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The taxonomy of *Acetosella*

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Abstract

Á. Löve (1983). The taxonomy of *Acetosella.* Bot. Helv. *93:* 145–168. The paper reports on a taxonomical study of the collective species *Rumex Acetosella* L., in continuation of a 1943 dissertation on the cytogenetics of this autoploid series of four taxa with the chromosome numbers 2n = 14, 28, 42 and 56. It discusses the reproductive isolation of the taxa concerned, and demonstrates by aid of much new material, that the diploid is incompatible to the three polyploids, which in turn are able to form highly sterile hybrids among themselves. After a discussion of the results and their evaluation in view of some modern concepts of the species and other categories, it is concluded that the group ought to be accepted as the distinct genus *Acetosella* rather than as a section or subgenus of the then unnaturally collective genus *Rumex* as conventionally maintained. The four taxa of the series are found to represent as many distinct biological species which are recognized by aid of a combination of several subtle and mainly quantitative characteristics that are closer analysed. These four species are shown to have been recognized long since by the intuition of skilled classical taxonomists, though their distinction has been controversial ever since Linnaeus proposed the first splitting in 1762. The paper concludes with a key to the taxa concerned and with a nomenclatural review of the four species and their subspecies in their valid combinations under *Acetosella* and their synonyms. The taxa are: *A. vulgaris* (Koch) Fourreau (2n = 42) with the gymnocarpous race ssp. *vulgaris,* which is a common central, north European and north and central Siberian weed that is naturalized in Britain, the North Atlantic islands and northeastern and northwestern North America; and the angiocarpous ssp. *pyrenaica* (Pourret) Á. Löve, which is an essentially west European race that has become an almost worldwide noxious weed; *A. multifida* (L.) Á. Löve (2n = 28), a mainly gymnocarpous originally Pontic-Southsiberian species which presently is common in central and northern Europe and naturalized in Britain, the North Atlantic islands, Greenland and northeastern North America; *A. graminifolia* (Rudolph) Á. Löve (2n = 56), of arctic Eurasia from Chuckchi west to northern Norway and northeastern Greenland; and *A. angiocarpa* (Murbeck) Á. Löve, (2n = 14) of Mediterranean-Pontic-Southsiberian distribution, angiocarpous in the western parts of its area, but mainly gymnocarpous in its eastern regions.

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Introduction

My first botanical study was an inquiry into the cytogenetics of Swedish and Icelandic populations of the species then generally accepted under the collective name *Rumex Acetosella* L. The results showed that this heterogenous dioecious species is in these countries represented by two different chromosome numbers, tetraploid and hexaploid, each of which was found to be characterized by certain morphological and ecological traits. In the initial report (Löve 1940a), the hexaploid was regarded as typical *R. Acetosella* L., whereas the tetraploid was identified as the variety *tenuifolius* Wallr., based on a description in the Central European flora manual by Ascherson & Graebner (1908–1913). In a second somewhat extended paper (Löve 1940b), the latter identification was augmented by mentioning the f. *multifidus* (L.) Murb. and f. *integrifolius* Wallr., since the leaves of the few initial specimens were not only narrow and glaucous with somewhat inrolled margins and a pair of hooked and forward pointed basal lobes, but sometimes also with divided or even palmate lobes or no lobes at all. Encouraged and advised by my floristics teacher at the University of Lund, Professor Henning Weimarck, my phytogeography adviser, Professor Eric Hultén, and then Professor emeritus Svante Murbeck, the outstanding authority on the collective genus *Rumex* his generation, my enthusiasm carried me to accept the tetraploid as a species in its own right, based on its morphological distinctions and the reproductive isolation as clearly indicated by the difference in chromosome number. At that time my knowledge of the philosophy and methods of plant taxonomy was vestigial, so I did not know better than to uncritically satisfy the recommendation of my elders by dismissing the Linnaean species name *R. multifidus* L., with which I already at that time had identified the tetraploid. Therefore, I (Löve 1941a) selected for the new species the name *R. tenuifolius* (Wallr.) Á. Löve with a new and detailed description and illustrations. Further observations on the tetraploid taxon were published in a short review of the polyploid series to which a diploid and an octoploid had then been added (Löve 1941b) and in my dissertation (Löve 1943), in the introduction of which a further taxonomical revision of the entire complex was pledged. For reasons beyond my control this pledge has not been fulfilled until with the present paper.

The first year of my investigation became the first year of the second world war, so there were difficulties in gathering live and herbarium material from other countries, even through the seed exchanges of Botanical Gardens still open, or by aid of foreign colleagues and friends on the continent. Nevertheless, I succeeded in building up a respectable living collection that started to flower in 1941, at about the time when the description of the tetraploid species was published. Although most of this material comprised the tetraploid and hexaploid taxa from northern and central Europe, some collections from southern and central regions from Portugal in the west to Yugoslavia in the east and northwards to southern Czechoslovakia were in 1941–1944 found to be characterized by the diploid chromosome number, and one collection made by Professor Alexandr Tolmachev, then in Arcangelsk, on the sandy banks of the river Pechora, was found to be octoploid. By aid of Professors Hultén and Murbeck, assisted by original descriptions and herbarium material that could be anatomically compared to microscopic detail of cell size and form, the diploid was firmly identified as *R. angiocarpus* Murbeck (1891), and the octoploid as *R. graminifolius* Rudolph ex Lambert (1811), as had also been ascertained by Professor Tolmachev for the latter material. When Professor Hultén urged me to map the general distribution of these four taxa, I

discovered that for that purpose material available in Nordic herbaria was too limited. However, since my own material was not heterogenous, I did not understand better than also to rely upon extensive notes on angiocarpous specimens in European herbaria given to me by Professor Murbeck, who felt safe to identify them as *R. angiocarpus* based on this character alone, and on notes and preliminary maps of *R. graminifolius* furnished by Professor Hultén, who afterwards (Hultén 1971) forgot this and unjustly criticized these maps as if they were my sole responsibility, and also admitted having had very little experience with that taxon outside the herbarium. As a matter of fact, I discovered much later that his notes and published maps included also eastern Asiatic and western Alaskan localities where the species is replaced by a perhaps only remotely related diploid and morphologically plastic amphipacific taxon, *R. aureostigmaticus* Komarov, races of which have recently been treated as distinct species by Yurtsev & alii (1973). It seems to me that that taxon may be close to the equally plastic but tetraploid western North American mountain species *R. paucifolius* Nuttall, locally reaching from southern California to Yukon (cf. Löve & Sarkar 1956; Smith 1968; Murray 1971). These taxa are generally misplaced in the subgenus *Acetosa* as a section *Paucifoliae,* but may be more appropriately regarded as a section of subgenus *Acetosella* or as an independent genus. That, however, is a story that has to wait for more experimental perusal. Similarly, the small and procumbent *R. atlanticus* Cosson ex Maire of the High Atlas Mountains of Morocco, which Rechinger (1954) placed in *Acetosella,* may be closer related to some of the Mediterranean sections of the collective genus *Acetosa;* it seems to have $2n = 16$ chromosomes.

When the war ended, the taxonomical studies of the already then considerable material added after the completion of the dissertation of 1943 had to be interrupted, when I moved to Iceland to take up duties in plant breeding, and later to Canada and the United States to teach botany at institutions with inferior research facilities and negative attitudes towards taxonomical and evolutionary botany. I kept, however, my interest in the group and intermittently accumulated considerable new experimental and herbarium evidence in support of a modern revision of the taxonomy of the group. The present paper briefly reports the essential results of that study, and may hopefully be accepted as a kind of a fulfillment of the pledge made in the introduction of the 1943 dissertation - four decades later.

Chromosome numbers

Since 1943 several authors have confirmed my cytological observations of the chromosome numbers $2n = 14$, 28, 42 and 56 for the taxa of the *Acetosella* group (cf. references in Löve & Löve 1974, 1975b, and below), and I have myself counted these numbers in samples of the collective taxon from numerous populations, either based on own collections on travels throughout the world or on material grown for a short time from seeds sent by various colleagues from all over the natural areas of the polyploid series and from regions where the taxa are established aliens, altogether 2620 population samples of at least ten specimens each. Of these, 459 represented diploid populations from various localities in Asiatic and European Turkey, the Caucasus, western Iran, Bulgaria, Greece, the Aegean Islands, Albania, Yugoslavia (including the type localitiy of *R. angiocarpus)*, Romania, Hungary, Austria, Switzerland, Czechoslovakia, Italy with Sicily and Sardinia, Corsica, southern and eastern France, lowland areas of

Spain, the Balearic Islands, Portugal, the Canary Islands, Azores, Madeira, and lowland Algeria, Morocco and Tunisia.

832 samples represented tetraploid populations from the Nordic countries and various parts of Russia and central and western Siberia, Armenia, Transcaucasia, Georgia, Armenia, Turkey (including the type locality of *R. acetoselloides)*, Ukraine, Romania, Bulgaria, Poland, Germany, Netherlands, Belgium, Luxembourg, Czechoslovakia, Yugoslavia, Hungary, Austria, Switzerland, southern and central France, northern Spain, Italy (including various possible type localities of *R. multifidus)*, Greece, the British Isles; and also samples from Iceland, Greenland, and a few localities in eastern Canada, where the taxon is naturalized.

Hexaploid populations were represented by 1287 new samples from localities all over the Nordic countries (including assumed topotypes from Uppsala in Sweden), the Soviet Union eastwards to Yensisej and south to Ukraine and the Caucasus region (including the type localities of *R. fascilobus)*, Turkey, Greece, Bulgaria, Romania, Poland, Czechoslovakia, Hungary, Yugoslavia, Austria, Germany, Switzerland, northern and western France, Belgium, the Netherlands, Luxembourg, the mountains of Spain and Morocco, the British Isles; as well as naturalized populations from the Faeroes, Iceland, Greenland, Svalbard, various parts of Canada and the United States including Alaska, the West Indies, Venezuela, Colombia, Brazil. Argentina, Peru, Juan Fernandez, the Falkland Islands, Hawaii, India, Japan, various parts of Australia, New Zealand, St. Helena, Tristan da Cunha, and South Africa.

The octoploid taxon was represented by samples of 39 populations from the Soviet Union from Kola and Lake Onega in the west to Yenisej and Chukotka in the east, all furnished by Professor A. Tolmachev; and one seed sample of each from the Tana River and Kirkenes in northern Norway, and from Eric the Red's Land in northeastern Greenland taken by Curator Johannes Lid from a then twenty year old specimen in the Oslo herbarium but still fully germinable.

Efforts were made to include in the collection samples of all the variations summarized by Ascherson & Graebner (1908–1913) and by Beck (1909) from within the natural area of distribution of the collective taxon.

Morphology

The *R. Acetosella* complex varies considerably in numerous morphological characters, several of which have been considered in attempts to subdivide it into more restricted taxa. Most of these characteristics, however, have been found to cut polyploid boundaries. Nevertheless, several botanists with a trained floristician eye, who have been shown cultivated samples of the series, seem to have no difficulty to distinguish its four members by some kind of an intuition that cannot be defined in strict terms. I myself have been unable to discover any single or even a pair of concrete characters other than the chromosome number that can be used for a safe identification of each of these taxa in any situation. But several quantitative characters show variation connected with the different stages of polyploidy; when these are combined, a reasonably secure identification is possible even without a statistical analysis, so to deny the importance of such differences would remind of the adage on pouring the child out with the bathwater. The following remarks are based on studies of hundreds of cultivated specimens of various origins, augmented by observations of natural populations and considerable herbarium material studied sporadically between 1940 and 1980.

Life form and rhizome. – The mature *diploid* taxon has an erect, stout and somewhat woody rhizome with winterbuds and branches at the tip, but without stolons or underground shoots. It may be classified as an hemicryptophyte in the life form system by Raunkiaer (1934). It is hemerophobous in the system by Linkola (1916) and is never met with as a real weed in gardens or agricultural lands, and is naturalized nowhere, as far as I am aware.

The polyploid taxa form more or less creeping, hypogaeus rhizomes typical of geophytes, with underground buds forming more or less dense mats of vegetative shoots. In the *tetraploid*, the horizontal rhizomes are short and the shoots are few and rather close. The tendency to vegetative propagation is limited, and so is also its occurrence as a weed or casual. The *hexaploid*, on the contrary, forms a profuse mat of shoots from a much branched system of the widely creeping rhizome, a character strongly furthering vegetative dispersal and enabling the plant to become a distinctly anthropochorous root-wandering universal weed. The *octoploid*, on the other hand, is essentially an arctic-subarctic plant with a thick, roughly erect rhizome with numerous more or less extended underground stolons, at least in cultivation. It seems to be distinctly hemerophobous and is not known ever to be connected with human habitation (Dorogostayskaya 1972).

Growth form. – The *diploid* plant has numerous erect or ascending slender and slightly woody stems in a rather dense tuft, frequently with a considerable amount of old leaf rests at the base and usually branched at or above the middle. The female plant is up to 40 cm tall, but the male plant is distinctly shorter. The *tetraploid* has more or less procumbent or ascending stems, usually branched below the middle and surrounded by groups of adventitious shoots from the rhizome; the female is often shorter than 30 cm and the male less than 15 cm tall. The *hexaploid* forms dense tufts of more or less erect stems, which branch at or above the middle; around the original tuft are numerous smaller tufts that have been formed by adventitious shoots from the rhizome or by stolons from the base of the original stem; the female is up to 55 cm tall but the male hardly 20 cm; in mountains and subarctic lowlands the stems tend to become procumbent and smaller. The *octoploid* forms a few, frequently only two or three, procumbent or ascending stems which are slightly thickened at the node and branch below the middle. The female stems are up to 25 cm long but usually much smaller, as are those of the male plant. Because of the occasionally long stolons from the young rhizomes, which are numerous in cultivation, the descendents of a single female plant seem to be able to cover considerable areas and survive for a long period, whereas that kind of vegetative propagation is much more restricted in the males, which are more shortlived and, therefore, appear to be less frequent than the female plants in established populations of all the polyploid taxa.

Leaves. – The basal leaves of the *diploid* taxon vary in size and outline, but they are generally lanceolate-hastate with a narrowly lanceolate to lanceolate-linear central lobe and a long stalk. Usually they have hooked and outward turned, triangular to narrow basal lobes, which most frequently are divided and often even palmately split, but rarely absent or replaced by toothlike appendices. The cauline leaves are lanceolate to narrowly linear and either with or without small basal lobes. The leaves are glabrous, thin with flat margins and with a single palisad layer, and of a slightly bitter rather than acid taste.

The central lobe of the basal leaves of the *tetraploid* are more often than not linear to threadlike rather than narrowly lanceolate, though in shaded places it tends to

become even ovate-lanceolate. The leaves have long, spreading, hooked basal lobes that are narrow and single and rarely divided in cooler climates, but usually divided or palmately split under more favorable conditions, rarely absent or reduced to toothlike appendices. The cauline leaves are linear with or without basal lobes. The leaves are thick with two palisad layers, glaucous, with inrolled margins, and distinctly bitter in taste.

The central lobe of the basal leaves of the *hexaploid* is more frequently lanceolate than ovate-lanceolate, with hooked and distinctly spreading, usually broad but sometimes narrow, basal lobes, that occasionally are missing but rarely divided in the material which I have cultivated or studied in nature, though divided lobes have been reported from Central Europe (den Nijs & van der Hulst 1982); such divided lobes are occasionally seen in Swedish populations, but even palmately split lobes are common in plants from Ukraine and Turkey, also when cultivated under more humid and cooler conditions. The leaves are thin with flat margins and a single palisad layer, at least in the North European material, glaucous-green, with a bitter and slightly acid taste.

The basal and cauline leaves of the *octoploid* are narrowly linear, either with or without short and then distinctly hooked basal lobes. They are thick with two palisade layers in the limited material studied anatomically, distinctly glaucous, and with a bitter, hardly even slightly acid taste.

The divided or palmately split leaf lobes of the diploid, tetraploid and hexaploid taxa are most frequent and almost ubiquitous in southeastern Europe and the Orient, where lobeless leaves are practically absent, but their frequency declines towards west and northwest, as observed by Murbeck (1891), Čelakovský (1892) and later authors. It was suggested by Harris (1968), who studied herbarium material from Europe, that this might indicate some kind of a clinal variation, a proposal sustained by den Nijs (1976), who also claimed to have observed a total lack of split basal lobes in western Europe. That observation, however, is contrary to the fact that even my first Swedish population from Uppsala produced this variation, which I even depicted (Löve 1940b), though I agree that there is a dearth of the character in west and north European populations of both the tetraploid and hexaploid. There seems to be an inherent difference in this character between the members of the series, and also between populations at each polyploid level, if my limited experiments may be accepted as a basis of such a conclusion. However, it is also possible that this is only a tendency to react against oceanity, humidity or temperature, since in my admittedly limited studies of small populations cultivated under controlled conditions in growth chambers and greenhouses, samples of the multifid diploid and tetraploid from the Balkans and Turkey were reduced to simple basal lobes in the coldest and most humid conditions, whereas tetraploid plants from Sweden with predominantly single-lobed leaves produced palmate basal lobes when grown in hot and dry situations. Even hexaploid plants varied similarly, and so did the Lake Onega population of the octoploid, which under natural conditions produces leaves with a single pair of basal lobes or none at all. The character of multifidy seems to be of controversial taxonomical importance, but it may be of ecological interest to study it closer by aid of more extensive experiments.

Male flowers. – The male flowers increase visibly and significantly in size from the diploid to the octoploid condition, both the inner ovate, and the outer oblong-lanceolate tepals and the stamens, though it was not found practicable to measure the diameter of the flowers or even the lenght of the tepals for a statistical comparison. However, ripe and undehisced anthers, carefully dissected from the flowers just before

dehiscence, were measured in 1942 and later, and also by Hadač & Hašek (1948) and Harris (1969). In my material, which by time has come to comprise over 1000 plants of various proveniences of each of the diploid, tetraploid and hexaploid levels and more than 100 individuals of the octoploid, the anthers of the diploid varied from 1.1 to 1.6 mm ($\bar{x} \pm S_{\bar{x}} = 1.16 \pm 0.06$), those of the tetraploid varied between 1.4 and 2.0 mm ($\bar{x} \pm S_{\bar{x}} = 1.68 \pm 0.05$), those of the hexaploid were between 1.7 and 2.4 mm long ($\bar{s} \pm S_{\bar{x}} = 1.92 \pm 0.08$), and the anthers of the octoploid were between 2.1 and 2.8 mm long ($\bar{x} \pm S_{\bar{x}} = 2.36 \pm 0.10$). (For statistical methods used, cf. Fisher 1944). The anthers of the octoploid have not been measured by other authors. These measurements fall within the limits of my earler report (Löve 1943) and that of Hadač & Hašek (1948) for the diploid to hexaploid levels, but they differ significantly from the measurements reported by Harris (1969), who concluded that although the diploids studied by him could be distinguished from the polyploids by their anther length, the difference between the tetraploids and hexaploids was not significant. Although there is evidently a statistical possibility to distinguish male plants of the polyploid series by aid of their mature anthers measured just prior to dehiscence, this is hardly a practical procedure of significance in the herbarium, in which shrunk anthers are almost the rule, and where even complex cell measurements may be more practical for the identification of the male specimens (Löve 1943).

Pollen grains. - As observed by me in 1943 and later and confirmed for the diploid to hexaploid by den Nijs, Hooghiemstra & Schalk (1980), the diameter of the pollen grains increases significantly from the diploid to the octoploid level. Although my analysis found this to be statistically significant, the Dutch workers claim this character to be of diagnostic significance only in exceptional cases. The diploids studied by me always had tricolpate pollen grains, though the Dutch workers indicate some exceptions from that rule, whereas I and they found considerable variation in this character in the polyploids. Together with other characteristics, however, this distinction is of value in identifying diploid male plants.

Female flowers. - In order to compare the size differences of the ovaries, which together with the two whorls of tepals constitute the female flowers, they were measured at anthesis before fertilization, excluding the stigma, on more than 500 flowers of each level of polyploidy. The female flowers of the diploid were found to vary between 0.7 and 1.0 mm ($\bar{x} \pm S_{\bar{x}} = 0.86 \pm 0.21$), the ovaries of the tetraploid were from 0.8 to 1.2 mm ($\bar{x} \pm S_{\bar{x}} = 1.10 \pm 0.20$), those of the hexaploid varied between 1.0 and 1.6 mm ($\bar{x} \pm S_{\bar{x}} = 1.39 \pm 0.24$) and those of the octoploid were between 1.5 and 2.2 mm ($\bar{x} \pm S_{\bar{x}} = 1.76 \pm 0.27$). Although the variation curves overlap in all cases, the increase in size is significant at all levels; there is little difficulty in distinguishing distant levels of polyploidy by aid of the relative size of the female flowers, though distinction between close levels would require an exact measurement of an impractically high number of mature ovaries.

Nutlets. - The fruit of *Rumex* is a nutlet or an achene formed from the single ovary and enclosed by the erect tepals, of which the inner whorl consists of three ovate valves that originally are shorter than the ovary in the *Acetosella* group, but later increase in size in pace with the fruit. Inside the inner tepals is a layer of rind cells that secrete some kind of a soluble gum at their base or all over the surface, depending upon the variable thickness of the rind. If the inner tepals discharge only a small amount of the gum and increase at a higher pace than the nutlet, and are only slightly pressed to it or tend to reflect a little during maturity, so that the gum is able to dry without touching the nutlet,

then the inner tepals will remain free from the mature fruit, except at the base. But if the inner tepals produce more gum and are thicker and pressed towards the achene during the drying process, then they will become cemented to the wall to form an organ that has been called an angiocarpous fruit, in contrast to the gymnocarpous nutlet that is free from the tepals at all times. The angiocarpous nutlet cannot be easily separated mechanically, not even by considerable rubbing between the fingers, but can be freed by aid of a time consuming process of scraping or dissolution in warm water or weak acids. The angiocarpous fruit in these plants is, thus, not a truly anatomical structure, as sometimes suggested, but a secondary product of the inherited production of gum between more or less appressed organs (cf. Campderà 1819; Čelakovský 1892). Gum production is most successful in the Mediterranean population of the diploid and in the western European race of the hexaploid, and it is practically absent in the octoploid. Under humid conditions in growth chambers the bonding between all or considerable part of the nuts may fail to a substantial degree, even in obligately angiocarpous populations. The taxonomical significance of the angiocarpous character must, thus, evidently be taken with a grain of salt and weighed together with other characteristics and with environmental conditions.

The size of the nutlets as measured or weighed including the tepals of the various polyploid stages, was found to correlate nicely with polyploidy by Löve (1943) and Hadač & Hašek (1948), whereas Harris (1969) challenged this. That disagreement may perhaps be caused by methodological differences, since my later studies of considerably larger collections from experimental material of known cytological distinction still confirm the results from 1943. In the new study 1000 seed weight was determined for 50 samples of each taxon, except only ten for the octoploid, both with tepals and without, in which latter case angiocarpous seeds were carefully cleaned of the glue and the tepals, and measured and compared with normally gymnocarpous diploid and polyploid seeds that had also been washed and dried. The results obtained are statistically compatible with the observations of 1943. The mean 1000-seed weight *with* tepals of 50 diploid samples of dry and well-filled seeds was found to be 274 ± 12 grams; that of 50 samples of the tetraploid was 373 ± 11 grams; that of 50 samples of the gymnocarpous hexaploid was 541 ± 15 grams; and that of 10 samples of the octoploid was 719 ± 23 grams. The average 1000 seed weight of the same number of samples of nutlets *without* tepals of the diploid, angiocarpous plants was found to be 163 ± 12 grams, of the diploid, gymnocarpous plants it was 159 ± 10 grams; the same for the tetraploid without tepals was 279 ± 11 grams, for the hexaploid it was 429 ± 14 grams, and for the octoploid 592 ± 24 grams. Although the tendency of increased weight is evident so the claim of 1943 is substantiated, the collecting and weighing of such amounts of seeds is hardly a practicable process for the identification of the various polyploid stages except in exceptional situations. The length of the nutlet, however, is a useful character. In my new material of the diploid taxon the angiocarpous nutlets were found to be as wide as or wider than long, as in the earlier study, and their average length as measured on 1000 seeds was 0.8 to 1.4 mm ($\bar{x} \pm S_{\bar{x}} = 1.1 \pm 0.02$ mm), whereas the nutlets of the hexaploid angiocarpous plants from western Europe and eastern North America were distinctly longer than wide and 1.6 to 1.8 mm long ($\bar{x} \pm S_{\bar{x}} = 1.7 \pm 0.02$ mm). Freed from the tepals, the nutlets of the angiocarpous diploid continued to be as wide as or wider than long, though they then were only 0.5 to 0.8 mm long ($\bar{x} \pm S_{\bar{x}} = 0.67 \pm 0.02$ mm), and the similar free nutlets of the gymnocarpous diploids were 0.6–0.8 mm long ($\bar{x} \pm S_{\bar{x}} = 0.69 \pm 0.02$ mm). The nutlets of the gymnocarpous polyploids, however, were

increasingly longer than wide, those of the tetraploid 0.9 to 1.5 mm long ($\bar{x} \pm S_{\bar{x}} = 1.2 \pm 0.04$ mm), of the hexaploid 1.2 to 1.6 mm ($\bar{x} \pm S_{\bar{x}} = 1.37 \pm 0.03$), and the nutlets of the octoploid varied between 1.5 and 1.9 mm ($\bar{x} \pm S_{\bar{x}} = 1.72 \pm 0.04$ mm). The inner valves were of about the same length as the ripe nutlet or only slightly longer in the diploid angiocarpous and gymnocarpous plants, whereas in the tetraploid and hexaploid they were on the average conceivably longer, even in the angiocarpous hexaploid in which they are wrinkled, and in the octoploid the valves were up to twice as long as the fruit. In my experience, seed size, both relative and exactly measured, is a useful character in identifying the members of the polyploid series, contrary to the conclusion by Harris (1969), although I am able to confirm his observations that there seems to be significant difference between populations at the same level of polyploidy, and even on branches of the same individual, that sometimes tend to reduce the usefulness of the character and make it unreliable except when combined with other similar measurements.

Most of the differences discussed above have been confirmed by the Dutch workers, who nevertheless claim inability to recognize them as useful in identifying the three lowest numbers of the polyploid series. In my opinion that kind of perhaps even preconceived tenacity is hardly logically constructive.

Hybridization and meiosis

Because of the mainly quantitative nature of the differences between the members of this autoploid series and the lack of truly qualitative distinctions, possible natural hybrids between the various taxa are not easily detected without the aid of a cytological study. Löve (1943) reported negative results from experimental attempts of hybridization between the diploid on one hand and the tetraploid or hexaploid on the other, but succeeded crossing the tetraploid and hexaploid, when the latter was the female parent. Later experiments on a much larger scale have confirmed that hybrids are never formed when the diploid is the mother, but some seeds have been collected after massive pollination of the tetraploid with pollen from the diploid, though their total lack of germination may indicate that the combination is not viable. The observation of a couple of triploids in the natural material studied by den Nijs (1976) is, therefore, more likely caused by fertilization by occasionally unreduced gametes, as suggested by him, rather than by natural hybridization between diploids and tetraploids, a suggestion strongly supported by the fact that no tetraploids were observed in the area. In my experimental fields triploids have never occurred.

Hybridization between the tetraploid and octoploid have been successful in both directions, and also that between the hexaploid and octoploid. Despite the extensive experimental material studied I have never been able to verify cytologically any assumed natural hybrid between any of the polyploid taxa, though natural hybrids between the tetraploid and hexaploid undoubtedly occur, as has been cytologically verified from the Alpique regions by den Nijs (1976). As could be expected, all the hybrids between members of the series are highly sterile and unable to produce fertile offspring, even the hexaploid hybrids between the tetraploid and octoploid taxa, so all geneflow between the polyploid levels is, at the best, drastically reduced. This claim may perhaps look contrary to the observation of filled pollen grains in the hybrids, both by Löve (1943) and den Nijs (1976). That, however, seems to be an illusion in the light

of the fact that Löve (1943) was able to demonstrate by aid of germination experiments that only very few filled pollen grains seem to be able to germinate in such hybrids, in addition to the more recent observation that female hybrid plants produce very few and then preferably non-germinable seeds. That does not invalidate the observation by den Nijs (1976) of individuals with deviating chromosome numbers that hardly are explainable except as results of some backcrossing to either parent.

Hybrids between geographically widely separated populations at the same level of polyploidy were produced by Löve (1943) from within the gymnocarpous complexes of both the tetraploid and hexaploid taxa. Later, similar hybrids have been made between both angiocarpous and gymnocarpous proveniences of the diploid, tetraploid and hexaploid; between highly multifid and distinctly simple-lobed groups of the diploid and tetraploid, between Swedish and Hungarian gymnocarpous tetraploids with simple lobes and palmate basal lobes respectively, between gymnocarpous hexaploid medium tall Swedish plants and more procumbent Icelandic plants; between angiocarpous and gymnocarpous European populations of the tetraploid and hexaploid, respectively; and between octoploid plants from the shores of Lake Onega and the Chukotka Peninsula. The hybrids between angiocarpous diploid, tetraploid and hexaploid taxa and their gymnocarpous counterparts always produced angiocarpous first generation hybrids, thus indicating strict dominance of the tendency to rich gum production. Six second generation populations of the diploid hybrids gave the following proportions of angiocarpous versus gymnocarpous females: 389:132; 355:121; 261:86; 253:82; 247:71, and 191:63. This seems to be close to the 3:1 frequency expected if the assumed gum producing gene, and thus the resulting angiocarpy, is dominant. The frequencies from second generation hybrids of angiocarpous and gymnocarpous tetraploids and hexaploids were, as expected, more complex and several of the plants produced both angiocarpous and gymnocarpous fruits. These observations are in conformity with the claim of dominance of angiocarpy by den Nijs & van der Hulst (1982).

It is of interest also to note, without giving the lengthy details of the observations that must be deferred to a more special report, that the meiosis of hybrids within the same degree of polyploidy was generally similar to that of natural populations, as had already been stated by Löve (1943) for the tetraploid and hexaploid hybrids. And those resulting from crosses between polyploid levels showed the same kind of disturbances typical of autoploids as were demonstrated earlier for similar hybrids between tetraploids and hexaploids.

It is my impression that it is legitimate and indeed logical to conclude from these results that although there is a very strong reproductive isolation between the different levels of polyploidy, no genetical blocks exist between geographically and morphologically even clearly distinct populations within each polyploid category. Or, in other words, this evidence strongly supports the view that the polyploid series actually represents only four reproductively isolated and variable interbreeding populations, irrespective of some minor geographical differences in morphology at each level.

Ecology and distribution

Because of the longtime confusion and the fact that the tetraploid has some tendency towards hemerophily so it evidently has spread somewhat by aid of human activities, and because the hexaploid is among the most widespread and noxious

agricultural weeds and extensively ruderal, there will always remain doubt as to their natural area and original ecology. The diploid and octoploid, however, seem to be either hemerophobous or at least hemerodiaphorous, in the terminology of Linkola (1916), so they either shun cultivated and inhabitated areas or are indifferent to human activities.

The preliminary maps of the general distribution of the four taxa presented by Löve (1943) have been found to be unreliable because they were based on studies of only the limited material in Nordic herbaria, before the reliability of useful morphological differences was established. The same is true for the map of *R. graminifolius* by Tolmachev (1966), because it excludes some localitites even in the Soviet Union and includes the unrelated diploid *R. aureostigmaticus* and its relatives from the Pacific and eastern Siberian area. In addition, botanical politics has been permitted to affect the maps of these taxa even in areas with reliable information, so biassed general maps of only a part of the areas have been presented (Jalas & Suominen 1979; Meusel, Jäger & Weinert 1965; Hultén 1968, 1971). All herbarium material available needs to be critically revised before it can be utilized as a basis for critical and exact maps of the real areas of the real taxa by aid of which reliable conclusions will hopefully be made on the origin and history and present distribution of the entire complex.

Despite the unreliability of available maps, it is nevertheless evident from available herbarium material studied after 1943 and from personal observation subsequent to the recognition of reliable morphological distinctions, that the *diploid* taxon is essentially a plant of rocky or sandy and sunny slopes or of sandy pine forests in the lowlands or foothills of the Mediterranean and Pontic-Southsiberian regions, in the system of Meusel, Jäger & Weinert (1965), reaching northwards to southern Czechoslovakia, Transsylvania and southern Ukraine, around the Black Sea and the Mediterranean and North Africa to Madeira and the Canary Islands and the Azores, and eastwards at least to western Iran. The western populations are preferably angiocarpous, the eastern mainly gymnocarpous. The *tetraploid* seems originally to have been a plant of the Pontic-Southsiberian region, where it prefers meagre and sterile grasslands and heaths, but presently its area reaches north and westwards into western Siberia and central and northern Europe as far as northern Russia and the arctic coasts of Scandinavia and to the coasts of western Europe south to France and northern Spain. It is probably originally introduced to much of its northern and Atlantic area, and certainly so in Great Britain, Iceland and Greenland and in its few localities in northeastern North America, although it is so thoroughly naturalized that it appears as an integral part of natural vegetation everywhere. It is predominantly gymnocarpous with only sporadic angiocarpous enclaves. The *hexaploid* is essentially a weed all over Europe, gymnocarpous in northern and eastern areas from which it has become naturalized in the North Atlantic arctic and in boreal regions on other continents, and angiocarpous in western Europe from where most introductions to foreign temperate and tropical regions seem to originate. It is difficult to establish its possible place of origin, though the present writer is of the impression that it may have risen in central or southeastern Europe, perhaps as late as at the onset of agriculture in the late Pleistocene. The *octoploid* is a plant of sandy beaches and riversides mainly in the arctic and subarctic Eurasia, reaching south to the sandy shores of Lake Baikal (Tolmachev 1966) and Lake Onega where it is evidently a relic of the Late Glacial Baltic Sea (cf. Magnusson, Lundqvist & Granlund 1957). It reaches northern Norway (Löve 1943; Elven 1977) and northeastern Greenland, but some localities marked on its maps by Löve (1943), Tolmachev

(1966) and Hultén (1968) from eastern Asia west to Yenisej and from boreal Alaska represent a misunderstood diploid of another relationship.

Taxonomical discussion

Although most botanists still blindly follow the traditional concept of a comprehensive genus *Rumex* as a conventional collective for its then about 230 highly variable taxa, many agree that its division into several subgenera, sections and subsections, as advocated by Rechinger (1937, 1949, 1954), Löve (1944) and Borodina (1977, 1979), is a considerable improvement. A biologically still more satisfactory solution seems to be to replace the collective taxon with the concept of the morphologically and biologically incompatible genera *Acetosa* Mill., *Acetosella* (Meisn.) Fourr., *Rumex* L. and *Bucephalophora* Pau, the first and third with several subdivisions, as recently advocated by Löve & Löve (1961) and Löve & Kapoor (1967) and accepted by Airy Shaw (in Willis 1966) and some others, despite the fact that even then the first genus remains a heterogenous unit in need of a more satisfactory treatment supported by further experiments. The small genus *Acetosella* clearly fits the definition of a natural genus as a cluster of genetically related species which, as far as possible, reflect cytogenetical and morphological evidence of having evolved from a single progenitor by linear branching and, therefore, being of common phylogeny as indicated by a single basic chromosome number, similar chromosome morphology, and a distinct haplomic and genomic relationship (Löve & Löve 1974, 1975a, b, Löve 1982). The genus *Acetosella* so restricted is dioecious and an obligate wind pollinator, and it is cytologically characterized also by its rather small chromosomes of the basic number $x = 7$ in a polyploid series, and by its XY sex mechanism based on a strong male determinant in the Y-chromosome that permits polyploidy and undisturbed dioecism up to at least the dodecaploid level in experimental material.

Classically, the genus *Acetosella* comprises the single collective species *A. vulgaris* (Koch) Fourr., or in the older conventional nomenclature, the species *Rumex Acetosella* L., which Linnaeus (1753) accepted in the first edition of Species plantarum and in his earlier works. In his opinion at that time, it comprised four varieties, three of which were copied from Bauhin (1623), who had accepted them from previous authors, and one borrowed from Boccone (1697). Linnaeus knew the first three from Sweden; they soon went into taxonomical oblivion and are long since out of the discussion. But in the second edition of Species plantarum (1762), he lifted the fourth to species rank as *Rumex multifidus* L., thus creating a controversy that still periodically gains some prominence.

Both the Linnaean species were accepted by all distinguished authors of the following half a century (cf. Willdenow 1799). At the end of that period, a new species, *R. graminifolius,* was added from Siberia by J.H. Rudolph, first as a name only in Georgi (1800), and then, after his death, with a formal description and picture, in Lambert (1811), and later as the synonymous *R. angustissimus* by Ledebour (1814), based on the same collection. The first monographer of the genus *Rumex,* Campderà (1819), accepted these three species, which he treated as a distinct group of section *Acetosa.* He suggested, however, that *R. multifidus,* which DeCandolle had reduced to a variety in Lamarck & DeCandolle (1815), might perhaps be more appropriately treated as a forma only of the classical species. Wallroth (1822) divided the single German

species, that he accepted as *R. Acetosella,* into three main varieties based on size, A. *major,* B. *minor* and C. *minima,* and included in each of the two first ones four formae based on leaf form. Two of these formae, A. *δ lacerus* and B. *γ multifidus,* replace the species *R. multifidus.*

The second monographer of the genus was Meisner (1856) in DeCandolle's Prodromus. He accepted only the single species *R. Acetosella,* with eight equivalent varieties.

New material was added to this brewing controversy, when Balansa (1854) observed fruit differences between French and Turkish populations, distinctions that later were termed angiocarpy and gymnocarpy. He assumed that the former, which he knew from France, were identical with the typical species of Linnaeus, and identified the latter, which in addition were characterized by palmate leaflobes, as *R. multifidus* L. That name, however, he rejected as being confusing, in favor of his new name *R. acetoselloides* Balansa. That is contrary to the International Code. When Murbeck (1891) encountered the same variations in Hercegovina, he ignored the leaf differences as of no taxonomical significance since in that area they were shared by populations with both fruit types, but observed that gymnocarpy is characteristic of the North European populations that he identified as typical *R. Acetosella* L., of which he regarded both *R. multifidus* and *R. acetoselloides* as simple synonyms. The angiocarpous plant that Balansa had identified with the Linnaean species was, however, described as new under the name *R. angiocarpus* Murbeck.

The controversy deepened when Čelakovský (1892) checked the observations of Murbeck (1891) on populations from Bohemia, where both fruit types are also met with, and rejected the difference in fruit as of little taxonomical importance on basis of a superficial observation of a single specimen of an angiocarpous plant with some gymnocarpous nutlets on a lower branch, though he admitted that angiocarpy is predominant in southern Europe. He was also critical of the significance of the divided or palmate lobes of the leaves of *R. acetoselloides* or *R. multifidus,* though he noted an increased frequency of this characteristics in Italy and the Orient, as contrasted to the prevalence of undivided lobes in central and northern Europe. Čelakovský (l. c.) concluded that the two taxa would be more appropriately accomodated as two varieties only of the classical species and proposed for these the names *angiocarpus* and *gymnocarpus.* This Murbeck (1899a, b, 1905, 1922) partly accepted, when reducing the southern taxon to a ssp. *angiocarpus* (Murbeck) Murbeck of *R. Acetosella* L., a nomenclature later followed by the few authors who during the first half of the 20th century felt a need to recognize any variations at all of the collective species (cf. Ascherson & Graebner 1908–1913), though Beck (1909) preferred to accept the five varieties *vulgaris, angiocarpus, multifidus, tenuifolius* and *integrifolius.*

Such was the situation, when I commenced my cytogenetical investigations the spring before the beginning of the second world war, and soon discovered that the *Acetosella* complex is composed of four stages of a polyploid series. These stages were later (Löve 1941b, 1943) preliminarily identified as the species *R. angiocarpus* ($2n = 14$), *R. tenuifolius* ($2n = 28$), *R. Acetosella* ($2n = 42$) and *R. graminifolius* ($2n = 56$), without even a vestigial key but with considerable information on their differences in the text for those, who might feel a need to study it closer. Five years later, Klokov (1948) added a new gymnocarpous species with much divided basal leaves, *R. fascilobus,* from central Ukraine, evidently unaware of my 1943 work and with a description so general as to render its identification with any of the three central and south European species

impossible without some kind of type material. I have been unable to borrow either the type specimen from near Zaporozh'hye or a neotype from near Krivoy Roy assigned by Borodina (1978), but have studied populations grown from seeds from near both of these places received from Professor Yu. N. Prokudin. Since they were found to be hexaploid it seems safe to suggest that they represent tallgrown plants of *R. Acetosella* s.str., as Rechinger (1964) also concluded.

When the diploid Portuguese population originally studied had been firmly identified with *R. angiocarpus,* Professor Murbeck and I concluded that all angiocarpous specimens must also belong to this species and be diploid. The general map of that species in my dissertation of 1943 was based on that conclusion. That deduction was, however, found to be overhasty already in the late summer of 1943, when plants grown from distinctly angiocarpous seeds from the seed exchange of the Botanical Garden at Liège in Belgium were found to be hexaploid. Later studies by Hadač & Hašek (1948), Pazourková (1966), Harris (1968, 1969, 1973), den Nijs (1974, 1976), Scheffer & den Nijs (1978), and den Nijs & van der Hulst (1982) have, indeed, thoroughly confirmed the diploid number for angiocarpous populations from various parts of southern Europe. However, angiocarpous plants from central and western Europe and from other continents have been reported as being hexaploid by Moore (1954), Mulligan (1959), Johnson & Briggs (1962), Harris (1968, 1969, 1973), Sterk & den Nijs (1971), den Nijs (1974, 1976), den Nijs, Hooghiemstra & Schalk (1980), and den Nijs & van der Hulst (1982). Both these observations I have also confirmed above on considerable material. In addition, den Nijs (1976) and Scheffer & den Nijs (1978) have discovered some populations of gymnocarpous diploids in central and southeastern Europe. That race I have found to be widespread at the coasts of the Black Sea in Turkey and the Orient north to the Caucasus and western Iran. However, den Nijs (1976) is mistaken when he refers to Hadač & Hašek (1948) and Pazourková (1966) as having reported gymnocarpous diploids from Czechoslovakia. There are even reports of tetraploid angiocarpous populations from the Pyrenées and Yugoslavia by Harris (1969), and from a few localities in central Europe by den Nijs (1976) and den Nijs & van der Hulst (1982), and I myself have observed and cultivated a sample of a small angiocarpous tetraploid population from the lower slopes of the eastern Alps near the Italian-Yugoslav border. But angiocarpy is certainly absent in the octoploid *R. graminifolius.*

When Hadač & Hašek (1948) verified my chromosome numbers for the three taxa that they also identified as *R. Acetosella, R. tenuifolius* and *R. angiocarpus,* they hesitated to accept my evaluation of their taxonomical level because the lack of qualitiative differences, and proposed instead the acceptance of three subspecies names, alternately in *Rumex Acetosella* or *Acetosella vulgaris,* or ssp. *angiocarpus,* ssp. *tenuifolius* and ssp. *euacetosella.*

When Rechinger (1949) published an extensive revision of the Asiatic *Rumices,* he could no more resist the temptation to construct a simple key for the four Asiatic species of the *Acetosella* group, in which he, unfortunately, mentioned only the angiocarpy as a key character of the diploid species. This key was repeated by Rechinger (1957, 1964) and has later been widely and uncritically copied by authors of flora manuals, and it has frequently been wrongly attributed to me, most recently by den Nijs (1974), who ought to have known better. Since it failed to mention other important distinctions of the diploid species, it has misled some into wrong conclusions, as did also my preliminary map of 1943. Much improved and detailed keys were constructed by W. Lemke (in Rothmaler 1963), Weinert (1963) and Weimarck (1963) for the boreal taxa and by

Elven (1977) for the entire group, though they have been thoroughly ignored in favor of the Rechinger effort.

When Moore (1954) reported the discovery of 42 chromosomes in the angiocarpous weed in New Zealand, she stated the fact and realized that the plant must be a race only of the species I had regarded as *R. Acetosella.* The reaction was similar, when Mulligan (1959) and Johnson & Briggs (1962) found the same to be true for the introduced weed in eastern Canada and southern Australia, respectively. It was not much different when the New Zealand agronomist Harris (1968, 1969, 1973) carried out a thorough agronomical investigation of many phases of the life history of the weed introduced in his homeland, in which a scrutiny of its morphological differences was an integral part. Most of his material was, understandably, from New Zealand, but a considerable sample of European herbarium and live material was included, though it was hardly better selected for widegoing conclusions than were my preliminary collections in 1943. He concluded in the classical manner of a good advisor in doubt, that more studies were needed for a better understanding of the problem, and then recommended that only the collective name *R. Acetosella* be used in the meantime. That, of course, contributes nothing to the clarification of the European controversy, though in New Zealand, where only the angiocarpous phase of this species in its strict sense is known to be naturalized as a noxious weed, it hardly needs to be hailed as a Solomonian resolution.

The most recent phase in the studies of the European *Acetosella* group comprises a seemingly thorough inventory of the factual distribution of the chromosome numbers and a critical evaluation of some selected characteristics, some of which I had reported on in 1943, with an implied disapproval of the genetical approach to such problems. That study was initiated by Sterk, van der Leeuw, Nienhuis & Simon (1969) and Sterk & den Nijs (1971) at the Hugo de Vries Laboratorium in Amsterdam, and has later been diligently carried out by den Nijs (1974, 1976), den Nijs, Hooghiemstra & Schalk (1980), Scheffer & den Nijs (1978), den Nijs & Panhorst (1980) and den Nijs & van der Hulst (1982). Although these Dutch authors seem to have some difficulty in rising over the level of trivial insinuations and prefer a polemic tone that is rare in scientific discussions, it does not affect their numerous factual observations which, in my opinion, add substantial strength to my original and later observations and conclusions, even those they set out to condemn and criticize. This is especially true regarding the fundamental conclusion that the series represents four well-defined biological species characterized by four chromosome numbers in a polyploid series and, thus, reproductively strongly isolated from each other and unable to exchange genes, although the authors themselves still prefer to ignore this division and avoid all mentioning of species concepts and other evolutionarily and taxonomically important matters, and instead recommend simply a return to the incomplete and, indeed, misleading taxonomy prevailing at least prior to my discovery of the polyploid series. That may perhaps reflect their implied indifference to the philosophy of evolutionary taxonomy as contrasted to their evident support of the contrary ideology of pheneticism, to which they are, naturally, perfectly entitled. In my opinion, however, their approach may perhaps constitute not a slight but a fatal misunderstanding of the principles of modern evolutionary taxonomy.

Here we must make some deviation for a review of the species concepts applicable to the material in question. The existence of the species category has been perceived since times immemorial, but its definition has long been arbitrary as have also been the means and methods of its recognition. When Linnaeus (1751) decided upon its standard to be followed in botanical taxonomy, he, thus, accepted a category which is a greater

reality in nature than are other taxonomical groups and which is, therefore, most distinct to human observation. It was evidently his intention that the species of plants ought to be of the same indisputable distinction as are man and ape, apple and pear, barley, rye and wheat. Although he did not define his standard from this point of view, probably because he was convinced that the number of species must be limited since they were an act of creation, or at least the result of differentiation by divine guidance from originally created generic prototypes, it is evident from his publications that he regarded the category of species to coincide largely with the cessation of hybridization possibilities or miscibility. To him the case of *R. Acetosella* and *R. multifidus* was beyond dispute. For the discrimination of the category he preferably selected conspicuous qualitative differences with no intermediates, if possible connected with reproduction, although in his later years some partially continuous quantitative characters were sometimes accepted.

Since Linnaeus did not feel a need to define his species standard, other botanists soon ventured to obtain a distinct guide to determine the category. The definition most closely related to the works of Linnaeus himself was phrased by DeCandolle (1813), who regarded the species as «la collection de tous les individus qui se ressemblent plus entr'eux qu'ils ne ressemblant à d'autres; qui peuvent, par une fécondation reciproque, produire des individus fertiles; et qui se reproduisent par la génération, de telle sorte qu'on peut par analogie les supposer tous sortis originairement d'un seul individu». If this definition had been generally taught to the new generations of botanists and adhered to by those practizing taxonomy, then no confusion in the species category would ever have arisen. The socalled biological species concept by which Mayr (1942) defined a species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" is evidently only a concentrated and semantic variation of the same phrase.

DeCandolle's (1813) definition, no less than the one by Mayr (1942), is distinctly evolutionary and genetical. Since there were at that time no known means to directly ascertain that reproductive isolation was involved, except the absence of hybrids or the presence of sterile hybrids, those, who tried to follow the advice, were frequently forced to rely upon intuition. Intuition has been and still remains the method largely employed by a considerable number of botanists and then especially by the antievolutionary group, which presently emphasizes its antigenetical leanings by calling their approach phenetics. The antievolutionists past and present have also enriched the field with innumerable more or less evasive definitions, of which one of the most recent is the rephrasing by Cronquist (1978) stating that "species are the smallest groups that are consistently and persistently distinct and distinguishable by ordinary means". In the phenetic definition, chromosomes play no role, whereas in the genetical concept they are of basic importance, because reproductive isolation is essentially caused by chromosomal changes, linear or numerical (Löve 1962, 1964).

Within the biological species, as in the Linnaean species, miscibility is not only permitted but directly required, irrespective of the strength of the morphological contrasts of various races. Therefore, sexual subspecies and varieties are defined as interfertile major or minor geographical races that are capable of mixing freely wherever they meet, subspecies being regional in their distribution, varieties more or less local (Hultén 1968; Löve & Löve 1976). Such taxa have been, and still frequently are, regarded as distinct species by the chorological or Kerner-Wettstein-Komarov school, the influence of which on Russian and North American and even Dutch botany

still is enormous. It deemphasizes the role of reproductive isolation and ignores cytogenetics and separates as species any morphologically distinguishable groups with a geographical area, large or small. The outcome of that school has been considerable, the most magnificent result being the great Flora SSSR; but it has also had disastrous biological influences by stimulating numerous ardent amateurs and botanists without a biological sense to separate as species innumerable pure lines of autogamous complexes of which the works on the genus *Astragalus* in the Soviet Union and North America is the most regrettable example, and to distinguish as species vegetatively reproduced lines of agamospermous complexes in the boreal zone, especially the meaningless microspecies of the genera *Hieracium* and *Taraxacum* in central and northern Europe.

Differences in chromosome number have long been known to result in incompatibility or in a high degree of sterility of the offspring that is caused by some disturbance of the numerical balance of the gene pool that in turn results in aborted ability to produce further offspring. That is just what has been observed in the hybridization experiments with the four members of the *Acetosella* series, in which the incompatibility between the diploid and the polyploids is complete, but decreases with increased polyploidy. That also confirms the correctness of treating the members of the polyploid series as independent biological species. Hybrids between morphologically, ecologically or geographically different races at each polyploid level, however, have been found to be as fertile and viable as the natural populations themselves, and their meiotic divisions reveal no increase in disturbances, which are of the typical autoploid nature. Therefore, these races could be logically accepted as subspecies or varieties. They will remain constant as long as their ecological or geographical isolation mechanisms are able to keep them separate, but their distinction ceases when this isolation is disturbed.

Although the biological species concept does not mention morphological differences because it accepts the fact that "to be a different species is not a matter of difference but of distinctness" (Mayr 1963), morphological characteristics of some kind or another are, of course, needed for the identification and recognition of any taxon in any system of definitions. In the phenetic concept, as in the classical Linnaean approach, such characters are preferably qualitative, whereas the biological concept is satisfied with either or both qualitative or quantitative characters, as long as they assist in securing proper identification of the taxa. This difference in requirement seems to be one of the essential causes of the present controversy over the acceptability of the four equivalent biological species of the *Acetosella* group, since few of their differences are distinctly qualitative and most of the quantitative characters differ only in degree and may leave certain overlapping that requires a complex statistical analysis or the concurrent use of two or more such characters for a safe identification. That, however, does not make them weaker species since their essential distinction remains biological and they are distinguishable by anyone with a well trained floristician eye, though perhaps not always without some efforts.

A key of a combination of characters for *Acetosella* is given in the nomenclatural synopsis below. The species themselves are also characterized by several other differences, macroscopical as well as microscopical, of which the essential ones are reviewed in the morphological chapter above.

There can be no argument about the identity of the gymnocarpous hexaploid taxon with the Linnaean *R. Acetosella* as typified by either or both the specimens on sheet "22" in the Linnaean herbarium in London (cf. Lindberg 1958), which also is doubtlessly identical with the weed still met with in the fields around Uppsala. In the genus

Acetosella it must be named *A. vulgaris* because of the tautonymy rule. It comprises considerable sporadical or essentially ecotypical or clinal variations that hardly warrant taxonomical recognition, but one of its interfertile digressions may merit taxonomical recognition at the level of subspecies, i.e., the originally western European but presently almost worldwide angiocarpous weed ssp. *pyrenaicus*, although its status as a major geographical race remains a matter of opinion. Despite of several attempts, I have been unable to locate any type collections of this race.

The diploid species was correctly and effectively described for the first and only time as *R. angiocarpus* by Murbeck (1891), as verified macroscopically and microscopically by comparison with its type specimen from Yugoslavia: "Hercegovina, am Fusse des Hunberges bei Mostar, 15/7, 1889. S. Murbeck", and on other specimens mentioned in the protolog and kept in the herbarium at Lund. This has also been verified by a cytological study of samples of the topotype population. The ubiquity of the name-giving character has no nomenclatural significance (cf. Mansfeld 1949; Stafleu & alii 1972). Although both angiocarpous and gymnocarpous as well as multifid and simply-lobed variations occur within the species, some with certain geographical connections, no proposal to recognize them as subspecies or varieties seems necessary. In the genus *Acetosella* the correct name of the species is *A. angiocarpa.*

The octoploid species has been accepted as *Rumex graminifolius* ever since it was first listed by J.H. Rudolph in Georgi (1800) as "eine noch unbeschriebene Art im nordöstlichen Siberien", and validated after Rudolph's death by a description in Lambert (1811), with the note "Habitat in Kamtchatkâ ad mare glaciale. Rudolph. In insulis Curilis. Pallas". Ledebour (1814) described the same species as *R. angustissimum* based on the same collection in the Pallas herbarium in Leningrad, and later (Ledebour 1850) validated the name *R. gramineus* Pallas as a synonym of the latter, evidently a *lapsus calami.* As mentioned above, the species in the sense of the description does not occur in Kamchatka proper or in the Kuril Islands, where it is replaced by the diploid species *R. aureostigmaticus* Komarov of doubtful relationship. At the time of Rudolph, Kamchatka province included a substantial part of eastern Siberia (cf. Hultén 1971). Therefore, Borodina (1979) selected for *R. graminifolius* as a lectotype a specimen in the Leningrad herbarium: "E Sibir. or. Hb. Pallas, leg. Steller, ex Herb. Fischer", evidently unaware of the fact that Hultén (1971) already, based on my observations in 1942, assigned as a cotype a specimen in the Stockholm herbarium: "Kamschatka, in vicina fluvii Wiluii, in campo arenoso. Herb Schwarzii", on which the note has been added: "Rumicis spec. nov. Ledebour?". That specimen seems to have been the basis of the drawing by Lambert (1811) with which it agrees in detail. It evidently comes from the sandy shores of the Vilyuy River, a tributary to the Lena River at the system of which numerous collections of the species have been made. In the *Acetosella* genus its correct name is *A. graminifolia.*

The nomenclature of the fourth species of the *Acetosella* group is somewhat more complicated because of my uncritical tendency to accept advice by my older and certainly wiser colleagues. I originally identified my Swedish tetraploid material with the species *R. multifidus* of southern Europe, recognized as such by Linnaeus (1762) on basis of its "auriculis palmatis" with reference to figure 126 by Boccone (1697), to which he had earlier referred for his *R. Acetosella* var. *δ, Acetosa minor erecta, lobis multifidis.* This species was later reduced to varietal status by DeCandolle (in Lamarck & DeCandolle 1815), and then rejected by Balansa (1854), who replaced it with the new name *R. acetoselloides* Balansa with a detailed description in which he contrasted the

gymnocarpy of his Turkish material with the angiocarpy of the plants he knew from France as *R. Acetosella.* When Murbeck (1891) studied his Hercegovinian material, which he found to be angiocarpous with palmate basal lobes, he observed that in the gymnocarpous character of the fruit, the Turkish and Balkan *R. acetoselloides* did not differ from typical *R. Acetosella* from northern Europe, but assumed that the palmate basal leaf lobes, shared by his *R. angiocarpus,* Balansa's *R. acetoselloides* and some of the north European plants, was a character that could be ignored, because of its apparent ubiquity. Of this he advised me in 1940, when I told him that the tetraploid narrow-leaved Swedish plants frequently have divided basal lobes and in this character at least reminded of the Linnaean *R. multifidus,* and recommended that the varietal name *tenuifolius* be lifted to the species level rather than accepting the misleading Linnaean name. That advice, however, was contrary to the International Code, of which I, a cytogeneticist, had at that time not been made aware, but my scrutiny of the drawing in Boccone's (1697) book, which is the type specimen of the Linnaean plant, left no doubt as to its identity to the tetraploid populations, which I also later had ample opportunities to study from various parts of the Apennines. The tetraploid species must, consequently, be identified as the usually but incorrectly rejected Linnaean species *R. multifidus* of which *R. tenuifolius* in the wide sense of Löve (1943) is a synonym. In the genus *Acetosella* its name must be *A. multifida.* Although it is a variable taxon in fruit characters and leaf form, its variations are hardly worthy of taxonomical recognition, not even the taxon *tenuifolius,* or the ecotype *campestris* of Turesson (1925), which is an extreme gymnocarpous and narrow-leaved form from meagre, sandy localities that occurs sporadically all over the area of the species itself.

This carries us to a declaration of the end of the controversy concerning the taxa of what we now recognize as the genus *Acetosella.* It seems to have been initiatied by the inablity of the intuitive approach to ascertain safe signs of reproductive isolation and its consequence, the reproductive gap, which experimental cytogenetics has now established. But perhaps even that solution is an illusion, because old arguments never die but only fade away to emerge when new generations find new reasons to argue about the trivialities of yesteryear?

Taxonomical and nomenclatural synopsis

Acetosella (Meisner) Fourreau, 1869, Ann. Soc. Linn. Lyon, n.s. 17:145;

Rumex sectio *Acetosella* Meisner, 1855, in Martius, Fl. Brasil. 14:10;

Rumex subgenus *Acetosella* (Meisner) K.H. Rechinger, 1937, Field Mus. Nat. Hist., Bot. Ser. 17, 1:6.

Typus generis: *Acetosella vulgaris* (Koch) Fourreau.

Dioecious plants of a polyploid series with small chromosomes in multiples of the basic number 7. Its leaves are ovate to lanceolate to linear, usually hastate because of hooked basal lobes, which sometimes are split or palmately divided, or absent. The fruit is gymnocarpous or angiocarpous and covered or enclosed by valves developed from the inner tepals, as long as or up to twice as long as the nutlet.

Key to the taxa

1a Rhizome and stem erect, flowering stem branched above the middle; stolons absent or vestigial; leaves thin with flat margins, narrowly lanceolate to lanceolate, with

basal lobes that sometimes are divided or palmately split; anthers 1.1–1.6 mm long; fruit angiocarpous or gymnocarpous, as wide as or wider than long, 0.8–1.4 mm long including attached tepals, 0.5–0.8 mm without tepals ..... *A. angiocarpa*

b Underground stolons; nutlet longer than wide 2

2a Rhizome horizontal, profusely branched; flowering stem ascending or erect, branched at or above the middle; leaves thin with flat margins, lanceolate to ovate-lanceolate, usually with broad basal lobes that rarely are divided; anthers 1.7–2.4 mm long; nutlet distinctly longer than wide, 1.2–1.6 mm long when gymnocarpous, 1.6–1.8 mm when angiocarpous 3

b Rhizone horizontal to erect, branched or with underground stolons; flowering stem procumbent or ascending, branched below the middle; leaves linear-lanceolate to linear, thick with inrolled margins, with or without basal lobes; nut gymnocarpous, rarely angiocarpous, slightly longer than wide 4

3a Fruit angiocarpous, fruit valves as long as the nutlet; stem erect or slightly procumbent, up to 50 cm tall, branched from the ground and up; leaves rather large with an oval-elliptical midlobe and uneven rather broad and sometimes divided basal lobes . *A. vulgaris* ssp. *pyrenaica*

b Fruit gymnocarpous, fruit valves as long as or slightly longer than nutlets; stem erect or procumbent, 5–30 cm tall; leaves elliptical-lanceolate with flat margins and broad and equally long, usually undivided basal lobes ..... *A. vulgaris* ssp. *vulgaris*

4a Rhizome branched with procumbent to ascending stems, branched below the middle; leaves linear to linear-lanceolate, with or without divided or palmate basal lobes; anthers 1.4–2.0 mm long; nutlets 0.9–1.5 mm long; fruit valves as long as or slightly longer than nutlet ..... *A. multifida*

b Rhizome thick with numerous underground stolons; flowering stems procumbent or ascending, branched below the middle; leaves linear, with or without basal lobes; anthers 2.1–2.8 mm long; nutlets 1.5–1.9 mm long, distinctly longer than wide; fruit valves up to twice as long as nutlet ..... *A. graminifolia*

Acetosella vulgaris (Koch) Fourreau, 1869, Ann. Soc. Linn. Lyon, n.s. 17:145;
Rumex Acetosella L., 1753, Spec. pl.:338;
Rumex Acetosella L. var. *vulgaris* Koch, 1837, Syn. Fl. Germ. Helv. 1:616;
Rumex infestus Salisb., 1796, Prodr.:258;
Rumex fascilobus Klokov, 1948, Bot. Zhurn. AN URSR 5:28;
Lapathum Acetosella Scopoli, 1772, Fl. Carn. ed. 2, I:261;
Acetosa hastata Moench, 1794, Meth.:357;
Acetosa Acetosella Miller, 1768, Gard. Dict. ed. 8, No. 2.
Acetosella Acetosella (L.) Small, 1933, Man. Southeast. Fl.:446.
Lectotypus: LINN. "22."
Chromosome number: 2n = 42.

ssp. *vulgaris*
Rumex Acetosella L. var. *gymnocarpus* Čelakovský, 1892, Sitzber. böhm. Ges. Wiss. 1892:402.

ssp. *pyrenaica* (Pourret) Á. Löve, comb. & stat. nov., based on *Rumex pyrenaicus* Pourret ex Lapeyrouse, 1818, Suppl. Hist. Pyrén.: 49;
Rumex arvensis Dulac, 1867, Fl. Hautes-Pyrén.: 165;
Rumex Acetosella Balansa, 1854, Bull. Soc. Bot. France 1: 282;
Lapathum arvense Lam., 1778, Fl. Franç. III: 8; p.p.;
Acetosa arvensis Montandon, 1856, Syn. Fl. Jura Sept.: 268.
Typus: unknown

Acetosella multifida (L.) Á. Löve, 1983, Fl. of Icel.: 168;
Rumex multifidus L., 1762, Spec. pl. ed. 2: 482;
Rumex acetoselloides Balansa, 1854, Bull. Soc. Bot. France 1: 282;
Rumex supinus Campderà, 1819, Monogr. Rumex: 147;
Rumex tenuifolius (Wallr.) Á. Löve, 1941, Bot. Notiser 1941: 99;
Rumex Acetosella ssp. *tenuifolius* (Wallr.) Hadač & Hašek, 1948, Sporn. Přírod. klubu v Pardubicich 1948: 6;
Rumex Acetosella var. *multifidus* (L.) DC., 1815, in Lam. & DC. Fl. Fr. ed. 3, III: 378;
Acetosa multifida Chaz. in Miller, 1768, Gard. Dict. ed. 8, Suppl. I: 8;
Acetosa repens S.F. Gray, 1821, Nat. Arr. Brit. Plants II: 276;
Acetosella tenuifolia (Wallr.) Á. Löve, 1948, Icel. Univ. Inst. Appl. Sci., Dept. Agric., Rep. B, 3: 108.
Lectotypus: Boccone, 1697, Mus. di Fisica, etc.: 164, t. 126.
Chromosome number: $2n = 28$.

Acetosella graminifolia (Rudolph) Á. Löve, 1948, Icel. Univ. Inst. Appl. Sci., Dept. Agric., Rep. B, 3: 109;
Rumex graminifolius Rudolph in Georgi, 1800, Beschr. Russ. Reichs 4, 3: 921, nomen;
Rumex graminifolius Rudolph ex Lambert, 1811, Trans. Linn. Soc. London 10: 264, tab. 10;
Rumex angustissimus Ledebour, 1814, Mém. Acad. Sci. Pétersb. 5: 536;
Rumex gramineus Pallas ex Ledebour, 1850, Fl. Ross. 3, 2: 512, pro syn.;
Rumex Acetosella var. *graminifolius* (Lamb.) Schrenk, 1854, Enum. pl.: 519.
Lectotypus: In vicinia fluvii Wiluii, in campo arenoso, Herb. Schwartzii, in LEN, cotypus in S.
Chromosome number: $2n = 56$.

Acetosella angiocarpa (Murbeck) Á. Löve, 1948, Icel. Univ. Inst. Appl. Sci., Dept. Agric., Rep. B, 3: 109;
Rumex angiocarpus Murbeck, 1891, Acta Univ. Lund 27: 46;
Rumex Acetosella ssp. *angiocarpus* (Murbeck) Murbeck, 1899, Bot. Notiser 899: 42;
Rumex Acetosella var. *angioccarpus* (Murbeck) Čelakovský, 1892, Sitzb. böhm. Ges. Wiss. 1892: 402;
Acetosella vulgaris ssp. *angiocarpa* (Murbeck) Hadač & Hašek, 1948, Sporn. Přírod. klubu v Pardubicich 1948: 6.
Holotypus: Hercegovina, am Fusse des Hunberges bei Mostar, 15/7 1889, S. Murbeck, in LD.
Chromosome number: $2n = 14$.

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