

**LINES OF EVOLUTION AND GEOGRAPHICAL DISTRIBUTION IN
RUMEX SUBGEN. LAPATHUM†**

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The docks, having no showy flowers, do not awake aesthetic feelings as do, for instance, brightly-coloured flowering plants or plants distinguished by a peculiar habit. The more intimate beauty which lies in the various graduated shades of red, brown and yellow of the ripe fruiting panicles, contrasting with the dull green willows accompanying the river banks, is not so obvious. Nevertheless, it belongs undoubtedly to the general impression of a landscape in autumn. On the other hand, when looked at with a certain attention the amazing variability in size and shape of the inner perianth segments at the fruiting period offer a great deal of pleasure.

The fact that they are weeds becomes clear when it is known that some of them are spread over the whole world, e.g. *R. crispus* and *R. conglomeratus*, and that it is hard to distinguish between the original and secondary part of their areas. On the contrary, there are among the docks many which have very limited areas and very pronounced ecological demands, and which show no tendency to secondary distribution. Some of them inhabit swamps, others are confined to the banks of certain big rivers and their tributaries, so that the Nile, the Volga and some of the large Asiatic rivers have docks of their own. Other species are confined to certain mountainous regions or islands of the tropics.

Collectors and plant-amateurs have not been alone in their apparent distaste for the genus. Scientific botanists, too, have obviously neglected it. It has been monographed only twice as a whole—by Campdera in 1819 and by Meisner in DC. *Prodromus* 1856. When glancing through Meisner's work one has the impression that it was not induced by a special interest but rather accomplished to fill a gap in De Candolle's encyclopaedic work. More modern papers on *Rumex*, such as those by Murbeck, Danser and Trelease, deal with species of limited regions and are not concerned with the natural arrangement of the whole genus.

The main groups of the genus—*Acetosella*, *Acetosa* and *Lapathum*—have nevertheless been distinguished since the earliest authors as well as by the public—the first two under the name of sorrels, the last as docks. I am dealing here only with the docks, the *Lapatha*, which include several hundred species and comprise the larger part of the genus.

I have already mentioned the amazing variability of the fruiting inner perianth segments, which have been termed valves. Being small and uniform in the flowering state, they increase and change their shapes

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in different manners indicating different and very distinct lines of evolution. Moreover, these transformations are combined with certain characters of the vegetative system, in this way furnishing the basis for a more natural arrangement of the species. The many transformations of the valves during the ripening process are easily reduced to three main types:—1. The valves increase, they become membranaceous and a network of nerves develops; 2. The midrib of one or of all three valves thickens more or less and is transformed into a callosity; 3. The margin of the valve grows out into teeth of various size and form. These types may occur separately or variously combined. In some cases one special type corresponds with a single species or group of species, in other cases all possibilities of combinations occur within a single very polymorphic species, thus causing many cases of parallelism and convergence. These phenomena, till now not clearly recognized, together with the frequent hybridization, give rise to the main difficulties of classification within the subgenus. No serious attempt has been made till now to establish a natural arrangement. Meisner's division of his section *Lapathum* into two groups—with entire and with dentate valves—is a mere artificial one. It separates species nearly related to each other and brings close together species showing superficial resemblance only. In contrast to this artificial arrangement I have tried to find out lines of development leading from more primitive forms to more differentiated ones. I think that a species may be regarded as more primitive the less the inner perianth segments are transformed during the ripening process.

Thus the first of the main types mentioned above represents the most primitive, the second—sometimes but not always combined with the first—is more advanced and the third—often combined with the second, sometimes more or less combined with the first—is the most differentiated. This interpretation is made more evident by the fact that annuals, which are generally regarded as more differentiated than perennials, occur only in groups characterized by the production of teeth and callosities. On the other hand, toothless taxonomic entities occurring exceptionally in annual groups can be regarded as reduced forms. I need not emphasize that I do not suppose the living species, regarded here as relatively primitive, to be the ancestors of the more advanced ones, but they may be similar to the presumed ancestors as far as the valves are concerned.

In addition to the characters of the valves, on which the lower taxonomic units are based, a vegetative character until now neglected proved to be very important and useful for separating two main groups of subgenus *Lapathum* as sections. These groups are: (1) the *Axillares*—characterised by producing regularly leafy axillary shoots which develop secondary inflorescences, often predominating the principal ones, the flowering and fruiting process therefore being practically unlimited; and (2) the *Simplices*, which have a single unbranched stem with a branching terminal inflorescence of limited flowering and fruiting

period. In genetic behaviour, also, these two groups show a very important difference. While the *Simplices* cross easily with each other and some also with the *Axillares*, there is no case of hybridization known within the *Axillares*. The importance of that division is still more evident from the fact that the geographical distributions of the two groups correspond with the morphological characters.

The *Axillares* have their principal area and their probably most important centre of development in North America and are, in contrast, completely lacking in Europe and the larger part of Asia. The section is represented in North America by the very polymorphic subsection *Salicifolii*. Only one species of this subsection is extra-American, that is *R. sibiricus* in north-eastern Asia. Other members of that section are widely distributed over South America, and the rest are scattered over Australia, New Zealand, the Hawaiian Islands, southwestern China, and South and Central Africa. Most of them are morphologically and geographically isolated from each other and very likely relics of ancient lines of development. A modification of the axillary type is no doubt represented by certain species with creeping rhizome-like stem, emitting axillary shoots. Species with this habit are found in South America, New Zealand and South Africa.

In the Section *Axillares* the shape of the fruiting perianth segments exhibits all the possibilities of this genus. The tendency to enlarge the surface is variously—sometimes exceedingly—prominent. *R. venosus* has the largest valves known. At the same time the nervation is developed very variously, strong or delicately graduated, or in nets of very different shape in the middle and on the border of the valves. The midrib is either not thickened (thus especially in the species with important developments of the surface of valves), or only little thickened, or transformed on one valve or on all three to a tubercle. Nevertheless, the characteristic shape and size of the tubercle and its proportion to the surface of the valve remain constant, within narrow limits for every species. The *Axillares* show little tendency toward dentation on the margins of the valves. It is developed considerably in one species only, the Australian *R. Brownii*, and in that to an extreme degree. Among the American *Axillares* only *R. californicus* shows small teeth.

Now to the second main group of *Lapathum*, the section *Simplices*. It is the larger one, and, besides the widespread weedy species already mentioned, includes others which are characteristic of every continent. The section is easily divided into natural groups in respect of the characters of the valves combined with the annual or perennial growth. Some of these groups show valves where only one of the above-mentioned main types is developed. Examples are the Subsections of *Hymenosepali*, *Densiflori*, *Alpini* and *Aquatici*. In these the valves are simply enlarged without any development of callosities or teeth. It is impossible to discuss in full all species of *Simplices*. Only groups show-

ing peculiarities of valve-development or geographical distribution will be mentioned.

The subsection *Hymenosepali* is monotypic; the only species, *R. hymenosepalus*, being confined to the south-western United States. The subsection *Densiflori*, in contrast, has a very large and very discontinuous area, several species being confined to the Rocky Mountains; a single species, very nearly related to these, is endemic in the high mountains of the western Balkan Peninsula. To the same subsection also belongs a plant well known under the name of *R. domesticus*, whose valid name is *R. longifolius* DC. It shows the unusual disjunction, Scandinavia—Scotland—Pyrenées Orientales, and very nearly related species have been found in Tibet and Korea. A very peculiar group of species agreeing with the former subsection in the entire valves without tubercles but differing in the gigantic habit and in the shape of the leathery leaves inhabits the mountains of Central and South America at an elevation of 9-14,000 ft., and so recalls the occurrence of equally gigantic representatives of the genera *Senecio* and *Lobelia* in the high mountains of tropical Africa. This group consists of *R. peruanus*, *R. tolimensis* and *R. costaricensis*. The last species attains a height of 15-20 ft., the stem measuring at the base 2-3 inches in diameter. It is by far the tallest plant among the docks.

The species forming the subsection *Aquatici* are extremely nearly related to each other so that they might even be united under one specific name. They inhabit swamp localities only and cover the northern temperate zone. At the northern limit of their area they merge into *R. arcticus*. *R. arcticus* itself is the only species of arctic circumpolar area. Only one species, very nearly related to the European *R. aquaticus*, occurs in the southern hemisphere, in western Patagonia near to the south end of S. America, thus adding a nearly antarctic area to the distribution of the subsection, and making it markedly discontinuous.

Another line of development leads to Subsection *Patientia*. The type of its distribution is Euro-Asiatic, and its members are confined to regions with a continental type of climate. The valves of this subsection enlarge their surface nearly to the same degree as in the subsections already discussed, but one or even more callosities are developed. Very short teeth occur in a few species only.

The subsection *Obtusifolii* furnishes good examples of various combinations of the two characters of callosity and dentation occurring within polymorphic species. *R. obtusifolius* is indigenous in Europe, except the Mediterranean region, and has been introduced into many other parts of the world. In Eastern Europe it is represented by ssp. *silvester* with small valves, all bearing a large callosity and very short teeth on the margin. In western Europe *R. obtusifolius* is represented by the contrasting ssp. *agrestis* with large valves, only one of them bearing a callosity, and with very pronounced teeth. In middle Europe the areas of these subspecies overlap and there frequently occur

intermediate forms not showing the characters usual in dock hybrids, such as diminished fertility. They are included under the name of ssp. *transiens*. In south-eastern Europe and western Asia the species is represented by ssp. *subalpinus*.

R. pulcher is as polymorphic as *R. obtusifolius*, the variability tending in the same directions. But its type of distribution is Mediterranean. The areas of its subspecies are not so clearly delimited, a fact perhaps due to the introduction of the ssp. *eupulcher* into the areas of other subspecies.

The subsection *Dentati* has a variability of the same type and the same degree as the last subsection, but differs obviously in the annual habit. The group consists of several species, all of them being inhabitants of wet or irrigated places in the tropics and sub-tropics. Remarkable is the occurrence of two subspecies, both characterised by very large callosities and small teeth, one on the banks of the Nile and the other along the Ganges and Brahmaputra—perhaps suggesting a connection between the development of callosities and the distribution by means of running water. In the New World the group is represented by two species in south-western North America and by two species in Paraguay and the Argentine.

The subsection *Maritimi* includes species of annual habit with small narrow valves bearing pronounced callosities and, usually, long and fine teeth. The group is widespread over the world and every continent has its own representatives. A very interesting fact is the occurrence of three species so similar that they would never have been described as species if not separated by thousands of miles—*R. garipensis* in South Africa, *R. comosus* in Egypt and *R. Marschallianus* in Southern Russia.

Till now the cytology has been studied of only a few species of *Lapathum*. There have been found extremely different numbers of chromosomes, some of them unusually high and, therefore, offering certain technical difficulties. Nevertheless, it is evident that certain basic numbers correspond with the main groups established by morphological researches.

It is clear that the study of this genus of world-wide distribution is of high interest. It shows, moreover, that by such comparative studies problems of general interest, such as those of evolution, of palaeogeography and palaeoclimatology may be resolved, especially when collaboration is established between cytology, genetics and the morphological method.