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Taxonomy of *Orchidaceae* tribus *Orchideae*, a traditional approach

Keywords

Orchideae, *Orchidinae*, chromosome numbers, labellum structure, taxonomy, tribal phylogeny, chorology.

Summary

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The taxonomy of tribe *Orchideae* is discussed on the basis of two traditional characters: chromosome number belonging to cytology and labellum structure belonging to morphology. Chromosome numbers combined with chorological data point to a base number of $x = 21$ in the tribe. By decreasing and increasing aneuploidization derived base numbers up to $x = 13$ and $x = 24$ evolved. The labellum structure is a useful character in taxonomical considerations. Starting from three basic types (entire labellum, three-lobed labellum with entire or two-lobed median lobe) several other types developed. The greatest variation is found in subtribe *Orchidinae*. In this group of presumed paleotropical origin three major evolutionary lines can be distinguished: a South-Asian-African, a Mediterranean-European and an East-Asian-North-American line. The latter has retained the original base number $x = 21$, whereas the Mediterranean and European species show a rapid chromosomal differentiation. On the basis of chromosome numbers and labellum structure the recently proposed re-arrangements of *Orchis* with *Neotinea* and *Anacamptis*, *Dactylochiza* with *Coeloglossum*, *Gymnadenia* with *Nigritella* as well as *Himantoglossum* with *Barlia* and *Comperia* are not recommended because of still insufficient insight. However, *Aceras* should be included in *Orchis*.

Zusammenfassung

Buttler, K. P. (2001): Die Systematik der *Orchidaceae* tribus *Orchideae*, ein traditioneller Ansatz. – Jour. Eur. Orch. 33(1): 7-32.

Die taxonomische Gliederung der Tribus *Orchideae* wird auf der Basis zweier traditioneller Merkmale aus Zytologie und Morphologie, der Chromosomenzahl und der Lippenstruktur, besprochen. Die Chromosomenzahlen sind von 325 Sippen (22 Prozent) bekannt, die sich auf 36 Gattungen (56 Prozent) verteilen. Die Zahlen werden kritisch geprüft, nicht berücksichtigt bleiben einige ungläubwürdige, überwiegend ältere Angaben. Unter Hinzuziehung vor allem chorologischer Aspekte wird $x = 21$ als die Basiszahl der Tribus angesehen. Durch ab- und aufsteigende Aneuploidisierung sind abgeleitete Basiszahlen bis $x = 13$ und $x = 24$ entstanden. Die Lippenstruktur erweist sich bei genauerer Betrachtung als taxonomisch relevant. Von drei Grundtypen (ungeteilte Lippe, dreilappige Lippe mit ungeteiltem oder zweiteiligem Mittellappen) leiten sich verschiedene weitere Typen ab. Während die Subtriben *Habenariinae* (mit *Hermiiniinae*) und *Platantherinae* im Lippenmerkmal relativ einheitlich sind, zeigen die *Orchidinae* eine große Variation. Innerhalb dieser Subtribus können ausgehend vom vermuteten Entstehungszentrum im tropischen Asien drei Entwicklungslinien unterschieden werden: 1. eine südasiatisch-afrikanische, 2. eine mediterran-europäische und 3. eine ostasiatisch-nordamerikanische. Die erste wird von hundert wenig bekannten Arten gebildet. Die beiden anderen Entwicklungslinien, fast dreihundert und hundert Arten stark, unterscheiden sich unter anderem darin, dass in dem mediterran-europäischen Zweig eine starke chromosomale Differenzierung eingesetzt hat, während im ostasiatisch-nordamerikanischen Zweig die ursprüngliche Basiszahl $x = 21$ erhalten blieb. Ein weiteres primitives Merkmal ist hier zum Beispiel die Rhizombildung in einigen Gattungen. Die neuerdings vorgeschlagenen Neugruppierungen von *Orchis* mit *Neotinea* und *Anacamptis*, von *Dactylorhiza* mit *Coeloglossum*, *Gymnadenia* mit *Nigritella* sowie *Himantoglossum* mit *Barlia* und *Comperia* werden mit Chromosomenzahlen und Lippentypen getestet und beim jetzigen Kenntnisstand als nicht abgesichert angesehen. Die Einbeziehung von *Aceras* in *Orchis* wird befürwortet.

* * *

Introduction

Contemporary students of orchid taxonomy in Europe are still mainly devoted to complete the inventory of taxa, their distribution and biology. The great number of papers on these subjects and the continuous detection of new species and sub-species even in otherwise well known areas illustrate that the orchid flora is still

in need of such basic research. Papers on tribal, subtribal or generic relationships are comparatively scarce during the last decades. Only in recent years the situation changed when new methods were introduced into orchid research. Among others, the papers of STRACK & al. (1989), PRIDGEON & al. (1997) and BATEMAN & al. (1997) received great attention, not only because of the new facts and interpretations, but also because of the nomenclatural consequences.

The taxonomy preferred in the present paper is traditional. The proposals to reorganize generic boundaries in subtribe *Orchidinae* seem premature and are not wholly convincing. Therefore *Orchis* is understood in a broad sense exclusive of the small satellite genera, *Gymnadenia* and *Dactylorhiza* are retained in a narrow sense. Some of the questions in this connection will be shortly discussed below.

Table 1. – Taxonomy of tribe *Orchideae*, subtribes by different authors.

SENGHAS (1973)	DRESSLER (1993)	SZLACHETKO (1995)	genera	species
Orchidinae	Orchidinae	Orchidinae	36	c. 458
Platantherinae		Bartholininae	1	3
Habenariinae	Habenariinae	Platantherinae	3	c. 63
		Platantherinae	2	13
		Habenariinae	14	c. 802
Androcoryfinae		Hermiiniinae	8	151
		Androcoryfinae	1	4
total			65	c. 1494

Number of genera after SZLACHETKO, of species after SENGHAS (number of *Orchidinae* revised, cf Table 10 on page 29). SZLACHETKO recognizes two evolutionary lines, marked by different frame. The total number of genera and species are variously calculated by different authors. To cite another opinion, BURNS-BALOGH & FUNK (1986) quote 57 genera with 1700 species. *Huittonaea*, placed by the latter authors and by SENGHAS in tribe *Orchideae*, is not treated here.

Table 1 on page 9 presents a survey of tribe *Orchideae* and its subtribes as proposed by different authors. The tribe has an almost worldwide distribution, its range comprises the tropical zone of all continents and reaches northwards to the arctic zone in Eurasia and North America and southwards to the temperate zone in South Africa. The tribe is not present in Australia and extratropical South America.

Concerning methodology, two traditional characters used in taxonomical research will be discussed in detail: chromosome number as part of cytology and labellum shape as part of morphology. There is a strong tendency in our days to disregard the so-called traditional methods as being out of date and giving no reliable results if applied. Modern methods as for example cladistics and molecular taxonomy are the present leaders and many researchers are convinced that these methods a priori yield the better results. The article intends to show that even out-dated morphology can contribute new aspects.

Chromosome numbers

General remarks

In many plant groups chromosome numbers are a useful tool to evaluate relationships, sometimes within genera, but more often within higher taxa above genera. There must of course be the cytological basis, that is a chromosomal differentiation in the group under investigation. This is true of the orchid family as a whole and of tribe *Orchideae* in particular.

The use of chromosome numbers in taxonomic considerations has to follow several precautions. First of all, obviously wrong numbers have to be excluded. Which counts fall into this category is often difficult to decide. Neither repeated nor recent publication are sufficient evidence for correctness. A well known example is *Nigritella*: The numbers $2n = 32$ und 64 have repeatedly been published, but are nevertheless wrong ($2n = 40$, 60 and 80 are correct, TEPPNER & KLEIN 1990).

Apart from the correct chromosome number, the second prerequisite is to find and compare small homogeneous groups of taxa. Any conclusion based on a heterogeneous set of data would from the beginning be defective or at least misleading. Such a wrong concept can be the mere calculation with numbers. If they vary and the chromosomes do not provide further information (size, structure, behaviour), additional data of morphology, chorology, genetics and further disciplines must be included. LOVE & LOVE (1961: 115), for example, tried to deter-

mine the base number of *Orchis*. Because they solely relied upon numbers their speculative proposal "x = 7?, 21?, 9, 10?, 19" is most irritating and does not at all clarify the structure of the genus.

For the purpose of this approach the large and variable genera *Orchis*, *Platanthera* and *Dactylorhiza* are split into small and homogeneous units, cf the tables in the appendix on pages 31, 30 and 32. These units are informally named with the epithet of the species that was first described. In many cases the units correspond to already proposed infragenetic taxa (sections, subsections, series, subseries).

Survey of *Orchideae* chromosome numbers

The chromosome numbers of *Orchideae* were extracted from literature and are compiled in the appendix. Several counts are not included in the tables because they are here considered as being wrong or at least doubtful. These are:

Anacamptis pyramidalis $2n = 20^*$, *Dactylorhiza „drudei“* $2n = 14^*$, *D. incarnata* $2n = 20^*$, *D. majalis* $2n = 20^*$, *D. maculata* $2n = 20^*$, *D. traunsteineri* $2n = (16, 17, 18)$ 20^* , *Gymnadenia conopsea* $2n = 20^*$, *G. odoratissima* $2n = 20^*$, *Herminium monorchis* $2n = 24-26$, *Himantoglossum hircinum* $2n = 24$, *Ophrys insectifera* $2n = 22-24$, *Orchis coriophora* $2n = 20^*$, *O. montana* $2n = 20^*$, *O. militaris* $2n = 20^*$, *O. purpurea* $2n = 40$, *O. ustulata* $2n = 20^*$, *Platanthera (Limnorchis) convallariifolia* $2n = 80$, *Pseudorchis alba* $2n = 40$, *Serapias pseudocordigera* $2n = 24$ (all cited in the index of chromosome numbers by BOLKHOVSKIKH & al. 1969).

Gymnadenia conopsea $2n = 30$ (CAUWET-MARC & BALAYER 1986)

Orchis coriophora $2n = 20$ (BALAYER 1986)

Platanthera bifolia $2n = 16$ (STEPANOV 1994)

Most of these numbers were published in the early phase of cytological research to the middle of the twentieth century and practical problems with counting chromosomes must be suspected. Those marked with an asterisk are from FUCHS & ZIEGENSPECK (1924) who had understanding problems, too, as they confused chromosome/chromomere and haploid/diploid.

In several species two chromosome numbers are known which at first glance both look probable. Whether one or both of them are correct cannot be decided without further investigation. The species are: *Dactylorhiza sambucina*, *Orchis pallens* and *O. spitzelii* $2n = 42/40$, *O. laxiflora* and *O. palustris* $2n = 42/36$, *O. collina* $2n = 40/36$, *O. coriophora* $2n = 38/36$. In some other taxa only single

Table 2. – Chromosome counts in subtribes *Orchidinae* and *Platantherinae* for genera and species arranged by regions.

area	total		counted		percentage	
	gen.	spec.	gen.	spec.	gen.	spec.
Europe/Mediterranean	18	324	17	185	94	57
east Asia/North America	15	108	11	27	73	25
Paleotropics/Africa	6	97	1	2	20	2
total	39	529	29	214	76	41

counts are available and the number therefore remains uncertain as for instance in *Comperia comperiana* and *Dactylorhiza insularis*.

At present chromosome numbers of 325 species, equalling 22 per cent of tribe *Orchideae* are known. The ratio for genera is markedly higher, cytological information exists for 36 genera, equalling 56 per cent. Our knowledge of the taxa in different parts of the distribution area is very unequal. While in Europe, including the Mediterranean and Southwest Asia, the species are relatively well investigated, the situation in other parts of the world is by far worse. In subtribe *Habenariinae* (*Hermiinae* included) with a mainly (sub)tropical distribution about 11 per cent of the approximately one thousand species are counted. Table 2 gives a summary for subtribes *Orchidinae* and *Platantherinae*.

Significance of chromosome numbers

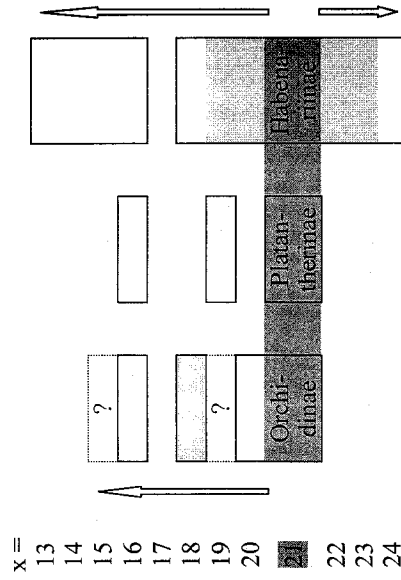
Chromosome numbers in tribe *Orchideae* show an enormous diversity. On the diploid level ($2n = 2x$) they range from 26 to 48, only 34 has not been counted yet. Polyploidy up to the octoploid level ($8x$) occurs infrequently.

The data set of chromosome numbers is still rather incomplete, as has been shown above. Nevertheless, the known numbers are adequate for further consideration if additional facts are incorporated. Many special questions cannot be answered on the basis of 36 genera out of 64, but it seems possible to reconstruct some general evolutionary patterns within the tribe. Good results are obtained if cytological data are combined with chorology and morphology.

“When faced with an array of chromosome numbers, cytologists almost always seek the base number in their study group.” (DRESSLER 1993: 70) Looking at tribe *Orchideae* in detail, evidence clearly points to a base number of $x = 21$. There exist several arguments that support the assumption:

- (1) The diploid number $2n = 2x = 42$ occurs in all subtribes.
- (2) It is the most frequent number within the tribe.
- (3) The number is distributed all over the area of the tribe.
- (4) The number predominates in the tropics, the supposed region of origin of the tribe and the family.
- (5) The number is positively correlated with primitive characters. Vice versa, genera with chromosome numbers other than 42 often show obviously derived characters.
- (6) Decreasing base numbers coincide with chorologically based evolutionary lines (see below on page 19).

Table 3. – *Orchideae*: occurrence of base numbers in the major subtribes.



Habenariinae including *Hermiinae*
 box dark shaded: frequent occurrence
 box light shaded: less frequent occurrence
 box not shaded: rare occurrence
 ? doubtful base number
 ⇐ direction of base number evolution

There is no evidence that the evolution of *Orchideae* started from a hypothetical ancestor with $x = 7$, as YOKOTA (1987) postulated. Diploid species with $2n = 14$ have so far not been found and the few species with $2n = 28$ that could be interpreted as tetraploids show otherwise derived characters. DRESSLER (1993) preferred not to specify the base number, he only stated the pre-dominance of 20, 21 and 22 as haploid numbers.

The tribal base number $x = 21$ cannot, of course, be interpreted as primitive within the family as a whole. It doubtless is derived, and possibly originated from the combination of two lower numbers by allopolyploidization what, however, is in need of further research. The increased base number does well agree with the opinion of several authors (e.g. DRESSLER's 1993) on the position of tribe *Orchideae* within the family. The tribe belongs to the most advanced groups, a secondary base number fits well in with the concept.

Labellum structure

General remarks

The labellum structure has only rarely been discussed and employed as an relevant character in *Orchideae* taxonomy, at least not if relationships between genera were concerned. The character was considered in those genera with a distinctive labellum, as for instance in *Himantoglossum*, *Serapias* and *Ophrys*, but was usually neglected in other groups with variable labellum types, especially in *Orchis*. The labellum was thought to be of little or no taxonomic importance. HAUTZINGER's comments may illustrate the opinion shared by many others. When discussing the relevancy of entire and three-lobed labella for the arrangement of *Orchis* species, he wrote (1978: 37, translated from German): "The lip, being the optically prominent perianth segment, is overvalued in the entire orchid family, yet it is nothing else but the landing-place for the pollinating insect. Furthermore especially the lip is subject to great modification even within one species." Yet there are a few contrasting examples. DELFORGE (1999) recently dealt with the labellum structure when reviewing *Himantoglossum* and resembling genera.

The facts, indeed, are different from HAUTZINGER's assumption. The structure of the labellum is not an accidental character. Like any other character, it is the result of evolutionary processes. If a certain structure has once been fixed, it does not easily convert into another. There may, however, be some variation, the structure may be modified by external or internal factors within the genetically based variability.

Figure 4. – Labellum types in tribe *Orchideae*.

lip entire	lip 2-lobed	lip 3-lobed, median lobe entire	lip 3-lobed, median lobe 2-lobed	lip 3-lobed, median lobe 3-lobed
E	2L	3L1	3L2	3L3
<p>P <i>Lysiella</i> P <i>Platanthera</i> O <i>Papilionaceae</i> Dactylorhiza</p>	<p>O <i>Laxiflorae</i></p>	<p>Neotianthe O <i>Coriophorae</i> Stevaniella Traunsteinera Anacamptis</p>	<p>O <i>Masculae</i> O <i>Moriones</i> Barlia</p>	<p>O <i>Militares</i> Aceras Neotinea</p>

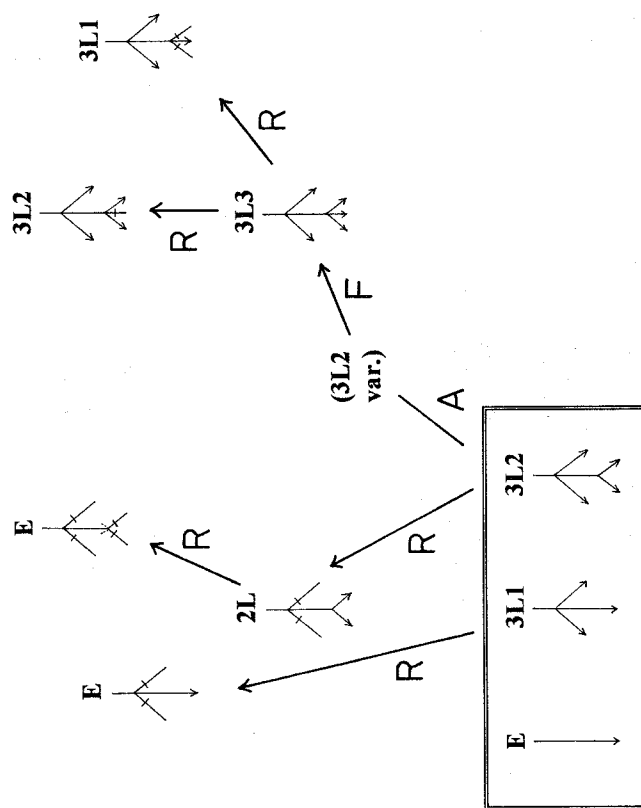
Subdivisions of genera are preceded by the genus abbreviation:

O = *Orchis* (sensu lato), P = *Platanthera* (sensu lato).

Survey of *Orchideae* labellum types

Using a descriptive approach, three basic labellum types occur in tribe *Orchideae*: undivided, two-lobed and three-lobed labella. The latter comprise three subtypes dependent upon the structure of the median lobe which itself may be entire, two-lobed or three-lobed. The labellum types are illustrated in Figure 4

Figure 5. - Supposed relationships of labellum types in subtribe *Orchidinae*.



Alteration of labellum structure through acquisition and/or loss of meristematic activity:

- reduced meristematic activity,
 - R, reduction, A, acquisition, F, fixation.
 - (3L2 var.) = hypothetical intermediate stage, variable 3L2 ↔ 3L3.
- Labellum formulae see Figure 4.

on page 15 with examples taken from European species mainly of the *Orchidinae* and some of the *Platantherinae*. To every type is added a sketch showing the growth direction during labellum development and a short formula that is hence used in the text.

If labellum types are to be used in taxonomic considerations, it is necessary to evaluate their relationships. New types evolve by alteration of the meristematic activity during labellum growth. Even without special investigation in developmental flower morphology, some general trends can be deduced from infraspecific labellum variation and interspecific labellum similarities. The main processes affecting the labellum type are the acquisition, the fixation and the reduction of meristems.

Figure 5 summarizes the supposed relationships in tribe *Orchideae*. Three of the labellum types observed are interpreted as primitive: the entire labellum (E), the three-lobed labella with entire median lobe (3L1) and two-lobed median lobe (3L2). The conclusion is drawn from the distribution pattern of different types in the subtribes. In *Habenariinae*, *Herminiinae* and *Platantherinae* the E and 3L1 types occur exclusively, in *Orchidinae* the 3L1 and 3L2 types are predominant in species which otherwise show primitive characters. What may be the common ancestor of these types cannot be assessed without further research.

The labellum variation is greatest in subtribe *Orchidinae* (see Table 6 on page 18). Starting from three-lobed labella (3L1 and 3L2) several other types evolved. The main process seems to have been the reduction of meristematic activity, which results in less complicated and finally entire labella (E). The acquisition of a new meristem, what equally could be the partition of an existing, is an obviously rarer event. Some species among *Orchis* sensu lato (the *Militares* group, also *Aceras* and *Neotinea*) have gained the new quality of developing a three-lobed median lobe (3L3). How evolution may have proceeded can be concluded from the labellum variation in related species. The *Anatolicae*, *Masculae* and *Patentes* groups of *Orchis* normally have a two-lobed median lobe, but occasionally a central tooth is present, too (3L2 variable). In case this tendency is being fixed, a qualitatively new labellum type has been reached. Interesting enough, the 3L3 type itself is modified by growth reduction what can be observed especially in species with small flowers like *Neotinea maculata*.

Superficially similar labella must not be equivalent, a certain character state can be primitive in one group and derived in another. In Figure 5 on the preceding page three such examples are shown:

- (1) The entire labellum (E) may be a primitive feature (e.g. in *Platanthera*) or may be derived, either by direct reduction from a three-lobed labellum with entire median lobe (3L1) (e.g. in *Dactylorhiza euxina*) or by reduction via a two-lobed labellum (3L2 → 2L) (e.g. in *Orchis palustris*).
- (2) The three-lobed labellum with entire median lobe (3L1) must be classified as primitive in several genera and *Orchis* subgroups (e.g. *Neottianthe*, *Stenella*, *Orchis Cortiophorae*), but is obviously derived from a three-lobed labellum with three-lobed median lobe (3L3) in *Neotinea maculata*.
- (3) The three-lobed labellum with two-lobed median lobe (3L2), being a primitive character for several taxa (e.g. for *Orchis Masculae*, *O. Moriones*), is derived by reduction from a three-lobed labellum with three-lobed median lobe (3L3) in *Aceras anthropophorum* and again in *Neotinea maculata*.

Table 6. — *Orchideae*: correlation between base numbers and labellum types in the major subtribes.

x =	?	?	Platantherinae	Habenariinae	labellum type
13					E
14					2L
15	?				3L1
16					3L2
17					3L3
18					
19	?				
20					
21					
22					
23					
24					

Concluding remarks

In the final chapter the attempt is made, by combining cytological and morphological with chorological data, to contribute some arguments to how tribe *Orchideae* has evolved. Because only two characters have been investigated somewhat closer, final conclusions are far from being possible. The discussion will therefore be focussed on two aspects, on geographical patterns of major evolutionary lines and on differentiation within subtribe *Orchidiinae*.

Chorology of tribe *Orchideae*

Judging from the present distribution pattern, the tribe *Orchideae* has originated in the tropics, what as well is most likely for the family as a whole. Subtribe *Habenariinae*, the largest group with more than half of the species, inhabits the tropics and subtropics of Asia, Africa and America. Only single members have an extratropical distribution as e.g. *Habenaria tridactylites*. The other major subtribes in SZLACHETKO's classification, *Orchidiinae*, *Hermiinae* and *Platantherinae* are concentrated outside the tropics, but are still connected to the supposed region of origin by a few genera and species.

Relatively detailed data are available for the *Orchidiinae*, especially from the species of Europe and the Mediterranean, because they are the best investigated. This subtribe consists of three chorological subgroups which represent major evolutionary lines:

- a south-Asian–African branch,
- a Mediterranean–European branch,
- an east-Asian–North-American branch.

The region where these evolutionary lines meet, and where also subtribes *Habenariinae*, *Hermiinae*, *Platantherinae* and *Androcoryninae* are present, are the tropics and subtropics of south Asia. This region may therefore well be the centre of origin for the tribe.

The south-Asian–African branch extends from tropical Asia westwards to tropical and temperate southern Africa. The largest genus is *Brachycorythis* covering almost the total area.

The two other branches radiated from the tropics towards the north, one in northwestern, the other in northeastern direction. The Mediterranean–European and the east-Asian–North-American branches are clearly distinct and display different evolutionary strategies. The latter group has retained several primitive

characters, for instance the original base number $x = 21$ except in very few species (which should again be examined to verify the numbers). The former group, on the other hand, is characterized by a rapid decrease of base numbers; aneuploidy plays a major role, and, to a lesser degree, also polyploidy. Starting from the original level $x = 21$ at least $x = 16$ has been reached, possibly $x = 15$ if the number will prove correct. The distinguishing characters, either primitive ("P: ") or derived ("D: "), are compiled in the following table:

character	EAs/NAm group	Med/Eur group
chromosome base number	P: $x = 21$, no polyploidy	D: decreasing aneuploidy, polyploidy in several genera
rhizomes	P: present in some genera	D: absent
labellum types	P: 3L1 and 3L2 types dominant	D: great variation, several derived types
plants	D?: slender growth	P?: robust growth
leaves	D: often reduced and scape leafless	P: often well developed and stem leafy
inflorescences	D: few-flowered	P: rich-flowered
bracts	P: mainly herbaceous	D: membranous in some genera
reproduction	?	D: occurrence of autogamy, apomixis and particular pollination mechanisms

If all arguments are considered together, the Mediterranean-European branch is the more advanced compared to the east-Asian-North-American one. The Mediterranean region became a secondary centre of speciation, caused by repeated drastic changes of environmental conditions during Pleistocene. Several genera are still in a state of active evolution.

The two northern evolutionary lines are not completely separated geographically, what probably is a secondary effect. Some genera were able to extend their distribution area by long distance migration. *Neottianthe cucullata* of east Asian origin has colonized all temperate continental Eurasia up to the fringe of central Europe. Good examples of the western group are *Orchis ustulata* and *O. militaris* which, also in the temperate zone, stretch eastward to the Ural

mountains and central Asia respectively (distribution maps by MEUSEL, JÄGER & WEINERT 1965: maps 109a, 109c). Also *Dactylorhiza* belongs here; the genus just reaches into North America across the Aleutian Islands represented by one species (*D. aristata*).

Besides in subtribe *Orchidinae*, great chromosomal diversity is found in subtribes *Habenaricinae* and *Herminiinae* (see Table 3 on page 13). The phenomenon must not necessarily point to a closer relationship of these taxa. It may rather indicate the general chromosomal variability being inherent in the tribe as a whole, meaning that aneuploidization may have occurred independently within several groups of the *Orchideae*.

Speciation pattern in subtribe *Orchidinae*

The interrelationship between chromosome number and labellum structure in subtribe *Orchidinae* is demonstrated in Table 7 on page 22. The diagram is not intended to present final conclusions, but to contribute some arguments to the discussion about subtribal taxonomy. The following conclusions can be drawn:

- * Within the *Orchidinae* three clearly separated labellum types have developed (**3L1**, **3L2** and **3L3**).
- * The taxa possessing the **3L1** type and palmate tubers form a well circumscribed lineage that is supposed to be monophyletic. The same interpretation applies to the taxa characterized by the **3L3** type.
- * The taxa grouped together under the **3L2** and **3L1** types reveal great differences in other characters and therefore both may be polyphyletic. The labellum type alone does not help to evaluate relationships.
- * The vertical lines in the diagram separating the different labellum types stand for factual barriers which cannot be crossed during speciation. This applies at least in those cases in which evolution has proceeded and the labellum type is fixed. A helpful marker is a derived base number. At the ancestral base number level ($x = 21$) an interchange between different labellum types may have been possible. One example, the supposed development of the **3L3** type from the **3L2** type via an intermediate stage has been discussed above. At present it is not known what are the relationships between the **3L1** and **3L2** types. A common ancestor must be expected in order to fulfil the condition of a monophyloous origin of the subtribe.

Taxonomical concepts in subtribe *Orchidinae*

The own results obtained from chromosome number and labellum structure investigation can be used to test different taxonomical concepts. In these days the generic boundaries within the *Orchidinae* are under discussion. Several proposals have been published recently to rearrange the species in better defined genera.

The most far-reaching proposal came from PRIDGEON & al. (1997) and BATEMAN & al. (1997) who split traditional *Orchis* into three genera and simultaneously incorporated *Aceras*, *Anacamptis* and *Neotinea* into the new entities. The new genera are the result of a molecular approach which is thought to be the ultimate methodological step in taxonomic research.

The differently circumscribed genera are marked in Table 8 on page 24. The diagram is basically the same as in Table 7 with the species groups arranged by chromosome number and labellum structure. The new genera do partly not reflect labellum morphology. This is especially true for *new Orchis* and *new Anacamptis* which both comprise several labellum types. On the other hand, the enlarged genera *new Dactylorhiza* (with *Coeloglossum*) and *new Gymnadenia* (with *Nigritella*) are not in disagreement with the own findings.

The enlarged genus *new Neotinea* including some of the former *Orchis* species (here called *Militares 2*) seems to be supported by a uniform labellum morphology. However, two more groups, *Aceras* and what is here called *Militares 1*, have the same labellum type (3L3), but are not included. If the conclusions based on molecular data were correct, the character state "three-lobed labellum with three-lobed median lobe" would have evolved two times independently. This assumption is unlikely and, to use cladistic terminology, is in conflict with the principle of parsimony. There exist further arguments speaking against the separate development: The labellum type parallels several other features as chromosome number, hood formation, spur structure and orientation. If all arguments are considered together, evidence supports a monophyletic origin of the four groups under discussion. *Aceras*, *Neotinea* and *Militares 1* and *2* are closely related and should not be separated. To place them in even different genera, *new Orchis* and *new Neotinea*, is artificial. The *Militares* subgroups are said to differ in flower size and bract length, but the postulated distinction does not pass a critical examination as intermediates occur.

The subgroups of *Orchis* and *Dactylorhiza* are printed in italics. The species are listed in Tables 12 and 13 respectively. The lower 40-chromosome row contains those groups in which also 42 chromosomes occur. For the smaller fraction the name is placed in parentheses. Uncertain (? alternative) chromosome numbers are marked with "[?]"

	3L1(E) palmate tubers	3L1	3L2	3L2 3L2/E	3L2+(3L3) variable (2L)	3L3
?	<i>Stenitella</i>					
30						
32					<i>Papilionaceae</i>	
34						
36	<i>Serapias</i> <i>Cortophorae</i> <i>Anacamptis</i>	<i>Himantoglossum</i> <i>Mortones</i> <i>Boryi</i> <i>Ophrys</i>		<i>Laxiflorae</i> <i>Collinae</i>	<i>Barlia</i>	
38						
40	<i>Gymnadenia</i> <i>Nigritella</i> <i>Coeloglossum</i> <i>Ibericae</i>					<i>Neotinea</i>
40	<i>Maculatae</i> <i>Romanae</i> <i>Sambucinae</i>				<i>(Masculae)</i> <i>Patentes</i>	
42	<i>(Maculatae)</i> <i>(Romanae)</i> <i>Pseudorchis</i>	<i>Neottianthe</i> <i>Chamorchis</i> <i>Branckfortii</i> <i>Transtseimera</i>	<i>Quadrupunctatae</i>	<i>[?]Laxiflorae</i>	<i>Masculae</i> <i>(Patentes)</i> <i>Anatolicae</i>	<i>Militares 2</i> <i>Militares 1</i> <i>Aceras</i>

Table 7. - Grouping of taxa of subtribe *Orchidinae* based on chromosome number (rows) and labellum structure (columns).

All the previously discussed proposals to rearrange the species in subtribe *Orchidinae* and to thereby achieve monophyly at the genus level seem premature for one or another reason. Unless additional arguments are available, changes in taxonomy causing nomenclatural irritation cannot be recommended. It remains, however, to examine the *Aceras* issue. The monotypic genus was almost unanimously accepted as independent from *Orchis* on the basis of some morphological peculiarities (lack of a spur, possession of a single viscidium and two callosities at the labellum base). These characters must not be overvalued, they are derived and mark the end of an evolutionary line. The close relationship with some *Orchis* species has several times been stressed (e.g. by NELSON 1968), but only recently BATEMAN & al. (1997) voted to draw the formal consequences. Chromosome numbers and labellum structure, too, favour the solution to merge *Aceras* with the *Militares* group of *Orchis*. For nomenclatural reasons the species must then be called *Orchis anthropophora*, as the type of the genus (*O. militaris*) belongs here.

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Appendix: Chromosome numbers in tribe Orchideae

The genera of *Orchideae* are arranged by subtribes. *Herminiinae* are included in one table with *Habenariinae* (Table 9, this page), as are *Platantherinae* with *Orchidiinae* (Table 10, page 29). The monotypic *Bartholininae* and *Androcorytinae* are not treated since no counts are known. Within *Orchidiinae* the chorological subgroups are presented separately. The heterogeneous genera *Platanthera*, *Orchis* and *Dactylophiza* are further subdivided (Tables 11, 12 and 13, pages 30, 31 and 32 respectively). Polyploid numbers are preceded by "P.". The distribution of the genera is indicated in the column "geography". The abbreviations stand for:

amphiatl amphiatlantic
 circpol circumpolar
 EAS east Asia
 Eur Europe
 Euras Eurasia
 Med Mediterranean
 NAM North America
 NTro Neotropics
 PTro Paleotropics
 SAfr southern Africa

Table 9. – Chromosome numbers in subtribe *Habenariinae*.

genera	number of species		geography	chromosome numbers (2n)
	total	counted		
Diplomeris	4	1	PTro	42
Gennaria	1	1	Eur	34/36?
Habenaria	c. 600	77	PTro/NTro/ NAM	(26 28 30 32) (40) 42 (44 46 48) P: (66) 84 (88 108 112 122 126 168)
Herminium	43	14	EAs/Eur	36 38 40 P: 76 114
Pecteilis	6	3	PTro	(32) 42
Peristylus	75	14	PTro/EAs	(36 38) 42 46 P: 88
Stenoglottis	3	1	SAfr	36
7 genera	c. 732	111	investigated	
17 genera	234		not investigated	

(rare numbers in parentheses)

Table 10. – Chromosome counts in subtribes *Orchidiinae* and *Platantherinae*.

genera	number of species		geography	chromosome numbers (2n)
	total	counted		
A) Paletropical and southern African taxa				
Brachycorythis	37	2	PTro/SAfr	42
1 genus	37	2	investigated	
5 genera	60		not investigated	
B) East Asian and North American taxa (except <i>Platanthera</i> , see Table 11)				
Amerorchis	1	1	NAM	42
Amitostigma	30	4	EAs	42 (44)
Blephariglossis	8	4	NAM	42
B. ciliaris	1	1	NAM	?32
Galearis	7	2	EAs/NAM	42
Gymnadeniopsis	3	2	NAM	(?42/?40)
Hempilia	17	1	EAs	42
Neotianthe	4	2	EAs/Eur	42
Piperia	4	3	NAM	42
Ponerorchis (Chusua)	20	4	EAs	42
Pseudodiphryllum	1	1	EAs/NAM	42
Tulotis (Perularia)	7	2	EAs/NAM	42
11 genera	103	27	investigated	
4 genera	6		not investigated	
C) Mediterranean and European/(Eurasian) taxa (except <i>Orchis</i> and <i>Dactylophiza</i> , see Tables 12 and 13)				
Aceras	1	1	Med/Eur	42

table continued on next page

Anacamptis	1	1	Med/Eur	36
Barlia	2*	1	Med	36 (?30)
Chamorchis	1	1	Eur	42
Coeloglossum	3	2	circpol	40
Comperia	1	1	Med	(?30)
Gymnadenia	c. 10*	7	Med/Euras	40
Himantoglossum	5*	3	Med/Eur	36
Neotinea	1	1	Med/Eur	40 (?42)
Nigritella	c. 16*	16	Med/Eur	40 P: 60 80 100 120
Ophrys	c. 130*	40	Med/Eur	36 (37-40) P: (54) 72 (73-76)
Pseudorchis	3*	2	Euras/amphiatl	42
Serapias	c. 20*	9	Med	36 P: 72
Traunsteinera	2*	2	Med/Eur	42
14 genera	c. 196	87	investigated	
1 genus	1		not investigated	

* Number of species deviating from the one given by SENGHAS (1973). Recently described species are included.
(rare numbers in parentheses)

Table 11. – Arrangement of *Platanthera* species into homogeneous groups and their chromosome numbers (mainly east Asian and North American taxa).

group	species	chromosome numbers (2n)
Limnorchis	c. 13 species, 8 counted	42 P: 84
Lysiella	6 species, all counted	42 P: 84 126
Platanthera	16 species, 13 counted 2 species	42 38

The grouping is provisional. The affinities of several species are uncertain. Species with deviating chromosome numbers may be wrongly placed, or the counts may be wrong.

Table 12. – Arrangement of *Orchis* species into homogeneous groups and their chromosome numbers (Mediterranean and European/(Eurasian) taxa).

group	species	chromosome numbers (2n)
Masculae	mascula • signifera scopulorum • olbiensis pinetorum • langei pallens • provincialis pauciflora • laeta	42 • 42 – • 42 – • – ?42/40 • 42 42 • –
Anatolicae	anatolica	42
Brancifortii	brancifortii	42
Quadrupunctatae	quadrupunctata	42
Patentes	spitzelii (s. l.) • canariensis patens • prisca	42/40 • P: 80 P: 80 • 40
Militares 1	punctulata • <u>galilaea</u> purpurea • stevenii <u>militaris</u> • italica • <u>simia</u>	42 • – 42 • – 42 • 42 • 42
Militares 2	tridentata • conica • lactea ustulata	42/P: 84 • – • 42 42
Laxiflorae	laxiflora • palustris	?42/36 • ?42/36
Collinae	collina	?40/36
Papilionaceae	papilionacea (s. l.)	32
Boryi	boryi • israelitica	36 • –
Moriones	morio (s. l.) • longicornu champagneuxii	36 • 36 36
Coriophorae	coriophora • sancta	38/36 • –

Underlined species: Flowers opening inversely (from top to bottom). The character state is derived and has developed independently in the two groups.

The division of the *Militares* group into two fractions follows BATEMAN & al. (1997) for solely practical reasons. The species all together form a homogeneous group.

The type of the genus is framed.

- : Chromosome number not known.

Table 13. – Arrangement of *Dactylorhiza* species into homogeneous groups and their chromosome numbers (Mediterranean and European/(Eurasian) taxa).

group	species	chromosome numbers (2n)
Sambucinae	sambucina	?40/42
Romanae	romana • flavescens	40 • 42
	markusii • insularis	– • (?760)
Maculatae	aristata	42
	c. 35 remaining species, 28 counted	40 P: 60 80 100 120
	iberica	40