its native range until the 1950s. Shortly afterwards, the species became invasive, but almost exclusively in higher upland ranges, unlike most Central European neophytes. At the higher altitudes it has reached, apparently by chance, some climatically and ecologically suitable spots, subsequently spreading in a radial manner (Rechinger 1990)¹. Considering this mode of

expansion, the colonization of individual areas should have proceeded, although simultaneously, separately from perhaps different regions of origin.

Different origins should result in morphological differences between the neophytic populations, because there is a geographical gradient of characters in the native range of *R. longifolius*. For example, plants from Central and Southeast Scandinavia and adjacent Russia have narrow (length/width ratio > 4) and strongly undulate basal leaf blades, in contrast to plants from the West (Pyrenees, France, Iceland, Denmark) and North (Scandinavia north of 67°), with broader and less undulate blades (Jalas & Lindholm 1975; Holm & Korpelainen 1999). Additionally, Kubát (1984) describes an even more broad-leaved form in the Krkonosé mountains as subsp. *sourekii*, with Central Russia as a putative area of origin.

Another variable feature is the tendency to bear tubercles on the valves (fruiting inner perianth segments). In contrast to information found in many floras, one of the valves of *R. longifolius* may develop small tubercles up to 1.0 mm × 0.6 mm (Kubát 1990; Castroviejo *et al.* 1990). Although there is no relevant information in the

¹ "Dort hat sie scheinbar sprunghaft einige klimatisch und ökologisch geeignete Punkte... erreicht und sich von diesen aus radial [ausgebreitet]."

literature about variation of this character in the native range of the species, at least neophytic populations in the mountains bordering Bohemia were found to differ in this respect (Sonnberger 2015).

A special question concerns the nativeness of *R. longifolius* in the Alps. Adler (1992) presents conclusive circumstantial evidence that the species is native to the Swiss Upper Engadin, where local botanists have confused it for several decades with *Rumex crispus* L., which is said to be absent from this area.

The main purpose of this work was a survey of the morphological variation of *R. longifolius* in Central Europe. The survey shall stimulate further, molecular-based research on the genetic composition of this unusual species, whose ecological behaviour (i.e. recent neophytic spread in cold environments) is contrary to the currently observed trend of global warming.

2. Material and methods

In 2014-2018, populations of *Rumex longifolius* in the Alps and mountains bordering Bohemia were sampled (Appendix 1). In February 2019, seeds of 11 representative parental specimens (P specimens) from 5 areas of origin were sown in the Botanical Garden in Frankfurt am Main, and the obtained total of 70 offspring individuals (OS specimens) were cultivated for 2 growing seasons. The plants that had not reached flowering on 1 August 2020, were transferred to my garden in Memmingen (southern Bavaria, Germany) and further cultivated until 25 July 2022.

Morphological comparison of the collected and cultivated plants was based on 5 characters considered to be of taxonomical importance: length/width ratio of the basal leaf blades (L/W-B); absolute length and width of the valves; length/width ratio of the valves (L/W-V); development of tubercles on the valves; absolute length and width of the tubercles.

The dried specimens listed in Appendix 1 and the examined material of the OS plants (basal leaves and infructescence fragments) are deposited in my herbarium.

2.1. Length/width ratio of the basal leaf blades

The measurements were made with an accuracy of 1 mm, using a ruler. In the case of the P specimens, all basal leaves in a suitably good state of preservation were used. In the OS generation, 5-9 basal leaves of each plant were examined in the first year (on 12 August 2019), in the second (on 22 May 2020), and for the plants cultivated further in my garden also in the third (on 11 May 2021) and fourth year of growth (on 12 May 2022).

2.2. Absolute length and width of the valves

Ten arbitrarily selected flowers with fully developed valves were taken from each specimen. One valve per

flower was examined, either the tubercle-bearing one, or, in the case of lacking tubercles, the visually largest valve.

The measurements were made with an accuracy of 0.1 mm by means of a scale loupe (Eschenbach Fadenzähler). As for the basal leaves, the width was defined as the maximum distance between the leaf margins along a line drawn orthogonally to the midrib. The length was defined as the distance between the tip of the valve and a tangent to the larger basal lobe, drawn orthogonally to the midrib.

2.3. Development of tubercles on the valves

The extent of development of tubercles on the valves was scored by semiquantitative estimation on a scale of 0-4, called the tubercle index. The index is based on the proportion of flowers bearing a valve with a tubercle: score 0 means <2%, 1 means 2-15%, 2 means 16-50%, 3 means 51-75%, and 4 means >75%.

In the (rather infrequent) cases of doubt whether a swelling of the midrib should be already regarded as tubercle, it was included in the tubercle index, even if measuring was not possible because of indistinct boundaries of the thickened area.

2.4. Absolute length and width of the tubercles

The measurements were limited to the tubercles formed on the valves selected as described above (see 2.2), with an accuracy of 0.05 mm by using again a scale loupe (Eschenbach Fadenzähler).

2.5. Statistics

First, mean values were determined for each population, i.e. over all sampled specimens of the same origin (Table 1). For the P vs OS comparison, the mean values were established individually for each P specimen, and for the cultivated plants in each case over all OS individuals stemming from that specimen (Tables 2 and 3). The statistical analysis included calculation of standard deviation. For reasons of readability, the latter together with the number of involved values are not given in the main body of the article but in Appendix 2.

3. Results and discussion

3.1. Life cycle

Almost all OS plants from the mountains bordering Bohemia, Arlberg Pass, and the offspring of specimen REN#5 from the Engadin developed inflorescences already in the second year. In contrast, the offspring of the other specimens from the Engadin, except for 2 individuals, formed only leaf rosettes (Fig. 1; Table 3,

Table 1. Morphological features of basal leaf blades (length-width ratio, L/W-B), valves and tubercles; populational means for the *Rumex longifolia* specimens collected in the field

Population	L/W-B	Valve length [mm]	Valve width [mm]	L/W-V	Tubercle index	Tubercle length [mm]	Tubercle width [mm]
Krkonoše mountains (RKr#xx)	2.3	4.5	5.2	0.88	4	0.7	0.4
Bohemian Forest (RSp#xx)	2.3	5.8	6.2	0.94	2	0.6	0.4
Bavarian Forest (RAr#xx)	3.5	5.1	5.8	0.87	1	0.6	0.3
Mount Ještěd (RJ#xx)	2.7	5.0	4.8	1.05	0	-	-
Upper Engadin (REN#xx)	3.6	6.4	6.6	0.97	0 (REN#6) 4 (other)	- 1.0	- 0.6
St. Anton am Arlberg (RAT#xx)	4.2	4.7	5.2	0.91	3 (RAT#4) 0 (other)	0.8 -	0.3 -

second column). After cultivation in the Botanical Garden for 2 years and transfer of these immature plants to my garden, their growth conditions seemed to be insufficient, despite climatic parameters rather favourable for

the species (foothills of the Bavarian Alps, 587 m asl). The plants showed poor growth, did not flower in the third year, and developed only a single inflorescence in the fourth year (Table 3).



Fig. 1. Cultures of *Rumex longifolius* in the Botanical Garden in Frankfurt a. M. on 22 May 2020. From left to right, offspring plants deriving from: RAT#1a (St. Anton am Arlberg), REN#8 (Upper Engadin), RAr#2a (Bavarian Forest), REN#4b (Upper Engadin)

Table 2. Length-width ratio of basal leafblades (L/W-B) of the cultivated offspring (OS) plants and the corresponding parental (P) specimens of *Rumex longifolia*

Population P specimen (no. of OS plants)	L/W-B (P)	L/W-B (OS) 12 Aug 2019	L/W-B (OS) 22 May 2020	L/W-B (OS) 11 May 2021	L/W-B (OS) 12 May 2022
Krkonoše mountains RKr#1 (4)	2.8	1.8	2.2	-	-
Bavarian Forest RAr#1 (7)	3.5	2.6	3.9	-	-
Bavarian Forest RAr#2a (5)	1.7	2.4	3.2	-	-
Mount Ještěd RJ#1 (7)	1.9	2.4	3.8	-	-
Upper Engadin REN#2b (7)	3.3	2.5	3.5	3.5	2.8
Upper Engadin REN#4b (6)	3.2	2.5	3.2	3.4	2.7
Upper Engadin REN#5 (6)	3.8	3.8	4.8	-	-
Upper Engadin REN#8 (7)	4.0	2.5	3.1	3.4	3.0
St. Anton am Arlberg RAT#1a (7)	4.1	3.3	4.9	-	-
St. Anton am Arlberg RAT#1d (7)	2.7	2.9	4.4	-	-
St. Anton am Arlberg RAT#5 (7)	4.5	2.6	3.8	-	-

Table 3. Perianth features of the cultivated offspring (OS) plants and the corresponding parental (P) specimens of *Rumex longifolia*

Population P specimen	Fruiting plants 1 Aug 2020	Valve length [mm]		Valve width [mm]		L/W-V		Tubercle index		Tubercle length [mm]		Tubercle width [mm]	
		P	OS	P	OS	P	OS	P	OS	P	OS	P	OS
Krkonoše mountains RKr#1	4 of 4	4.7	4.5	5.4	4.9	0.88	0.91	4	4	0.7	0.9	0.3	0.3
Bavarian Forest RAr#1	7 of 7	5.6	4.7	6.2	5.2	0.90	0.90	2	2	0.6	0.5	0.2	0.2
Bavarian Forest RAr#2a	5 of 5	4.5	4.9	5.4	5.2	0.84	0.94	0	1	-	0.7	-	0.2
Mount Ještěd RJ#1	7 of 7	4.3	5.1	4.6	5.0	0.95	1.02	0	0	-	-	-	-
Upper Engadin REN#2b	1 of 7 25 Jul 2022 (1 plant)	6.3	6.0 5.2	6.9	6.1 5.3	0.92	0.98 0.99	4	3 4	0.8	0.7 1.1	0.5	0.4 0.7
Upper Engadin REN#4b	1 of 6	6.6	6.2	6.8	6.6	0.97	0.93	4	4	1.1	1.1	0.6	0.7
Upper Engadin REN#5	6 of 6	5.7	5.8	6.1	6.1	0.93	0.97	4	4	1.7	1.5	0.9	0.8
Upper Engadin REN#8	0 of 7	6.7	-	7.2	-	0.93	-	4	-	1.2	-	0.7	-
St. Anton am Arlberg RAT#1a	7 of 7	4.6	4.9	5.1	5.5	0.91	0.89	0	1	-	0.7	-	0.3
St. Anton am Arlberg RAT#1d	7 of 7	4.2	4.8	4.6	5.3	0.91	0.90	0	0	-	-	-	-
St. Anton am Arlberg RAT#5	6 of 7	4.6	4.7	5.1	5.3	0.90	0.89	0	1	-	0.5	-	0.3

3.2. Leaf features

If only the specimens collected in the field are considered, the length-width ratio of the basal leaf blades differentiate the studied populations into 3 groups (Table 1). The plants from the Czech Republic (Krkonoše mountains, Mount Ještěd, Bohemian Forest) have broad blades ($L/W-B$ ca. 2.5) and may therefore be assigned to subsp. *sourekii*, in accordance with the opinion of Czech researchers (e.g. Kubát 1990). The plants from the Bavarian Forest and the Engadin, with $L/W-B$ ca. 3.5, correspond to the nominate form (Castroviejo *et al.* 1990), while the Arlberg population, with $L/W-B > 4$, to the Southeast Scandinavian group (taxonomically yet not described) in the sense of Holm & Korpelainen (1999).

These features are superimposed by the developmental stage of the plants (Table 2). In the OS generation, the differences observed in the parental generation appear only in the second year, while the vegetative rosettes of the first year, as well as the poorly growing plants of the fourth year, are characterized by broader leaves. This finding provides a possible explanation for the leaf shape of P specimen RAT#1d, which deviates from that of the other Arlberg plants by its much smaller $L/W-B$ (Table 2). The specimen consists of a leaf rosette (formed during the current growing season), which is connected to a withered fruiting stalk (Fig. 2). Obviously, such a secondary shoot tends to develop broader leaves in the same way as an immature individual in its first year.



Fig. 2. *Rumex longifolius*: parental specimen RAT#1d, collected on 1 Sep 2018. Top right and bottom middle: second-year basal leaves of its offspring plants, sampled on 22 May 2020



Fig. 3. Valves of *Rumex longifolius* from the Alps. Top row: Upper Engadin, specimen REN#2b. Bottom row: St. Anton am Arlberg, specimen RAT#5. Scale bar = 1 mm

3.3. Perianth features

In the Alps, the specimens from the Engadin are distinguished by their large valves, always bearing tubercles, except for specimen REN#6. In contrast, valves of the Arlberg plants are markedly smaller and always lack tubercles, except for specimen RAT#4 (Tables 1 and 3, Fig. 3). These differences persist – more or less – in the OS generation (Table 3), hence obviously

are genetically fixed. Taking into account the above-mentioned leaf traits it therefore can be concluded that the population on Mount Arlberg, which exists at least since the early 1990s (Willner 1994), originated by a discrete introduction, rather than – as supposed recently (Sonnberger 2018) – by migration from the Engadin down the upper Inn valley. This can be seen also from the aspect of the stands above St. Anton. The plants concentrate at 1850 m asl around the cableway building

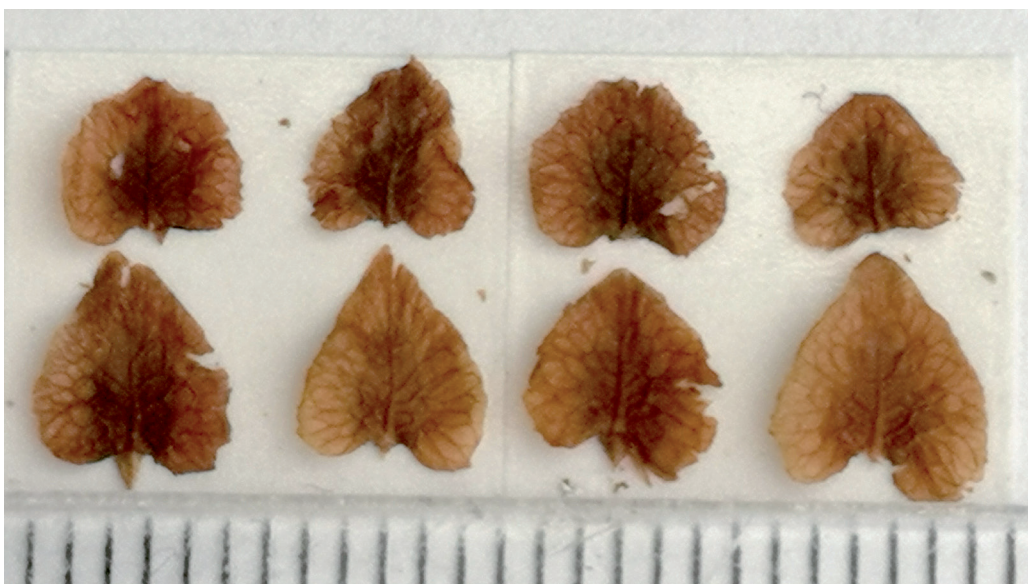


Fig. 4. Valves of *Rumex longifolius* from Mount Ještěd, specimen RJ#1. Top row: parental specimen, 14 Aug 2018. Bottom row: offspring plant, 1 Aug 2020. Scale bar = 1 mm



Fig. 5. Valves of *Rumex longifolius* from the mountains bordering Bohemia. Top row: Krkonoše mountains, specimen RKr#1; middle row: Mount Ještěd, specimen RJ#2; bottom row: Bavarian Forest, specimen RAr#1. Scale bar = 1 mm

complex “upper terminus Gampenbahn / lower terminus Kapallbahn”, from which they descend ca. 100 m downhill along the Gampenbahn cableway line. Here we are obviously dealing with the scheme described by Rechinger (1990): a onetime introduction followed by subsequent expansion.

The valves of the plants from Mount Ještěd differ from those of all the other examined populations by invariably lacking tubercles and a larger length-width ratio. The first trait is stably inherited (tubercle index = 0 in P as well as OS), while the latter is varying between the generations, as $L/W-V = 0.95$ in P and 1.02 in OS (Table 3; Fig. 4). The plants from Krkonoše mountains and the Bavarian Forest, both with smaller $L/W-V$ and tubercles often present, differ from each other in $L/W-B$

and tubercle index in both generations (Tables 2 and 3). It can therefore be assumed that 3 genetically different populations occur in the mountains bordering Bohemia (Fig. 5).

3.4. Synopsis of morphological findings

Combining the data obtained from the original collections and the OS cultures, the studied populations can be distinguished from one another (Table 4). The values are sufficiently dissimilar to demonstrate that geographical separation is associated with morphological differences. This allows the conclusion that each of the populations originated by a singular introduction event. Unfortunately, because no ripe seeds were available, it was not possible to include the Bohemian Forest

Table 4. Approximate values of length-width ratio of basal leaf blades ($L/W-B$) and perianth features of combined parental and offspring plants of *Rumex longifolia*

Population	$L/W-B$ on current year's flowering shoots	Valve length [mm]	$L/W-V$	% of flowers with a mature valve bearing a tubercle
Krkonoše mountains	2-3	4-5	0.85-0.95	>50
Bavarian Forest	3-4	4.5-5.5	0.85-0.95	<50
Mount Ještěd	3-4	4.5-5.5	0.95-1.05	0 (no exception)
Upper Engadin	3-4	6-7	0.90-1.00	100 (except for REN#6)
St. Anton am Arlberg	>4	4-5	0.85-0.95	0 (except for RAT#4)

population (see Table 1) in the cultivation experiments. In the Czech literature, the plants occurring there as well as those naturalized in the Krkonoše mountains are assigned to a distinct subsp. *sourekii* Kubát, which differs from the nominal taxon by broader leaves (Kubát 1990). Although this trait could be confirmed here for the collections from the Krkonoše mountains, its taxonomical relevance should be assessed against the variability of the species, and the dependence of just this character from development stage and growth conditions (see 3.2). Considering the general polymorphism of *R. longifolius*, a categorisation based on a single character does not seem appropriate anyway. The rank of a subspecies clearly overemphasizes the taxonomical status of subsp. *sourekii* as defined hitherto².

4. Occurrence of *Rumex crispus* in the Engadin

Specimen REN#5 has been suspected already in the field to be *R. × propinquus* Aresch. (*R. crispus* × *R. longifolius*) because of its tubercles measuring on average 1.7 mm × 0.9 mm as well as its smaller valves and narrower leaves as compared with the other Engadin specimens. These traits are essentially inherited by the OS generation (Tables 2 and 3), so it can be concluded that the specimen derived from a fertile introgression with *R. crispus*. Its narrow leaves and invariably entire valves allow to exclude other tubercle-bearing species, like *R. obtusifolius* L. (which occurs in the region, see specimen REN#7, Appendix 1) and *R. patientia* L. The other specimens from the Engadin are characterized by unusually (as for *R. longifolius*) large tubercles, too. REN#4b and REN#8 exceed the maximum value given in the literature (1 mm × 0.6 mm, see Kubát 1990; Castroviejo *et al.* 1990), and although the P specimen REN#2b itself has “normally sized” tubercles, the single OS plant reaching flowering in the fourth year again exceeds the above-mentioned limit. The latter also developed distinctly smaller valves (Table 3), but this may be due to the unfavourable growth conditions in that year (see 3.1).

Hence, contrary to the hypothesis formulated by Adler (1992), *R. crispus* apparently occurs in the Engadin or at least occurred there in the past. It is possible, for example, that the subalpine climatic conditions prevailing here constitute a severe growth limit for this species, normally restricted to lower elevations. Since *R. longifolius* became invasive in the mid-20th century, it may have quickly replaced and genetically assimilated its ecologically poorly adapted relative.

5. Nativeness of *Rumex longifolius* in the Engadin

The current or earlier occurrence of *R. crispus* in the Engadin does not disprove the hypothesis of *R. longifolius* being native in this area. The former species, recently no more recorded there, may have been sufficiently rare already in the 19th and early 20th century to doubt the reliability of its records by contemporary botanists. Many records of *R. crispus* at that time probably refer to introgression forms with *R. longifolius* or to the latter species itself.

The OS plants from the Engadin (except for the offspring of specimen REN#5, considered as *R. × propinquus*) did not reach flowering in the second year and developed only occasional inflorescences, respectively – in contrast to the offspring of all other, certainly neophytic populations (Fig. 1; Table 3). This obvious developmental distinctiveness may be taken as another indication of the nativeness of *R. longifolius* in the Engadin. Further evidence results from its preference for wet habitats, which was observed only here. Specimens REN#1 and REN#6 grew in natural biotopes (riverbank and marsh, see Appendix 1), to which they might have spread from the adjacent ruderal habitats. On the other hand, the ruderal stands prevailing today in the Engadin may have originated just in the mid-20th century, after transition of the species to invasive behaviour, with natural habitats in the flood plains of the Inn as an area of origin and source of diaspores.

6. Other records from Austria

Fischer *et al.* (2008) mention records of *R. longifolius* from the upper Tyrolean Inn valley and the Steiermark, which date back to the second half of the 20th century. They are documented by 4 sheets in the herbarium of the Natural History Museum Vienna (W) and one sheet in the herbarium of the Biology Centre Linz (LI), with a duplicate in the herbarium of the University of Graz (Table 5). The Tyrolean specimens have comparatively large valves, regularly bearing tubercles, similarly to the Engadin plants investigated in this paper. Although origin from this region seems likely because of short physical distance, this assumption should be verified statistically by more material. Two other specimens from Austria in the herbarium of the Tyrolean State Museum in Hall in Tirol (Matrei in Eastern Tyrol, 26 Sep 2009; Ötztaler Ache North of Sölden, 28 Aug 1999) have not been examined in this study.

7. Putative hybrid origin of *R. longifolius*

The original description of *R. longifolius* by DeCandolle in 1815 (Fig. 6) was translated by me as follows: “This species has many common features with

² According to Plants of the World Online (<https://powo.science.kew.org/>, visited Nov 15, 2024) *R. longifolius* subsp. *sourekii* Kubát, meanwhile, has been synonymized with *R. longifolius* DC.

Table 5. Herbarium specimens of *Rumex longifolius* from the upper Tyrolean Inn valley [Oberinntal] and the Steiermark

Herbarium code, specimen no.	Original label text in German and its translation into English	Specimen description
W, specimen 1, sheet 1	Oberinntal, unmittelbares linkes Innufer zwischen Stuben/Pfunds und Maria-Stein, ca. 955 m, 12.09.1983, leg. A. Polatschek, det. W. Forstner (als <i>R. patientia</i>), rev. K. H. Rechinger	1 (presumably) basal leaf 24.7 cm x 7.8 cm → length/width = 3.2; 1 immature infructescence with green-brown valves
W, specimen 1, sheet 2	[Upper Inn valley, immediate bank of river Inn between Stuben / Pfunds and Maria-Stein, ca. 955 m, 12 Sep 1983, leg. Al Polatschek, det. W. Forstner (as <i>R. patientia</i>), rev. K. H. Rechinger]	1 (presumably) basal leaf 32.3 cm x 12.4 cm → length/width = 2.6; 1 mature infructescence with brown valves bearing occasional tubercles; mean of 8 valves: length = 6.6 mm, width = 7.1 mm → length/width = 0.93; tubercles up to 1.5 mm x 0.8 mm
W, specimen 2	Oberinntal: linkes Innufer zw. Schönwies und Imsterberg, Aubereich, 31.08.1972, leg. A. Polatschek, det. K. H. Rechinger [Upper Inn valley: left bank of river Inn between Schönwies and Imsterberg, flood plain zone, 31 Aug 1972, leg. A. Polatschek, det. K. H. Rechinger]	1 (presumably) basal leaf 19.3 cm x 6.6 cm → length/width = 2.9; 1 (presumably) stem leaf; 1 mature infructescence with brown valves bearing occasional tubercles; mean of 12 valves: length = 5.8 mm, width = 6.1 mm → length/width = 0.96; tubercles up to 0.9 mm x 0.5 mm
W, specimen 3	Oberinntal, rechte Inn-Au zwischen Gh. "Neuer Zoll" und der Pontlatz-Brücke bei Prutz, ca. 860 m, 04.09.1983, leg. A. Polatschek (als <i>R. patientia</i>), det. K. H. Rechinger. [Upper Inn valley, right flood plain of river Inn between inn "Neuer Zoll" and Pontlatz bridge near Prutz, ca. 860 m, 4 Sep 1983, leg. A. Polatschek (as <i>R. patientia</i>), det. K. H. Rechinger.	1 (presumably) basal leaf 27.4 cm x 13.1 cm → length/width = 2.1; 1 mature infructescence with brown valves bearing numerous tubercles; mean of 10 valves: length = 5.4 mm, width = 5.9 mm → length/width = 0.91; tubercles up to 1.0 mm x 0.6 mm
LI	Steiermark, oberes Murtal, nordöstl. von Kraubat auf einer Anschwemmung der Mur gegen St. Stefan zu, 24.08.1988, H. Melzer [Steiermark, upper Mur valley, northeast of Kraubat on alluvia of river Mur towards St. Stefan, 24 Aug 1988, H. Melzer]	1 (presumably) basal leaf 23.5 cm x 8.3 cm → length/width = 2.8; 1 mature infructescence with brown valves without or with only rudimentary tubercles; mean of 10 valves: length = 5.0 mm, width = 5.3 mm → length/width = 0.94

R. aquaticus and *crispus*. The stem is straight, high, furrowed; the leaves are very long, in the lower parts of the plant long-stalked; they are elongated, acute, attenuated at both ends, undulate-crispate at the margins;

the flowers are in whorls, which are arranged in long spikes, these mostly simple, sometimes branched, usually paired in the leaf axils; the valves of the perianth are highly entire, obtuse, and bear instead of tubercles just

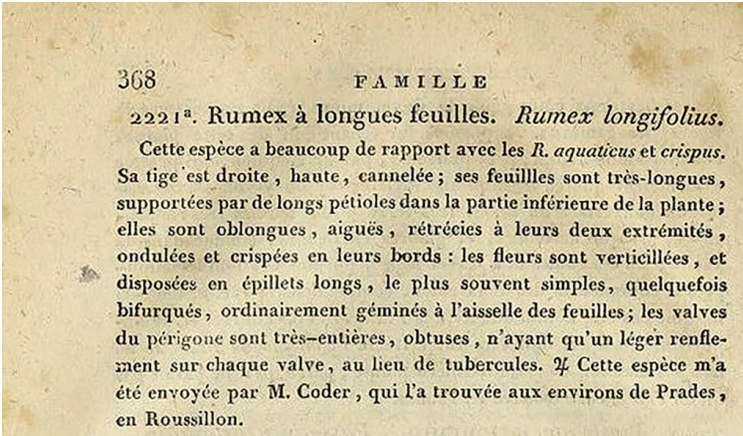


Fig. 6. Original description of *Rumex longifolius* by DeCandolle from the year 1815

a slight swelling. This species has been sent to me by Mr. Coder, who found it in the surroundings of Prades, in Roussillon”.

This description already points to a possible relation to *R. aquaticus* and *R. crispus*. Kubát (1990) suggests hybrid origin, with these 2 species as parents, but does not cite any references. Because a literature search did not yield any pertinent information, it can be assumed that we are dealing here with an unverified hypothesis, which nevertheless is very plausible from both morphological and ecological points of view. For example, the morphological variability of *R. longifolius* described in this paper is reflected by various combinations of traits of *R. aquaticus* (large valves without tubercles, broad, marginally not undulate leaves) and *R. crispus* (medium-sized valves with tubercles, narrow, strongly undulate leaves). Moreover, the limitation to higher mountain

ranges, which is unusual for an invasive species, may be explained by humidity rather than temperature. An increased demand for moisture inherited by *R. aquaticus* should be met here much easier than in similar ruderal lowland habitats. As compared to Kubínová & Krahulec (1998), who explained the success of *R. longifolius* at higher altitudes by its adaptation to a cold environment and short growing seasons, this hypothesis better reflects an invasive behaviour antithetical to the much-discussed global warming.

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Appendix 1. Overview of the collected specimens of *Rumex longifolius* and closely related taxa

Code	Date	Locality	Specimen	
Krkonoše mountains (Czech Republic)				
RKr#1 P	4 Oct 2014	ruderal site in Temný Důl, west of Horní Maršov, 600 m asl	<i>R. longifolius</i> , 1 mature infructescence with brown valves and 2 separate basal leaves	
RKr#2	5 Oct 2014	Richterovy Boudy, west of Pec pod Sněžkou, ca. 1200 m asl	<i>R. longifolius</i> , 1 immature infructescence with green-brown valves and 2 separate basal leaves	
Bavarian Forest (Germany)				
RAr#1 P	20 Aug 2015	roadside between Bayerisch Häusel and Brennes, 1000 m asl	<i>R. longifolius</i> , 1 mature infructescence with brown valves and 3 attached basal leaves	
RAr#2a P	21 Aug 2015	Brennes, roadside opposite to hotel Arberalm, 1030 m asl	<i>R. longifolius</i> ; 1 mature infructescence with brown valves and 1 separate basal leaf	
RAr#2b			1 immature infructescence with green valves	
RAr#3	6 Aug 2016	Bayerisch Häusel, grassy verge in front of youth hostel, 800 m asl	<i>R. longifolius</i> 1 immature infructescence with green valves and a separate rosette with 7 leaves	
RAr#4	6 Aug 2016	roadside between Bayerisch Häusel and Brennes, 1000 m asl	<i>R. longifolius</i> , 2 immature infructescences with green valves, one of them with 3 attached basal leaves	
RAr#5	6 Aug 2016	roadside between Bayerisch Häusel and Brennes, 1000 m asl	<i>R. longifolius</i> , 2 inflorescences (one of them with 7 basal leaves), 4 separate basal leaves (valves not developed yet)	
RAr#6	6 Aug 2016	road embankment ca. 500 m east of Brennes, 1050 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves	
RAr#7	16 Jul 2017	road verge ca. 650 m south-west of viewing platform Hindenburgkanzel, 1040 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves and 1 separate basal leaf	
Bohemian Forest (Czech Republic)				
RSpl	15 Jul 2017	Špičák Pass above Železná Ruda, 930 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves	
RSpot	15 Jul 2017	road verge near parking lot “Kaskady” in Špičák village above Železná Ruda, 860 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves and 2 separate basal leaves	
Mount Ještěd above Liberec (Czech Republic)				
RJ#1 P	14 Aug 2018	near summit, ca. 1010 m asl	<i>R. longifolius</i> , 1 mature infructescence with brown valves and 7 attached basal leaves	
RJ#2	14 Aug 2018	near summit, ca. 1010 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves	
RJ#3	14 Aug 2018	near summit, ca. 1010 m asl	<i>R. longifolius</i> , 4 separate rosettes with a total of 3+2+4+6 = 15 leaves	
RJ#F	29 Jul 2016 (leg. S. E. Fröhner)	near summit, ca. 1000 m asl	<i>R. longifolius</i> , 1 immature infructescence with brown-green valves	
Upper Engadin (Switzerland)				
REN#1	20 Aug 2018	Inn river bank ca. 100 m north of parking lot between Samedan and Celerina, ca. halfway between parking lot and bridge, ca. 1720 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves and 1 separate rosette with 4 leaves	
REN#2a	20 Aug 2018	grassy verge ca. 50 m north of that parking lot (see REN#1), ca. 8 m away from road, ca. 1720 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves and 2 separate basal leaves	
REN#2b P			<i>R. longifolius</i> , 1 mature infructescence with brown valves and 8 separate basal leaves	
REN#3	20 Aug 2018	grassy verge ca. 10 m north of that parking lot (see REN#1), between bikeway and road, ca. 1720 m asl	<i>R. alpinus</i>	
REN#4a	20 Aug 2018	meadow ca. 100 m south of “Classi Car Engadin” (last house east of that road, at southern outskirts of Samedan village), ca. 1720 m asl	<i>R. longifolius</i> > <i>R. cf. × propinquus</i> , 1 partly mature infructescence with green and brown valves	1 secondary rosette with 3 leaves
REN#4b P			<i>R. longifolius</i> > <i>R. cf. × propinquus</i> , 1 mature infructescence with brown valves	

REN#5 P	20 Aug 2018	same as above: meadow ca. 100 m south of “Classi Car Engadin” (last house east of that road, at southern outskirts of Samedan village), ca. 1720 m asl	<i>R. cf. × propinquus</i> , 1 mature infructescence with brown valves bearing a basal branch with immature (green) valves; 1 separate rosette with 4 leaves
REN#6	20 Aug 2018	bottle sedge bog, right of brook Flaxvegl, close to its junction with river Inn, ca. 200 m east of above-mentioned bridge (see REN#1), ca. 1720 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves and 1 separate rosette with 9 leaves
REN#7	21 Aug 2018	meadow slope ca. 50 m above bus station “Hauptpost” in St. Moritz, intermixed with <i>R. alpinus</i> and <i>R. longifolius</i> , ca. 1800 m asl	<i>R. obtusifolius</i>
REN#8 P	21 Aug 2018	meadow by “Sothebys” house above road from railway station to St. Moritz Dorf, ca. 1800 m asl	<i>R. longifolius</i> > <i>R. cf. × propinquus</i> , 1 mature infructescence with brown valves and 3 separate basal leaves
REN#9	21 Aug 2018	upper terminus Chantavella / lower terminus Corviglia funicular above St. Moritz, ca. 2010 m asl	<i>R. longifolius</i> , 1 immature infructescence with green valves and 3 separate basal leaves
REN#F	17 Jul 2018 (leg. S. E. Fröhner)	meadow edge within Sils-Maria village, ca. 1810 m asl	<i>R. longifolius</i> , 1 inflorescence (valves not developed yet) and 3 separate basal leaves

St. Anton am Arlberg (Austria), 1850-1750 m asl

RAT#1a P	1 Sep 2018	meadow below a small building below lower terminus of cableway Kapallbahn; mixed stand of <i>R. longifolius</i> and <i>R. alpinus</i>	<i>R. longifolius</i> , 1 mature infructescence with brown valves and secondary rosettes with a total of 8 leaves
RAT#1b	1 Sep 2018		<i>R. longifolius</i> , 1 mature infructescence with brown valves
RAT#1c	1 Sep 2018		<i>R. longifolius</i> , 1 mature infructescence with brown valves and separate rosettes with a total of 13 leaves
RAT#1d P	1 Sep 2018	path ca. 5 m east of that building (see RAT#1a)	<i>R. longifolius</i> , 1 mature infructescence with brown valves and secondary rosette with 6 leaves
RAT#1e	1 Sep 2018	path ca. 5 m north of that building (see RAT#1a)	<i>R. longifolius</i> , 2 mature infructescences with brown valves and 12 separate basal leaves
RAT#1f	1 Sep 2018	south verge of way between that building (see RAT#1a) and lower terminus of cableway Kapallbahn	<i>R. obtusifolius</i>
RAT#2a	1 Sep 2018	ca. 75 m south-east of upper terminus of cableway Gampenbahn, together with <i>R. obtusifolius</i>	<i>R. longifolius</i> , 1 immature infructescence with green valves 1 secondary rosette with 6 leaves
RAT#2b			<i>R. longifolius</i> , 1 mature infructescence with brown valves
RAT#3	1 Sep 2018	cableway of Gampenbahn, near third pillar from above, together with <i>R. obtusifolius</i>	<i>R. longifolius</i> , 1 mature infructescence with brown valves and separate rosettes with a total of 5 leaves
RAT#4	1 Sep 2018	cableway of Gampenbahn, near second pillar from above, together with <i>R. acetosa</i>	<i>R. longifolius</i> , 1 immature infructescence with green valves and a secondary rosette with 4 leaves
RAT#5 P	1 Sep 2018	cableway of Gampenbahn, between terminus building and first pillar from above	<i>R. longifolius</i> , 1 mature infructescence with brown valves and a secondary rosette with 6 leaves
RAT#Fa	25 Aug 2017 (leg. S. E. Fröhner)	upper terminus of cableway Gampenbahn, 1860 m asl	<i>R. longifolius</i> , 1 inflorescence (valves yet not developed) and 4 separate basal leaves
RAT#Fb			<i>R. longifolius</i> , 1 mature infructescence with brown valves

Explanations: Unless otherwise noted, specimens were collected by B. Sonnberger. **P** – plants used for cultivation experiments

Appendix 2. Statistical data of parental (P) and offspring (OS) plants of *Rumex longifolius*

Parameter	Number of values	Mean value	Standard deviation
Table 1, RKr#xx, L/W-B	4	2.32	0.59
Table 1, RKr#xx, valve length [mm]	17	4.54	0.44
Table 1, RKr#xx, valve width [mm]	17	5.15	0.59
Table 1, RKr#xx, L/W-V	17	0.88	0.05
Table 1, RKr#xx, tubercle length [mm]	14	0.73	0.19
Table 1, RKr#xx, tubercle width [mm]	14	0.36	0.24
Table 1, RSp#xx, L/W-B	2	2.29	0.23
Table 1, RSp#xx, valve length [mm]	20	5.84	0.54
Table 1, RSp#xx, valve width [mm]	20	6.24	0.66
Table 1, RSp#xx, L/W-V	20	0.94	0.09
Table 1, RSp#xx, tubercle length [mm]	5	0.60	0.07
Table 1, RSp#xx, tubercle width [mm]	5	0.38	0.09
Table 1, RAr#xx, L/W-B	26	3.50	0.86
Table 1, RAr#xx, valve length [mm]	70	5.06	0.65
Table 1, RAr#xx, valve width [mm]	70	5.80	0.63
Table 1, RAr#xx, L/W-V	70	0.87	0.09
Table 1, RAr#xx, tubercle length [mm]	9	0.56	0.11
Table 1, RAr#xx, tubercle width [mm]	9	0.27	0.09
Table 1, RJ#xx, L/W-B	22	2.71	0.62
Table 1, RJ#xx, valve length [mm]	30	5.00	0.71
Table 1, RJ#xx, valve width [mm]	30	4.76	0.44
Table 1, RJ#xx, L/W-V	30	1.05	0.12
Table 1, REN#xx, L/W-B	39	3.61	0.67
Table 1, REN#xx, valve length [mm]	93	6.39	0.77
Table 1, REN#xx, valve width [mm]	93	6.62	0.77
Table 1, REN#xx, L/W-V	93	0.97	0.08
Table 1, REN#xx, tubercle length [mm]	73	1.03	0.50
Table 1, REN#xx, tubercle width [mm]	73	0.59	0.28
Table 1, RAT#xx, L/W-B	64	4.21	0.89
Table 1, RAT#xx, valve length [mm]	110	4.72	0.64
Table 1, RAT#xx, valve width [mm]	110	5.18	0.68
Table 1, RAT#xx, L/W-V	110	0.91	0.06
Table 1, RAT#xx, tubercle length [mm]	7	0.76	0.17
Table 1, RAT#xx, tubercle width [mm]	7	0.34	0.05
Table 2, RKr#1, P, L/W-B	2	2.76	0.48
Table 2, RKr#1, OS, L/W-B, 12 Aug 2019	18	1.81	0.43
Table 2, RKr#1, OS, L/W-B, 22 May 2020	29	2.24	0.23
Table 2, RAr#1, P, L/W-B	3	3.50	0.29
Table 2, RAr#1, OS, L/W-B, 12 Aug 2019	29	2.59	0.34
Table 2, RAr#1, OS, L/W-B, 22 May 2020	44	3.87	0.45
Table 2, RAr#2a, P, L/W-B	1	1.70	-
Table 2, RAr#2a, OS, L/W-B, 12 Aug 2019	28	2.37	0.36
Table 2, RAr#2a, OS, L/W-B, 22 May 2020	30	3.24	0.38
Table 2, RJ#1, P, L/W-B	7	1.94	0.21
Table 2, RJ#1, OS, L/W-B, 12 Aug 2019	36	2.42	0.37
Table 2, RJ#1, OS, L/W-B, 22 May 2020	44	3.76	0.60
Table 2, REN#2b, P, L/W-B	10	3.33	0.58
Table 2, REN#2b, OS, L/W-B, 12 Aug 2019	33	2.50	0.31
Table 2, REN#2b, OS, L/W-B, 22 May 2020	46	3.50	0.48
Table 2, REN#2b, OS, L/W-B, 11 May 2021	31	3.49	0.59
Table 2, REN#2b, OS, L/W-B, 12 May 2022	17	2.83	0.59
Table 2, REN#4b, P, L/W-B	3	3.18	0.45
Table 2, REN#4b, OS, L/W-B, 12 Aug 2019	33	2.53	0.34
Table 2, REN#4b, OS, L/W-B, 22 May 2020	37	3.16	0.39
Table 2, REN#4b, OS, L/W-B, 11 May 2021	25	3.37	0.57
Table 2, REN#4b, OS, L/W-B, 12 May 2022	14	2.74	0.53

Table 2, REN#5, P, L/W-B	4	3.79	0.36
Table 2, REN#5, OS, L/W-B, 12 Aug 2019	21	3.82	0.92
Table 2, REN#5, OS, L/W-B, 22 May 2020	49	4.82	0.96
Table 2, REN#8, P, L/W-B	3	3.96	0.30
Table 2, REN#8, OS, L/W-B, 12 Aug 2019	37	2.48	0.29
Table 2, REN#8, OS, L/W-B, 22 May 2020	36	3.10	0.31
Table 2, REN#8, OS, L/W-B, 11 May 2021	35	3.37	0.79
Table 2, REN#8, OS, L/W-B, 12 May 2022	10	3.01	0.36
Table 2, RAT#1a, P, L/W-B	8	4.07	0.53
Table 2, RAT#1a, OS, L/W-B, 12 Aug 2019	34	3.26	0.46
Table 2, RAT#1a, OS, L/W-B, 22 May 2020	35	4.92	0.60
Table 2, RAT#1d, P, L/W-B	6	2.65	0.57
Table 2, RAT#1d, OS, L/W-B, 12 Aug 2019	38	2.90	0.52
Table 2, RAT#1d, OS, L/W-B, 22 May 2020	44	4.40	0.46
Table 2, RAT#5, P, L/W-B	6	4.46	0.85
Table 2, RAT#5, OS, L/W-B, 12 Aug 2019	32	2.56	0.47
Table 2, RAT#5, OS, L/W-B, 22 May 2020	47	3.82	0.70
Table 3, RKr#1, P, valve length [mm]	10	4.73	0.38
Table 3, RKr#1, OS, valve length [mm]	40	4.48	0.43
Table 3, RKr#1, P, valve width [mm]	10	5.41	0.44
Table 3, RKr#1, OS, valve width [mm]	40	4.93	0.41
Table 3, RKr#1, P, L/W-V	10	0.88	0.06
Table 3, RKr#1, OS, L/W-V	40	0.91	0.07
Table 3, RKr#1, P, tubercle length [mm]	7	0.73	0.14
Table 3, RKr#1, OS, tubercle length [mm]	38	0.94	0.19
Table 3, RKr#1, P, tubercle width [mm]	7	0.29	0.10
Table 3, RKr#1, OS, tubercle width [mm]	38	0.32	0.08
Table 3, RAr#1, P, valve length [mm]	10	5.58	0.54
Table 3, RAr#1, OS, valve length [mm]	70	4.71	0.47
Table 3, RAr#1, P, valve width [mm]	10	6.20	0.60
Table 3, RAr#1, OS, valve width [mm]	70	5.24	0.54
Table 3, RAr#1, P, L/W-V	10	0.90	0.04
Table 3, RAr#1, OS, L/W-V	70	0.90	0.06
Table 3, RAr#1, P, tubercle length [mm]	2	0.65	0.07
Table 3, RAr#1, OS, tubercle length [mm]	14	0.53	0.14
Table 3, RAr#1, P, tubercle width [mm]	2	0.23	0.04
Table 3, RAr#1, OS, tubercle width [mm]	14	0.21	0.04
Table 3, RAr#2a, P, valve length [mm]	10	4.53	0.57
Table 3, RAr#2a, OS, valve length [mm]	50	4.89	0.56
Table 3, RAr#2a, P, valve width [mm]	10	5.43	0.55
Table 3, RAr#2a, OS, valve width [mm]	50	5.20	0.52
Table 3, RAr#2a, P, L/W-V	10	0.84	0.11
Table 3, RAr#2a, OS, L/W-V	50	0.94	0.06
Table 3, RAr#2a, OS, tubercle length [mm]	1	0.70	-
Table 3, RAr#2a, OS, tubercle width [mm]	1	0.20	-
Table 3, RJ#1, P, valve length [mm]	10	4.34	0.41
Table 3, RJ#1, OS, valve length [mm]	70	5.07	0.59
Table 3, RJ#1, P, valve width [mm]	10	4.59	0.34
Table 3, RJ#1, OS, valve width [mm]	70	4.97	0.39
Table 3, RJ#1, P, L/W-V	10	0.95	0.10
Table 3, RJ#1, OS, L/W-V	70	1.02	0.08
Table 3, REN#2b, P, valve length [mm]	10	6.31	0.43
Table 3, REN#2b, OS, valve length [mm]; 1 Aug 2020	10	6.00	0.63
Table 3, REN#2b, OS, valve length [mm]; 27 Jul 2022	15	5.23	0.62
Table 3, REN#2b, P, valve width [mm]	10	6.89	0.39
Table 3, REN#2b, OS, valve width [mm]; 1 Aug 2020	10	6.14	0.67
Table 3, REN#2b, OS, valve width [mm]; 27 Jul 2022	15	5.29	0.57
Table 3, REN#2b, P, L/W-V	10	0.92	0.02
Table 3, REN#2b, OS, L/W-V; 1 Aug 2020	10	0.98	0.05
Table 3, REN#2b, OS, L/W-V; 27 Jul 2022	15	0.99	0.10
Table 3, REN#2b, P, tubercle length [mm]	10	0.76	0.16

Table 3, REN#2b, OS, tubercle length [mm]; 1 Aug 2020	7	0.71	0.22
Table 3, REN#2b, OS, tubercle length [mm]; 27 Jul 2022	14	1.14	0.23
Table 3, REN#2b, P, tubercle width [mm];	10	0.45	0.09
Table 3, REN#2b, OS, tubercle width [mm]; 1 Aug 2020	7	0.36	0.08
Table 3, REN#2b, OS, tubercle width [mm]; 27 Jul 2022	14	0.67	0.16
Table 3, REN#4b, P, valve length [mm]	10	6.57	0.53
Table 3, REN#4b, OS, valve length [mm]	10	6.16	0.78
Table 3, REN#4b, P, valve width [mm]	10	6.81	0.34
Table 3, REN#4b, OS, valve width [mm]	10	6.64	0.67
Table 3, REN#4b, P, L/W-V	10	0.97	0.07
Table 3, REN#4b, OS, L/W-V	10	0.93	0.08
Table 3, REN#4b, P, tubercle length [mm]	10	1.11	0.16
Table 3, REN#4b, OS, tubercle length [mm]	10	1.09	0.26
Table 3, REN#4b, P, tubercle width [mm]	10	0.64	0.13
Table 3, REN#4b, OS, tubercle width [mm]	10	0.71	0.15
Table 3, REN#5, P, valve length [mm]	13	5.65	0.69
Table 3, REN#5, OS, valve length [mm]	60	5.84	1.53
Table 3, REN#5, P, valve width [mm]	13	6.11	0.89
Table 3, REN#5, OS, valve width [mm]	60	6.05	1.48
Table 3, REN#5, P, L/W-V	13	0.93	0.09
Table 3, REN#5, OS, L/W-V	60	0.97	0.10
Table 3, REN#5, P, tubercle length [mm]	13	1.73	0.68
Table 3, REN#5, OS, tubercle length [mm]	29	1.53	0.54
Table 3, REN#5, P, tubercle width [mm]	13	0.94	0.34
Table 3, REN#5, OS, tubercle width [mm]	49	0.81	0.30
Table 3, REN#8, P, valve length [mm]	10	6.72	0.72
Table 3, REN#8, P, valve width [mm]	10	7.21	0.84
Table 3, REN#8, P, L/W-V	10	0.93	0.05
Table 3, REN#8, P, tubercle length [mm]	9	1.18	0.31
Table 3, REN#8, P, tubercle width [mm]	9	0.74	0.12
Table 3, RAT#1a, P, valve length [mm]	10	4.62	0.52
Table 3, RAT#1a, OS, valve length [mm]	70	4.88	0.72
Table 3, RAT#1a, P, valve width [mm]	10	5.08	0.44
Table 3, RAT#1a, OS, valve width [mm]	70	5.47	0.73
Table 3, RAT#1a, P, L/W-V	10	0.91	0.05
Table 3, RAT#1a, OS, L/W-V	70	0.89	0.07
Table 3, RAT#1a, OS, tubercle length [mm]	3	0.67	0.21
Table 3, RAT#1a, OS, tubercle width [mm]	3	0.32	0.16
Table 3, RAT#1d, P, valve length [mm]	10	4.22	0.34
Table 3, RAT#1d, OS, valve length [mm]	70	4.83	0.66
Table 3, RAT#1d, P, valve width [mm]	10	4.64	0.44
Table 3, RAT#1d, OS, valve width [mm]	70	5.34	0.61
Table 3, RAT#1d, P, L/W-V	10	0.91	0.07
Table 3, RAT#1d, OS, L/W-V	70	0.90	0.08
Table 3, RAT#5, P, valve length [mm]	10	4.59	0.44
Table 3, RAT#5, OS, valve length [mm]	60	4.71	0.68
Table 3, RAT#5, P, valve width [mm]	10	5.07	0.39
Table 3, RAT#5, OS, valve width [mm]	60	5.34	0.80
Table 3, RAT#5, P, L/W-V	10	0.90	0.06
Table 3, RAT#5, OS, L/W-V	60	0.89	0.08
Table 3, RAT#5, OS, tubercle length [mm]	4	0.46	0.16
Table 3, RAT#5, OS, tubercle width [mm]	4	0.33	0.06