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A Review of the Genus *Dactylorhiza**

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Introduction

The genus *Dactylorhiza*^a, which at one time was combined with *Orchis*, the type genus of the family Orchidaceae, belongs to the subtribe Orchidinae, tribe Orchideae, subfamily Orchidoideae (Dressler, 1981). This is the largest genus in the group of genera, which forms the so-called "*Dactylorhiza*-alliance". From the evolutionary point of view it represents an intermediate stage in one of the geophytic directions in the evolution of orchids starting with hypothetical primitive *Cephalanthera*-like ancestors and extending to such highly specialized terrestrial genera from the ancient Mediterranean area as *Orchis*, *Ophrys*, *Serapias*, *Himantoglossum*, *Steveniella*, etc. The study of dactylorchids is therefore very important for an understanding of the adaptations of orchids to terrestrial habitats under conditions of pronounced seasonal changes. Two previous works were devoted to the study of the genus *Dactylorhiza* (Klinge, 1898; Vermeulen, 1947). Questions of nomenclature were dealt with by a number of contributors (Soó, 1962; Hunt and Summerhayes, 1965; Averyanov, 1986). Species of dactylorchids which occur in Europe (Soó, 1980), Asia (Renz, 1978; Renz and Taubenheim, 1984) and the Soviet Union (Averyanov, 1982, 1983a, b) were studied during the last decade. More extensive reviews of dactylorchids are available in a number of monographs (Sundermann, 1975; Nelson, 1976, 1979; Fuller, 1983; Averyanov, 1983c).

Anatomy and Morphology of Dactylorchids

All species of the genus *Dactylorhiza* are perennial herbs with an unbranched erect stem, a spiral arrangement of leaves and terminal spicate inflorescence. They are similar to tuber-forming geophytes.

The evolutionary appearance and development of the tuberoid, also known as the "sinker" (Dressler, 1981), are undoubtedly due to the seasonal climatic changes, which necessitate nutrient storage for the following year's growth. Formation of the tuberoid probably evolved as a consequence of the thickening of the root base. This resulted at first in the formation of finger-like tuberoids which occur in relatively primitive dactylorchids (aggr. *D. fuchsii*, aggr. *D. incarnata*). Further evolution proceeded along lines of greater specialization and resulted in a cylindrical tuberoid structure in more advanced species of *Dactylorhiza* (aggr. *D. sambucina*, aggr. *D. sulphurea*) and in the closely related genus *Orchis* (Fig. 5-1e; Averyanov, 1983a, c). This structure is often polystelic, that is, it includes several vascular cylinders, as though several roots have grown together (Ogura, 1953; Dressler, 1981).

Evolutionary changes in the stems of specialized forms of the genus consisted mainly in reduction of the number of nodes (for example, in high mountain and northern species; Fig. 5-1c). The formation of subterranean creeping shoots in *D. iberica* (Fig. 5-1f) is a unique modification of the stem. This character is, apparently, an evolutionary adaptation which compensates for limited seed production by the species and prevents extinction (Averyanov, 1983a).

Anatomically the stems of all species in the genus are very similar. They are formed by an apical meristem and have no intercalary meristems in their nodes. The mature stem is

^aThe name of the genus (and the common name for all its species—dactylorchid) is derived from the Ancient Greek δαχτυλοζ (finger) and reflects the characteristic form of the tubers of these plants.

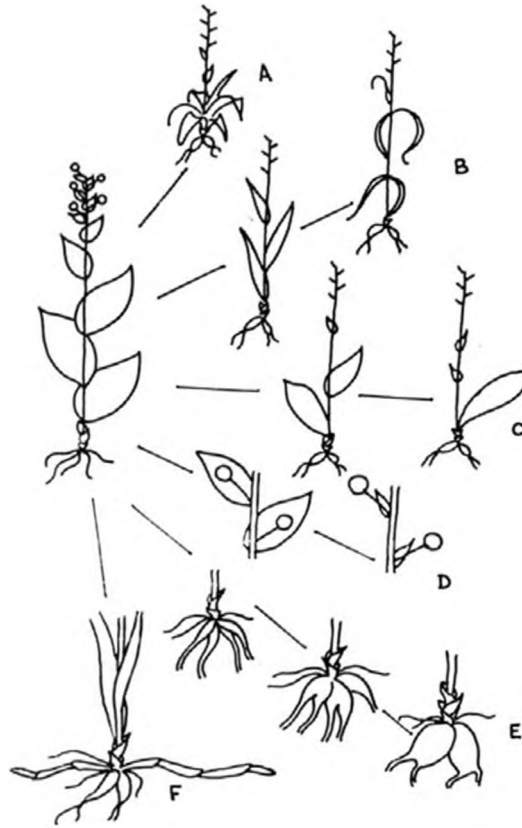


Fig. 5-1. The evolutionary trends of vegetative organs in the genus *Dactylorhiza* (Averyanov, 1983c).

covered by a layer of epidermal cells enveloped by an external cuticle. Next to the epidermis is a 3–6 layered chlorenchyma consisting of rounded cells with many chloroplasts and numerous large intercellular spaces. A 3–5 layered cylinder of sclerenchyma cells, usually more or less lignified, is located inside the chlorenchyma. As a rule, the sclerenchyma also surrounds the vascular bundles. The central part of the stem consists of parenchyma which disappears as the plant matures and is replaced by a cavity. Appearance during ontogenesis and the size of this cavity is an important systematic character for the genus (Borsos, 1980).

The leaves of dactylorchids are formed by an intercalary meristem, situated at their bases. At the end of its activity this meristem widens, surrounds the stem and forms a leaf sheath.

The stomata, situated on the lower surface of the leaf and on the stem are anomocytic. However, their development can be either azenous or hemimesogenous, and the former is always dominant. The hemiperigenous and hemimesoperigenous type of stomatal development has also been observed, but occurs very rarely. The ratio of developmental types of stomata varies even in closely related species of the genus *Dactylorhiza* (Rasmussen, 1981).

Ancestors of dactylorchids probably had a large number of wide leaves attached at approximately equal distances on the shoot as occurs in most primitive species of the genus. In more recently evolved species the leaves vary from almost rounded to linear. Specialization in this case proceeded from wide ovate leaves to narrow-lanceolate and linear ones (Fig 5-1b). The most specialized are the linear, longitudinally folded, curved leaves of a number of northern and mountain species. Specialization of bracts tends mainly toward reduction (Fig 5-1d). The rosettelike arrangement of leaves at the stem

base (Fig. 5-1a) in some high mountain and arid species (Averyanov, 1983a) is a more advanced specialization within the genus.

The edges of the leaves and bracts in species of the genus consist of epidermal cells which bear papillae covered with large numbers of cuticular folds. The size of the papillae and the character of the cuticular folds vary considerably among species (Fig 5-2). This and other vegetative characters can be used taxonomically within *Dactylorhiza* and for the delimitation of the genus itself.

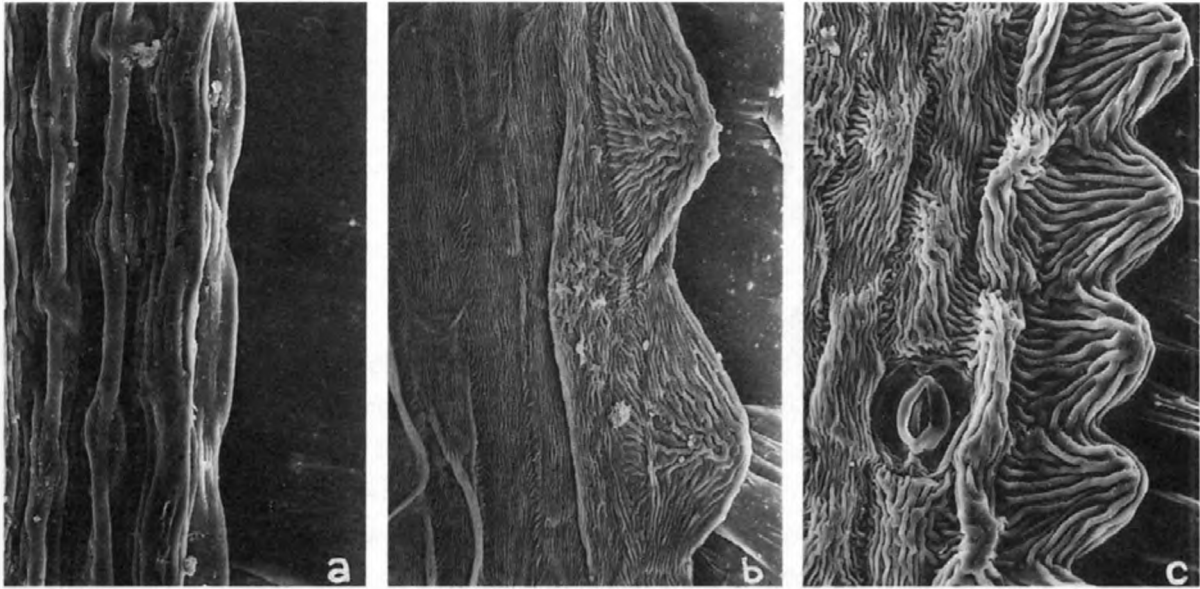


Fig. 5-2. Micromorphology of the leaf edge in different species of the genus *Dactylorhiza* (Averyanov, 1983c). Explanation of symbols: a, *D. incarnata*. $\times 275$; b, *D. sambucina*. $\times 275$; c, *D. salina*. $\times 275$.

Flowers

Flowers of dactylorchids are highly zygomorphic and have six free perianth segments. Segments of the outer and inner whorls (except the labellum) are similar in form and size. The well developed lip is of different form and extends at the base to form a cylindrical spur. Stamens of the inner whorl are completely reduced. Only one (the median stamen of the outer whorl) functions normally. The other two are modified into barely visible staminodes situated on the sides of the anther. Columns are rather small and the sessile stigma consists of three lobes situated at the base of the anther above the entrance to the spur (Vermeulen, 1947; Averyanov, 1983; Fig. 5-3.).

The pollen grains of dactylorchids occur in polyades (Kuprianova and Alioschina, 1967) or massulae (Caspers and Caspers, 1976) within a two-celled anther. Polyades are connected to each other with mucilaginous strands of a polysaccharide and form clavate pollinia. The central sterile axis of the pollinium is extended into a more or less elongated caudicle which terminates in a retinaculum or viscidium (Fig. 5-3). These structures play an important part in the pollination process. In the flower of dactylorchids, the two pollinaria are completely divided. Pollinia are completely hidden within the anther cells and the caudicles lie freely in tissue folds of the anther base where they are separated by a small rostellum. In the base of the anther, the caudicles are combined and their retinacula or viscidia are covered by a small bilocular operculum which is located

over the stigma itself (Fig. 5-3). The operculum opens easily when the insect-pollinator contacts it and tries to penetrate into the spur. In this case, the viscidia become exposed and on touching the body of the insect-pollinator become attached to it (usually to its anterior part or head).

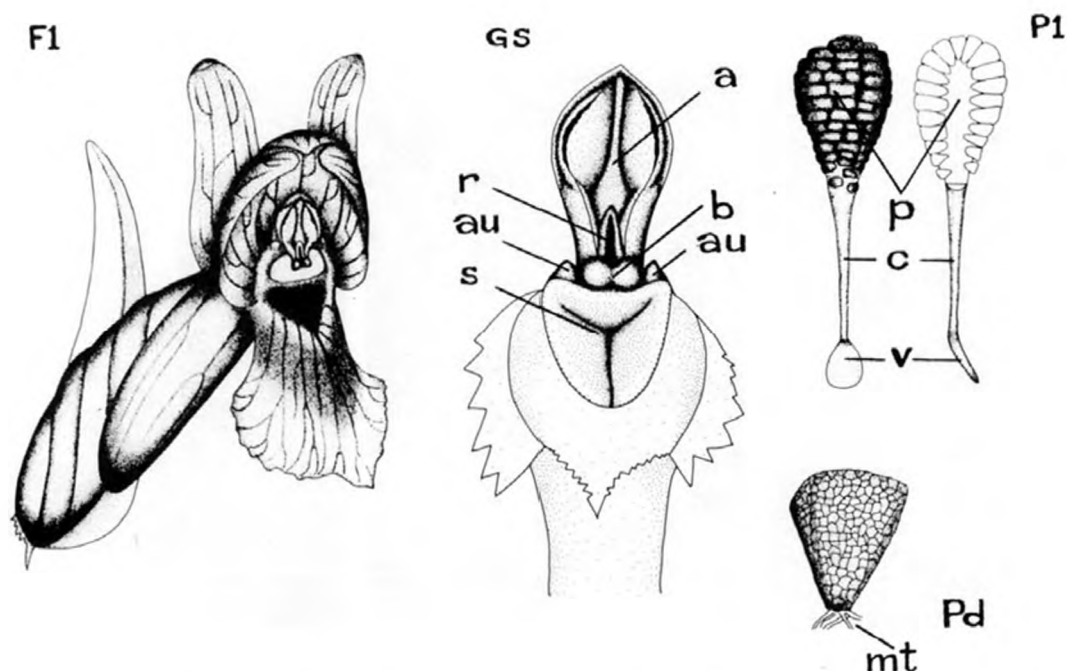


Fig. 5-3. Structure of the dactylorchid flower (Averyanov, 1983c). a, anther; au, auricle; b, bursicle; c, caudicle; Fl, flower (*D. incarnata*). Explanation of symbols: GS, gynostemium or column; mt, mucilaginous threads; p, pollinium; Pd, polyade; Pl, pollinarium; r, rostellum; s, stigma; v, viscidium.

The pollinaria can be pulled easily from the anther cells and carried away by pollinators. In the air the caudicle of the pollinium dries very quickly and bends in a specific manner positioning the pollinium so that during a subsequent visit of the insect to another flower of the same species of dactylorchids, it touches the stigma. Some portion or the entire pollinium remains on the sticky surface of the stigma.

Flowers of dactylorchids are entirely lacking in nectar and no other attractants have been discovered to date (Darwin, 1877; Faegri and van der Pijl, 1979). Specific pollinators are unknown. The flowers of all species are pollinated by bumblebees (Nilsson, 1980, 1981), bees and flies (Faegri and van der Pijl, 1979). Some of the pollinators (*Apis mellifera*, *Bombus lapidarius* and *B. terrestris*) probably exploit the stigmatic exudate of the flowers (*Dactylorhiza fuchsii*) which contains glucose and amino acids (Dafni and Woodel, 1986). Food deception has been shown to exist in *D. sambucina* (Nilsson, 1980, 1981).

The most primitive flower in the genus *Dactylorhiza* is small, faintly colored and has a small lip with a short saccate spur (*D. incarnata*). Evolution of this organ has proceeded in the direction of enlargement and strengthening of the zygomorphy. The increasing level of zygomorphy of the flower consists mainly of 1) enlargement and elaboration of the lip, 2) lengthening of the spur (*D. umbrosa*), 3) increasing proximity of perianth segments (except the lip), 4) formation of a helmet (*D. iberica*), and 5) the appearance of

awn-shaped tips in the petals of the inner and outer whorl (*D. aristata*). In more advanced dactylorchids, the lip differs sharply from other perianth segments and often consists of three lobes. Its surface is covered with epidermal papillae which are externally similar to those on the edges of the leaves and bracts. They are usually 50–60 μm long, but sometimes may reach 120–150 μm (*D. iberica*). Their width is 20–30 μm (Averyanov, 1983c).

Flower color has changed during the evolution of the genus from relatively pale pink and yellowish flowers in relatively primitive species to bright-lilac (*D. traunsteineri*, *D. euxina*, *D. umbrosa*) and dark-violet ones (*D. cordigera*) in more advanced dactylorchids. The selective forces of this evolutionary trend are still unclear.

Ovaries in all species are tricarpelate, inferior, twisted and consist of one chamber with parietal placentation. Flowers are sessile.

Pollen

Like most orchids, all species of the genus *Dactylorhiza* have highly specialized pollen grains. They occur in tetrahedral polyades 140–300 μm long and 80–200 μm wide in pollinia that are typical for the tribe Orchideae. The polyade usually contains a large number of pollen grains with greatly reduced walls. No typical pollen structure is common to the various species. A distinct exine exists only on the outward side of peripheral pollen grains in the polyade. The attachment between peripheral pollen grains is so intimate that they are often almost indistinguishable. Fused outward walls of peripheral pollen cells result in a rigid "exine" polyade envelope. The structure of this envelope in orchids and especially in members of the tribe Orchideae is very variable and therefore useful in taxonomy (Caspers and Caspers, 1976; Schill and Pfeiffer, 1977; Dressler, 1981).

In dactylorchids the pollen cells which form the surface of tetrahedral polyades are polygonal in shape. They are usually slightly elongated along the edges and sides of the polyade. At the base of polyade, they are elongated along the pollinium axis. Cell size varies from 10–14 μm in length and 10–20 μm in width. Sculpturing on the surface of the pollen grains is of three types, established in the Orchidaceae (Schill and Pfeiffer, 1977).

Type I ("laevigat-scabros"—Schill and Pfeiffer, 1977) the surface is slightly rough with the surface of the exine covered with small torulae (Fig. 5-4a). This type is characteristic for most species of the genus *Dactylorhiza* in the sections of *Dactylorhiza*, *Sambucinae* and *Aristatae*.

Type II ("verrucos-hamulat"—Schill and Pfeiffer, 1977) possesses a very variable exine surface, which is formed by short, curved semicylinder-like excrescences (Fig. 5-4b). These excrescences can fuse fully with each other and form either a finely perforated or a finely reticulate surface texture. This type occur in some of species of the section *Dactylorhiza*.

Type III ("reticulat-fragmentimurat"—Schill and Pfeiffer, 1977) has a surface formed by irregular torulose excrescences which are fused in a pectinaceous structure which covers the exine with a continuous net (Fig. 5-4c). This type is characteristic only of the monotypic section *Iberanthus*.

Exine structures in the genus *Dactylorhiza* are shown in Fig. 5-5. The morphological variations in exine structure have no clear adaptive value.

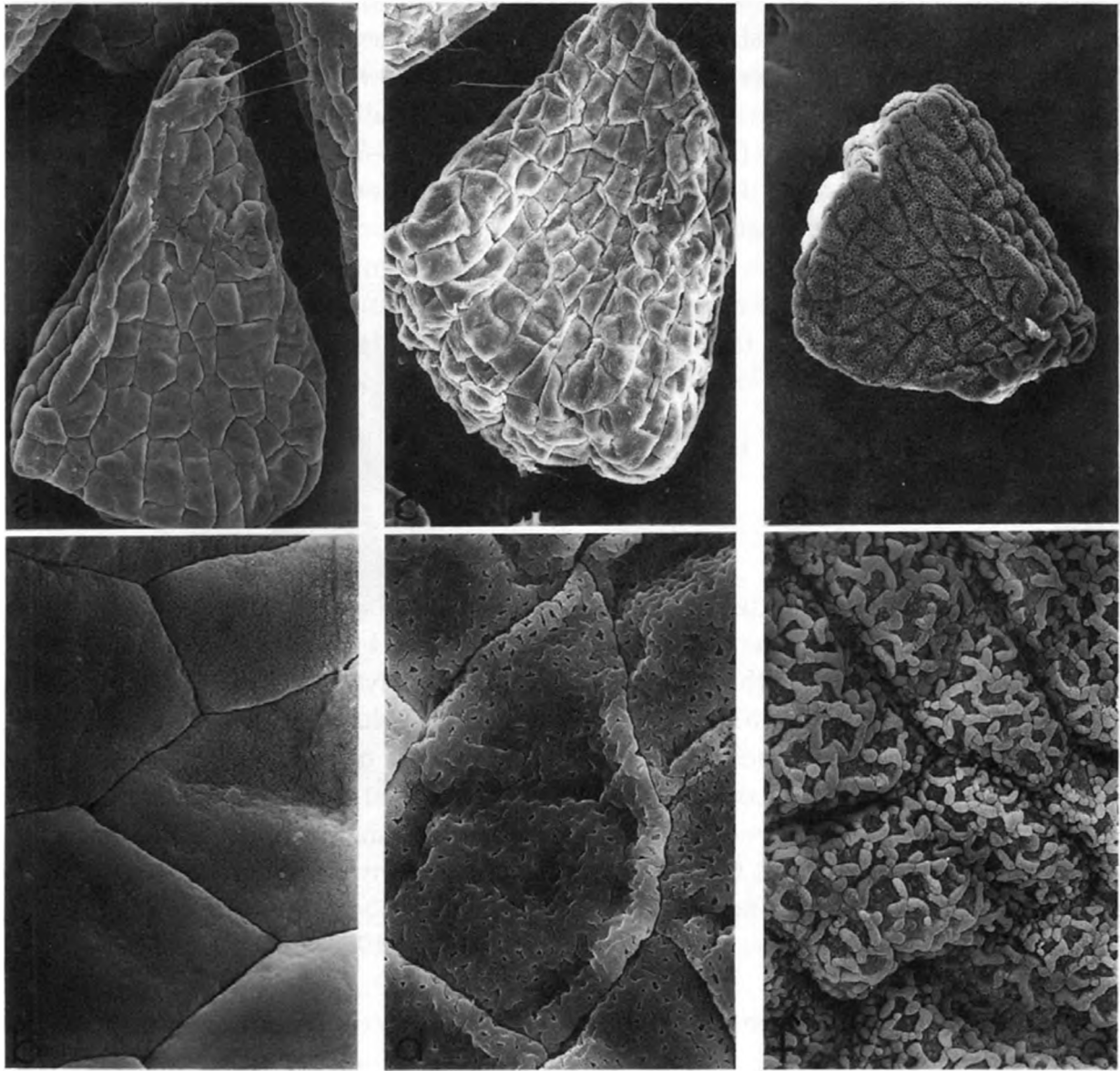


Fig. 5-4. Different surface types of pollen grains in the genus *Dactylorhiza*. a,b, type 1 (*D. flavescens*). $\times 250$, $\times 1700$; c,d, type 2 (*D. majalis*). $\times 250$, $\times 1700$; e, f, type 3 (*D. iberica*). $\times 250$, $\times 1700$ (Averyanov, 1983c).

Seeds

Species of the genus *Dactylorhiza* have seeds similar to those of most orchids. Their number is large and can reach (in *D. maculata* for example) 6,000 seeds per capsule (Darwin, 1877). A considerable reduction, which is typical for orchid seeds, exists in combination with specialized structures that enable them to float in the air. In dactylorchids and related genera, such a highly specialized tissue is the seed coat or testa. When mature it is a thin membrane that surrounds the embryo and contains a considerable volume of air. This allows the seed to float in the air for long periods, and "fly" to cover large distances. It has an important adaptive value.

The testa in orchids is extremely variable (Arditti et al., 1979, 1980a, b; Barthlott and Ziegler, 1981). In dactylorchids it is spindle-like, widest in the middle where the embryo

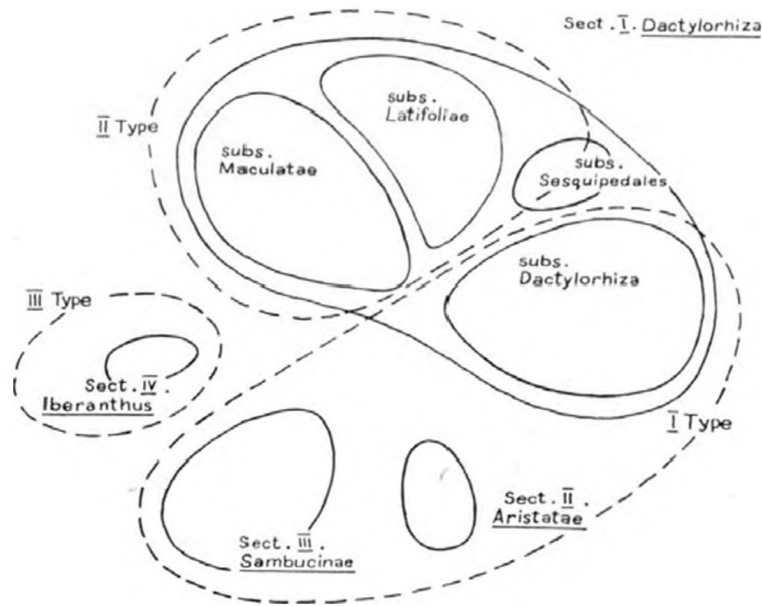


Fig. 5-5. Occurrence of different pollen grains surface types in the genus *Dactylorhiza*. Explanation of symbols: Solid line indicates the taxonomic affiliations within the genus; the occurrence of different pollen grain surface types is marked by the dotted line.

is located. The size of testae varies from 350 to 1100 μm in length and from 150 to 300 μm in width. The smallest seeds are those of *D. aristata* (350–500 \times 200–250 μm) and the largest are produced by *D. urvilleana* (900–1100 \times 150–250 μm) (Averyanov, 1983c).

Cells of the testa are polygonal in shape, bounded by thickened lignified anticlinal walls. In most species of *Dactylorhiza* they are elongated along the seed axes. The length of the testa cells is almost equal to their width in *D. incarnata* and *D. aristata*, the species with the smallest seeds (Averyanov, 1983c). Their shape as well as the ratio of their number on the transverse and longitudinal axes, is an important diagnostic character that permits the separation of the closely related *Dactylorhiza* and *Orchis* (Fig. 5-6; Tohda, 1983). The direction of specialization is from seeds with a relatively multicellular testa in *Dactylorhiza* to an extremely simplified seed coat consisting of a very small number of cells in *Orchis*.

In dactylorchids anticlinal cell walls in the testa are closely attached to each other. There are no intercellular spaces. The walls of the seed coat are very thin, membranous and stretched (like in drum skin) along thickened and lignified anticlinal cell walls. As seeds mature, cells of the one-layered testa lose their cytoplasm and the periclinal walls fuse with one another, at least in the center.

The surface structure of periclinal walls of the testa in dactylorchids is very variable. In one group of species the surfaces of the periclinal walls are not sculptured, in others sculpturing is present. Sculpturing of the periclinal walls is geographically variable in some species (Tohda, 1983). The form and presence of trabeculae is the basis of the classification of the structure of periclinal walls of testa cells of the genus into 4 types.

Type I (*D. incarnata*-type). The absence of trabeculae on periclinal walls of testa cells is typical for this class (Fig. 5-7a).

Type II (*D. maculata*-type). Periclinal walls of testa cells have transverse, sometimes dichotomously branching trabeculae which extend at right angles from the anticlinal cell walls (Fig. 5-7b).

Type III (*D. romana*-type). Trabeculae exhibit curved branching and anastomose with each other. Some do not join the anticlinal wall, become thinner and disappear on the

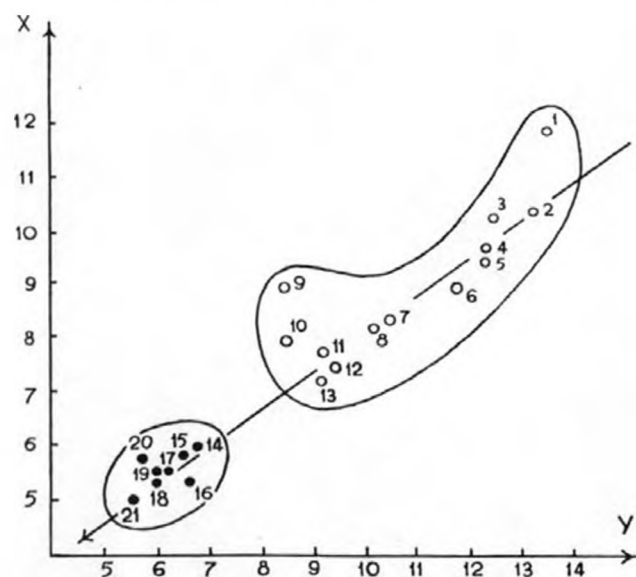


Fig. 5-6. Relation between cell numbers at the longest and widest axes of the testa in different dactylorhizid species and *Orchis* species (Tohda, 1983). X — number of testa cells at the widest axis; Y — number of testa cells at the longest axis; the direction of testa specialization is shown by the arrow. Key: 1, *Dactylorhiza sphagnicola*; 2, *D. sambucina*; 3, *D. incarnata*; 4, *D. integrata*; 5, *D. sp.*; 6, *D. majalis*; 7, *D. purpurella*; 8, *D. traunsteineri*; 9, *D. foliosa*; 10, *D. aristata*; 11, *D. maculata*; 12, *D. ericetorum*; 13, *D. fuchsii*; 14, *Orchis morio*; 15, *O. simia*; 16, *O. laxiflora*; 17, *O. coriophora*; 18, *O. picta*; 19, *O. mascula*; 20, *O. longicruris*; 21, *O. purpurea*.

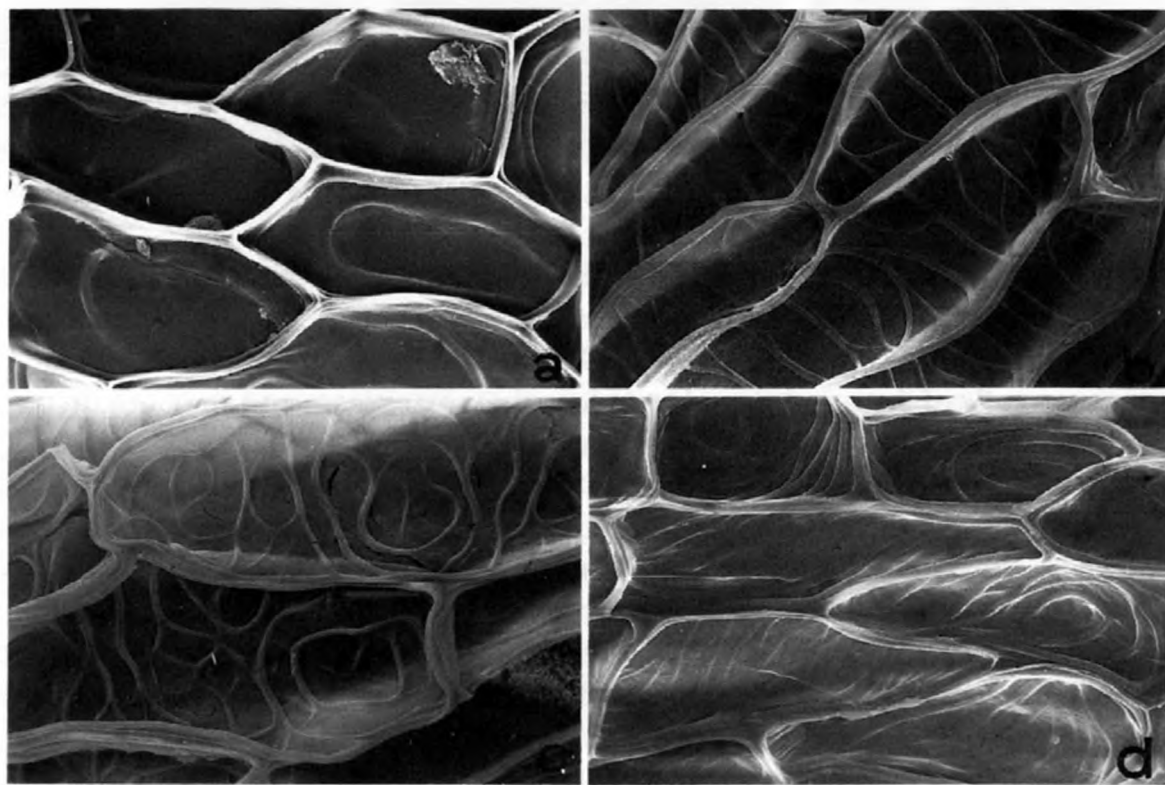


Fig. 5-7. Different morphological types of periclinal testa walls in seeds of *Dactylorhiza* species (Averyanov, 1983c). a, type 1 (*D. incarnata*). $\times 400$; b, type 2 (*D. maculata*). $\times 400$; c, type 3 (*D. romana*). $\times 400$; d, type 4 (*D. aristata*). $\times 400$.

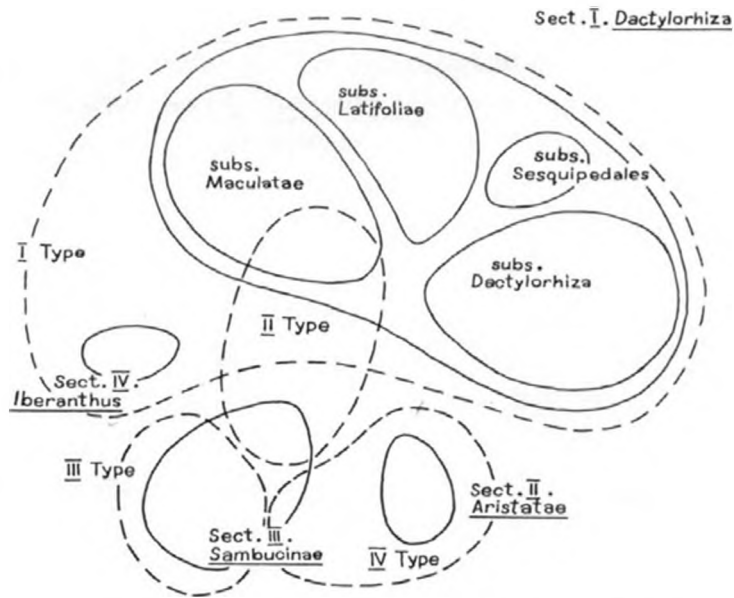


Fig. 5-8. Occurrence of different morphological types of periclinal testa walls in seeds of the genus *Dactylorhiza*. Explanation of symbols: The solid line indicates the taxonomic groups within the genus; the occurrence of different types of periclinal testa walls in seeds is marked by the dotted line.

periclinal membrane (Fig. 5-7c).

Type IV (*D. aristata*-type). The trabeculae are "concentric" and arch-shaped. They extend at a sharp angle from the anticlinal walls and anastomose with each other in a pattern similar to the outline of the cell (Fig. 5-7d).

Schematically, the occurrence of these types in the genus *Dactylorhiza* is shown in Fig. 5-8. These types are, on the whole, similar to each other and therefore intermediate morphological variants can occur in a number of cases. The form of the trabeculae has no clear adaptive value.

The embryo in dactylorchids seeds is very small and essentially undifferentiated. In longitudinal sections it has a slightly bipolar structure because of larger cells which form one of its poles.

Chromosomes

The basic chromosome number for species of the tribe Orchideae as well as for the genus *Dactylorhiza* is $2n=40$. This chromosome number is found in most members of this tribe (Duncan, 1959; Feodorov, 1969). Specimens of this tribe are polyploids (but diploids in their function) in comparison with the most primitive orchid karyotype ($2n=20$ in *Cypripedium* for example). The basic chromosome number for orchids as an evolutionary group is $x=10$.

Morphologically similar metacentric chromosomes with very short arms are typical for *Dactylorhiza* and most members of the subtribe Orchidinae. On metaphase plates of root meristems, they appear as rounded or oval bodies which stain well with Heidenhein's ferrous hematoxylin or Schiff's reactive. Their length in species of the genus *Dactylorhiza* is within 1–2 (2,5) μm . The primary constriction is hard to see. There are no B-chromosomes (Averyanov, 1983c).

Autopolyploidy, aneuployploidy and allopolyploidy were involved in the evolution of the karyotype of dactylorchids (Fig. 5-9). Karyotypes of the primary kind ($2n=40$) are

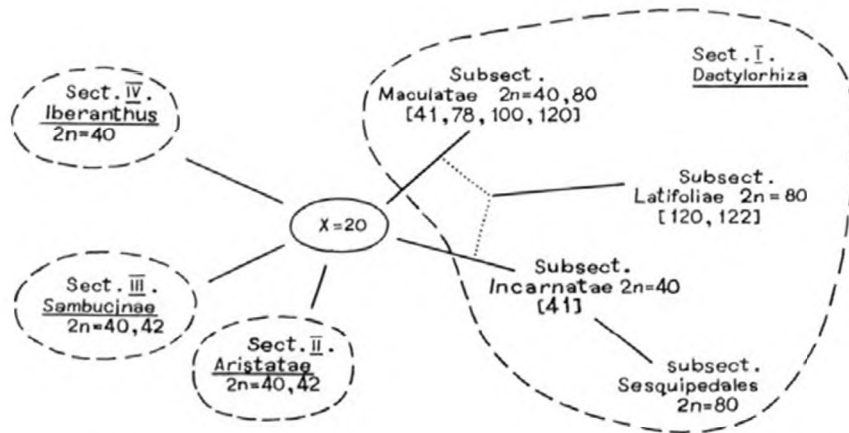


Fig. 5-9. Diagram of karyotype evolution in the genus *Dactylorhiza* from a basic chromosome number $X = 20$ (Averyanov, 1983c).

present in the only species of the monotypic section *Iberanthus* and in some of species of the section *Dactylorhiza*. The evolution of species in the subsection *Dactylorhiza* of the type section (sect. *Dactylorhiza*) proceeded at the diploid level. The primary chromosome number ($2n=40$) is also typical for many species in the subsection *Maculatae*. Tetraploid species of this subsection with $2n=80$ arose by autopolyploidy (or allopolyploidy). The same process in species of the subsection *Dactylorhiza* led to tetraploids in the subsection *Sesquipedales*. Allopolyploid stabilization of hybrids between species of the subsections *Dactylorhiza* and *Maculatae* resulted in tetraploids among primary species of the hybridogenic subsection *Latifoliae* (Heslop-Harrison, 1954, 1957). Aneuploid change of the karyotype ($2n=40 \rightarrow 42$) is typical for species of the section *Sambucinae* and *Aristatae*. This rearrangement is still evolving and in many species of these sections the norm is two chromosome numbers $2n=40$ and $2n=42$.

Polyploid plants with $2n=100, 120, 122$ sometimes occur in populations of *D. maculata* and *D. russowii* (Vermeulen, 1938; Kliphuis, 1963; Averyanov, 1979b). Aneuploid forms with $2n=41, 78$ can be found in *D. merovensis*, *D. hebridensis*, *D. psychrophila* and *D. maculata* (Averyanov et al., 1982a, b, 1985). Plants with such karyotypic anomalies are very rare. Morphologically and taxonomically they are similar to the parental species. In Fig. 5-9 and Table 5-1 they are presented in square brackets.

Somatic polyploidy was observed in several species of dactylorchids, when in a karyologically normal plants some tissues (or part of a tissue) have an anomalous chromosome number (Perring, 1968; Averyanov et al., 1982b).

Triploid hybrids ($2n=60$) are formed as a result of frequent hybridization between diploid and tetraploid species of dactylorchids. Sometimes they are very numerous and found in nature in large groups. Usually they are completely sterile. In a number of instances they can form up to 4% of normal seeds (Heslop-Harrison, 1957). Such seeds are formed either by parthenogenesis (Heslop-Harrison, 1959) or through the fusion of gametes produced by anomalous meiosis. This leads to further degradation of the karyotype in the progeny and to the appearance of plants with $2n=44, 48, 52, 72$ etc. (Lord and Richards, 1977). As a rule this is associated with anthropogenic influence on populations, which probably disturb existing isolation mechanisms among existing species.

In the subsection *Maculatae* some diploid and tetraploid species are morphologically very similar. This is particularly true for *D. fuchsii* ($2n=40$) and *D. maculata* ($2n=80$); *D.*

hebridensis ($2n=40$) and *D. elodes* ($2n=80$) as well as *D. psychrophila* ($2n=40$) and *D. sudetica* ($2n=80$). Most anatomical and morphological characters of these species correlate somewhat poorly with the ploidy level (Averyanov, 1979a). However, tetraploid and diploid species in this group prefer soils of different acidity and podzolization and they have not been observed to coexist in nature (Averyanov, 1982; Averyanov et al., 1982a, b). Although their triploid hybrids are sterile, all of these species are sometimes considered belonging to *D. maculata* s.l.

Relatively frequent changes of the ploidy level in progeny of one plant have been shown to occur in diploid and tetraploid species of *D. maculata* s.l. (Hagerup, 1944). The cases of haploidy ($2n=40 \rightarrow 2n=20$ and $2n=80 \rightarrow 2n=40$) can be explained by the development of an embryo from an unfertilized egg or another haploid cell in the embryo sac (Hagerup, 1944). This has been shown to also occur in other orchids related to dactylorhichid genera (Hagerup, 1947; Heslop-Harrison, 1959).

Polyploidy can be explained by fertilization of unreduced eggs ($2n=40 \rightarrow 2n=60^b$ and $2n=80 \rightarrow 2n=120$) and by autopolyploidization at an earlier stage of ontogenesis ($2n=40 \rightarrow 2n=80$; Averyanov, 1979a). On the whole, development and fusion of the overwhelming majority of gametes proceeds normally. In the hypothetical scheme (Fig. 5-10) this is marked with boldface arrows. All plants with unusual chromosome numbers are sterile and relatively rare in nature; in Fig. 5-10 they are marked with an asterisk^c.

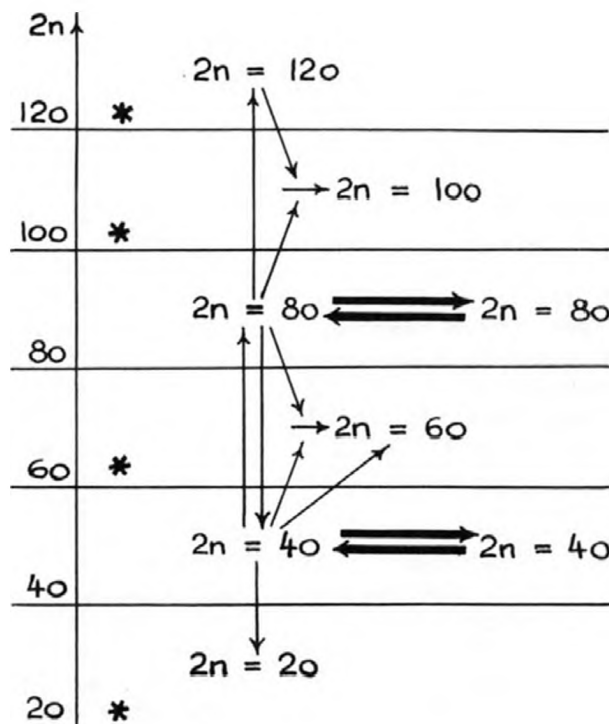


Fig. 5-10. Chart of possible spontaneous variations of the ploidy level in populations of *Dactylorhiza maculata* s.l. (Averyanov, 1979a).

^bIn most cases triploids result from hybridization of diploid and tetraploid plants.

^c*D. maculata* s.l. with $2n=20$ is known only in the embryo stage. Adult plants with such a chromosome number have not been observed in nature.

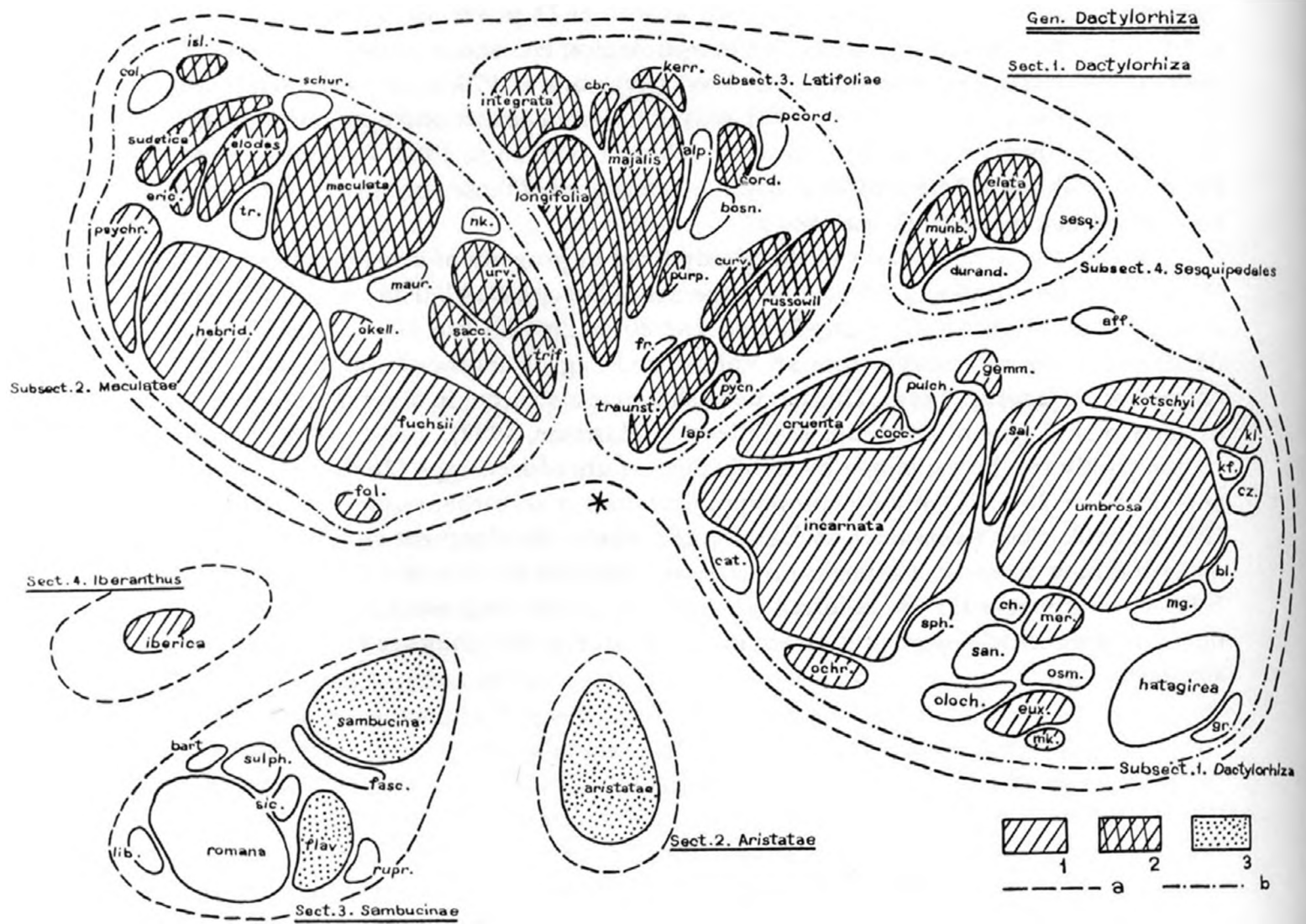


Fig. 5-11. Diagram of phylogenetic interrelations in *Dactylorhiza* species. Explanation of symbols: Distances between zones which designate species are an approximation of their affinity and their areas represent the relative extent of their distribution in combination with the polymorphism and the magnitude of the general species population. The approximate position of the ancestral complex is marked with an asterisk, and the distance from it is indicative of degree of evolutionary advancement (specialization) of taxa. Differences in species karyotypes are marked with shading: 1, $2n=40$; 2, $2n=80$; 3, $2n=40, 42$, bodies designating karyologically unstudied species are not shaded. Sections limits are marked by line "a"; subsections limits—by line "b".

Abbreviations of species names in the diagram:

- | | | | |
|-----------------------------------|------------------------------------|--------------------------------------|-----------------------------------|
| Sect. 1. <i>Dactylorhiza</i> | 20. <i>D. baldshuanica</i> bl. | 40. <i>D. transsilvanica</i> tr. | 60. <i>D. lapponica</i> lap. |
| Subsect. 1. <i>Dactylorhiza</i> | 21. <i>D. czerniakowskiae</i> cz. | 41. <i>D. ericetorum</i> eric. | Subsect. 4. <i>Sesquipedales</i> |
| 1. <i>D. incarnata</i> incarnata | 22. <i>D. kafiriana</i> kf. | 42. <i>D. sudetica</i> sudetica | 61. <i>D. durandii</i> durand. |
| 2. <i>D. cataonica</i> cat. | 23. <i>D. kulikalonica</i> kl. | 43. <i>D. colaënsis</i> col. | 62. <i>D. munbyana</i> munb. |
| 3. <i>D. ochroleuca</i> ochr. | 24. <i>D. hatagirea</i> hatagirea | 44. <i>D. islandica</i> isl. | 63. <i>D. elata</i> elata |
| 4. <i>D. cruenta</i> cruenta | 25. <i>D. graggeriana</i> gr. | Subsect. 3. <i>Latifoliae</i> | 64. <i>D. sesquipedalis</i> sesq. |
| 5. <i>D. coccinea</i> cocc. | 26. <i>D. affinis</i> aff. | 45. <i>D. majalis</i> majalis | Sect. 2. <i>Aristatae</i> |
| 6. <i>D. pulchella</i> pulch. | Subsect. 2. <i>Maculatae</i> | 46. <i>D. kerryensis</i> kerr. | 65. <i>D. aristata</i> aristata |
| 7. <i>D. sphagnicola</i> sph. | 27. <i>D. triphylla</i> trif. | 47. <i>D. cambrensis</i> cbr. | Sect. 3. <i>Sambucinae</i> |
| 8. <i>D. gemmana</i> gemm. | 28. <i>D. urvilleana</i> urv. | 48. <i>D. purpurella</i> purp. | 66. <i>D. sambucina</i> sambucina |
| 9. <i>D. olocheilos</i> oloch. | 29. <i>D. nieschalkiorum</i> nk. | 49. <i>D. alpestris</i> alp. | 67. <i>D. fasciculata</i> fasc. |
| 10. <i>D. osmanica</i> osm. | 30. <i>D. saccifera</i> sacc. | 50. <i>D. integrata</i> integrata | 68. <i>D. sulphurea</i> sulph. |
| 11. <i>D. euxina</i> eux. | 31. <i>D. foliosa</i> fol. | 51. <i>D. longifolia</i> longifolia | 69. <i>D. sicula</i> sic. |
| 12. <i>D. markowitschii</i> mk. | 32. <i>D. fuchsii</i> fuchsii | 52. <i>D. bosniaca</i> bosn. | 70. <i>D. bartonii</i> bart. |
| 13. <i>D. sanasunitensis</i> san. | 33. <i>D. okellyi</i> okell. | 53. <i>D. cordigera</i> cord. | 71. <i>D. flavescens</i> flav. |
| 14. <i>D. merovensis</i> mer. | 34. <i>D. hebridensis</i> hebrid. | 54. <i>D. pseudocordigera</i> pcord. | 72. <i>D. ruprechtii</i> rupr. |
| 15. <i>D. chuhensis</i> ch. | 35. <i>D. psychrophila</i> psychr. | 55. <i>D. traunsteineri</i> traunst. | 73. <i>D. romana</i> romana |
| 16. <i>D. salina</i> sal. | 36. <i>D. maculata</i> maculata | 56. <i>D. francis-drucei</i> fr. | 74. <i>D. libanotica</i> lib. |
| 17. <i>D. umbrosa</i> umbrosa | 37. <i>D. maurusia</i> maur. | 57. <i>D. russowii</i> russowii | Sect. 4. <i>Iberanthus</i> |
| 18. <i>D. kotschyi</i> kotschyi | 38. <i>D. elodes</i> elodes | 58. <i>D. curvifolia</i> curv. | 75. <i>D. iberica</i> iberica |
| 19. <i>D. magna</i> mg. | 39. <i>D. schurii</i> schur. | 59. <i>D. pycnantha</i> pycn. | |

As indicated in the scheme, diploid and tetraploid plants can exchange genetic information irrespective of the sterility of their hybrids. This fact probably has a great adaptive value for *D. maculata* s.l. The genotype of diploids (similarly as it takes place in haploids) can change much faster than that of tetraploids under selection pressure. However, intensification of strong selection pressure can result in a considerable impoverishment of the gene pool of diploid populations and even put them on the verge of extinction. Therefore, it is possible that the flow of genetic information into such populations from closely related tetraploid species can avert extinction of the diploid species. Such interrelations may exist, for example, among *D. fuschii* and *D. maculata*; *D. hebridensis* and *D. maculata* and *D. elodes*; *D. psychrophila* and *D. sudetica*. On the other hand, useful and new genes can flow from diploids into tetraploids. In such cases, the tetraploid species can function as a reservoir and repository of genotypic variations which are constantly expressed and "tested" in diploids. Thus, hypothetically, related diploid and tetraploid species, which form the group "*D. maculata* s.l.", maintain their integrity and mutually determine the success of evolution (Averyanov, 1979a, 1983c).

Data on the karyology of *Dactylorhiza* species are brought together in Fig. 5-11 and Table 5-1.

Table 5-1. The taxonomy of dactylorchids.

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- Genus *Dactylorhiza* Necker ex Nevski, 1937, *Tr. Bot. Inst. Ac. Sci. USSR*, Ser. 1,4:332.
 Lectotype: *D. incarnata* (L.) Soó (*Orchis incarnata* L.)^a
- Section 1. *Dactylorhiza*.
 Subsection 1. *Dactylorhiza*.
 1-8. Aggregate *D. incarnata*.
1. *D. incarnata* (L.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 3
 Basionym: *Orchis incarnata* L., 1755, *Fl. Suec.*, ed. 2:312.
 Syn.: *Orchis impudica* Haller, 1769, in Crantz, *Stirp. Austr.* 2, 6:497.
 Orchis divaricata Rich., 1812, *Mer. Fl. Par.* 2:94.
 Orchis latifolia L. var. *angustifolia* Lois., 1828, *Fl. Gall.* 2:267.
 Orchis angustifolia Lois. ex Wimm. et Grabowski, 1829, *Fl. Siles.* 2, 2:252.
 Orchis lanceata Dietri, 1833, *Fl. Boruss.* 5.
 Orchis angustifolia Reichenb. var. *haussknechtii* Klinge, 1893, *Revis. Orch. cord. Orch. angustif.*: 70.
 2n = 40. Europe, W. Asia Minor, Crimea, N. Caucasus, Siberia, N. Central Asia, N. China, Mongolia.
 2. *D. cataonica* (Fleischm.) Holub, 1964, *Preslia*, 36,3:252.
 Basionym: *Orchis cataonica* Fleischm., 1914, *Ann. Naturh. Mus. (Wien)* 28:34.
 Asia Minor, Transcaucasia.
 3. *D. ochroleuca* (Wüstrn. ex Boll.) Holub, 1974, *Folia Geobot. Phyt. Tax.* 9,3:272.
 Basionym: *Orchis incarnata* L. var. *ochroleuca* Wüstrn. ex Boll., 1860, *Arch. Ver. Fr. Nat. Macklenb.* 14:307.
 Syn.: *Orchis incarnata* L. var. *straminea* Reichenb. f. ex Soó, 1933, in Keller et Schlechter, *Monogr. Icon. Orch. Europ. Mittelmeer.* 2,6-7:209.
 2n = 40. Central and N. Europe.
 4. *D. cruenta* (O. F. Müll.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
 Basionym: *Orchis cruenta* O. F. Müll., 1782, *Fl. Dan.* 5,15:4.
 Syn.: *Orchis haematodes* Reichenb., 1830, *Fl. Germ. Exc.*: 126.
 Orchis cruentiformis Neuman, 1909, *Bot. Not. (Lund)* 1909: 243.
 Orchis incarnata L. var. *hyphaematodes* Neuman, 1909, *Bot. Not. (Lund)* 1909:244.
 Orchis incarnata L. ssp. *guttata* Ugrinsky, 1911, *Tr. Obsch. Ispit. Prir. Chark. Univ.* 44:295.
 2n = 40. Central and N. Europe, Siberia.
 5. *D. coccinea* (Pugsley) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis latifolia* L. var. *coccinea* Pugsley, 1935, *J. Linn. Soc. London (Bot.)* 49,332:579.
 2n = 40. British Islands.
 6. *D. pulchella* (Druce) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis incarnata* L. var. *pulchella* Druce, 1918, *Rep. Bot. Exch. Club Brit. Isl.* 1918:167.
 British Islands.

^aThe term *Dactylorhiza*, introduced by Sergei Arsenievich Nevski (1908-1938) in 1937 as a generic name, was based on specimens of dactylorchids occurring in Europe (Necker, 1790). Therefore *Orchis incarnata* should be considered as the lectotype of the genus (Vermeulen, 1947; Smolyaninova, 1976), and not *Orchis umbrosa* (Farr, Leussink, Stafleu, 1979) which was the first dactylorchid known under the generic name *Dactylorhiza* (*Dactylorhiza umbrosa* Nevski, 1937).

Table 5-1. Continued.

7. *D. sphagnicola* (Höppn. ex Soó) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 6.
Basionym: *Orchis sphagnicola* Höppn. ex Soó, 1933, in Keller et Schlechter, *Monogr. Icon. Orch. Europ. Mittelmeer.* 2, 6-7:259.
W. Europe.
8. *D. gemmana* (Pugsley) Aver., 1984, *Bot. J.* 69:875.
Basionym: *Orchis latifolia* L. var. *gemmana* Pugsley, 1935, *Journ. Linn. Soc. London (Bot.)* 49, 332:578.
2n = 40. British Islands.
- 9-12. Aggregate *D. olocheilos*.
9. *D. olocheilos* (Boiss.) Aver., 1984, *Bot. J.* 69:875.
Basionym: *Orchis incarnata* L. var. *olocheilos* Boiss., 1884, *Fl. Orient.* 5:71.
Syn.: *Orchis orientalis* Klinge ssp. *cilicica* Klinge, 1898, *Dactylorh. Monogr. Prodr.*: 41.
Asia Minor.
10. *D. osmanica* (Klinge) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
Basionym: *Orchis orientalis* Klinge ssp. *osmanica* Klinge, *Dactylorh. Monogr. Prodr.*: 42.
Asia Minor.
11. *D. euxina* (Nevski) Czer., 1981, *Sosud. Rast. USSR*: 308.
Basionym: *Orchis euxina* Nevski, 1935, *Fl. USSR* 4:709.
Syn.: *Orchis cordigera* Fries var. *caucasica* Klinge ex Lipsky, 1897, *Acta Horti Petropol.* 14, 10:306, nom. nud.
Orchis monticola Klinge ssp. *caucasica* Klinge, 1898, *Dactylorh. Monogr. Prodr.*: 35.
Orchis caucasica (Klinge) Medwedev, 1919, *Tr. Tiflissk. Bot. Gard.* 18, 2:476, non Regel, 1869.
2n = 40. Caucasus, Transcaucasia.
12. *D. markowitschii* (Soó) Aver., 1983, *Bot. J.* 68:893.
Basionym: *Orchis caucasica* (Klinge) Medwedev var. *markowitschii* Soó, 1926, *Notizbl. Bot. Gart. Berlin* 9, 89:909.
Syn.: *Orchis caucasica* (Klinge) Medwedev var. *alpina* Schlechter, 1927, in Keller et Schlechter, *Monogr. Orch. Europ. Mittelmeer.* 1:173.
2n = 40. Caucasus, Transcaucasia.
- 13-15. Aggregate *D. sanasunitensis*.
13. *D. sanasunitensis* (Fleischm.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
Basionym: *Orchis sanasunitensis* Fleischm., 1914, *Ann. Naturh. Mus. (Wien)* 28:35.
Asia Minor.
14. *D. merovensis* (Grosheim) Aver., 1983, *Bot. J.* 68:894.
Basionym: *Orchis merovensis* Grosheim, 1928, *Beih. Bot. Centralbl.* 44:207.
Syn.: *Dactylorhiza umbrosa* (Kar. et Kir.) Nevski var. *longibracteata* Renz, 1978, *Fl. Iran.* 126:131.
2n = 40 [41]. Transcaucasia, N.-E. Turkey, N. Iran.
15. *D. chuhensis* Renz et Taub., 1984, *Fl. Turkey* 8:564.
Syn.: *Dactylorhiza renzii* Aver., 1983, *Bot. J.* 68:893, non H. Baumann et Künkele, 1981.
Transcaucasia, E. Turkey.
- 16-23. Aggregate *D. salina*.
16. *D. salina* (Turcz. ex Lindl.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
Basionym: *Orchis salina* Turcz. ex Lindl., 1835, *Gen. Sp. Orch. Pl.*: 259.
Syn.: *Orchis incarnata* L. var. *rhombilabia acroglossa* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:53.
2n = 40. E. Caucasus, E. Transcaucasia, N. Central Asia, S. Siberia, N. China, Mongolia.
17. *D. umbrosa* (Kar. et Kir.) Nevski, 1937, *Tr. Bot. Inst. Ac. Sci. USSR, Ser. 1*, 4:332.
Basionym: *Orchis umbrosa* Kar. et Kir., 1842, *Bull. Soc. Nat. Moscou* 15:504.
Syn.: *Orchis incarnata* L. var. *sesquipedalis altaica* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:53.
Orchis orientalis Klinge ssp. *turcestanica* Klinge, 1898, *Dactylorh. Monogr. Prodr.*: 37.
Orchis persica Schlechter, 1918, *Feddes Repert.* 15:290.
Orchis hatagirea Don var. *afganica* Soó, *J. Bot. (London)* 66:17.
Orchis altaica (Reichenb. f.) Soó, 1933, in Keller et Schlechter, *Monogr. Icon. Orch. Europ. Mittelmeer.* 2, 6-7:214.
2n = 40. Iran, Afghanistan, Pakistan, Central Asia, S. Siberia, N. China, Mongolia.
18. *D. kotschyi* (Reichenb. f.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
Basionym: *Orchis incarnata* L. var. *kotschyi* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:53.
Syn.: *Orchis incarnata* L. var. *knorringiana* Kraenzl., 1931, *Feddes Repert. (Beih.)* 65:34.
2n = 40. Iran, Afghanistan, Pakistan, Central Asia, S. Siberia, N.-W. China, Mongolia.
19. *D. magna* (Czerniak.) Iconn., 1972, *Nov. Syst. Visch. Rast.* 9:303.
Basionym: *Orchis magna* Czerniak., 1941, *Fl. Uzbek.* 1:528, 546.
Afghanistan, Pakistan, Central Asia.
20. *D. baldshuanica* Czerniak. ex Aver., 1983, *Bot. J.* 68:534.
Tadjikistan.
21. *D. czerniakowskiae* Aver., 1983, *Bot. J.* 68:536.
N.-E. Afghanistan, N. Pakistan, S.-E. USSR (Middle Asia), N.-W. China.
22. *D. kafiriana* Renz, 1978, *Fl. Iran.* 126:125.
N.-E. Afghanistan, N. Pakistan.
23. *D. kulikalonica* Czerniak. ex Aver., 1983, *Bot. J.* 68:535.
2n = 40. N.-E. Afghanistan, N. Pakistan, S.-E. USSR (Middle Asia), N.-W. China.
- 24-25. Aggregate *D. hatagirea*.

24. *D. hatagirea* (Don) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
 Basionym: *Orchis hatagirea* Don, 1825, *Prodr. Fl. Nepal.*: 23.
 Syn.: *Orchis latifolia* L. var. *indica* Lindl., 1835, *Gen. Sp. Orch. Pl.*: 260.
 E. Pakistan, N. India, Nepal, S.-W. China, Bhutan.
25. *D. graggeriana* (Soó) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
 Basionym: *Orchis graggeriana* Soó, 1928, *J. Bot. (London)* 66:15.
 N. India.
26. *D. affinis* (C. Koch) Aver., 1983, *Bot. J.* 68:895.
 Basionym: *Orchis affinis* C. Koch, 1849, *Linnaea* 22:284.
 Asia Minor, Transcaucasia.
- Subsection 2. *Maculatae* (Parl.) Aver., 1983, *Bot. J.* 68:1160.
 Type: *D. maculata* (L.) Soó (*Orchis maculata* L.).
- 27–30. Aggregate *D. saccifera*.
27. *D. triphylla* (C. Koch) Czer., 1981, *Sosud. Rast. USSR*: 309.
 Basionym: *Orchis triphylla* C. Koch, 1849, *Linnaea* 22:283.
 Syn.: *Orchis basilica* L. ssp. *cartaliniae* Klinge, 1898, *Dactylorch. Monogr. Prodr.*: 50, p.p.
Orchis amblyoloba Nevski, 1935, *Fl. USSR* 4:707.
 2n = 80. Asia Minor, Caucasus, Transcaucasia.
28. *D. urvilleana* (Steudel) Baumann et Kuenkele, 1981, *Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ.* 13:240.
 Basionym: *Orchis urvilleana* Steudel, 1841, *Nomencl.* 2ed., 2:225.
 Syn.: *Orchis saccata* d'Urv., 1822, *Pl. Ins. Ponti Eus.*: 119, non Ten., 1811.
Orchis lancibracteata C. Koch, 1849, *Linnaea* 22:284.
Orchis basilica L. ssp. *cartaliniae* Klinge, 1898, *Dactylorch. Monogr. Prodr.*: 50, p.p.
Orchis maculata L. var. *brotheri* Somm. et Lev. 1900, *Acta Horti Petropol.* 16:419.
Orchis pontica Fleischm. et Handel-Mazzetti, 1909, *Ann. Naturh. Mus. (Wien)* 23, 1–2:208.
 2n = 80. Asia Minor, Iran, Caucasus, Transcaucasia.
29. *D. nieschalkiorum* H. Baumann et Kuenkele, 1981, *Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ.* 13:259.
 N.-W. Turkey.
30. *D. saccifera* (Brongn.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 8.
 Basionym: *Orchis saccifera* Brongn., 1832, in Bory, *Exp. Scient. Moree* 3,2:259.
 Syn.: *Orchis tetragona* Heuffel, 1933, *Fl. Oder Allgem. Bot. Zeit.* 23:363.
Orchis macedonica Griseb., 1841, *Reise Rumel.* 2:219, 302, nom. nud.
Orchis macrostachys Tineo, 1846, *Pl. Rar. Sic.*: 7.
Orchis maculata L. var. *cartalinoides* Klinge ex Fleischm., 1908, *Mitt. Nat. Ver. Steierm.* 45:176.
 2n = 40, 80 [42]. S. Europe, Asia Minor, Syria, Lebanon.
31. *D. foliosa* (Soland.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 7.
 Basionym: *Orchis foliosa* Soland., 1831, in Lowe, *Trans. Cambr. Phil. Soc.* 4:13.
 2n = 40. Madeira Islands.
- 32–35. Aggregate *D. fuchsii*.
32. *D. fuchsii* (Druce) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 8.
 Basionym: *Orchis fuchsii* Druce, 1914, *Rep. Bot. Exch. Club Brit. Isl.* 4:105.
 Syn.: *Orchis maculata* L. var. *obscura* Neuman, 1909, *Bot. Not. (Lund)* 1909:152.
 2n = 40. Europe, Siberia, N.-W. China, Mongolia.
33. *D. okellyi* (Druce) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis maculata* L. var. *Okellyi* Druce, 1909, *Irish Natur.*: 221.
 2n = 40. British Islands.
34. *D. hebridensis* (Wilmott) Aver., 1986, *Bot. J.* 71:92.
 Basionym: *Orchis hebridensis* Wilmott, 1939, *J. Bot. (London)* 77:192.
 Syn.: *Orchis maculata* L. var. *meyeri* Reichenb. f., 1851, *Icon. Fl. Germ.* 13–14:67.
Orchis fuchsii Druce ssp. *rhoumensis* H.-Harrison f., 1949, *Trans. Proc. Bot. Soc. Edinburg* 35,1:53.
 2n = 40 [41, 80]. Europe, Siberia, Mongolia.
35. *D. psychrophila* (Schlechter) Aver., 1982, *Bot. J.* 67:308.
 Basionym: *Orchis maculata* L. var. *psychrophila* Schlechter, 1927, in Keller et Schlechter, *Monogr. Icon. Orch. Europ. Mittelmeer.* 1:183.
 2n = 40 [41]. N. Europe, Siberia (mountains).
- 36–44. Aggregate *D. maculata*.
36. *D. maculata* (L.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 7.
 Basionym: *Orchis maculata* L., 1753, *Sp. Pl.*: 942.
 Syn.: *Orchis candidissima* Krocke, 1814, *Fl. Siles.*: 16.
Orchis angustifolia Krocke, 1814, *Fl. Siles.*: 16.
 2n = 80 [78, 100, 120]. Europe, W. Siberia.
37. *D. maurusia* (Emberger et Maire) Holub, 1973, *Folia Geobot. Phyt. Tax.* 8, 2:176.
 Basionym: *Orchis maurusia* Emberger et Maire, 1931, *Bull. Soc. Sci. Natur. Maroc.* 11, 4–6:109.
 Syn.: *Orchis maculata* L. ssp. *aborica* Maire et Weiller., 1959, in Maire, *Fl. Afr. Nord.* 6:309.
 N. Africa (Atlas Mountains).
38. *D. elodes* (Griseb.) Aver., 1982, *Bot. J.* 67:309.
 Basionym: *Orchis elodes* Griseb., 1846, *Über Bildung Torfs*: 25.
 2n = 80 [40]. Europe.

Table 5-1. Continued.

39. *D. schurii* (Klinge) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis angustifolia* Reichenb. var. *recurva* Klinge f. *schurii* Klinge, 1893, *Revis. Orch. cord. Orch. angustif.*: 83.
 E. Europe (Carpathian Mountains).
40. *D. transsilvanica* (Schur) Aver., 1982, *Bot. J.* 67:309.
 Basionym: *Orchis transsilvanica* Schur, 1866, *Enum. Pl. Transsilv.*: 643.
 E. Europe (Carpathian Mountains).
41. *D. ericetorum* (Linton) Aver., 1982, *Bot. J.* 67:309.
 Basionym: *Orchis maculata* L. ssp. *ericetorum* Linton, 1900, *Fl. Bournemouth*: 208.
 2n = 80. Central and N. Europe.
42. *D. sudetica* (Poch ex Reichenb. f.) Aver., 1982, *Bot. J.* 67:310.
 Basionym: *Orchis maculata* L. var. *sudetica* Poch ex Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:66.
 Syn.: *Orchis maculata* L. var. *praecox* Webster, 1886, *Brit. Orch.*: 54.
Orchis maculata L. var. *pumila* Neuman, 1909, *Bot. Not. (Lund)* 1909:245.
 2n = 80. Central and N. Europe, N.-W. Siberia.
43. *D. kolaënsis* (Montell) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis maculata* L. var. *kolaënsis* Montell, 1947, *Mem. Soc. Fauna Fl. Fenn.* 23:166.
 Syn.: *Dactylorchis maculata* (L.) Vermeulen ssp. *montellii* Vermeulen, 1947, *Stud. Dactylorch.*: 141.
 N. Europe.
44. *D. islandica* (A. Löve et D. Löve) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Dactylorchis maculata* (L.) Vermeulen ssp. *islandica* A. Löve et D. Löve, 1948, *Chrom. numb. North. Pl. Sp.*: 106.
 2n = 80. Iceland.
- Subsection 3. *Latifoliae* (Reichenb. f.) Aver., 1983, *Bot. J.* 68:1162.
 Type: *D. majalis* (Reichenb.) P. F. Hunt et Summerhayes (*Orchis majalis* Reichenb.).
- 45-49. Aggregate *D. majalis*.
45. *D. majalis* (Reichenb.) P. F. Hunt et Summerhayes, 1965, *Watsonia* 6,2:130.
 Basionym: *Orchis majalis* Reichenb., 1828, *Icon. Bot. Pl. Crit.*, 6,7:7.
 Syn.: *Orchis latifolia* L., 1753, *Sp. Pl.*: 941, p.p., nom. confus.
Orchis comosa Scop., 1772, *Fl. Carn.* 2:198, nom. illeg.
Orchis fistulosa Moench, 1794, *Meth. Pl. Horti Marburg.*: 713, nom. illeg.
 2n = 80. Central and N. Europe.
46. *D. kerryensis* (Wilmott) P. F. Hunt et Summerhayes, 1965, *Watsonia* 6,2:131.
 Basionym: *Orchis kerryensis* Wilmott, 1936, *Proc. Linn. Soc. London* 148:126.
 Syn.: *Orchis majalis* Reichenb. var. *occidentalis* Pugsley, 1935, *Journ. Linn. Soc. London (Bot.)* 49, 332:586.
 2n = 80. British Islands.
47. *D. cambrensis* (Roberts) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Dactylorchis majalis* (Reichenb.) Vermeulen ssp. *cambrensis* Roberts, 1961, *Watsonia* 5,1:41.
 2n = 80. British Islands.
48. *D. purpurella* (T. Stephenson et T. A. Stephenson) Soó, 1962, *Nom. Nov. Gen. Dactylorch.*: 5.
 Basionym: *Orchis purpurella* T. Stephenson et T. A. Stephenson, 1920, *J. Bot. (London)* 58:164.
 Syn.: *Orchis praetermissa* Druce var. *pulchella* Druce, 1920, *Rep. Bot. Exch. Club Brit. Isl.* 5:577.
 2n = 80. N.-W. Europe.
49. *D. alpestris* (Pugsley) Aver., 1983, *Bot. J.* 68:1164.
 Basionym: *Orchis alpestris* Pugsley, 1935, *J. Linn. Soc. London (Bot.)* 49, 332:587.
 Syn.: *Orchis cordigera* Fries ssp. *sicolorum* Soó, 1927, *Feddes Repert.* 24:31.
Dactylorchis majalis (Reichenb.) Vermeulen var. *alpestroides* Vermeulen, 1949, *Nederl. Kruidk. Arch.* 56:215.
 Europe.
- 50-51. Aggregate *D. integrata*.
50. *D. integrata* (E. G. Camus) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis incarnata* L. var. *integrata* E. G. Camus, 1891, in Fourcy, *Vadem. Herb. Paris* ed. 6:325.
 Syn.: *Orchis integrata* (E. G. Camus) E. G. Camus, 1892, *Monogr. Orch. Fr.*: 48.
Orchis praetermissa Druce, 1913, *Rep. Bot. Exch. Club Brit. Isl.* 3:341.
 2n = 80. N.-W. Europe.
51. *D. longifolia* (Neuman) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis longifolia* Neuman, 1909, *Bot. Not. (Lund)* 1909:241.
 Syn.: *Orchis latifolia* L. var. *dunensis* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:59, non Druce, 1917.
Orchis latifolia L. ssp. *baltica* Klinge, 1898, *Dactylorch. Monogr. Prodr.*: 24.
 2n = 80. Central and N. Europe, Siberia, N. Central Asia, N.-W. China.
- 52-54. Aggregate *D. cordigera*.
52. *D. bosniaca* (G. Beck) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis bosniaca* G. Beck, 1887, *Ann. Naturh. Mus. (Wien)* 2:53.
 Syn.: *Orchis latifolia* L. var. *lagotis* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:58.
Orchis latifolia L. var. *rochelii* Grisebach et Schenk, 1852, *Arch. Naturg. (Berlin)* 18,1:355.
 S.-E. Europe (Carpathian and Balkan Mountains).
53. *D. cordigera* (Fries) Soó, 1962, *Nom. Nov. Gen. Dactylorch.*: 5.
 Basionym: *Orchis cordigera* Fries, 1842, *Nov. Fl. Suec.* 3:130.
 Syn.: *Orchis latifolia* L. var. *conica* Lindl., 1935, *Gen. Sp. Orch. Pl.*: 260.
Orchis rivularis Heuff. ex Schur., 1866, *Enum. Pl. Transsilv.*: 642.
 2n = 80. E. Europe (Carpathian Mountains).

54. *D. pseudocordigera* (Neuman) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 4.
 Basionym: *Orchis pseudocordigera* Neuman, 1909, *Bot. Not. (Lund)* 1909:236.
 Syn.: *Orchis latifolia* L. var. *conica* Blyttii Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:60.
 N. Europe (Scandinavian Peninsula).
- 55-60. Aggregate *D. traunsteineri*.
55. *D. traunsteineri* (Saut.) Soó, *Nom. Nov. Gen. Dactylorh.*: 5.
 Basionym: *Orchis traunsteineri* Saut., 1837, *Fl. Regensb.* 20, 1 Beibl. 3:36.
 Syn.: *Orchis angustifolia* Lois. ex Reichenb., 1831, *Icon. Bot. Pl. Crit.* 9:17, non Bieb., 1808, nec Wimm. et Grab., 1829.
Orchis latifolia L. var. *eborensis* Godfery, 1933, *Monogr. Icon. Nat. Brit. Orch.*: 166, 219.
Orchis majalis Reichenb. ssp. *traunsteinerioides* Pugsley, 1936, *Proc. Linn. Soc. London* 148:124.
 2n = 80. Central and N. Europe, Urals.
56. *D. francis-drucei* (Wilmott) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis francis-drucei* Wilmott, 1936, *Proc. Linn. Soc. London* 148:128.
 Scotland, Hebrides.
57. *D. russowii* (Klinge) Holub, 1964, *Preslia* 36,3:253.
 Basionym: *Orchis angustifolia* Lois. ex Reichenb. var. *russowii* Klinge, 1893, *Revis. Orch. cord. Orch. angustif.*: 84.
 Syn.: *Dactylorhiza deweveri* Vermeulen, 1949, *Nederl. Kruidk. Arch.* 56:227.
 2n = 80 [120, 122]. Central and N. Europe, Siberia.
58. *D. curvifolia* (Nyl.) Czer., 1981, *Sosud. Rast. USSR*: 307.
 Basionym: *Orchis curvifolia* Nyl., 1844, *Spicil. Pl. Fenn.* 2:12.
 Syn.: *Orchis recurva* Nyl. ex Fries, 1846, *Summa Veget. Scand.* 1:61, nom. nud.
Orchis angustifolia Lois. ex Reichenb. var. *recurva* Klinge, 1893, *Revis. Orch. cord. Orch. angustif.*: 82.
 2n = 80. Central and N. Europe.
59. *D. pycnantha* (Neuman) Aver., 1983, *Bot. J.* 68:1163.
 Basionym: *Orchis angustifolia* Lois. ex Reichenb. ssp. *pycnantha* Neuman, 1909, *Bot. Not. (Lund)* 1909:232.
 Syn.: *Orchis angustifolia* Lois. ex Reichenb. var. *Blyttii* Klinge, 1893, *Revis. Orch. cord. Orch. angustif.*: 79.
 2n = 80. N. Europe.
60. *D. lapponica* (Laest.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 5.
 Basionym: *Orchis angustifolia* Krockner var. *lapponica* Laest., 1843, in Hartm., *Skand. Fl.* 4:281.
 Syn.: *Orchis latifolia* L. var. *lapponica* Laest. ex Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:58.
Orchis angustifolia Lois. var. *pusilla* Neuman, 1909, *Bot. Not. (Lund)* 1909:233.
 N. Europe.
- Subsection 4. *Sesquipedales* (Vermeulen) Aver., 1983, *Bot. J.* 68:895.
 Type: *D. elata* (Poir.) Soó (*Orchis elata* Poir.).
- 61-64. Aggregate *D. elata*.
61. *D. durandii* (Boiss. et Reut.) M. Lainz., 1971, *Aport. Conocim. Fl. Gallega* 7:31.
 Basionym: *Orchis durandii* Boiss. et Reut., 1852, *Pugill. Pl. Nov.*: 111.
 Syn.: *Orchis orientalis* Klinge ssp. *africana* Klinge, 1898, *Dactylorh. Monogr. Prodr.*: 40.
 S.-W. Europe, N.-W. Africa.
62. *D. munbyana* (Boiss. et Reut.) Holub, 1981, *Folia Geobot. Phytotax* 19, 2:214.
 Basionym: *Orchis munbyana* Boiss. et Reut., 1852, *Pugill. Pl. Nov.*: 112.
 Syn.: *Orchis incarnata* L. var. *foliosa* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:52.
 2n = 80. S.-W. Europe, N.-W. Africa.
63. *D. elata* (Poir.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 7.
 Basionym: *Orchis elata* Poir., 1789, *Voy. Barb.* 2:248.
 Syn.: *Orchis incarnata* L. var. *sesquipedalis algerica* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:53.
Orchis latifolia L. var. *elatior* Afz. ex Batt. et Trab., 1884, *Fl. Alger.*: 196.
Orchis sesquipedalis Willd. var. *algerica* Briq., 1910, *Prodr. Fl. Corse* 1:169.
 2n = 80. N. Africa, Sicily.
64. *D. sesquipedalis* (Willd.) M. Lainz, 1971, *Aport. Conocim. Fl. Gallega* 7:31.
 Basionym: *Orchis sesquipedalis* Willd., 1805, *Sp. Pl.* 4:30.
 Syn.: *Orchis lusitanica* Steudel, 1841, *Nomencl. Bot.* 2ed. 2:224.
Orchis incarnata L. var. *sesquipedalis genuina* Reichenb. f., 1851, *Icon. Fl. Germ.* 13-14:53.
Orchis latifolia L. var. *corsica* Reverchom ex E. G. Camus, 1892, *Monogr. Orch. Fr.*: 158.
Orchis elata Poir. ssp. *ambigua* Mart.-Donos ex Soó, 1927, *Feddes Repert.* 24:31.
 S.-W. Europe.
- Section 2. *Aristate* Aver., 1983, *Bot. J.* 68:895.
65. *D. aristata* (Fisch. ex Lindl.) Soó, *Nom. Nov. Gen. Dactylorh.*: 5.
 Basionym: *Orchis aristata* Fisch. ex Lindl., 1835, *Gen. Sp. Orch. Pl.*: 262.
 Syn.: *Orchis latifolia* L. var. *beeringiana* Chamisso, 1828, in Chamisso et Schlechter, *Linnaea* 3:26.
 2n = 40,42. Korea, Japan, Kuril and Aleutian Islands, S. Sakhalin, S. Kamchatka, W. Alaska.
- Section 3. *Sambucinae* (Parl.) Smoljian., 1976, *Fl. Europ. Czasti USSR* 2:52.
 Type: *D. sambucina* (L.) Soó (*Orchis sambucina* L.).
- 66-67. Aggregate *D. sambucina*.
66. *D. sambucina* (L.) Soó, 1962, *Nom. Nov. Gen. Dactylorh.*: 3.
 Basionym: *Orchis sambucina* L., 1755, *Fl. Suec.* 2ed.:312.
 2n = 40,42. Central Europe.

Table 5-1. Continued.

67. *D. fasciculata* (Tin. in Guss.) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis fasciculata* Tin. in Guss., 1844, *Fl. Siculae Synops.* 2,2:875.
 Syn.: *Orchis insularis* Sommier, 1895, *Bull. Soc. Bot. Ital.*: 247.
 S. Europe.
- 68–74. Aggregate *D. sulphurea*.
68. *D. sulphurea* (Link) Franko, 1978, *J. Linn. Soc. London (Bot.)* 76,4:366.
 Basionym: *Orchis sulphurea* Link, 1806, in Schrader, *Neues Journ. Bot. (Schrad.)* 1,3:132.
 S.-W. Europe.
69. *D. sicula* (Tin. ex Reichenb. f.) Aver., 1984, *Bot. J.* 69:875.
 Basionym: *Orchis sicula* Tin. ex Reichenb. f., 1851, *Icon. Fl. Germ.* 13–14:63.
 Syn.: *Orchis markusii* Tin. ex Reichenb. f., 1851, *Icon. Fl. Germ.* 13–14:63.
Orchis mediterranea Klinge ssp. *siciliensis* Klinge, 1898, *Dactylorch. Monogr. Prodr.*: 19.
 S. Europe.
70. *D. bartonii* (Huxley et P. F. Hunt) Aver., 1984, *Bot. J.* 69:876.
 Basionym: *Dactylorhiza romana* (Seb.) Soó ssp. *bartonii* Huxley et P. F. Hunt, 1967, *J. Roy. Hort. Soc. (London)* 92,7:309.
 E. Spain.
71. *D. flavescens* (C. Koch) Holub, 1976, *Folia Geobot. Phytotax.* 11,1:83.
 Basionym: *Orchis flavescens* C. Koch, 1849, *Linnaea*, 22:281.
 Syn.: *Orchis tenuifolia* C. Koch, 1849, *Linnaea*, 22:281.
Orchis mediterranea Klinge ssp. *georgica* Klinge, 1898, *Dactylorch. Monogr. Prodr.*: 20.
 2n = 42. E. Asia Minor, Caucasus, Transcaucasia, Iran, E. Central Asia (Kopetdag Mountains).
72. *D. ruprechtii* Aver., 1983, *Bot. J.* 68:537.
 Caucasus, Transcaucasia.
73. *D. romana* (Seb.) Soó, 1962, *Nom. Nov. Gen. Dactylorch.*: 3.
 Basionym: *Orchis romana* Seb., 1813, *Pl. Rom.* 1:12.
 Syn. *Orchis pseudosambucina* Ten., 1815, *Syn. Nov. Pl.* 1ed:72.
 S. Europe, Crimea, W. Asia Minor, Syria, Lebanon, Cyprus.
74. *D. libanotica* (Mouterde) Aver., 1984, *Bot. J.* 69:876.
 Basionym: *Orchis romana* Seb. ssp. *libanotica* Mouterde, 1966, *Nouv. Fl. Liban, Syrie* 1:342.
 Section 4. *Iberanthus* (Schlechter) Smoljjan., 1976, *Fl. Europ. Czasti USSR* 2:51.
75. *D. iberica* (Bieb. ex Willd.) Soó, 1962, *Nom. Nov. Gen. Dactylorch.*: 3.
 Basionym: *Orchis iberica* Bieb. ex Willd., 1805, *Sp. Pl.* 4:25.
 Syn.: *Orchis angustifolia* Bieb., 1808, *Fl. Taur. Cauc.* 2:368.
Gymnadenia angustifolia Spreng., 1826, *Syst. Veg.* 3:693.
Orchis leptophylla C. Koch, 1849, *Linnaea* 22:282.
Orchis natolica Fisch. et Mey., 1854, *Ann. Sci. Nat. (Paris)* Ser. 4, 1:30.
 2n = 40. S.-E. Europe, Asia Minor, Lebanon, Syria, Crimea, Caucasus, Transcaucasia.

Taxonomy of the Genus *Dactylorhiza*

The name *Dactylorhiza* for dactylorchids was introduced in 1790 by N. J. Necker, but its use as a generic term for *Dactylorhiza* was established formally much later by S. A. Nevski (1937). Several elements of the dactylorchid taxonomy were established during the last 150 years by a number of authors (Reichenbach fil., 1851; Parlato, 1858; Schlechter, 1927). This taxonomy system was augmented subsequently by additional authors (Nevski, 1935; Pugsley, 1935; Vermeulen, 1947; Heslop-Harrison, 1954; Soó, 1960; Nelson, 1976, 1979; Smolyaninova, 1976). The latest classification of the genus *Dactylorhiza* was formulated by Averyanov (1983a, b; Table 5-1). Groups of closely related species are combined in so-called "species-aggregates", the use of which was proposed by Heywood (Heywood, 1963). Modern data on karyology and distribution of species are given in Table 5-1.

In Fig. 5-11 a phylogenetic scheme of the genus *Dactylorhiza* is shown. It represents a cross-section of "the genealogical tree" at the modern stage (Averyanov, 1983b, c). Differences in karyotypes of species are shown with different shading.

Hypothetical historical interrelations of the main taxa of the genus are given in Fig. 5-12. The thickness of the trunks, which designate taxa, reflects the number of presently existing species (their number is indicated over the cuts of the corresponding trunks made at the modern stage of evolution of the genus).

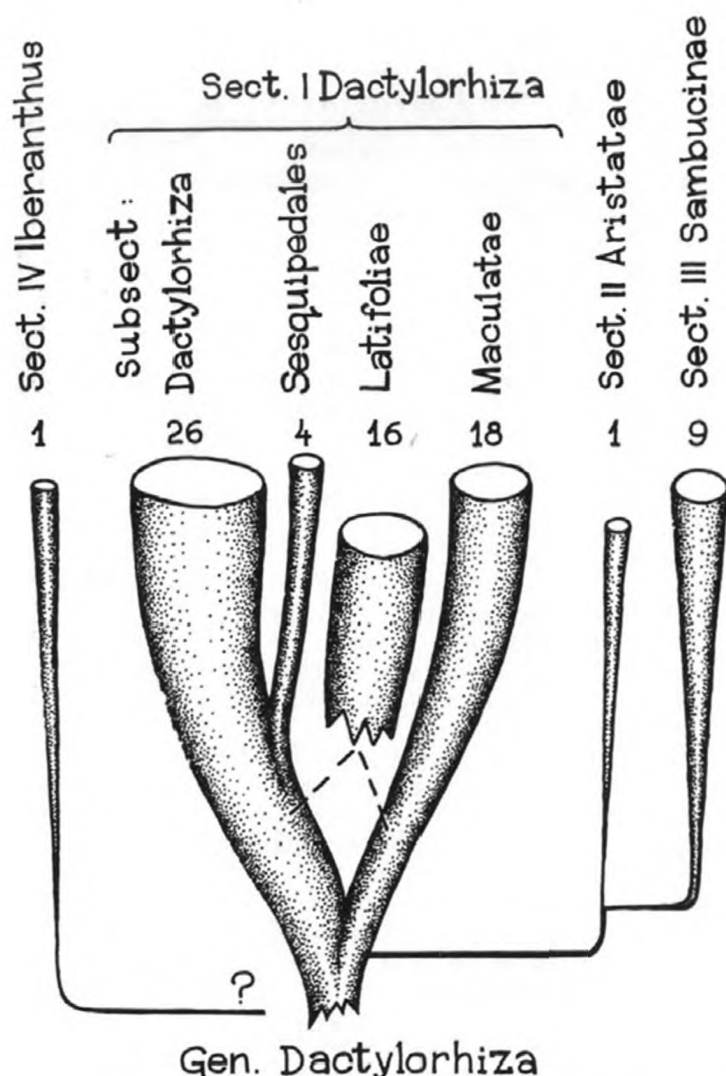


Fig. 5-12. Diagram of presumed historical interrelations of the main taxa of the genus *Dactylorhiza*. Thickness of the trunks designating taxa reflects their species richness (the number of presently existing species is marked above the cuts of the corresponding trunks).

Hybridization

Interspecific hybridization takes place very often in the genus *Dactylorhiza*. The data concerning hybrids among species of dactylorchids are given in numerous papers and several extensive reviews (Schlechter, 1927; Camus and Camus, 1928; Soó, 1933a, 1960, 1962; Dandy, 1958; Sundermann, 1975). According to some reports, hybrids may sometimes arise from more than two parent species^d. Many of the hybrids known at present have binominal names.

Hybrids among species of the type section (sect. *Dactylorhiza*) of the genus *Dactylorhiza* are most common. This section contains 141 pairs of species which hybridize relatively often with each other in nature. Hybrids which have binominal names are listed in Table 5-2. Hybridization among species of this section is outlined in Fig. 4-13.

Hybrids are often also observed within the section *Sambucinae*. Most species of this section are sympatric and form a large area of intogression. Known hybrids of these species are indicated in Table 5-3. Only one of them has a binominal name.

^dUnder cultivation, triple hybrids of the kind *D. foliosa* × *D. maculata* × *D. majalis* (= *D. hepburnii* (Druce) Soó) are known (Soó, 1960). In nature formation of such "triple" hybrids is possible only between closely related species which produce relatively fertile progeny.

Table 5-2. Natural interspecific hybrid names of dactylorchids in section *Dactylorhiza*.

- D. incarnata* × *D. cruenta* (= *D. × krylowii* (Soó) Soó).
D. incarnata × *D. saccifera* (= *D. × serbica* (Fleischm.) Soó).
D. incarnata × *D. nieschalkiorum* (= *D. × renzii* H. Baumann et Kuenkele).
D. incarnata × *D. fuchsii* (= *D. × kerneriorum* (Soó) Soó).
D. incarnata × *D. maculata* (= *D. × ambigua* (Kerner) Sundermann). Morphologically derived types: *D. × beckeriana* (Höppner) Soó; *D. × elatior* (Afz.) Soó; *D. × gracilis* (Höppner) Soó; *D. × hoeppneri* (A. Fuchs) Soó; *D. × koningweniana* (A. Fuchs) Soó; *D. × rhenana* (Höppner) Soó; *D. × rigida* (Höppner) Soó; *D. × ruthei* (Schulze) Soó; *D. × steegeri* (Höppner) Soó; *D. × surensis* (Gsell) Soó; *D. × wirtgenii* (Höppner) Soó.^a
D. incarnata × *D. elodes* (= *D. × carnea* (E. G. Camus) Soó).
D. incarnata × *D. schurii* (= *D. × claudiopolitana* (Simk.) Soó).
D. incarnata × *D. majalis* (= *D. × aschersoniana* (Hauskn.) Soó). Morphologically derived types: *D. × bavaria* (A. Fuchs) Soó; *D. × gennachiensis* (A. Fuchs) Soó; *D. × mulignensis* (Gsell) Soó; *D. × pseudotraunsteineri* (A. Fuchs) Soó; *D. × suevica* (A. Fuchs) Soó.
D. incarnata × *D. purpurella* (= *D. × latirella* (Hall) Soó).
D. incarnata × *D. alpestris* (= *D. × hochreutinerana* (Hellmayr) Aver.).
D. incarnata × *D. integrata* (= *D. × wintoni* (Druce) Soó).
D. incarnata × *D. longifolia* (= *D. × ishorica* Aver.).
D. incarnata × *D. traunsteineri* (= *D. × stenostachys* (J. Murr.) Rauschert). Morphologically derived types: *D. × flixensis* (Gsell) Soó; *D. × thellungiana* (Br.-Bl.) Soó.
D. incarnata × *D. russowii* (= *D. × lehmannii* (Klinge) Soó).
D. incarnata × *D. sesquipetalis* (= *D. × dubreuilhi* (Keller et Jeanjean) Soó).
D. ochroleuca × *D. majalis* (= *D. × templinensis* Potucek).
D. cruenta × *D. salina* (= *D. × baicalica* Aver.).
D. cruenta × *D. maculata* (= *D. × samnaunensis* (Gsell) Soó).
D. cruenta × *D. majalis* (= *D. × predaensis* (Gsell) Soó).
D. cruenta × *D. traunsteineri* (= *D. × engadinensis* (Ciferri et Giacomini) Soó).
D. coccinea × *D. hebridensis* (= *D. × variabilis* (Heslop-Harrison f.) Soó).
D. osmanica × *D. urvilleana* (= *D. × breviceras* Renz et Taub.).
D. osmanica × *D. umbrosa* (= *D. × nevskii* H. Baumann et Kuenkele).
D. euxina × *D. umbrosa* (= *D. × bayburtiana* H. Baumann).
D. euxina × *D. urvilleana* (= *D. × rizeana* Renz et Taub.).
D. umbrosa × *D. urvilleana* (= *D. × sivasiana* H. Baumann et Kuenkele).
D. nieschalkiorum × *D. saccifera* (= *D. × boluiana* H. Baumann).
D. fuchsii × *D. maculata* (= *D. × transiens* (Druce) Soó).
D. fuchsii × *D. majalis* (= *D. × braunii* (Halacsy) Borsos et Soó).
D. fuchsii × *D. purpurella* (= *D. × venusta* (T. Stephenson et T. A. Stephenson) Soó).
D. fuchsii × *D. integrata* (= *D. × mortonii* (Druce) Soó).
D. fuchsii × *D. traunsteineri* (= *D. × kelleriana* (Ciferri et Giacomini) Soó).
D. fuchsii × *D. russowii* (= *D. × megapolitana* (Bisse) Soó).
D. hebridensis × *D. maculata* (= *D. × komiensis* Aver.).
D. hebridensis × *D. ericetorum* (= *D. × corylensis* (Heslop-Harrison f.) Soó).
D. hebridensis × *D. purpurella* (= *D. × hebridella* (Wilmott) Soó).
D. maculata × *D. majalis* (= *D. × vermeuleniana* Soó). Morphologically derived type: *D. × eifliaca* (A. Fuchs) Soó.
D. maculata × *D. alpestris* (= *D. × czatoi* (Soó) Soó).
D. maculata × *D. integrata* (= *D. × batavica* Soó).
D. maculata × *D. traunsteineri* (= *D. × jenensis* (Brand-Soó)).
D. maculata × *D. sesquipetalis* (= *D. × delamainii* (Keller et Stephenson) Soó).
D. elodes × *D. majalis* (= *D. × nummiana* (P. Fournier) Soó). Morphologically derived types: *Orchis × danguyi* P. Fournier; *Orchis × guffroyi* P. Fournier.
D. elodes × *D. integrata* (= *D. × hallii* (Druce) Soó).
D. elodes × *D. durandii* (= *D. × stephensonii* Soó).
D. schurii × *D. cordigera* (= *D. × szaboiana* (Soó) Soó).
D. ericetorum × *D. majalis* (= *D. × townsendiana* (Rouy) Soó).
D. ericetorum × *D. kerryensis* (= *D. × dingleensis* (Wilmott) Soó).
D. ericetorum × *D. purpurella* (= *D. × formosa* (T. Stephenson et T. A. Stephenson) Soó).
D. ericetorum × *D. traunsteineri* (= *D. × robertsii* Aver.).
D. majalis × *D. integrata* (= *D. × godferyana* Soó).
D. majalis × *D. traunsteineri* (= *D. × dufftiana* (Schulze) Soó).
D. purpurella × *D. integrata* (= *D. × insignis* (T. Stephenson et T. A. Stephenson) Soó).
D. integrata × *D. longifolia* Morphologically derived type: *D. × pardalina* (Pugsley) Aver.

^aIt is possible that *D. majalis* also took part in the formation of these derivative types.

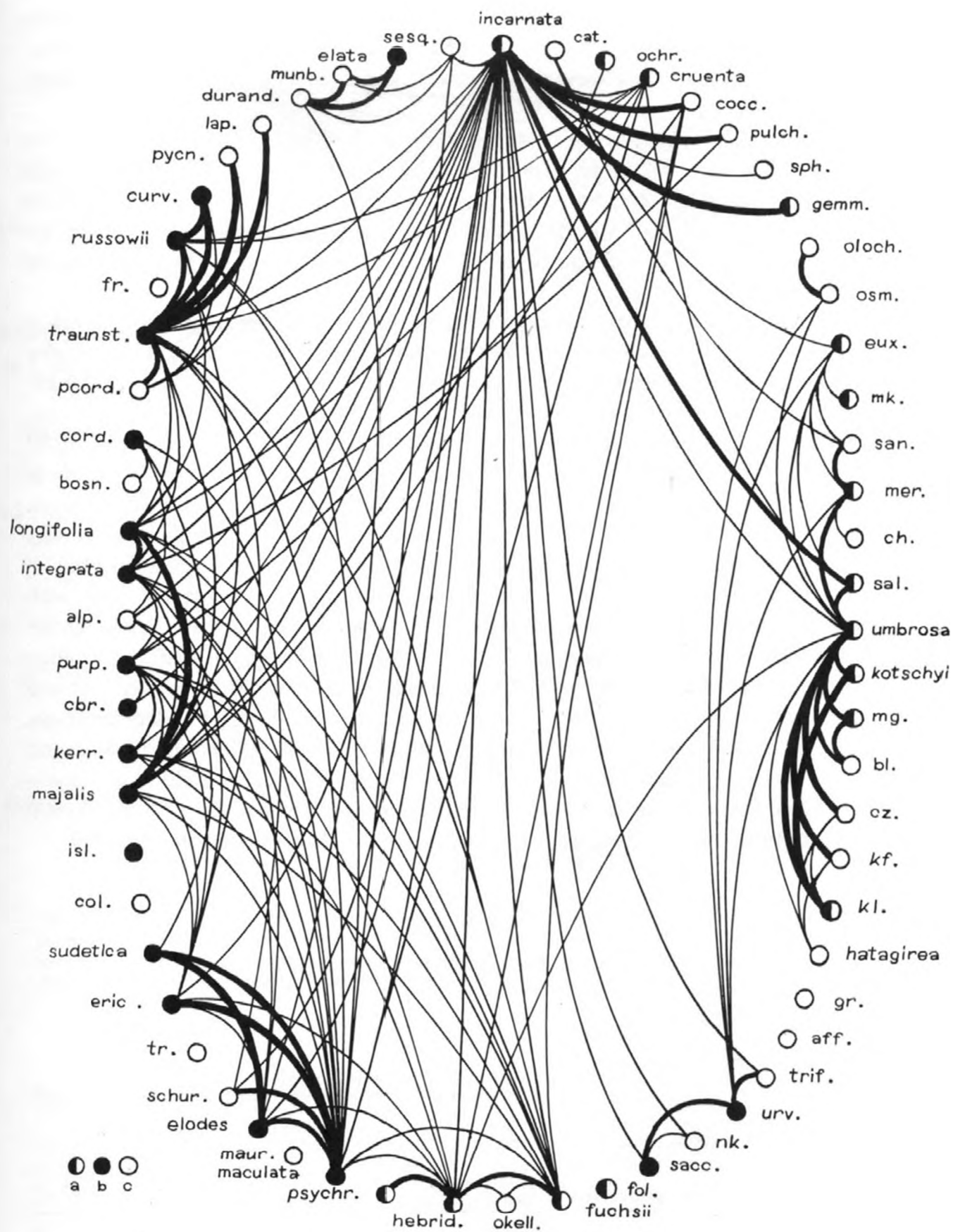


Fig. 5-13. Diagram of hybridization among species of the genus *Dactylorhiza*, section *Dactylorhiza*. Explanation of symbols: Species forming hybrids in nature are connected by lines (thin line, hybrids rare and sporadic; thick line, hybrids are numerous, sometimes form an introgression zone); a-diploid species ($2n=40$); b-tetraploid species ($2n=80$); c-species, the chromosome number of which is not yet known. Abbreviations of species names as in Fig. 5-11.

Intersectional hybrids of dactylorchids are considerably rarer and known only between species of sect. *Dactylorhiza* and those of the sections *Sambucinae* and *Iberanthus*. They occur in Europe and Asia Minor. All known hybrids of this type are listed in Table 5-4.

The formation of hybrids among several species of dactylorchids with very different genomes like *D. sambucina* ($2n=40, 42$) \times *D. maculata* ($2n=80$) \times *D. majalis* ($2n=80$) (= *D. x gabretana* (A. Fuchs) Soó, suggested by Soó (Soó, 1960, 1962), is highly unlikely in nature. Their presumed complex nature may have arisen due to morphologically different hybrid individuals produced by a cross between only two species of dactylorchids.

In nature dactylorchids hybridize relatively easily with species of related genera of the subtribe Orchidinae. Such hybrids have been reported often (Klinge, 1898; Fuchs, 1921; Stephenson and Stephenson, 1922; Soó, 1933a, b; Dahl, 1941; Dandy, 1958; Malmgren and Segelberg, 1965; Hylander, 1966; Garay and Sweet, 1966; Soó and Borsos, 1966; Danielsson, 1970; Schmid et al., 1974; Sundermann, 1975; Wennerberg, 1978; Ericsson, 1980; Schmid, 1980; Savelsberg, 1981). All known intergeneric hybrids of dactylorchids have generic names (Hunt and Summerhayes, 1965; Garay and Sweet, 1966, 1969; Soó and Borsos, 1966). The interbreeding of dactylorchids with closely related genera is presented in Fig. 5-14. Dactylorchids form the largest number of intergeneric hybrids with *Gymnadenia conopsea* (15 hybrids), considerably fewer—with *Coeloglossum viride* (5) and *Platanthera bifolia* (5), all of whose flowers have nectar. Dactylorchids hybridize relatively often with *Orchis* species which have similar ecology and may coexist with them in one habitat, specifically *O. laxiflora* (5), *O. palustris* (6) and *O. morio* (4). Hybrids with other genera are considerably rarer. Among the dactylorchids, the largest number of intergeneric hybrids involve the most widely distributed and common species, *D. maculata* (10). Hybrids involving other species include, *D. majalis* (9), *D. incarnata* (7) and the now endangered species *D. sambucina* (9). All known intergeneric hybrids of dactylorchids and their binomials are listed in Table 5-5.

Table 5-3. Natural interspecific hybrids of dactylorchids in the section *Sambucinae*.

<i>D. sambucina</i> \times <i>D. fasciculata</i>
<i>D. sambucina</i> \times <i>D. sulphurea</i>
<i>D. romana</i> \times <i>D. flavescens</i>
<i>D. flavescens</i> \times <i>D. ruprechtii</i>
<i>D. sambucina</i> \times <i>D. romana</i> (= <i>D. x rombucina</i> (Ciferri et Giacomini) Soó).

Table 5-4. Natural intrasectional hybrids of dactylorchids.

<i>D. sambucina</i> \times <i>D. incarnata</i> (= <i>D. x guillaumeae</i> B. Christian).
<i>D. sambucina</i> \times <i>D. fuchsii</i> (= <i>D. x influenza</i> (Sennholz) Soó).
<i>D. sambucina</i> \times <i>D. maculata</i> (= <i>D. x altobracensis</i> (Coste) Soó).
<i>D. sambucina</i> \times <i>D. majalis</i> (= <i>D. x rupperii</i> (Schulze) Soó).
<i>D. romana</i> \times <i>D. maculata</i> (= <i>D. x maculana</i> (Ciferri et Giacomini) Soó).
<i>D. iberica</i> \times <i>D. incarnata</i> (= <i>D. x vogtiana</i> H. Baumann).
<i>D. iberica</i> \times <i>D. nieschalkiorum</i> (= <i>D. x abantiana</i> H. Baumann et Kuenkele).
<i>D. iberica</i> \times <i>D. osmanica</i> .
<i>D. iberica</i> \times <i>D. saccifera</i> (= <i>D. x sultandagi</i> Renz et Taub.; <i>D. x gustavssonii</i> H. Baumann).
<i>D. iberica</i> \times <i>D. umbrosa</i> (= <i>D. x kopdagiana</i> H. Baumann).
<i>D. iberica</i> \times <i>D. urvilleana</i> (= <i>D. x balabiana</i> H. Baumann).

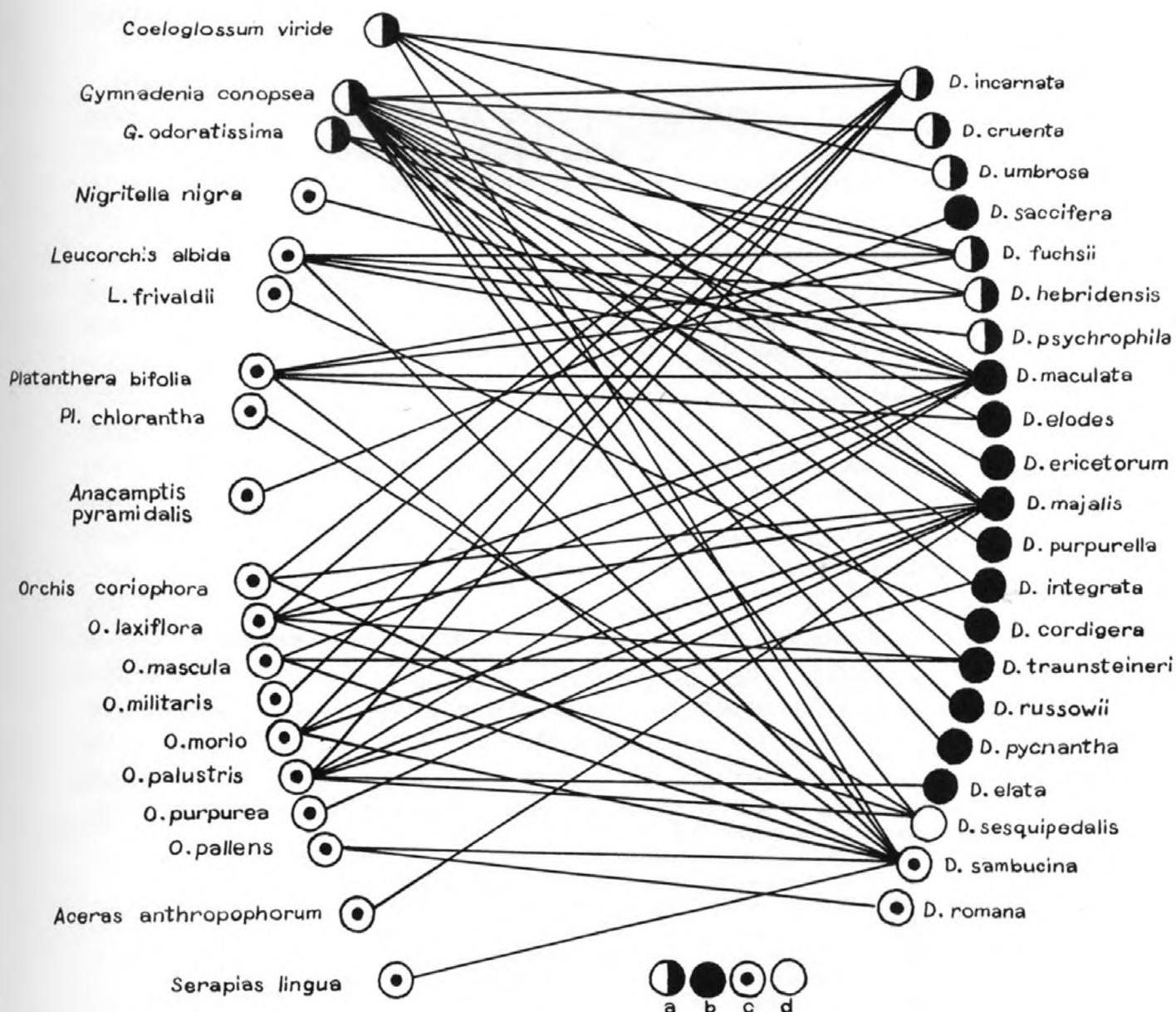


Fig. 5-14. Diagram of hybridization of dactylorchids with species of phylogenetically related orchid genera. Explanation of symbols: Species forming hybrids in nature are connected by lines; a, diploid species ($2n=40$); b, tetraploid species ($2n=80$); c, aneuploid species ($2n=36-42$); d, species, the chromosome number of which is not yet known.

Table 5-5. Natural intergeneric hybrids of dactylorchids.

<i>Dactylorhiza</i> × <i>Coeloglossum</i> C. Hartm. (= × <i>Dactyloglossum</i> P. F. Hunt et Summerhayes).
<i>Dactylorhiza incarnata</i> × <i>Coeloglossum viride</i> (L.) C. Hartm. (= × <i>Dactyloglossum guilhotii</i> (E. G. Camus) Soó).
<i>D. umbrosa</i> × <i>C. viride</i> (= × <i>D. turcestanicum</i> (C. Keller et Soó) Soó).
<i>D. maculata</i> × <i>C. viride</i> (= × <i>D. conigerum</i> (Norman) Rauschert).
<i>D. majalis</i> × <i>C. viride</i> (= × <i>D. drucei</i> (E. G. Camus) Soó).
<i>D. sambucina</i> × <i>C. viride</i> (= × <i>D. erdingeri</i> (Kerner) Janchen).
<i>Dactylorhiza</i> × <i>Gymnadenia</i> R. Br. (= × <i>Dactylodenia</i> Garay et Sweet).
<i>Dactylorhiza incarnata</i> × <i>Gymnadenia conopsea</i> (L.) R. Br. (= × <i>Dactylodenia vollmannii</i> (Schulze) Aver.).
<i>D. cruenta</i> × <i>G. conopsea</i> (= × <i>D. raetica</i> (Paroz et Reinhard) Peitz).
<i>D. fuchsii</i> × <i>G. conopsea</i> (= × <i>D. gracilis</i> (A. Camus) Aver.).
<i>D. fuchsii</i> × <i>G. odoratissima</i> (L.) Rich. (= × <i>D. lawalree</i> Dalforge et Tyteca).
<i>D. hebridensis</i> × <i>G. conopsea</i> .
<i>D. maculata</i> × <i>G. conopsea</i> (= × <i>D. heinzliana</i> (Reichardt) Aver.). Morphologically derived type: × <i>D. st. quintinii</i> (Godfery) Aver.
<i>D. maculata</i> × <i>G. odoratissima</i> (= × <i>D. regeliana</i> (Bruegger) Peitz).
<i>D. elodes</i> × <i>G. conopsea</i> (= × <i>D. souppensis</i> (E. G. Camus) Aver.).

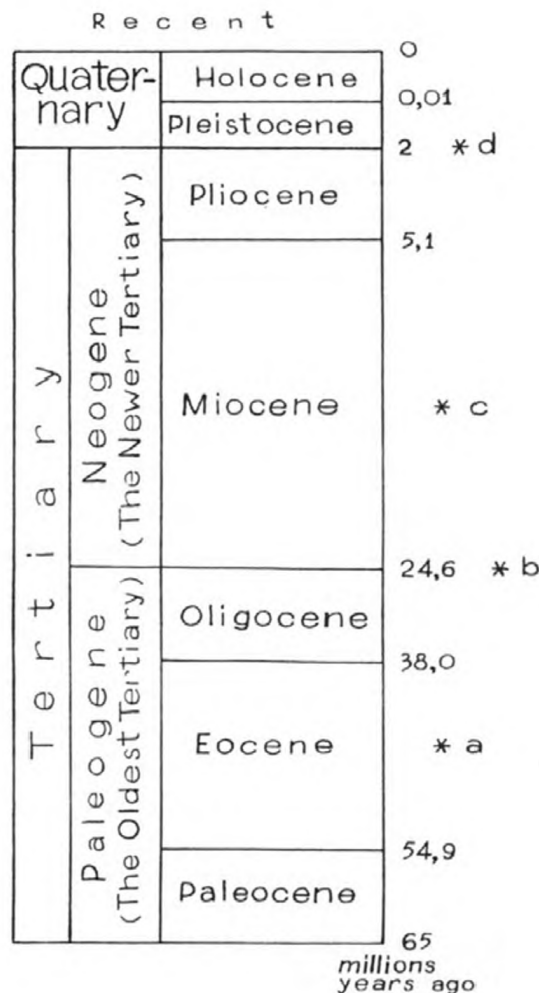
Table 5-5. Continued.

D. ericetorum × *G. conopsea* (= × *D. evansii* (Druce ex T. Stephenson et T. A. Stephenson) Aver.).
D. majalis × *G. conopsea* (= × *D. comigera* (Reichenb.) Aver.).
D. majalis × *G. odoratissima*.
D. purpurella × *G. conopsea* (= × *D. varia* (T. Stephenson et T. A. Stephenson) Aver.).
D. integrata × *G. conopsea* (= × *D. wintonii* (Druce) Aver.).
D. traunsteineri × *G. conopsea* (= × *D. fuchsii* (G. Keller et Soó) Aver.).
D. russowii × *G. conopsea* (= × *D. klingiana* (Aschers. et Graebn.) Aver.).
D. pycnantha × *G. conopsea*.
D. sesquipedalis × *G. conopsea* (= × *D. jeanjeanii* (G. Keller) Aver.).
D. sambucina × *G. conopsea* (= × *D. zollikoferi* (Stojan.) Peitz).
Dactylorhiza × *Nigritella* Rich. (= × *Dactylitella* P. F. Hunt et Summerhayes).
Dactylorhiza maculata × *Nigritella nigra* (L.) Rich. (= × *Dactylitella tourensis* (Godfery) Janchen).
Dactylorhiza × *Leucorchis* E. Mey. (= × *Dactyleucorchis* Soó).
Dactylorhiza fuchsii × *Leucorchis albida* (L.) E. Mey. (= × *Dactyleucorchis nieschalkii* Senghas).
D. psychrophila × *L. albida* (= × *D. nieschalkii* var. *minor* (Potucek) Kumpel).
D. maculata × *L. albida* (= × *D. bruniana* (Bruegger) Soó).
D. cordigera × *L. frivaldii* (Hampe ex Griseb.) Schlechter (= × *D. illyrica* Jahn et Kumpel).
D. sambucina × *L. albida* (= × *D. albucina* (Ciferri et Giacomini) Aver.).
Dactylorhiza × *Platanthera* Rich. (= × *Rhizantha* P. F. Hunt et Summerhayes).
Dactylorhiza fuchsii × *Platanthera bifolia* (L.) Rich.
D. hebridensis × *Pl. bifolia*.
D. maculata × *Pl. bifolia* (= × *Rh. somersetiensis* (A. Camus) Soó).
D. elodes × *Pl. bifolia* (= × *Rh. chevalleriana* (E. G. Camus) Soó).
D. sesquipedalis × *Pl. chlorantha* (Cust.) Reichenb. (= × *Rh. thilensis* (G. Keller et Jeanjean) Aver.).
D. sambucina × *Pl. bifolia* (= × *Rh. fournieri* (Royer) Soó).
Dactylorhiza × *Anacamptis* Rich. (= × *Dactylocamptis* P. F. Hunt et Summerhayes).
Dactylorhiza saccifera × *Anacamptis pyramidalis* (L.) Rich. (= × *Dactylocamptis weberi* (Schulze) Soó).
Dactylorhiza × *Orchis* L. (= × *Orchidactyla* P. F. Hunt et Summerhayes).
Dactylorhiza incarnata × *Orchis coriophora* L. (= × *Orchidactyla drucei* (Schulze) Borsos et Soó).
D. incarnata × *O. laxiflora* Lam. (= × *O. legueri* (E. G. Camus) Borsos et Soó).
D. incarnata × *O. militaris* L. (= × *O. jeanpertia* (E. G. Camus et Luis) Borsos et Soó).
D. incarnata × *O. morio* L. (= × *O. arborescens* (E. G. Camus) Borsos et Soó).
D. incarnata × *O. palustris* Jacq. (= × *O. uechtritziana* (Hausskn.) Borsos et Soó).
D. maculata × *O. laxiflora* (= × *O. valoni* (E. G. Camus) Borsos et Soó).
D. maculata × *O. mascula* L. (= × *O. pentecostalis* (Wettst. et Sennholz) Borsos et Soó).
D. maculata × *O. morio* (= × *O. timbaliana* (E. G. Camus) Borsos et Soó).
D. maculata × *O. palustris* (= × *O. neglecta* (E. G. Camus) Borsos et Soó).
D. majalis × *O. coriophora* (= × *O. sauzaiana* (E. G. Camus) Rauschert).
D. majalis × *O. laxiflora* (= × *O. chassagnei* (Alleizette) Borsos et Soó).
D. majalis × *O. morio* (= × *O. boudieri* (E. G. Camus) Borsos et Soó).
D. majalis × *O. palustris* (= × *O. rouyana* (E. G. Camus) Borsos et Soó).
D. majalis × *O. purpurea* Huds. (= × *O. questphalica* (Richter) Borsos et Soó).
D. integrata × *O. palustris* (= × *O. luizetiana* (E. G. Camus) Borsos et Soó).
D. traunsteineri × *O. laxiflora*.
D. traunsteineri × *O. mascula* (= × *O. masteyneri* (Ciferri et Giacomini) Aver.).
D. elata × *O. palustris* (= × *O. kabyliensis* (G. Keller) Aver.).
D. sesquipedalis × *O. laxiflora* (= × *O. aquitaniensis* (G. Keller et Jeanjean) Aver.).
D. sesquipedalis × *O. palustris* (= × *O. lamarquei* (G. Keller et Jeanjean) Aver.).
D. sambucina × *O. coriophora* (= × *O. carpetana* (Willk.) Borsos et Soó).
D. sambucina × *O. mascula* (= × *O. speciosissima* (Wettst. et Sennholz) Soó).
D. sambucina × *O. morio* (= × *O. luciae* (Royer) Borsos et Soó).
D. sambucina × *O. pallens* L. (= × *O. chenevardii* (Schulze) Borsos et Soó).
D. romana × *O. pallens* (= × *O. romanallens* (Ciferri et Giacomini) Aver.).
Dactylorhiza × *Aceras* R. Br. (= × *Dactyloceras* Garay et Sweet).
Dactylorhiza majalis × *Aceras anthropophorum* (L.) R. Br. (= × *Dactyloceras helveticum* (Ciferri et Giacomini) Garay et Sweet).
Dactylorhiza × *Serapias* L. (= × *Serapirhiza* Potucek).
Dactylorhiza sambucina × *Serapias lingua* L. (= × *Serapirhiza sambucino-lingua* (Barla) Garay et Sweet).

Fig. 5-15. The Kainozoic era subdivisions (Harland *et al.*, 1982). The principal events of this era mentioned in the text are marked with asterisks (the time is indicated very roughly): a, the existence of the ancient heat-loving flora (Poltava flora) which included in its composition the dactylorchids ancestors; b, Great Tertiary or Alpine earth-movements (Alpine orogenesis) which resulted in the elevation of most of the major mountain chains of the world, such as the Alps, Himalayas, Rockies and Andes; c, period of origin of the primary ancient dactylorchids species (it was in the Miocene period that the geography of Europe and Northern Asia began to assume its present day form); d, a period of intense coolings usually known as the Glacial period or the Great Ice age.

Natural History of the Genus *Dactylorchiza* and Its Species

It is supposed that the ancestors of dactylorchids were not very specialized terrestrial heat-loving orchids of the Poltava flora, which were widely distributed in the Paleogene. Their thickened specialized roots were not evolved yet and in outward appearance the plants resembled primitive species of *Epipactis* and *Cephalanthera* (Dressler and Dodson, 1960). Formation of primary dactylorchid species and related tuber forming orchids is associated with powerful mountain raisings (Alpine orogenesis) in what is modern Europe at the end of the Paleogene or early Neogene. The more severe climate of relatively high mountains and especially the increased seasonal fluctuations and the cooler temperatures lead to the formations of subterranean storage organs in the ancestral forms which were located in the plains. As a result of the cooling at the end of Neogene and in the Pleistocene, the climatic conditions in the plains became similar to the climate of the ancient high mountains. Under these conditions, early species of dactylorchids could occupy plains areas where the degradation of thermophilic tertiary flora was proceeding. Most dactylorchids and the related genera *Gymnadenia*, *Leucorchis* and *Coeloglossum* as well as their Paleogene ancestors remained primarily hydrophilous plants. All of them have relatively primitive palmate (finger-like) tubers. The formation of such tubers was a "preadaptation" to existence in drier and arid conditions. The adaptation to arid climate proved to be an evolutionary response to development of such conditions in the territories of the ancient Mediterranean basin and has resulted in the evolution of a number of highly specialized genera (*Orchis*, *Ophrys*, *Himantoglossum*, *Aceras*, *Anacamptis*, *Comperia*, *Serapias*, *Steveniella* and *Traunsteinera*; Averyanov, 1983a, c).



The direct ancestors of the genus *Dactylorhiza* were in existence toward the end of Paleogene and inhabited a vast area. Growth of mountains during the Alpine orogenesis in Eurasia led to the simultaneous formation of dactylorchids in a large area. Formation of the primary species of this genus occurred in the large mountain regions of modern Europe, Asia Minor, the Caucasus, Middle and Central Asia and, possibly, also those of North Africa (Fig. 5-16).

Later, as a result of Pleistocene cooling of the climate, a mass occupation of the plains of Europe and subsequently also of temperate Asia by species of dactylorchids took place. These species were formed originally in mountain ranges. The climatic changes during the Pleistocene are responsible for migrations of *Dactylorhiza* species and this contributed to hybridization and speciation. Periodically the most hydrophilous species of the genus (Sect. *Dactylorhiza*) expanded their territories considerably and after the disappearance of the glaciers they occupied habitats which were most similar to the habitats of the high mountains (Fig. 5-16). However, during the xerothermic maxima of the interglacial periods, their territories diminished to some extent. Extinction took place in regions subjected to especially severe aridization in the south of Siberia and north of Middle Asia. These facts can explain the disjunctions in the distribution of some present species. Several species, however, could adapt to life under the rather arid conditions of the ancient Mediterranean basin (Sect. *Sambucinae* and *Iberanthus*) owing to the formation of more specialized cylindrical, scarcely palmate tubers.

At present the genus *Dactylorhiza* comprises 75 species.

Section 1. *Dactylorhiza*.

The largest section contains 64 of the most primitive species, which were originally hydrophilous. This section covers the largest geographical area coinciding in general with the present distribution of the genus (Fig. 5-17).

Subsection I. *Dactylorhiza*.

This subsection includes 26 species. Its distribution coincides with that of the type section (except for North Africa and the region beyond the polar circle). All species are of mountainous origins. Some authors (Nelson, 1976, 1979) separate them in two series—Ser. *Dactylorhiza* (=Ser. *Septentrionales* Nelson nom.invalid^e) and Ser. *Orientalis* Nelson.

1–8. Aggregate *D. incarnata*.

The species of this aggregate, particularly *D. incarnata* and *D. cataonoca* have many characters which make them the most primitive in the genus.

The main species of the aggregate, *D. incarnata*, originated in Europe and is now found throughout this continent, Siberia, Crimea, the Northern Caucasus, Northern Central Asia, China and Mongolia. A number of its southern populations (Crimea, North Caucasus etc.) are presently isolated from the main distribution area.

Closely related to *D. incarnata* (and as ancient) is *D. cataonoca*. This species occurs in Eastern Asia Minor and in Transcaucasia. It has not migrated extensively.

Unlike the overwhelming majority of species in the genus, *D. ochroleuca* has yellowish-white flowers^f and is endemic to Central and Western Europe reaching

^eThis taxon includes the type of the genus (*D. incarnata*) and according to nomenclature rules its name should be repeated in the name of the genus.

^fSuch plants should be distinguished from albino forms which occur from time to time in all species of the genus and have purely white flowers.

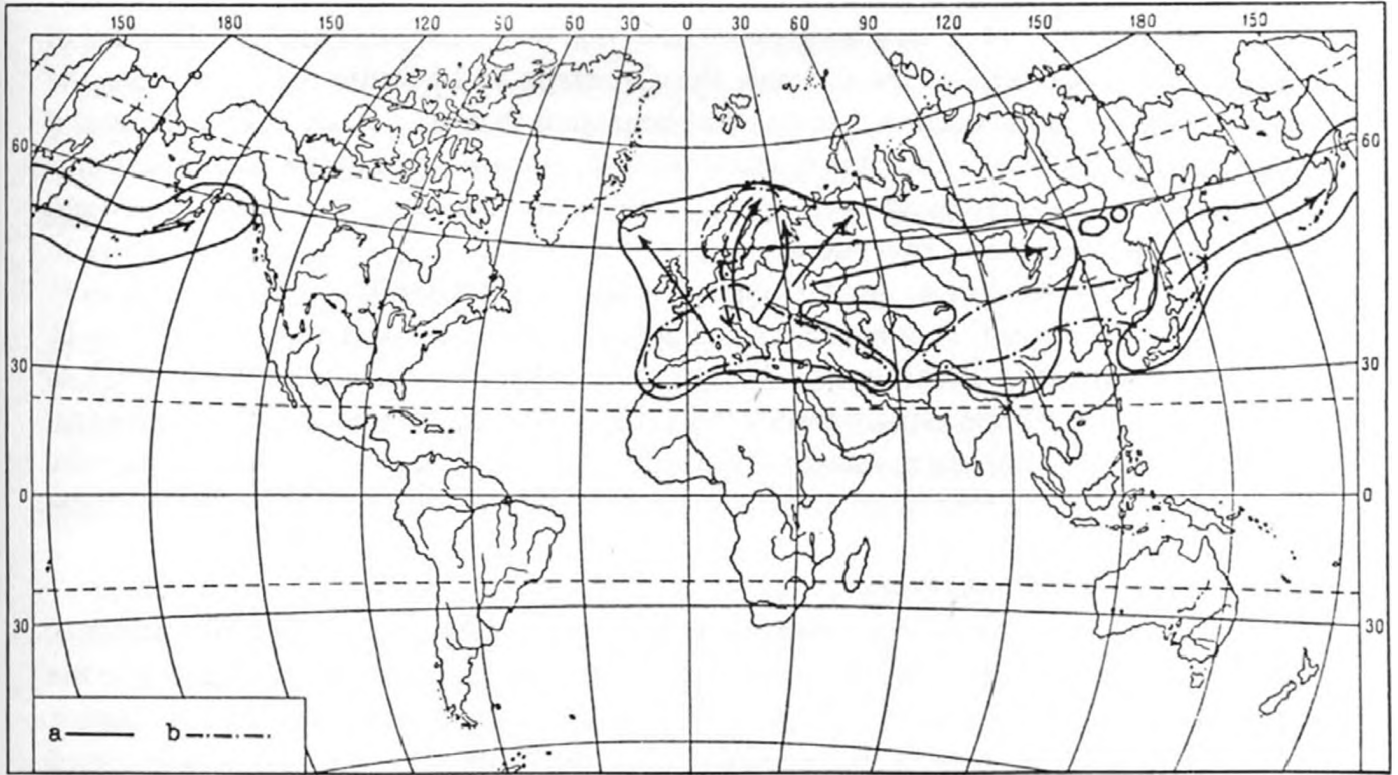


Fig. 5-16. Regions of formation of *Dactylorhiza* species and main paths of their migrations. Explanation of symbols: a, boundary of the present area of the genus; b, boundary of presumed primary area of the genus (arrows indicate the main paths of migrations of the species; broken line, the early quaternary migrations; solid line, quaternary and Holocene migrations) (Averyanov, 1983c).

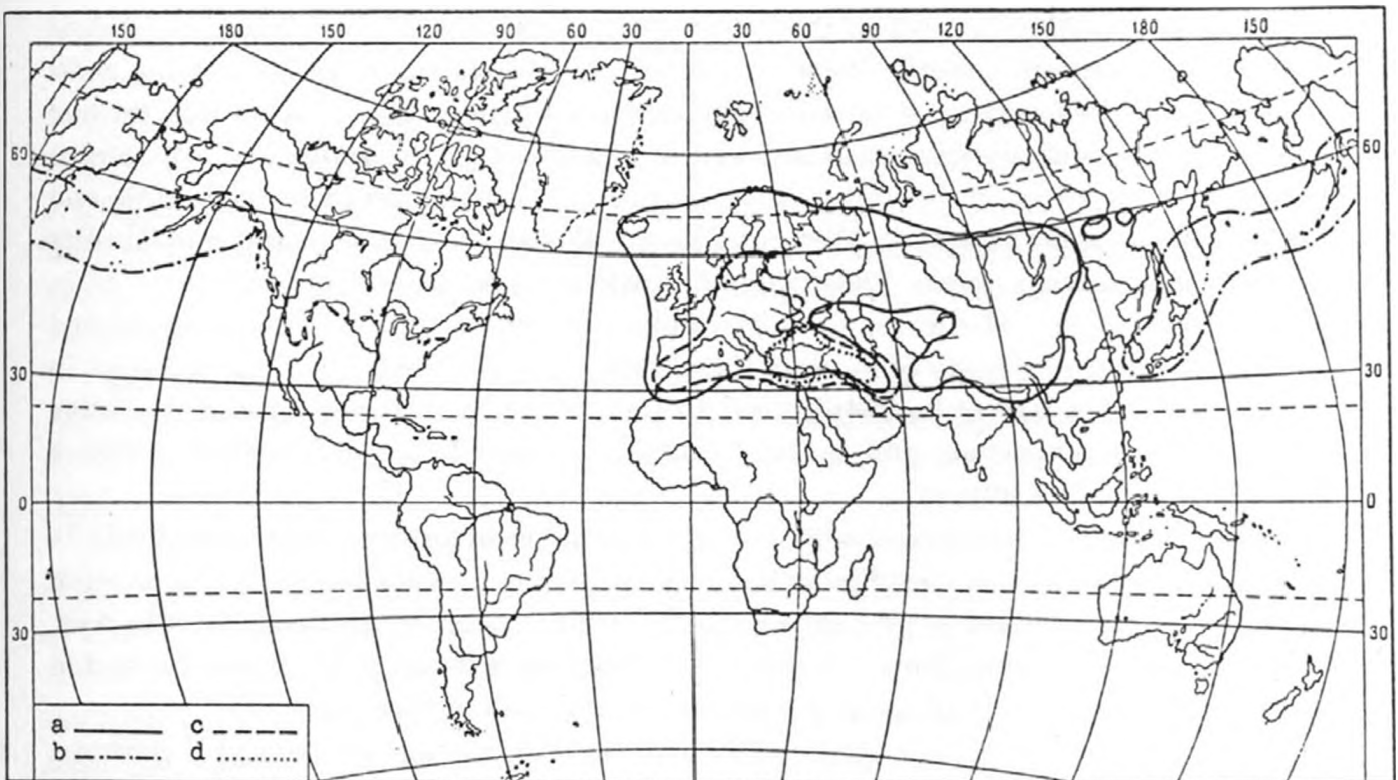


Fig. 5-17. Distribution of the genus *Dactylorhiza* sections. a, Sect. *Dactylorhiza*; b, Sect. *Aristatae*; c, Sect. *Sambucinae*; d, Sect. *Iberanthus* (Averyanov, 1983c).

Saaremaa island (Estonia, USSR) on the east. Ecologically it prefers carbonate fens.

The distribution of *D. cruenta* is very similar to that of *D. incarnata* but this species is not found in the mountains of the Crimea, the Caucasus and Middle Asia. Probably the migration of *D. cruenta* occurred somewhat later than that of *D. incarnata*. To the east it almost reaches the Sea of Okhotsk together with *D. incarnata*, and in the south it extends to Mongolia. *D. cruenta* has spotted leaves, a character found only in *D. chuhensis* and sometimes in *D. euxina* in this subsection.

The remaining species of aggr. *D. incarnata* are stenoendemics in West Europe. *D. coccinea*, *D. pulchella* and *D. gemmana* occur in the British Isles and adjacent islands. *D. sphagnicola* is found in Belgium, the Netherlands, West Germany and in the north of France. These species are usually associated with *D. incarnata* by introgressive hybridization. All of these are the youngest species of aggr. *D. incarnata* and their origin reflects the general process of the formation and development of the European flora after the most powerful glaciations.

9–12. Aggregate *D. olocheilos*.

All species of this group originated in the mountains of Asia Minor and the Caucasus. They have not migrated extensively during their evolution. *D. olocheilos* is endemic to the mountains of Southern Turkey. In the north (Pontic Ridge), it is replaced by *D. osmanica*. Both of these species in Transcaucasia and in the mountains of the Caucasus are replaced by *D. euxina* and its alpine derivate *D. markowitschii*.

13–15. Aggregate *D. sanasunitensis*.

Species of this group are close to aggr. *D. olocheilos* but differ from them by a longer spur which is also found in species aggr. *D. salina*. All of them evolved within regions of their origin without apparent migrations. *D. sanasunitensis* is found in the mountains of Asia Minor. In the east, in Iran and the Transcaucasia mountains, it is replaced by *D. merovensis*. *D. chuhensis* is a rare species, endemic to Armenia.

16–23. Aggregate *D. salina*.

The main distribution area of this aggregate includes the Middle and Central Asia mountains, Southern Siberia, Western China and Mongolia. *D. umbrosa* is the most widely distributed and most ancient species of this group. This species was formed simultaneously with the European and Asia Minor species of the genus, but, apparently, separately from them in the Tethys isles. Its present distribution includes Middle and Central Asia, Southern Siberia, Western China, Pakistan, Afghanistan and Iran. During the periodic coolings of the Pleistocene *D. umbrosa* repeatedly migrated north of its present distribution. The traces of these migrations can be seen at present as isolated populations in the territory of modern Kazakhstan (USSR) in the Turgai depression. In the western boundary of its distribution, in Iran, *D. umbrosa* comes into introgressive contact with *D. merovensis*, and in the mountains of Kun-Lun and Nanshan in China hybridizes with *D. hatagirea*.

In the north of its distribution area, *D. umbrosa* reaches in introgressive contact with *D. incarnata* s.str. and this has resulted in the polytopic formation of a hybridogenic species, *D. salina*. Its distribution at present includes southern Siberia, northern Middle Asia, Mongolia and Northern China. An isolated population is found in the Caucasus and in eastern Transcaucasia. Ecologically it prefers weakly saline meadows.

The remaining species of aggr. *D. salina* are relatively young derivatives of *D. umbrosa*. The altitudinal zone differentiation of *D. umbrosa* gave rise to the formation of *D. kotschy* and *D. magna*. Their distribution areas are similar to those of the parent species.

D. baldshuanica, *D. kulikalonica* and *D. kafiriana* are stenoendemic mountain species.

The first two are endemic to the mountains of Tajikistan (USSR). *D. kafiriana* occurs only in the north of Hindu-Kush (N. E. Afghanistan and N. Pakistan).

More widespread is *D. czerniakowskiae* which occurs in the mountains of Middle Asia, Afghanistan, Pakistan and Northwestern China. All species of this aggregate hybridize easily with each other when they come in contact and rarer species can sometimes be fully "absorbed" by the more common one as a result of introgressive hybridization.

24–25. Aggregate *D. hatagirea*.

Species of this aggregate represent the Himalayan center of development of dactylorchids. *D. hatagirea* occur in Pakistan, northern India, Nepal, Butan and in the mountains of China near these countries. This species and *D. umbrosa* hybridize freely when the two come into contact. *D. graggeriana* is endemic to Kashmir.

D. affinis, a rather taxonomically isolated rare species, is found in eastern Turkey and Transcaucasia.

Subsection II. *Maculatae*.

This subsection includes 18 species of mountain origin. Its distribution area coincides with that of section *Dactylorhiza* except in the easternmost part.

27–30. Aggregate *D. saccifera*.

The central species of this group, *D. saccifera*, evolved in the mountains of Europe. The last cooling diminished its distribution and at present it can be found only in the mountains of Southern Europe and in the North of Asia Minor. In the eastern part of its distribution in Turkey, it is gradually replaced by two related species, *D. urvilleana* and *D. triphylla* which are also found in Iran and the Caucasus. The very large-flowered stenoendemic species *D. nieschalkiorum* which has been recorded only in Central Turkey adjoins this group. *D. foliosa*, a species endemic to the Madeira Isles, has no evident affinity with other members of the subsection. This species is cultivated in Europe as a horticultural plant (Regel, 1866) and freely hybridizes with other dactylorchids (Soó, 1960).

32–35. Aggregate *D. fuchsii*.

36–44. Aggregate *D. maculata*.

Species in these groups have evolved adaptations to the most rigorous conditions of high mountains, and this gave obvious advantages during Pleistocene glaciations. These aggregates were undergoing intensive development and differentiation at that time. This was accompanied by extensive migrations of some species throughout Europe, Siberia and North Africa. Their areas of distribution assumed the modern outlines in the Holocene.

Aggr. *D. fuchsii* includes diploid ($2n=40$) species, aggr. *D. maculata* has tetraploid ($2n=80$) species and taxa whose chromosome numbers are unknown. Both aggregates exhibit parallel variations, but they are seldom sympatric since their soil requirements differ.

The most primitive species of aggr. *D. fuchsii* is *D. fuchsii* s.str., which is widely distributed in Europe and Siberia. This species prefers rich, high pH soils. A more northern derivative of this species found in eutrophic peatlands is *D. hebridensis*. An alpine derivative of this aggregate occurring also in the north and in the Arctic is *D. psychrophilla*. This cryophilic species grew extensively in the periglacial zone of Pleistocene glaciers and migrated together with them. At present it occurs in the mountains of Europe, Northern Europe and in Southern Siberia (Altai, Sajan ridge). The calciphilous species *D. okellyi* which occurs throughout the British Isles and represents young European endemism adjoins this aggregate.

Tetraploid species of aggr. *D. maculata* were evolved from diploid species of aggr. *D. fuchsii*. Most of these species replace aggr. *D. fuchsii* species in swampy habitats with different levels of soil acidity. Active spreading of these species started rather recently when podzolization and oligotrophic soil swamping in Europe became fairly frequent after the last glaciation. Areas occupied by these species are apparently expanding at present. The most widespread species of this aggregate is *D. maculata*. Its area extends through Central and Northern Europe, and Western Siberia. During the intense cold periods of the Quaternary, *D. maculata* was found in Southern Europe. It also reached Northern Africa, where in the Atlas Mountains the related species *D. maurusia* evolved. This species is now endemic to the Atlas Mountains and completely isolated from *D. maculata*.

D. ericetorum and *D. elodes* are endemic to Europe. Both are found especially in poor soils. The former occurs in Central and Northern Europe and the latter reaches the Urals and grows in sphagnum upland bogs.

D. schurii and *D. transsilvanica* are endemic to the Carpathian Mountains, *D. islandica* occurs only in the south of Iceland and *D. colaënsis* is found in the north of Europe. These species represent young endemism in the European flora.

D. sudetica and the related species *D. psychrophila* (aggr. *D. fuchsii*) occur in the high mountains of Europe, in the European north, and in northern Siberia. Both species grow further north than other dactylorchids and reach the extreme north of Scandinavia. As usual all species of the aggregates are interrelated by introgressive hybridization. Hybrids between species of different aggregates are sterile.

Subsection III. *Latifoliae*.

This subsection numbers 16 species which evolved under mountainous or plains conditions through allopolyploid stabilization of hybrids between species of the subsection *Dactylorhiza* and *Maculatae*. Most are of European origin. Some authors assign the rank of a section (Smolyaninova, 1976) or a series (Nelson, 1976, 1979) to all species of this subsection.

45–49. Aggregate *D. majalis*.

The central species of the aggregate *D. majalis* was originally a plains species which is presently distributed in Western Europe. *D. kerryensis* and *D. cambrensis* in the British Isles are closely related to it. These species do not occur on the continent. They were formed as a result of relatively recent isolation of separate populations of *D. majalis*. Both hybridize easily with other species of the subsection (with *D. integrata*, *D. purpurella* and *D. traunsteineri*), but they do not exhibit a trend toward full absorption by more common species. *D. alpestris* was formed as a result of hybridization between *D. majalis* and *D. cordigera*. Distribution of this species throughout Europe clearly shows the paths of Holocene migrations of *D. cordigera* which is now extinct in most areas and can be found only in the Carpathians.

50–51. Aggregate *D. integrata*.

Both species of this aggregate evolved in European plains. *D. integrata* occurs in the Atlantic countries of Western Europe. On the other hand, *D. longifolia*, having evolved in the Baltic countries, migrated eastward. At present it is distributed widely in Eastern Europe and in the south of the Ural Mountains. An isolated part of its area includes the southern portion of Eastern Siberia, the north of Middle Asia and Mongolia. In Europe both species are associated through introgressive hybridization with each other and *D. majalis*.

52-54. Aggregate *D. cordigera*.

D. bosniaca and *D. cordigera* are mountain species and at present limited to the mountains of the Balkan Peninsula and the Carpathians. During the climatic pulsations of the Pleistocene, *D. cordigera* often migrated from its mountain habitats to the plains of Europe. This reached Scandinavia during its most intensive expansion where, in the mountains, the closely related endemic species *D. pseudocordigera* evolved. At present all three species of of aggregate *D. cordigera* have very limited distributions.

55-60. Aggregate *D. traunsteineri*.

This aggregate unites a group of very closely related species, all which originated in the European mountains. Some of them have very local distributions. *D. francis-drucei* is endemic to Scotland. *D. lapponica* and *D. pycnantha* occur only in Northern Europe. *D. traunsteineri* s.str. and *D. curvifolia* have wider distributions in practically the entire area of Central and Northern Europe. In the east both are gradually being replaced by the more active species *D. russowii* which in the past often migrated to the east reaching to the Baikal lake. At present the area of *D. russowii* is disjunctive and consists of a number of isolated populations. All species of this group are often interrelated by introgressive hybridization in areas where they come in contact with each other.

Subsection IV. *Sesquipedales*.

This subsection includes 4 species which are distributed in southern Europe and northern Africa. Nelson (1976, 1979) combined them as the series *Meridionales* Nelson.

61-64. Aggregate. *D. sesquipedalis*.

Species of this group evolved from an ancestor which was isolated as far back as the Neogene. This ancestral form was subject to increasing drought conditions for a long period. It gave rise to four modern species, *D. durandii* and *D. munbyana* which occur in the western Atlas mountains and in the south of the Pyrenees; *D. elata* which is distributed through the Atlas mountains and reaches the mountains of Sicily; and *D. sesquipedalis* which occurs in the south of Western Europe and in Corsica. In contact zones, these species show introgressive hybridization. They did not migrate extensively while evolving.

Section 2. *Aristatae*.

The only species of this monotypic section evolved from primary dactylorchids found in the thermophilic forest flora of Northern Eurasia during the early Neogene. As a result of general cooling and drying of the climate in the late Neogene, the distribution of primary dactylorchids became limited to the western and eastern parts of its original general area. At present the climate in the area of this disjunction is sharply continental (Tolmaczov, 1954, 1974). The extinction of dactylorchid ancestors in the south of Eastern Siberia has isolated the ancestors of *D. aristata* from the main area of the genus a long time ago. Later it migrated to the east and became established in the Aleutian Isles and Western Alaska (Fig. 5-16). At present the distribution of this species has a marked oceanic nature (Fig. 5-17).

Section 3. *Sambucinae*.

This section includes 9 evolutionarily advanced species. Its distribution at present includes mostly the mountain regions of the Ancient Mediterranean (Fig. 5-17). Floral color dimorphism is typical of all species in this section.

66–67. Aggregate *D. sambucina*.

The most primitive species in the section is *D. sambucina*. It evolved in Europe and had its widest distribution during the Atlantic period of the Holocene. At present its distribution is more limited and it is found primarily in the Baltic Sea regions of Central Europe. The species is primary hydrophilous. In the south of Western Europe it is replaced by closely related species *D. fasciculata*.

68–74. Aggregate *D. sulphurea*.

All species of this group evolved from *D. sambucina*-like ancestors by adapting to relatively dry and arid habitats. Their life cycle is similar to that of ephemeroïds. These species did not migrate extensively during their evolution. *D. sulphurea* occurs in the Pyrenees Mountains; *D. sicula* is found in the south of Italy, Sicily and Sardinia; *D. bartonii* is a stenoendemic of the Eastern Pyrenees; *D. libanotica* was evolved in what is now Lebanon. *D. romana* is the most widely distributed species of this aggregate. It occurs in low mountains in countries adjacent to the Mediterranean, and also in Asia Minor and the Crimea. It is related to all species of this aggregate through introgressive hybridization. In Turkey and further to the East, this species is completely replaced by *D. flavescens* which extends to the Caucasus, Iran and western Turkmenia (Kopet-dag mountains). A related alpine species in the mountains of Asia Minor and in the Caucasus is the *D. rupprechtii*. These species did not substantially change their distribution areas during the Quaternary.

Section 4. *Iberanthus*.

The single, ancient and very isolated species of this section, *D. iberica* is distributed in the mountains of the eastern Mediterranean basin in the Crimea, Transcaucasia, Asia Minor and Iran (Fig. 5-17). The habitats of the species apparently did not change during the Quaternary and its present distribution reflects the region of origin and formation of *D. iberica*.

A schematic map of species frequency in *Dactylorhiza* populated area is given in Fig. 5-18. The largest concentration of *Dactylorhiza* species is found in Western Europe (W. European center). There are from 13 to 18 species of dactylorchids in some sections of this region. Species that are equally widely distributed are *D. incarnata*, *D. cruenta*, *D. fuchsii*, *D. hebridensis*, *D. maculata*, *D. elodes*, *D. traunsteineri*, *D. russowii*. Stenoendemic species also occur in this center (*D. ericetorum*, *D. majalis*, *D. alpestris*, *D. purpurella*, *D. integrata*, *D. sambucina*). Areas of these species define the boundaries of the center. Moreover, the specific character of some regions of this center is defined by local endemic races. For the British Isles these are: *D. coccinea*, *D. pulchella*, *D. gemmana*, *D. okellyi*, *D. kerryensis*, *D. cambrensis*, *D. francis-drucei*. In the continental part of Western Europe the species is *D. sphagnicola*. For Scandinavia they are *D. pseudocordigera*, *D. pycnantha*, *D. lapponica*. Their evolution is associated closely with the last glaciation and occupation of the European territories which became free of ice in the early Holocene.

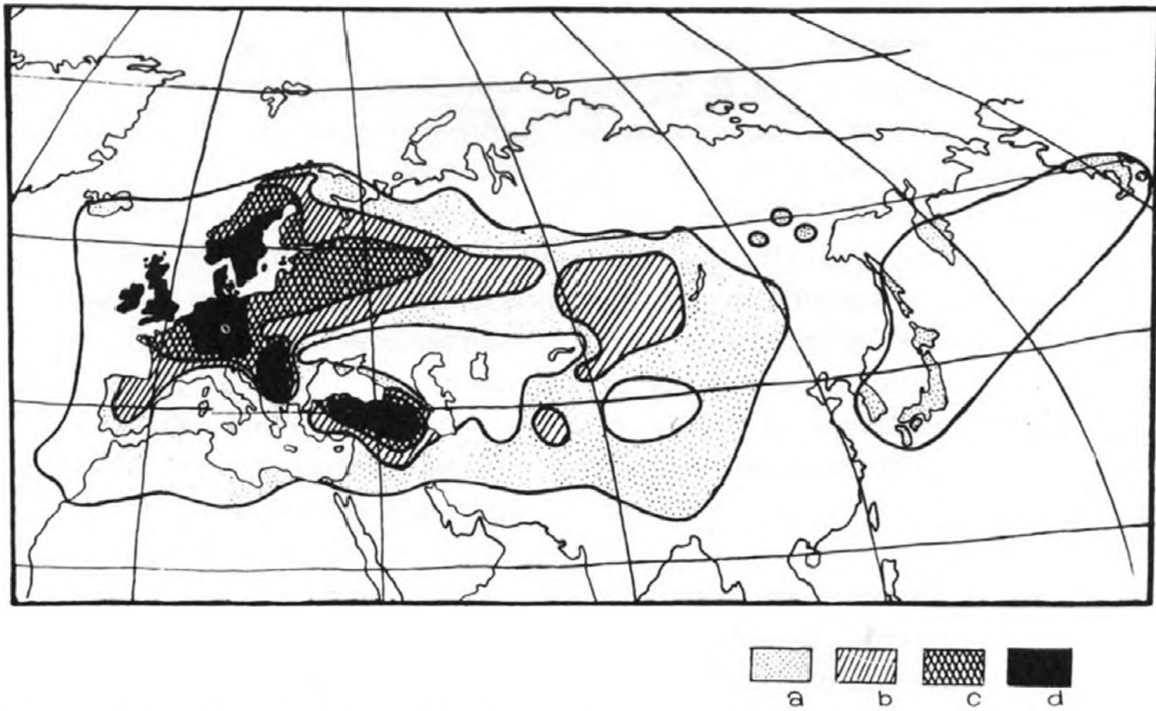


Fig. 5-18. A schematic map of dactylorchids species concentration in the general distribution area of the genus *Dactylorhiza*. Explanation of symbols: Territories where different numbers of species occur are indicated with shading; a, 1-5; b, 6-9; c, 10-12; d, more than 12 species. Species of the genus do not occur in unshaded territories (Averyanov, 1983c).

On the whole, young endemism is typical for this center.

The influence of the Western European center of the genus on the abundance of species is very significant and pronounced especially toward the north and east. Owing to Gulf Stream influence *D. maculata*, *D. elodes*, *D. sudetica*, *D. hebridensis*, *D. psychrophila*, *D. colaënsis*, *D. pycnantha* and *D. lapponica* extend from the center into the far north of Scandinavia.

A considerable number of species radiates from the center eastwards. Only some of the species (*D. ochroleuca*, *D. ericetorum*, *D. majalis*, *D. pycnantha*, *D. lapponica*, *D. sambucina*) disappear just beyond the boundary of the center. Such species as *D. maculata*, *D. elodes*, *D. traunsteineri* and *D. curvifolia* reach almost to the Ural Mountains. *D. longifolia* and *D. russowii* extend practically to the Baikal region. Species of European origin such as *D. incarnata*, *D. cruenta*, *D. fuchsii* and *D. hebridensis* extend considerably eastwards.

In the southern direction the influence of the Western European center of dactylorchids on the abundance of species is not clearly marked. There are substantial differences between the Southern European flora of dactylorchids and that of Northern Africa. *D. maurusia* (aggr. *D. maculata*) is the only African species to show close affinity with European dactylorchids. The character of this part of the distribution of the genus is determined by the species aggr. *D. sesquipedalis* and aggr. *D. sulphurea*. In the extreme southwest of the area populated by the genus, the sole representative is *D. foliosa* (Madeira Isles).

The Carpathian-Balkan center of species abundance for the genus adjoins the Western European center from the southeast. Both of them are related in their species composition. *D. ochroleuca*, *D. sudetica*, *D. saccifera*, *D. majalis*, *D. alpestris*, *D. sambucina* and also more widespread dactylorchids species are common to both centers. Specificity of the Carpathian-Balkan center is defined by the species which are endemic to it: *D. schurii*, *D. transsilvanica*, *D. cordigera* and *D. bosniaca*.

A more isolated and third center of species abundance for dactylorchids is in Asia Minor (Asia Minor center). This center has only one common species (*D. iberica*) with the dactylorchid European flora. *D. triphylla*, *D. urvilleana*, *D. nieschalkiorum*, *D. cataonica*, *D. olocheilos*, *D. osmanica*, *D. sanasunitensis*, *D. merovenssis*, *D. chuhensis*, *D. affinis*, *D. flavescens* and *D. ruprechtii* occur only here. Two additional species, *D. euxina* and *D. markowitschii* join the ones listed above in the Caucasus and Transcaucasia.

The second, and especially the third center of the species abundance of dactylorchids represent more ancient endemism of the genus *Dactylorhiza*. Species in these centers have undergone no substantial migrations in comparison with those of the Western European center of species abundance for the genus.

Considerable abundance of dactylorchids species in the Hindu-Kush and Pamir Mountains is defined by the widespread and common *D. umbrosa*, *D. salina*, *D. kotschyi*, *D. magna*, *D. czerniakowskiae*, and the stenoendemic species *D. baldschuanica*, *D. kafiriana* and *D. kulikalonica*.

The genus is represented only by *D. hatagirea* and *D. graggeriana* in the Himalayas. In Southern Siberia a rather high level of dactylorchid species abundance is caused by penetration into the region of both European (*D. incarnata*, *D. fuchsii*, *D. hebridensis*, *D. russowii* and *D. longifolia*) and Central Asian species (*D. salina*, *D. umbrosa* and *D. kotschyi*). The eastern isolated part of the genus territory is represented by a single species, *D. aristata*.

On the whole the existence of the many still insufficiently studied, young, morphologically rather poorly defined, often stenoendemic species is characteristic of the genus *Dactylorhiza*. This is indirect evidence that intensive species radiation of the genus is proceeding at its present stage of development.

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Glossary

- Agene cell.** Any protodermal cell, adjacent to the guard cells and which remains in this position without dividing.
- Agenuous.** Type of development where the stomatal meristemoid forms two guard-cells only. The stomatal complex at the end of the development is surrounded solely by agene cells. This term is applied in accordance with the origin of the cells and their position during development.
- Aggregate.** A group of closely related species which is named as the oldest specific epithet among species that form it. The term was introduced by Heywood in 1963.
- Allopolyploid stabilization.** Stabilization of hybrids by means of polyploidy as a result of which these hybrids between species with different genomes became capable of producing fertile seeds.
- Allopolyploidy.** A number of chromosomes equal to the total of both parents in hybridization between species which contain different chromosome numbers.
- Alpine orogenesis.** A series of orogenic events in Southern Europe and Asia during the Tertiary when the Alps were largely raised.
- Aneuploidy.** A somatic chromosome number which is not the same or even a multiple of the basic haploid number.
- Anomocytic.** A type of stomate in which subsidiary cells are not associated with the guard cells. The term is applied in accordance with purely morphological criteria.
- Anther.** The pollen-forming part of the stamen.
- Anthropogenic.** A factor produced by human activities.
- Anticlinal.** Perpendicular to the surface.
- Apical meristem.** A group of meristematic cells at the tip of a shoot from which all the tissues of the mature axis are ultimately formed.
- Autopolyploidy.** Formation a polyploid organism which has three or more sets of chromosomes, all of which come from the same species. This usually results from the doubling of chromosomes in a single individual.
- Bilocular.** Two-celled, or with two locules.
- b.m.** Bicrometer = 1/1000 of a mm, 1/1,000,000 of a m.
- Bract.** A modified, often much reduced leaf subtending a flower or inflorescence; morphologically a foliar organ.
- Calciphilous.** Plants growing on the soils containing lime; e.g. calcium carbonate, calcite, or magnesium carbonate.
- Carpels.** The ovule-bearing structure (megasporophyll) of a flower, regarded as a single, modified, seed-bearing leaf.
- Caudicle.** A slender, mealy, or elastic extension of the pollinium which is produced within the anther.
- Chlorenchyma.** Parenchyma cells that contains chloroplasts.
- Chloroplasts.** A cellular organelle in photosynthetic eukaryotes that contains chlorophyll; the site of photosynthesis.
- Clavate.** Club-shaped; gradually thickened toward the apex from a slender base.
- Cryophilic.** Cool loving, adapted to live in tundra or in polar regions.
- Derivate.** A divergent part of an entity; a daughter taxon evolved by divergence from its ancestral form.
- Disjunct distribution.** The occurrence of one species in widely isolated geographical areas. Disjunction is the region between such isolated areas where the species does not occur.
- Egg.** A female gamete.
- Ephemeroïds.** Perennial herbaceous plants in deserts with different underground storage organs (bulbs, tubers, etc.) which have a very short annual growth period.
- Eutrophic.** A body of water or marsh which is rich in organic and inorganic nutrients.
- Exine.** The outer wall layer of pollen grains.
- Gene pool.** The genetic constitution of a population.
- Geophytic.** Adapted to the terrestrial mode of life.
- Geophytes.** Plants with meristematic portions located below the soil surface, as on bulbs or rhizomes.
- Hemimesogenous.** Type of stomata development where one or more mesogene cells are formed by the meristemoid, incompletely surrounding the stomatal complex. The stomatal complex at the end of the development is surrounded by agene and mesogene cells. This term is applied in accordance with the origin of the cells and their position during development.
- Hemimesoperigenous.** Type of stomata development where both the mesogene and perigene cells are formed by the meristemoid, incompletely surrounding the stomatal complex. The stomatal complex at the end of the development is surrounded by agene, perigene and mesogene cells. This term is applied in accordance with the origin of the cells and their position during development.
- Hemiperigenous.** Type of stomata development when the perigene cells are formed by the meristemoid, incompletely surrounding the stomatal complex. The stomatal complex at the end of

- the development is surrounded by agene and perigene cells. This term is applied in accordance with to the origin of the cells and their position during development.
- Hybridogenic. Originated by means of hybridization.
- Hydrophilous. Water loving, growing in moist places.
- Inferior ovary. An ovary that is situated below the point of insertion of the other floral organs.
- Intercalary meristem. A localized meristematic region in an elongating internode; a meristem that lies between areas that are more or less mature (differentiated).
- Introggressive hybridization. Genetic modification of one species by another though the intermediacy of hybrids.
- Karyotype. The general appearance of the chromosome complement of an individual or a group of related individuals, with regard to their number, size, shape, etc.; usually based on observations of chromosomes in mitotic metaphase.
- Lobes of stigma. Segments of lobed stigma, the portion of a carpel upon which pollen germinates.
- Massula (pl. Massulae). See polyade.
- Mesogene cell. Any cell derived by division of a stomatal meristemoid before it divides into the two guard cells.
- Metacentric chromosome. A chromosome which has a centrally located centromere.
- Middle Asia. A modern term (replacing the old name Turkistan) widely used in Soviet literature. It designates the North West regions of Central Asia which at present are within the limits of the USSR (Uzbek, Turkmen, Kazakh, Kirghiz and Tadzhik Socialist Soviet Republics).
- Mucilaginous. Having the character of, or containing mucilage; being gelatinous, gummy or sticky.
- Nom.invalid. Taxonomical abbreviation from Latin "*nomen invalidum*," i.e. incorrect name.
- Ontogenesis. The entire development of an organism from the zygote to maturity.
- Operculum. A lid, or cap, covering the retinacula in dactylorchid flowers.
- Paleogene. The span of time comprising Paleocene, Eocene and Oligocene. The Lower Tertiary. Also, corresponds to the division of rocks of respective age.
- Palmate. Having lobes, veins or divisions radiating from a common point, as in palmately lobed, palmately veined or palmately compound.
- Papilla (pl. Papillae). A soft, nipple-shaped protuberance, a type of trichome.
- Parallel placentation. The arrangement and distribution of placentae and ovules within the ovary forming lines which are parallel to the axis of the ovary.
- Parenchyma. Tissue composed of parenchymous cells.
- Parenchyma cell. The most common cell type in plants; the cells are characteristically alive at maturity, usually thin-walled and exhibit a variety of sizes and shape. Functions include photosynthesis, storage, secretion, transport of water and food substances.
- Parietal placentation. Placentation with ovules or placenta attached on the inner wall of the ovary.
- Pectinaceous. Comblike; having closely parallel, narrow, toothlike projections.
- Pedicel. The stalk of an individual flower in an inflorescence.
- Periclinal. Parallel to the surface.
- Perigene cell. Any daughter cell formed by one or more divisions in a protodermal cell adjacent to the guard-cells.
- Phylogenetic. Pertaining to the evolutionary history and relationships among a group of organisms.
- Pleistocene. The epoch of the Quarternary following the Pliocene and preceding the Holocene, also corresponds to the division of rocks of the respective age.
- Pollinarium (pl. Pollinaria). The complete set of pollinia from an anther, with associated parts, retinaculum or retinacula and stipe (caudicle).
- Pollinium (pl. Pollinia). A more or less compact and coherent mass of pollen (in dactylorchids consists of polyades).
- Poltava flora. Term pertaining to the fossil flora which existed in the para-Tetis region about Eocene time. Made up mainly of tropical and subtropical plants.
- Polyade. A packet of pollen in those genera in which the pollinium is subdivided into small packets usually connected by elastic threads.
- Polytopic formation. Origin and development of a taxon in two or more separate areas.
- Retinaculum (pl. Retinacula). A viscid part of the rostellum which is clearly defined and removed with the pollinia as a unit, and serving to attach the pollinia to an insect or other agent.
- Rosette. A crowded, circular cluster of leaves or other organs; often in reference to a growth habit in which leaves radiate from a crown, close to the ground.
- Rostellum. The tissue which separates the anther from the fertile stigma; a modified portion of stigma.
- Saccate. Sacklike, deeply concave.
- Sclerenchyma. A tissue composed of sclerenchyma cells, including fibers, fiber-sclereids and sclereids; functions include support and sometimes protection.
- Series. A taxonomic rank usually comprising a group of closely related allopatric species.

Sessile. Without a stalk; sitting directly on its base.

s.l. Taxonomical abbreviation from Latin "*sensu lato*" i.g., in a wide sense. It means a taxon which includes taxa which sometimes are considered as independent.

s.str. Taxonomical abbreviation from Latin "*sensu stricto*" i.g., in a narrow sense. It means a taxon which includes only one taxon (including the nomenclatural type) and no other similar taxa.

Spur. A slender, tubular or sacklike projection from a flower part, usually a nectary, commonly formed by the base of the labellum.

Staminode. A sterile stamen which does not produce pollen; staminodes in orchids are variable in form.

Stenodemic. Native or confined naturally to a particular and very restricted geographical area or region.

Sympatric. Originating in, or occupying the same geographical region; species or populations which occur close enough together to be within the range of mutual pollinating vectors.

Taxon (pl. Taxa). A taxonomic group of any rank.

Testa. The outer seed coat, which is derived from the outer integument of the ovule.

Thermophilic. Heat-loving.

Torulose excrescences. Minutely torose projections.

Trabecula (pl. Trabeculae). A rodlike part of a cell wall extending across the lumen; structure which partially or completely traverses an intercellular space.

Type section. Section which includes the type species of a genus.

Vascular bundle. A strand of vascular tissue composed of xylem, phloem and procambium.

Whorl. A circle of floral organs; e.g., stamens, petals, carpels.

Xerothermic maximum. Driest and hottest period.

Zygomorphous. Bilaterally symmetrical.

Zygomorphy. The condition of being bilaterally symmetrical.