

CLASSIFICATION AND PHYLOGENY IN THE ORCHIDACEAE

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ABSTRACT

The nomenclature of tribes and subtribes in the Orchidaceae is reviewed, and brought into line with the rules of botanical nomenclature. Tribal definition is discussed, and a different delineation of the Neottieae and Epidendreae is proposed. The Apostasiae are considered to be primitive orchids. The Vandae are not considered to be clearly separable from the Epidendreae. A "phylogenetic" arrangement of recognized subtribes is proposed, and keys are given. A broader interpretation is given, especially of the subtribes Chloraeinae, Spiranthiniae, Cyrtopodiinae, Epidendrinae, Maxillariinae and Oncidiinae. About 40 subtribes are recognized (as compared to 80 in Schlechter's system). The need for further revision is recognized. Evolutionary patterns are discussed for several features of the orchid plant, and the phylogeny of the family briefly considered. ROBERT L. DRESSLER, Missouri Botanical Garden, 2315 Tower Grove Ave., St. Louis 10, Missouri; CALAWAY H. DODSON, Instituto Botánico, Universidad de Guayaquil, Guayaquil, Ecuador.

INTRODUCTION

The Orchidaceae form one of the largest families of angiosperms, as well as one of the most fascinating by reason of their diversity and specialization in floral structure. A satisfactory classification of the orchids into tribes and subtribes is not yet available. The most commonly used system, that of Schlechter, has for some time not been in accord with the rules of nomenclature, and has many features which may be questioned on botanical grounds. The recent International Botanical Congress has clarified the rules concerning the nomenclature of categories between family and genus, and provides an occasion for a reevaluation of nomenclature in the Orchidaceae. In reviewing the groups within the Orchidaceae we have, of necessity, made a number of observations on relationships and probable phylogeny within the family. These form the final portion of this paper.

While many workers have described new genera and species of orchids, there has been very little monographic work, and we may safely say that the family has really been very little studied, considering its size and complexity. Until there has been a great deal more systematic study of the family it will not be possible to present a finished system of tribes and subtribes. Consequently, no new taxa are presented in this paper, but we have attempted only to review and evaluate previous systems of classification, and to present a tentative system, with synonymy.

Swartz, in 1880, first divided the orchids into those with a single fertile anther and those with two fertile anthers, thus providing the basis for the subfamilial divisions now recognized. Lindley, in his "Orchidearum sceletos" (1827), was the first to divide the family into tribes. In this work he recognized eight tribes. Later, in "The Genera and Species of Orchidaceous plants," only seven tribes were maintained, with "sections" or "divisions" recognized under some of these. Reichenbach never presented a detailed system of orchid classification, and his categories were vague and inconsistent in both rank and spelling (1852, 1884). Bentham (1881), in preparing a system for *Genera Plantarum*, recognized only five tribes, and delineated 27 subtribes under these. Pfitzer (1887) criticized the classification of Bentham and offered a revised system, based primarily on vegetative features. While the rank of Pfitzer's categories was not very clearly indicated,

one finds that the groups with names ending in "-inae" are referred to as "Tribus." Thus Pfitzer's classification recognized 32 tribes, with a number of subtribes. This same system was followed in "Die Natürlichen Pflanzenfamilien," with only minor changes. Pfitzer's classification was the basis for Schlechter's posthumously published "System der Orchidaceen" (1926). Schlechter, however, recognized only four tribes and treated the remaining tribes and subtribes of Pfitzer all as subtribes, of which he enumerated eighty. Some of Schlechter's subtribes were characterized in earlier papers (1911, 1915) as "Gruppen," but only in the 1926 paper were they treated as subtribes. In studying Schlechter's work, one often feels that his system was published in unfinished form, and that he might have presented a much more coherent system, had he lived to complete it. Mansfeld (1937) has reviewed Schlechter's system and made some modifications, but most recent authors have followed Schlechter's original system with little change. Recently Hawkes and Heller (1959) have presented a list of subtribes and genera in which they recognize no less than 88 subtribes.

Schlechter might well be characterized as a "splitter"; he followed very narrow concepts at all levels of his classification. Subsequent workers have reduced a large proportion of his genera and species to synonymy, but most have accepted his tribes and subtribes with little question. Actually, many of the subtribal boundaries drawn by Schlechter have proven to separate closely related genera. In several cases genera assigned to different subtribes have proven interfertile. While Schlechter recognized eighty subtribes in the subfamily Orchidoideae and several others have since been proposed, we tentatively recognize only about forty in our proposed revision. We believe that future study may further reduce the number of subtribes to be recognized. While the rules of nomenclature permit an almost excessive number of categories between genus and species (subgenus, section, subsection, series and subseries), there are relatively few categories between family and genus. Where Schlechter's subtribes seem useful, even though too closely related or too poorly defined, we have indicated them as "alliances." These are not intended to have formal nomenclatural status. To recognize them as subtribes would tend too much toward taxonomic inflation, and would tend to obscure the really close relationships which exist within the family.

Some authors have cast doubt on the validity of genera which are interfertile. While we do not believe that a fertility criterion (alone) can be applied for generic status in the orchids, we do feel that interfertile genera should not be placed in separate subtribes. In every case where authentic hybrids have been reported between subtribes, however, the morphological evidence, alone, favors their union into a single group. In those cases where we feel quite sure that closely related genera were separated in Schlechter's system, we have united them into a single subtribe. In other cases, however, we have deferred judgment because of insufficient familiarity with the plants involved.

The main difference between Schlechter's system and our own is that he emphasized differences, while we are seeking resemblances. His system was primarily analytical and aimed at identification (though often faulty for that purpose), while our own is synthetic, as we believe these higher categories should be. This

is not to belittle the key features used by Schlechter. Where valid, these are still available for keying groups within the subtribes, but relationships are, we hope, more clearly shown in our system. In many cases the key features chosen by Schlechter will separate only a portion of the genera in closely related or artificial groups.

There are primarily three features of the International Code of Botanical Nomenclature which affect the choice or form of names used in this paper. In the case of subfamilies, tribes or subtribes, the name of any taxon which includes the type of the next higher taxon must be based on the same stem as the name of the next higher taxon. Thus "Ophrydeae" and "Platantherinae," for example, must be replaced by Orchideae and Orchidinae, respectively. This requirement, which was only recently added to the rules (by the 1959 Congress) causes a few changes, but should cause no confusion, and in general makes the taxonomy at this level more logical. The requirement of the suffixes *-oideae*, *-eae* and *-inae* for subfamilies, tribes and subtribes has been in the rules for some time, but has often been ignored by those dealing with orchid nomenclature. The same is true of the principle of priority, which demands the use of names proposed by Bentham, where these differ from those used by later workers.

TRIBAL DELINEATION

The separation and characterization of the tribes Apostasiae and Cypripediae is relatively clear. Each forms a distinctive and natural group which is easily recognized. In the subfamily Orchidoideae the situation is rather different. The tribe Orchideae is distinctive and rather easily characterized, though clearly related to the Neottieae. The distinction of further tribes is much less clear. In Schlechter's system all of the genera with mealy or sectile pollen (except the Orchideae) are grouped in the tribe Polychondreae (= Neottieae), while the genera with hard, waxy pollinia are separated as the more advanced tribe Kerosphaerae (= Epidendreae). As Mansfeld has shown, the distinction between mealy and waxy pollinia is neither practical nor natural. Some genera of the Bletinae have, according to Mansfeld, mealy pollinia. Certainly most of the remaining genera have rather soft pollinia. Some genera of the Sobraliinae have hard pollinia and this subtribe shows close affinity to the Thuniinae and the Epidendrinae. Similarly, the Arethusinae have mealy pollinia, but *Crybe* and *Jimensia* (*Bletilla*) are closely related to *Bletia*. There is a complete series ranging from free pollen grains to the hard ceraceous pollinia of the Oncidiinae and Sarcanthinae. Any arbitrary degree of cohesion chosen as a dividing line would split natural genera and subtribes. Mansfeld (1937) placed the Arethusinae and Sobraliinae in the Epidendreae, and this action is supported by the morphological studies of Hirmer (1920). Such a system, though, leaves no practical way of distinguishing the Epidendreae and Neottieae and is, we believe, still unnatural. The subtribes Vanillinae, Pogoniinae and Gastrodiinae seem to show much closer relationship to the Sobraliinae and Arethusinae than to the other subtribes of the Neottieae. By placing these subtribes in the Epidendreae one achieves a system which is both

more natural and more practical. By this arrangement the great majority of the primitive Epidendreae (with mealy pollinia) have incumbent, operculate anthers, like those of *Phajus* or *Cattleya* (see fig. 3D). The position of the anther in the more advanced Epidendreae is extremely diverse, but these are easily distinguished by the truly hard pollinia. A few species of primitive Epidendreae, such as *Triphora* and some species of *Epistephium* and *Elleanthus*, have erect anthers. Thus the position of the anther is not a fool-proof key feature, but it does seem to provide a better practical separation, as well as a more natural classification.

Several authors have distinguished the tribes Epidendreae and Vandae on the basis of pollinia structure, but a clear distinction proves to be difficult. The presence or absence of a stipe is one feature which has been used for this purpose, but some genera which would unquestionably belong in the "Vandae" have little or no stipe, while a few other genera which are not closely related have stipes or stipe-like structures (Genyorchidinae, Thecostelinae, some species of *Polystachya*). Another feature which is characteristic of the "Vandae" is the presence of superposed pollinia; yet *Coelogyne* and some species of Thuniinae and *Polystachya* have more or less superposed pollinia, but seem otherwise not referable to the "Vandae." There seems to be no feature or combination of features which will serve to separate the more advanced Orchidoideae into two clear-cut main groups. There is a general trend from plants with terminal inflorescence and relatively simple pollinia to those with a lateral inflorescence and highly specialized pollinia, but there is no sharp break and the relationships seem too reticulate to admit the separation of two tribes on this basis. The subtribes of the "Vandae" (Cyrtopodiinae to Oncidiinae as listed on p. 29) seem to represent a relatively homogeneous and more specialized offshoot from some of the several evolutionary lines within the remainder of the Epidendreae. All of these subtribes appear to have been derived from more or less *Eulophia*-like ancestors. For this reason, it is sometimes convenient to consider them as a unit, and a better understanding of the subtribes related to the Cyrtopodiinae may indicate a sharper break between the two main divisions of the Epidendreae than is now evident.

While the Epidendreae form a natural and closely knit group, the Neottieae are more diverse in terms of relationship. Even with the removal of the Vanillinae, Pogoniinae and Gastrodiinae, it is not certain that the Neottieae form a really natural group. Including all of these genera in one tribe because they all possess mealy pollen is somewhat comparable to a hypothetical grouping of *Vanilla*, *Selenipedium*, and *Apostasia* into a single taxon because of seed characteristics. Mealy pollen, like the sclerotic seed coat and the lateral anthers of the Cyripedioideae, is a feature which was doubtless found in all orchids at an early stage in orchid evolution. Its occurrence in two or more otherwise dissimilar groups is scarcely strong evidence of relationship. Since the present paper is primarily a review of orchid classification, any major reorganization of the Neottieae or the Cyripedioideae must be deferred for the present. The possible groupings within these taxa are discussed in the final section on tribal phylogeny (p. 62).

Subfamily Cypripedioideae	Tribe 5. Epidendreae (Continued)
Tribe 1. Apostasiae	Subtribe Coelogyninae
Tribe 2. Cypripedieae	Epidendrinae
Subfamily Orchidoideae	a. <i>Epidendrum</i> alliance
Tribe 3. Neottieae	b. <i>Eria</i> alliance
Subtribe Limodorinae	c. <i>Polystachya</i> alliance
Chloraeinae	d. <i>Glomera</i> alliance
Rhizanthellinae	e. <i>Podochilus</i> alliance
Pterostylidinae	f. <i>Arpophyllum</i> alliance
-----	Pleurothallidinae
Neottiinae	Adrorhizinae
-----	Thelasiinae
Diuridinae	Ridleyellinae
Cryptostylidinae	Liparidinae
Prasophyllinae	Dendrobiinae
-----	Genyorchidinae
Spiranthinae	Thecostelinae
a. <i>Tropidia</i> alliance	-----
b. <i>Goodyera</i> alliance	Cyrtopodiinae
c. <i>Spiranthes</i> alliance	Catasetinae
d. <i>Cranichis</i> alliance	Cymbidiinae
Tribe 4. Orchideae	Sarcanthinae
Subtribe Epipogiinae	Stanhopeinae
Orchidinae	Maxillariinae
Disinae	a. <i>Zygopetalum</i> alliance
a. <i>Disa</i> alliance	b. <i>Lycaste</i> alliance
b. <i>Satyrium</i> alliance	c. <i>Maxillaria</i> alliance
Coryciinae	Pachyphyllinae
Tribe 5. Epidendreae	Cryptocentrinae
Subtribe Vanillinae	Oncidiinae
Gastrodiinae	a. <i>Oncidium</i> alliance
Pogoniinae	b. <i>Ornithocephalus</i> alliance
Sobraliinae	c. <i>Dichaea</i> alliance
Thuniinae	-----
Arethusinae	Subtribes of uncertain position
Bletiinae	Grobyinae
Collabiinae	Pachyplectrinae

A PROPOSED PHYLOGENETIC LIST OF SUBTRIBES

Above is given a list of the tribes and subtribes which we recognize, followed by a tentative key to tribes. We have, in nearly all cases, changed the endings of the group names to accord with the rules of nomenclature. Very few of them were published in the appropriate form, though status was clearly indicated. We have attempted to arrange the groups in a "phylogenetic" sequence; that is, we

have tried to place the more primitive members at the beginning of each group, and we have tried to place closely allied groups together, where possible. The limitations of a one-dimensional scheme are obvious; there are, for example, a number of subtribes which should be immediately adjacent to the Epidendrinae in any "natural" system, but only two can be so placed. We have indicated groups of related subtribes by lines, but interrelationships within the Epidendreae are better shown in figure 1 (p. 51).

KEYS

As Schweinfurth has indicated (1959, p. 528), orchid identification has continued to be more of an art than a science. This is, in part, due to continued reliance on unworkable keys. Since previously published keys to the Orchidaceae have proven to be inadequate in many features, we have prepared these keys *de novo*, as much as possible. Comparison will show Schlechter's key to be much simpler in many respects. To this we can only reply, "Yes, but his key doesn't work." There will surely be many sections in these keys where a similar complaint is justified. It is extremely difficult to write a workable key to the orchids of the world. The person working in a single continent has an easier time of it, and would do well to prepare his keys independently, rather than trying to adapt either these or Schlechter's keys. An English translation of Schlechter's key, with some revision, is given in Withner's recent book (Schweinfurth, 1959).

KEY TO SUBFAMILIES AND TRIBES

1. Fertile anthers 2 or 3; filaments more or less united to the style, but arising below the level of the stigma; the stigma and terminal portion of the style free; no rostellum present.....subfamily CYPRIPEIDIOIDEAE.....2
1. Fertile anther 1 (or 3 as an abnormality and in some autogamous forms); filaments united with the style to form a distinct column, united for the full length of the style or the anther and stigma connected by a terminal rostellum.....subfamily ORCHIDOIDEAE.....3
- 2(1). Perianth essentially regular, the lip never deeply saccate; fertile anthers 2 or 3, elongate; style slender.....APOSTASIEAE
2. Perianth irregular, with a deeply saccate lip; fertile anthers 2, subglobose; a conspicuous, flattened median staminode present; style relatively thick.....CYPRIPEIDIEAE
- 3(1). Pollinia 2 to 8, hard, waxy; anther usually caducous; leaves various, often articulate; habit of growth various.....EPIDENDREAE
3. Pollinia 2 or 4, soft, mealy, in tetrads or granular masses; anther persistent or deciduous; leaves usually herbaceous, not articulate; growth usually sympodial with a terminal inflorescence.....4
- 4(3). Anther erect or reclinate (rarely incumbent), persistent, usually broadly joined to the column; pollinia in soft masses (sectile), caudicles arising from the base of the pollinia.....ORCHIDEAE
4. Anther erect or incumbent, narrowly joined to the column, commonly caducous or withering; pollinia mealy or sectile, without caudicles or these indistinct and terminal.....5
- 5(4). Anther terminal and operculate (incumbent) or rarely erect, usually more or less versatile; stems often with corms or corm-like thickenings.....EPIDENDREAE
5. Anther more or less erect, often dorsal (terminal and operculate in some species of *Acianthus*); stems without corms or other thickenings.....NEOTTIEAE

SYNONYMY AND DISCUSSION

In the following section we give keys to subtribes and list the subtribes alpha-

betically under the tribes, with synonymy and discussion where appropriate. We have not given full citations with the names of tribes and subtribes, but the papers containing new tribes or subtribes are indicated by an asterisk in the bibliography. We estimate that there are about 600 distinct, valid genera in the Orchidaceae. A really critical enumeration of genera is not yet possible. The lists given here are based primarily on Schlechter (1926), and doubtless contain some genera which do not merit recognition, while omitting others which should be listed. Only for the *Epidendrum* and *Oncidium* alliances can we indicate with some confidence the genera which will be maintained by critical revision; and, even here, there are genera of which we have not yet seen adequate or living material. If these alliances are representative of the family, the total number of valid genera may be well under 600.

Subfamily CYPRIPEDIOIDEAE Lindley (Diandrae Kunth, Pleonandrae Pfitzer [1903], Apostasioideae Wettstein)

Tribe 1. APOSTASIEAE R. Brown (Pulverae Blume, in part)

Some authors have excluded the Apostasiae as a separate family. We, however, agree with Rolfe (1909), J. J. Smith (1934), Mansfeld (1934) and Holttum (1953), that these plants cannot logically be excluded from the family without also excluding the Cyripedieae, and we feel that neither action is desirable. A classification which excludes the Apostasiae because they are inconspicuous and retains the Cyripedieae because they are showy is scarcely acceptable. It is possible, of course, that detailed study will show the Apostasiae to be basically different from other orchids in some features. As far as present knowledge goes, they are primitive orchids, and quite as closely related to some Neottieae as these are to the other orchids. As Godfery (1932) indicates, there is little evidence of close relationship between the Apostasiae and Cyripedieae, even though they show the same basic plan of flower structure. It is quite possible that the current subfamilial division is artificial.

Apostasia, Neuwiedia.

Tribe 2. CYPRIPEDIEAE

The four genera of ladyslippers form a relatively uniform relic group. They are markedly divergent from most other orchids in that the median anther is represented by a large shield-like staminode. In spite of their differences, the ladyslippers are orchids in good standing. The three abaxial stamens, resupination, reduction in seed structure, mycorrhizal relationship, and the less obvious features which predispose the family to evolution as epiphytes are themes which run throughout the family. The primitive features to be found in *Selenipedium* are strongly reminiscent of those found in other primitive orchids, though they do not, of course, necessarily indicate close relationship. Mansfeld (1937a) notes some resemblances between the Cyripedieae and *Epipactis*.

Cypripedium, Paphiopedilum, Phragmipedium, Selenipedium.

Subfamily ORCHIDOIDEAE (Monandrae Kunth)

Tribe 3. NEOTTIEAE Lindley (Granulosae Blume [in part], Pulverae Blume [in part], Goodyereae King & Pantling, Listereae King & Pantling, Polychondreae Schltr., Epipactieae Hatch [illegitimate, because nomenclaturally superfluous when published])

KEY TO SUBTRIBES

1. Anther more or less terminal, erect or inclined, projecting beyond the stigma or rostellum; viscidium, if present, commonly attaching to the base or ventral surface of the pollinia, rarely to the apex.....2
1. Anther dorsal, not projecting beyond the erect rostellum; pollinia usually attached to a terminal viscidium.....6
- 2 (1). Plants subterranean, or the flowers scarcely penetrating the surface of the soil; leafless saprophytes with the flowers in dense bracteate heads (Australia).....RHIZANTHELLINAE
2. Plants appearing above the soil, usually forming leaves.....3
- 3 (2). Rostellum sensitive, secreting a viscid drop when touched, or appearing to form a viscidium; small, slender-stemmed plants with 2 sub-opposite cauline leaves (leafless saprophytes in *Neottia*) (north temperate).....NEOTTIINAE
3. Rostellum not sensitive, with or without a viscidium; leaves usually either several or basal.....4
- 4 (3). Leaves cauline, spiral (absent in *Limodorum* and *Aphyllorchis*); lip usually divided into a basal, more or less saccate portion and a terminal, often hinged, portion (sub-entire and spurred in *Limodorum*); rostellum present or absent (largely north temperate).....LIMODORINAE
4. Leaves often basal; lip not as above; rostellum usually present.....5
- 5 (4). Lip hinged, with a retrorse appendage at the hinge, actively motile (sensitive) (Australasia).....PTEROSTYLIDINAE
5. Lip various, but not actively motile (South America and Australasia).....CHLORAEINAE
- 6 (1). Column with distinct lateral wings or staminodia; plants with fascicled roots and basal leaves.....7
6. Column usually without distinct wings or staminodia; habit various.....9
- 7 (6). Pollinia with a distinct caudicle-like stipe (Australasia).....PRASOPHYLLINAE
7. Pollinia without a stipe.....8
- 8 (7). Staminodia very prominent, scarcely adnate to the style; column not more or less hidden by the enfolding lip base; sepals or petals relatively broad (Australasia).....DIURIDINAE
8. Staminodia relatively small; column very short, nearly hidden by the base of the lip; both sepals and petals very narrow (Australasia).....CRYPTOSTYLIDINAE
- 9 (6). Rostellum sensitive, secreting a viscid drop when touched, or appearing to form a viscidium; small, slender-stemmed plants with 2 subopposite cauline leaves (leafless saprophytes in *Neottia*) (north temperate).....NEOTTIINAE
9. Rostellum not sensitive, usually with a distinct viscidium; habit not as above (wide-spread).....SPIRANTHINAE

CHLORAEINAE Pfitzer (Caladeniinae Pfitzer, Thelymitrinae Pfitzer, Acianthinae Schltr., Corysanthinae Schltr., Megastylidinae Schltr., Corybasinae Mansf. [not validly published, unless later (1954) reference to Corysanthinae Schltr. be taken to validate its publication as a new name. Corysanthinae, however, is a valid name, though based on a synonym])

This is the group which includes most of the bizarre Australian genera. The striking modifications have led to the naming of several subtribes, but these do not seem tenable, at least as previously delimited. *Thelymitra* is distinctive because of its nearly regular perianth, which is frequently blue, but it is closely allied to the

other genera through *Calochilus*, *Adenochilus* and *Glossodia*. Some species of *Thelymitra* are unusual for this group in the attachment of the rostellum or viscidium to the apex of the pollinia, but this is not consistent within the genus. Some species of *Acianthus* are very unusual in the form of the column and the position of the anther (operculate), but *A. reniformis* is more representative of the subtribe in these features; Mansfeld's action in grouping *Acianthus* with *Caladenia*, thus seems correct. *Corybas* is closely related to *Caladenia*. The three American genera *Chloraea*, *Bipinnula* and *Asarca* are somewhat distinctive in habit, but the other American genus, *Codonorchis*, is closely related to both *Chloraea* and *Caladenia*. Most of the Australian genera show a characteristic pitted, conic anther.

Acianthus, *Adenochilus*, *Asarca*, *Bipinnula*, *Burnettia*, *Caladenia*, *Calochilus*, *Chiloglottis*, *Chloraea*, *Codonorchis*, *Corybas*, *Epiblema*, *Eriochilus*, *Glossodia*, *Leptoceras*, *Lyperanthus*, *Megastylis*, *Rimacola*, *Thelymitra*, *Townsonia*.

CRYPTOSTYLIDINAE Schltr.

Cryptostylis is a distinctive genus, though without striking key features. Some species mimic insects and are involved in the strange relationship of pseudo-copulation. This subtribe, the Diuridinae and the Prasophyllinae seem to form a distinct group with column structure similar to that of the Spiranthinae. The degree of relationship to the Spiranthinae is uncertain.

Coilochilus, *Cryptostylis*.

DIURIDINAE Bentham

This group is of special morphological interest because of the large staminodia and because the filament and style are scarcely united into a column. Some Spiranthinae show similar columnar structure, though without the staminodia.

Diuris, *Orthoceras*.

LIMODORINAE Bentham (Cephalantherinae Pfitzer, Epipactiinae Godfrey)

The Limodorinae include genera which are quite primitive in some respects, and, being largely European, they have been studied much more than other primitive orchids.

Aphyllorchis, *Cephalanthera*, *Epipactis*, *Limodorum*.

NEOTTIINAE (Listerinae Schltr.)

These genera are distinctive in the sensitive rostellum, which forcibly extrudes a viscid droplet when touched. The anther is either erect or somewhat incumbent on the subequal rostellum. These genera show some resemblances to the Limodorinae, and, like that group, have relatively large chromosomes (Duncan, 1959).

Listera, *Neottia*.

PRASOPHYLLINAE Schltr.

Mansfeld placed these genera with *Thelymitra*, but they are distinctive in aspect, and unusual in the possession of stipes. These are generally described as

caudicles, but are not derived from the pollinia (see Vermeulen, 1959). This group seems more nearly allied to the Diuridinae and Cryptostylidinae.

Corunastylis, Goadbyella, Microtis, Prasophyllum.

PTEROSTYLIDINAE Pfitzer (Drakaeinae Schltr.)

These Australian genera are remarkable for their sensitive, motile lip, but very closely allied to the Chloraeinae, and especially to *Chiloglottis*.

Caleana, Drakaea, Pterostylis, Spiculaea.

RHIZANTHELLINAE Rogers

Rogers placed this group near the Gastrodiinae, but the form of the lip, column and anther indicate that they are allied to *Caladenia*.

Cryptanthemis, Rbizanthella.

SPIRANTHINAE Bentham (Corymbidinae Bentham [based on *Corymbis*, an orthographic variant of *Corymborchis*], Cranichidinae Pfitzer, Physurinae Pfitzer [based on *Physurus* L. C. Rich., nom. nud.], Tropidiinae Pfitzer, Maniellinae Schltr.)

We feel confident that the Spiranthinae and Cranichidinae should be merged. These groups have much the same floral structure, and we see little justification for separating them, especially if some American authors are correct in reducing Schlechter's Spiranthinae nearly to a single genus. The genera included in the *Goodyera* alliance are somewhat distinct in habit (rooting at the nodes, rather than roots fascicled), but agree well in floral features. Here, too, there seem to be too many genera. If future study should indicate the advisability of segregating the group as a separate subtribe, the name might be based on the familiar genus *Goodyera*. The *Tropidia* alliance seems to have the strongest claim to subtribal distinction, but no differences in floral structure have been demonstrated. In habit, these genera resemble *Palmorchis*, of the Sobraliinae, and *Apostasia*. The earliest subtribal name, Corymbidinae, should be changed in form, if it is to be used.

KEY TO ALLIANCES

1. Stem hard, woody; leaves subcoriaceous, strongly plicate, with several prominent nerves beneath (widespread).....*Tropidia* alliance
1. Stem and leaves herbaceous, leaves not strongly plicate.....2
- 2(1). Roots not fascicled, scattered along the stem or rhizome; pollinia often sectile (widespread).....*Goodyera* alliance
2. Roots usually fascicled; pollinia not sectile.....3
- 3(2). Flower resupinate, lip lowermost (widespread, but predominantly American).....*Spiranthes* alliance
3. Flower not resupinate, lip uppermost (American).....*Cranichis* alliance
 - a. GOODYERA ALLIANCE: *Anoectochilus, Cheirostylis, Cystopus, Cystorchis, Dicrostylis, Dossinia, Erythrodus (Physurus), Eucosia, Eurycentrum, Gonatostylis, Goodyera, Gymnochilus, Haemaria, Herpysma, Hetaeria, Hylophila, Kublbasseltia, Lepidogyne, Macodes, Moerenhoutia, Myrmechis, Odontochilus, Orchipedum, Papuaea, Platylepis, Tubilabium, Vrydagzynea, Zeuxine.*
 - b. CRANICHIS ALLIANCE: *Altensteinia, Baskervillea, Cranichis, Fuertesella, Pontbeiva, Porphyrostachys, Prescottia, Pseudocentrum, Pterichis, Solenocentrum, Stenoptera, Wullschlaegelia.*

c. SPIRANTHES ALLIANCE: *Centrogenium*, *Eurystyles*, *Lankesterella*, *Manniella*, *Pelexia*, *Sarcoglottis*, *Sauroglossum*, *Spiranthes*.

d. TROPIDIA ALLIANCE: *Corymborchis*, *Tropidia*.

Tribe 4. ORCHIDEAE (Granulosae Blume. [in part], Ophrydeae Lindley, Epipogiaceae Parlatore)

Here, except for the inclusion of the Epipogiinae in this tribe, we have followed essentially the classification of Bentham, which seems to be the best. There are still several problems in the morphological interpretation of flower structure in the Orchideae. Until this is better understood, it is difficult to consider the evolution or relationships of the group. As Godfery (1933) and Swamy (1949) have indicated, the Orchideae are clearly more highly specialized than the majority of Neottieae, and should not precede them in a phylogenetic scheme.

KEY TO SUBTRIBES

1. Lip erect, adnate to the face of the column, commonly bearing an appendage which overtops the anther; dorsal sepal and petals commonly forming a hood (Old World).....CORYCIINAE
1. Lip free from the column.....2
- 2(1). Leafless saprophytes; the anther erect or incumbent, narrowly attached to the column (Old World).....EPIPOGIINAE
2. Autophytes with green leaves (except for *Silvorchis*); the anther erect or reclinate, broadly attached to the column.....3
- 3(2). Anther erect or suberect, not projecting dorsally from the column; stigma simple or often divided into 2 separate, often stipitate, lobes; spur, if present, single and formed by lip (widespread).....ORCHIDINAE
3. Anther more or less reclinate, projecting dorsally from the column, or recumbent, with the base uppermost, rarely suberect; stigma not divided into two completely separate lobes; median sepal sometimes spurred (Old World, predominantly African).....DISINAE

CORYCIINAE Bentham (Disperidinae Schltr.)

Ceratandra, *Corycium*, *Disperis*, *Pterygodium*.

DISINAE Bentham (Satyriinae Pfitzer)

These genera seem better treated as a single subtribe. The position of the saprophytic *Silvorchis* is uncertain.

KEY TO ALLIANCES

1. Flowers resupinate; spur, when present, formed by median sepal; column relatively short (Africa).....*Disa* alliance
1. Flowers not resupinate; spur or spurs, when present, formed by lip; column usually elongate (Old World).....*Satyrium* alliance
 - a. DISA ALLIANCE: *Brownleea*, *Disa*, *Schizodium*.
 - b. SATYRIUM ALLIANCE: *Pachites*, *Satyrium*, *Silvorchis*?

EPIPOGIINAE Schltr.

Recent authors have placed these genera in the Neottieae, but the persistent anther and the sectile pollinia with basal caudicles indicate a much closer affinity with the Orchideae. Godfery (1933) followed Parlatore (1858) in treating

Epipogium as the type of a separate tribe. In *Epipogium apbyllum* the anther is incumbent and the pollinia are parallel with the caudicles, which attach to a viscidium near the apices of the pollinia. It is not clear that the incumbent anther indicates a relationship with the primitive Epidendreae; the peculiar orientation of the caudicles suggests that it is a derived condition in this species. Rohrbach (1866) gives detailed illustrations of *E. apbyllum*. The anther is erect in the autogamous *E. roseum* (as it is in the young bud of *E. apbyllum*) and the caudicles are apparently functionless. The detailed structure of *Stereosandra* is not well known, but the anther is erect and the pollinia bear caudicles. These genera probably are not very closely related to the Gastrodiinae, though, being saprophytes, they are superficially similar.

Epipogium, Stereosandra.

ORCHIDINAE (Angiadeniae Parlature, Habenariinae Bentham, Serapiadinae Bentham, Ophrydinae Bentham & Hooker, Gymnadeniinae Pfitzer, Androcorydinae Schltr., Huttonaeinae Schltr., Platantherinae Schltr.)

The union of the Platantherinae and Habenariinae of Schlechter is certainly appropriate, when there is yet disagreement as to whether or not *Habenaria* and *Platanthera* are distinct genera. This group is seriously in need of monographic attention. The extreme "splitting" of European workers combined with the (equally unrealistic) extreme "lumping" of recent American workers has led to taxonomic chaos.

Aceratorchis, Aceras, Acrostylia, Amitostigma, Anacamptis, Androcorys, Arnottia, Bartholina, Benthamia, Bicornella, Bonatea, Brachycorythis, Centrostigma, Chamaeorchis, Coeloglossum, Cynorchis, Dactylorchis, Deroemera, Diphylax, Diplacorchis, Diplomeris, Dithrix, Galeorchis, Gennaria, Gyaladenia, Gymnadenia, Habenaria, Herminium, Himantoglossum, Holothrix, Huttonaea, Leucorchis, Loriglossum, Neobolusia, Neotinea, Neottianthe, Nigritella, Ophrys, Orchis, Peristylus, Perularia, Phyllomphax, Platanthera, Platycoryne, Roeperorchis, Schizochilus, Schwartzkopffia, Serapias, Stenoglottis, Steveniella, Traunsteinera, Tylostigma.

Tribe 5. EPIDENDREAE Lindley (Cereaceae Blume, Arethuseae Lindley, Gastrodieae Lindley, Malaxideae Lindley, Vandae Lindley, Kerosphaerae Schltr., all but 4 of Pfitzer's 31 tribes [1887], Sturmieae Pfitzer [1897]).

KEY TO SUBTRIBES

1. Growth sympodial, each shoot of limited growth and followed by other shoots from (usually basal) axillary buds (except *Vanilla* and *Galeola*, which are fleshy vines).....2
1. Growth monopodial, the inflorescence axillary and the stem usually growing indefinitely in length.....38
- 2 (1). Pollinia soft, mealy.....3
2. Pollinia in compact masses, more or less hard, waxy in texture.....7
- 3 (2). Sepals and petals more or less united (except in *Stigmatodactylus*); flowers often tubular; plants saprophytic (widespread).....GASTRODIINAE
3. Sepals and petals not united; plants autophytes or saprophytes.....4
- 4 (3). Plants with corms; stems short; leaves narrow and grass-like (North America and temperate Asia).....ARETHUSINAE
4. Plants without corms (except in *Nervilia*), stems elongate; leaves various.....5
- 5 (4). Leaves articulated at the base, deciduous (America and Africa).....SOBRALIINAE
5. Leaves not articulated, persistent.....6

6(5).	Seed with wing or sclerotic testa; fleshy vines, or sub-shrubs with a distinct calyculus below the ovary (widespread).....	VANILLINAE
6.	Seed without wing or sclerotic testa, seed coat thin and reticulate; plants not as above (widespread).....	POGONIINAE
7(2).	Inflorescence terminal or upper axillary, occasionally on young shoots before leaves develop (lateral and basal in a few species of <i>Epidendrum</i> , <i>Dendrobium</i> , <i>Coelogyne</i> and <i>Pleurothallis</i>).....	8
7.	Inflorescence lateral, usually basal.....	25
8(7).	Leaves plicate.....	9
8.	Leaves conduplicate.....	16
9(8).	Flowers borne on separate leafless shoots which alternate with the unifoliate vegetative shoots (Asia).....	COLLABIINAE
9.	Flowers and foliage borne on same shoot.....	10
10(9).	The pollinia naked, without caudicles (see also <i>Pseuderia</i> , Dendrobiinae) (widespread).....	LIPARIDINAE
10.	The pollinia bearing caudicles.....	11
11(10).	Pollinia 8.....	12
11.	Pollinia 2 or 4.....	13
12(11).	Flower with a distinct column foot and mentum (Asia, <i>Eria</i> alliance).....	EPIDENDRINAE
12.	Flower without a column foot or mentum (America and Africa).....	SOBRALIINAE
13(11).	Pseudobulbs or corms of a single internode; pollinia 4, usually without a viscidium (Asia).....	COEOLOGYNINAE
13.	Pseudobulbs or corms, if present, usually of several internodes.....	14
14(13).	Stems usually forming either corms or pseudobulbs; rostellum with a distinct viscidium (widespread).....	CYRTOPODIINAE
14.	Stems elongate, not forming corms or pseudobulbs; viscidium present or absent.....	15
15(14).	Plants Asiatic, usually with large, showy flowers.....	THUNIINAE
15.	Plants American, with small, inconspicuous flowers (<i>Palmorchis</i>).....	SOBRALIINAE
16(8).	Pollinia 2, 4, 6 or 8, clavate or laterally flattened.....	17
16.	Pollinia 2 and semi-globose or 4 and superposed.....	22
17(16).	Asiatic plants with elongate stems and terminal inflorescence of large showy flowers; pollinia 8.....	THUNIINAE
17.	Not with the above combination of features.....	18
18(17).	The ovary articulated to the pedicel, the pedicel persisting; pollinia clavate; plants without pseudobulbs (America).....	PLEUROTHALLIDINAE
18.	The ovary not articulated to the pedicel, the pedicel falling with the flower.....	19
19(18).	Pollinia naked, without caudicles (rarely with viscidium).....	20
19.	Pollinia with caudicles.....	21
20(19).	Flowers with a distinct column foot and mentum (except in <i>Pseuderia</i>) (widespread, predominantly Asiatic).....	DENDROBIINAE
20.	Flowers without a column foot or mentum (widespread).....	LIPARIDINAE
21(19).	Clinandrium more or less petaloid, overtopping the anther; pollinia 4; pseudobulbs of a single internode; inflorescence terminal (Asia).....	COEOLOGYNINAE
21.	Clinandrium usually not petaloid nor overtopping the anther; pollinia 2-8; pseudobulbs usually of several internodes; inflorescence often upper axillary (widespread).....	EPIDENDRINAE
22(16).	Plants with pseudobulbs.....	23
22.	Plants without pseudobulbs, stems elongate.....	24
23(22).	Pseudobulbs of a single internode; clinandrium petaloid and overtopping the anther; pollinia without a viscidium (Asia).....	COEOLOGYNINAE
23.	Pseudobulbs of several internodes; clinandrium not petaloid, nor overtopping anther, pollinia with a viscidium (<i>Polystachya</i> , largely African).....	EPIDENDRINAE
24(22).	Lip free from the column; flowers large (Asia).....	THUNIINAE
24.	Lip completely adnate to the column; flowers very small (<i>Epidanthus</i> , America).....	EPIDENDRINAE
25(7).	Leaves plicate.....	26
25.	Leaves conduplicate.....	30

26 (25).	Pseudobulbs or corms of several internodes, when present.....	27
26.	Pseudobulbs usually of a single internode (rarely absent in the <i>Zygopetalum</i> alliance).....	29
27 (26).	Pollinia 4 or (usually) 8, clavate or laterally flattened, without stipe and usually without viscidium (widespread).....	BLETHINAE
27.	Pollinia 2, or 4 and superposed, with a distinct viscidium and usually with a stipe.....	28
28 (27).	Pollinia 2 or 4; plants usually with corms, sometimes with elongate pseudobulbs and basal inflorescence; lip often hinged or spurred (widespread).....	CYRTOPODIINAE
28.	Pollinia 4; plants with elongate pseudobulbs; inflorescences usually lateral on the pseudobulb; lip often saccate, but neither hinged nor spurred; anther usually sensitive, forcibly expelling the pollinia when triggered (America).....	CATASETINAE
29 (26).	Lip immobile, often with antenna-like processes; flowers usually racemose (America).....	STANHOPEINAE
29.	Lip usually hinged at base and mobile, without antenna-like processes; flowers often solitary (America).....	MAXILLARIINAE
30 (25).	Pollinia 2-8 (usually 4), clavate or laterally flattened, often without caudicle or stipe.....	31
30.	Pollinia 2, or 4 and superposed, usually with stipe and viscidium.....	36
31 (30).	Pollinia naked, without caudicles, usually without a viscidium, never with stipe or caudicles.....	32
31.	Pollinia not naked, usually with distinct viscidium and stipe or caudicles.....	33
32 (31).	Pollinia 2 or 4; inflorescence various (widespread, predominantly Old World).....	DENDROBIINAE
32.	Pollinia 8; inflorescence paniculate (New Guinea).....	RIDLEYELLINAE
33 (31).	Flower with a pronounced column foot; stipe present, frequently double.....	34
33.	Column foot slight or absent; no true stipe present.....	35
34 (33).	Lip and base of column more or less united into a tubular structure (Asia).....	THECOSTELINAE
34.	Lip free from column, not forming a tubular structure (Old World).....	GENYORCHIDINAE
35 (33).	Pollinia 4, the caudicles inconspicuous; roots extremely thick (Ceylon and South India).....	ADRORHIZINAE
35.	Pollinia 8, with a long caudicle; roots not especially thick (Asia).....	THELASHINAE
36 (30).	Pseudobulbs usually of several internodes (Old World).....	CYMBIDIINAE
36.	Pseudobulbs of a single internode.....	37
37 (36).	Lip usually hinged to the base of the column, mobile; flowers usually solitary; often with a wide semilunate viscidium and short indistinct stipe (America).....	MAXILLARIINAE
37.	Lip not hinged to the base of the column, immobile; viscidium usually compact, clearly differentiated from the stipe (America).....	ONCIDIINAE
38 (1).	Clinandrium petaloid, overtopping anther; small American plants.....	PACHYPHYLLINAE
38.	Clinandrium not petaloid, not overtopping the anther.....	39
39 (38).	Old World plants.....	40
39.	American plants.....	41
40 (39).	Pollinia 8, without a stipe (but with a long caudicle).....	THELASHINAE
40.	Pollinia 2 or 4, with a distinct stipe (see also <i>Dipodium</i> , <i>Cymbidiinae</i>).....	SARCANTHINAE
41 (39).	Flower with a distinct spur.....	42
41.	Flowers without spurs (except in <i>Rodriguezia</i> , <i>Oncidiinae</i>).....	43
42 (41).	Flowers in racemes, or plants leafless; spur not concealed by a bract.....	SARCANTHINAE
42.	Flowers solitary; spur parallel with the pedicel and usually concealed by a bract; plants leafy.....	CRYPTOCENTRINAE
43 (41).	Lip hinged to the base of the column, mobile; flowers usually solitary, often with a wide semilunate viscidium and a short indistinct stipe.....	MAXILLARIINAE
43.	Lip not hinged to the base of the column, immobile; viscidium usually compact, clearly differentiated from the stipe.....	ONCIDIINAE

ADRRORHIZINAE Schltr.

Schlechter placed this group near the Coelogyninae, while Kränzlin allied them to *Dendrobium* or *Eria*. These views are not necessarily opposed, as we believe the Coelogyninae and Epidendrinae (esp. *Eria*) to be closely related. These genera appear to be closest to *Eria*, but are distinguished by the lateral inflorescence and fewer pollinia.

Adrorhizon, *Josephia*.

ARETHUSINAE Bentham (Bletillinae Schltr.)

These largely north temperate genera have corms or fleshy rhizomes and closely resemble the Bletinae, but the pollinia are mealy and without caudicles. *Crybe* and *Jimensia* may well be more closely related to *Bletia* than to *Arethusa*.

Arethusa, *Calopogon*, *Crybe*, *Jimensia* (*Bletilla*).

BLETIINAE Bentham (Chysiinae Schltr., Phajinae Schltr.)

Chysis is apparently allied to *Acanthephippium*. *Coelia* and *Bothriochilus* are placed here on the subplicate leaves, the lateral inflorescence and the relatively soft, subclavate pollinia. They do not show close relationship to the genera of the Epidendrinae. *Basiphyllaea*, similarly, is out of place among the Epidendrinae; it seems to differ from *Bletia* primarily in size. *Hexalectris* is closely allied to *Bletia*, and less so to *Chysis*. *Bletia* closely resembles some species of *Laelia* (Epidendrinae) in flower structure, and these genera may be more closely related than is indicated by our present classification.

Acanthephippium, *Ancistrochilus*, *Anthogonium*, *Ascotaenia*, *Aulostylis*, *Basiphyllaea*, *Bletia*, *Bothriochilus*, *Calanthe*, *Chysis*, *Coelia*, *Gastorchis*, *Hexalectris*, *Ipsea*, *Pachystoma*, *Phajus*, *Plocoglottis*, *Spathoglottis*, *Taeniopsis*.

CATASETINAE Schltr.

This is an interesting group because of the usually sensitive anther, but some species of *Catasetum* (or *Clowesia*) lack this feature. These genera are apparently related to the Cyrtopodiinae (especially *Cyrtopodium* and *Galeandra*).

Catasetum, *Cycnoces*, *Mormodes*.

COELOGYNINAE Bentham

The flower structure of this group is close to that of the Epidendrinae and Bletinae, but the habit is distinctive, and the pollinia are superposed in some genera.

Acoridium, *Basigyne*, *Bulleyia*, *Coelogyne*, *Dendrochilum*, *Dickasonia*, *Gynoglottis*, *Ischnogyne*, *Nabalua*, *Neogyne*, *Otochilus*, *Panisea*, *Pholidota*, *Pleione*, *Pseudacroridium*, *Sigmatogyne*.

COLLABIINAE Schltr.

These genera seem to be very closely allied to both the Bletinae and the Cyrtopodiinae. *Tainia* and *Nephelaphyllum* are certainly allied to *Eulophia*. The

habit of this group is relatively distinctive, while the structure of the pollinia is somewhat diverse.

Chrysoglossum, *Collabium*, *Diglyphosa*, *Hancockia*, *Mischobulbon*, *Nephelaphyllum*, *Pilophyllum*, *Tainia*.

CRYPTOCENTRINAE Garay

These genera were placed in the Maxillariinae by Schlechter, apparently because of the habit and 1-flowered inflorescence. Schlechter considered *Sepalosaccus* (which we have not seen) to be intermediate between *Maxillaria* and *Cryptocentrum*. Garay has created a separate subtribe for *Cryptocentrum*, on the basis of the conspicuous spur (other features listed by Garay are present in the *Maxillaria* alliance or are different aspects of the spur). According to Garay, *Cryptocentrum* would find its closest affinity in the Oncidiinae, but we are unable to agree with this conclusion. We believe that the genus most closely approaches *Trigonidium* (Maxillariinae). *Cryptocentrum* is usually monopodial, but sympodial species occur. The genus is rather distinctive and may merit a separate subtribe, but further study is needed.

Anthosiphon, *Cryptocentrum*.

CYMBIDIINAE Benthams

The Cymbidiinae bear a general resemblance to the Blettiinae, but seem to be distinct in both habit and structure of pollinia. A single hybrid between *Pbajus* and *Cymbidium* is recorded. Rolfe (1911) has shown that this parentage is probably in error. Many more recent attempts to cross these genera have failed. *Ansellia* closely resembles *Grammatophyllum* and, like that genus, has conduplicate leaves and sometimes bears lateral inflorescences (while *Grammatophyllum* may rarely produce a terminal inflorescence). *Ansellia* must be placed in the Cymbidiinae, if this group can be maintained separate from the Cyrtopodiinae. Perrier (1941) assigns *Grammangis* and *Cymbidiella* to the Cyrtopodiinae and suggests that the two groups cannot be separated. The Cymbidiinae generally have elongate stems or pseudobulbs with several or many leaves, while the few Cyrtopodiinae which have conduplicate leaves usually have very short, unifoliate pseudobulbs, but this is surely not a very convincing separation; further study is needed. Holttum (1958) indicates the probable relationships of this subtribe to the Sarcanthinae, from which a few monopodial species are not easily distinguished by any "key" feature. *Acriopsis* resembles *Porphyroglottis*, but is unusual in the petaloid clinandrium, the union of the lip and column, and the form of the pollinia. It may deserve a separate subtribe, but it is not closely allied to *Thecostele*.

Acriopsis?, *Ansellia*, *Caloglossum*, *Cymbidiella*, *Cymbidium*, *Cyperorchis*, *Dipodium*, *Grammangis*, *Grammatophyllum*, *Poicilantbe*, *Porphyroglottis*.

CYRTOPODIINAE Benthams (Eulophiinae Benthams, Corallorhizinae Schltr., Calypsoinae Schltr., Eulophidiinae Schltr.)

Several of these genera were placed in the Polystachyinae by Schlechter, but they show little affinity to *Polystachya*, and are separated from the Cyrtopodiinae only by the position of the inflorescence. The peculiar anther of *Galeandra* is duplicated

in some species of *Eulophia* (and among the Collabiinae). *Corallorbiza* is clearly allied to *Oreorchis* and *Aplectrum*. While brought together from diverse parts of Schlechter's system, this forms one of the more natural subtribes. It is usually characterized by corms (rhizomes in the saprophytes, pseudobulbs in some species of *Galeandra*, *Eulophia* and *Cyrtopodium*), plicate leaves and 2 or 4 (superposed) pollinia with a distinct viscid disk, but little or no stipe. The lip and column of *Calypso* are distinctive, but it is apparently related to *Dactylostalix* and *Yoania*, which are more characteristic of the subtribe. For the placement of *Yoania* in this group, see Finet (1896). *Cyrtopodium* is somewhat distinctive in habit and the form of the lip, but the habit is approached by some species of *Eulophia* and *Galeandra*. Schlechter's inclusion of *Eulophia* in the Cyrtopodiinae would seem to require the use of this name, rather than Eulophiinae, for this group.

Schlechter assigns *Eulophidium* to a separate subtribe, but Mansfeld places it in the Cyrtopodiinae. Perrier (1941) goes so far as to treat *Eulophidium* as a subgenus of *Lissochilus*. The American species are distinctive in habit and closely resemble *Oncidium* section *Miltoniastrum*. This section of *Oncidium* has relatively simple rostellar structure, and it is possible that *Eulophidium* represents a phyletic link between the Cyrtopodiinae and the Oncidiinae.

Acrolophia, *Calypso*, *Corallorbiza*, *Cremastra*, *Cyanaeorchis*, *Cyrtopodium*, *Dactylostalix*, *Eulophia*, *Eulophidium*, *Eulophiella*, *Galeandra*, *Geodorum*, *Govenia*, *Graphorkis*, *Lissochilus*, *Pteroglossaspis*, *Tipularia*, *Warrea*, *Yoania*.

DENDROBIINAE Bentham (Bulbophyllinae Schltr.)

We follow Bentham in associating *Dendrobium* and *Bulbophyllum* in a separate subtribe. We do not doubt that *Dendrobium* is related to *Eria*, but the relationship to *Bulbophyllum* is much closer, and the naked pollinia of this group are quite distinctive. *Dendrobium* and *Bulbophyllum* are primarily distinguished by the position of the inflorescence, and even this is subject to exceptions, as in *D. laterale* L. Wms. The embryological data also support a close relationship between these genera (Swamy, 1949). These are probably the largest genera of the orchids, as now treated. Holttum (1953) notes that the sections of *Dendrobium* are biologically far more distinct than many orchid genera in other subtribes. It may be that the naked pollinia severely limit the possibilities of morphological variation in flower structure. Generic limits in the Liparidinae (with naked pollinia) are similarly difficult. If this hypothesis is correct, the Genyorchidinae, which are surely derived from *Bulbophyllum*-like ancestors, may have escaped these limitations by the development of stipes, and show correspondingly greater variation in flower structure.

Bulbophyllum, *Dendrobium*, *Epigeneium*, *Pedilochilus*, *Pseuderia*, *Saccoglossum*.

EPIDENDRINAE (Eriinae Bentham, Laeliinae Bentham, Stenoglossinae Bentham, Podochilinae Bentham & Hooker, Cattleyinae Pfitzer, Ponerinae Pfitzer, Glomerinae Schltr., Polystachyinae Schltr., Epidanthinae L. Wms.)

We are relatively familiar with the genera of this group, especially the American ones, and we have found it necessary to unite several previously recognized

subtribes under this one. It is quite possible that some of the alliances which are discussed below will eventually prove to deserve subtribal status, but we are unable to find any feature or combination of features which will convincingly separate them. The key features which have been used are largely imaginary. The name Epidendrinae is required for the subtribe of the Epidendreae which includes the type genus. Hawkes and Heller (1959) list the "subtribe Stolziinae," but we have not been able to locate any valid publication of such a name. Schlechter (1926) and Summerhayes (1953) agree that *Stolzia* is closely related to *Polystachya*.

KEY TO ALLIANCES

1. Pollinia laterally flattened or subglobose, 2-8.....2
1. Pollinia clavate, 4-8.....4
- 2(1). Plants African (except for some species of *Polystachya*—pseudobulbous plants with terminal raceme, a distinct column foot, 2-4 pollinia, a distinct viscidium, and the callus of the lip usually with mealy hairs).....*Polystachya* alliance
2. Plants not African.....3
- 3(2). Plants American; pollinia 2-8; inflorescence usually terminal.....*Epidendrum* alliance
3. Plants Asiatic; pollinia 8; inflorescence usually upper axillary.....*Eria* alliance
- 4(1). Rostellum elongate, beak-like; anther dorsal.....7
4. Rostellum short, not markedly projecting nor beak-like; anther more or less terminal.....5
- 5(4). Plants American, with slender, unifoliate stems, fleshy leaves and a dense spike of small rose-purple flowers.....*Arpophyllum* alliance
5. Plants of Old World.....6
- 6(5). Viscidium well developed; flowers usually in dense subcapitate clusters.....*Glomera* alliance
6. Viscidium usually absent; flowers not in dense subcapitate clusters.....*Eria* alliance
- 7(4). Asiatic plants with elongate stems and distichous leaves.....*Podochilus* alliance
7. American plants with short, unifoliate stems (*Meiracyllium*).....*Arpophyllum* alliance

a. ARPOPHYLLUM ALLIANCE

These two genera stand apart from the *Epidendrum* alliance in the possession of clavate rather than laterally flattened pollinia. The form of the pollinia and viscidium ally them to the *Glomera* and *Podochilus* alliances, and, especially, to the Pleurothallidinae, with which they agree in habit. They probably represent the ancestral stock of this distinctive American subtribe.

Arpophyllum, *Meiracyllium*.

b. EPIDENDRUM ALLIANCE

The classic distinction between the Laeliinae and the Ponerinae; the presence or absence of a column foot, is clearly an unnatural one, and largely a matter of degree. The column foot is slight in several of the genera, and, in fact, is present in some species of *Laelia* (in the section *Schomburgkia*). Several genera have been repeatedly shifted between the two groups, as for example *Domingoa*, *Nageliella* and *Hexisea*. *Domingoa*, though closely related to *Nageliella* and *Scaphyglottis*, has been crossed with *Encyclia*. *Nageliella* is clearly allied to some of the elements of the *Scaphyglottis* complex; and *Homalopetalum*, *Hexisea* and *Nidema*, similarly, show greater affinity to *Scaphyglottis* than to the other plants customarily included in the Laeliinae.

Williams has separated *Epidanthus* as a subtribe, on the basis of a distinct

viscidium. Such a viscidium, however, is found in most species of *Epidendrum*. *Epidanthus* is distinctive in the possession of only two pollinia, but in all other features it resembles true *Epidendrum*.

This alliance appears to be the most distinctive of those included here, and it is possible that it is not as closely related to *Eria* as the structure of *Ponera*, especially, suggests. It may be that the resemblances between *Ponera* and *Eria* are parallelisms, and not indicative of close relationship. We are reluctant, though, to recognize subtribes on the basis of distribution alone.

Alamania, *Barkeria*, *Brassavola*, *Broughtonia*, *Cattleya*, *Caularthron*, *Constantia*, *Dimerandra*, *Diothonea*, *Domingoa*, *Encyclia*, *Epidanthus*, *Epidendrum*, *Hexisea*, *Homalopetalum*, *Isabelia*, *Isobilus*, *Jacquiella*, *Laelia*, *Leptotes*, *Loefgrenianthus*, *Nageliella*, *Neocogniauxia*, *Nidema*, *Octadesmia*, *Orleanesia*, *Platyglottis*, *Ponera*, *Scaphyglottis*, *Sophronitella*, *Sophronitis*, *Tetramicra*.

c. ERIA ALLIANCE

This group is not clearly separable from either the *Epidendrum* alliance or the *Polystachya* alliance. The three may be thought of as the American, Asiatic and African segments of a single complex, though a few species of *Polystachya* are widespread.

Cryptochilus, *Eria*, *Porpax*.

d. GLOMERA ALLIANCE

These genera are very closely allied to *Eria*, though the viscidium is better developed. The two groups may not merit separation, even as alliances.

Aglossorhyncha, *Agrostophyllum*, *Ceratostylis*, *Chitonochilus*, *Cyphochilus*, *Earina*, *Epiblastus*, *Giulianettia*, *Glomera*, *Glossorhyncha*, *Ischnocentrum*, *Mediocalcar*, *Poaephyllum*, *Sarcostoma*, *Sepalosiphon*.

e. PODOCHILUS ALLIANCE

This group is closely allied to the *Glomera* alliance, and differentiated primarily by the more elongate rostellum.

Appendicula, *Chilopogon*, *Podochilus*.

f. POLYSTACHYA ALLIANCE

These genera show little affinity to the other genera grouped in the Polystachyinae by Schlechter. *Neobenthamia* has four laterally flattened pollinia and an indistinct viscidium (many species in the *Epidendrum* alliance have the viscidium better developed), while *Stolzia* has eight pollinia and no viscidium. *Polystachya* has a distinct viscidium and the pollinia are united into two in some species, while others bear four laterally flattened pollinia, as in the majority of the Epidendrinae. Some species of *Polystachya* have a small but distinct stipe, while this is not evident in other species which we have examined.

Neobenthamia, *Polystachya*, *Stolzia*.

GASTRODIINAE Pfitzer

The Gastrodiinae are all saprophytic, and the flowers are tubular in most species.

They are apparently allied to the Vanillinae and Pogoniinae. *Stigmatodactylus* is clearly out of place in the Chloraeinae (Acianthinae), and appears to be closely allied to *Didymoplexis* section *Leucolaena* (*Didymoplexiella*).

Auxopus, *Didymoplexis*, *Gastrodia*, *Stigmatodactylus*?, *Uleiorchis*.

GENYORCHIDINAE Schltr.

This group is allied to the Dendrobiinae, and especially to *Bulbophyllum*, but apparently differs in the possession of a distinct stipe or stipes.

Drymoda, *Genyorchis*, *Ione*, *Monomeria*.

LIPARIDINAE Benth (Microstylidinae Benth, Malaxidinae Benth & Hooker, Vargasiellinae C. Schweinf. [not validly published])

This subtribe, like the Dendrobiinae, is distinctive in the possession of completely naked pollinia. A viscidium is sometimes developed, but caudicles are lacking. The systematic position of the Liparidinae is not well understood. Mansfeld suggests a relationship to the Cyrtopodiinae (Calypsinae), as well as to the Neottiinae (tribe Neottieae), but neither relationship is well documented. Clearly, this group deserves further study.

The subtribe Vargasiellinae was proposed without description, and is thus not validly published. The only clear feature we can find which might be taken to distinguish *Vargasiella* from the Liparidinae is the distinct claw of the lip. The habit is distinctive among the American genera, but is less so when Old World genera are considered. This genus should also be compared with *Pseuderia* (Dendrobiinae).

Didicicia?, *Ephippiantibus*?, *Hippeophyllum*, *Imerinaea*, *Liparis*, *Malaxis*, *Oberonia*, *Orestia*, *Risleya*, *Vargasiella*.

MAXILLARIINAE Benth (Huntleyinae Schltr., Lycastinae Schltr., Zygopetalinae Schltr.)

We are unable to separate the Huntleyinae and Zygopetalinae even as alliances (see below). The close relationship between the *Lycaste* and *Zygopetalum* alliances is confirmed by artificial hybrids such as *Zygocaste*. The *Maxillaria* alliance is superficially separated from the *Lycaste* alliance by the conduplicate leaves, but floral structure indicates a close relationship. The structure of the pollinia is similar in *Xylobium*, *Bifrenaria* and *Maxillaria*. Of interest is *Bifrenaria minuta* Garay, which has slightly plicate leaves, but is otherwise a *Maxillaria*. We know of a hybrid between *Lycaste virginalis* and *Maxillaria variabilis*, though none of the plants has yet flowered. The difficulty of raising *Lycaste* seedlings to maturity is probably one reason that no such hybrids are yet registered.

KEY TO ALLIANCES

1. Callus usually wide, with conspicuous longitudinal ridges.....*Zygopetalum* alliance
2. Callus usually narrow, smooth.....2
- 2(1). Leaves plicate.....*Lycaste* alliance
2. Leaves conduplicate.....*Maxillaria* alliance

a. LYCASTE ALLIANCE

We have placed *Teuscheria* here, though its author assigned it to the *Bletiinae*. The shape of the anther and the four superposed pollinia with a distinct viscidium (large in *T. pickiana*, quite small in *T. venezuelana*) support this classification. The genus is described as lacking a viscidium, but we do not understand "Pollinia . . . inappendiculata, visco parco cohaerentia, sine glandula." The viscidium (and the resupinate flower) is clearly shown in Mrs. Allen's illustration of *T. pickiana* (Ceiba 4:272. 1955). *Neomoorea* and *Eriopsis* are assigned to the *Zygopetalinae* by Mansfeld (1937), but appear to fit as well or better in the *Lycaste* alliance.

Anguloa, *Bifrenaria*, *Eriopsis?*, *Lycaste*, *Neomoorea?*, *Rudolfiella*, *Teuscheria*, *Xylobium*.

b. MAXILLARIA ALLIANCE

Hoehne has separated some of the monopodial *Maxillarias* as a distinct genus, *Marsupiarina*, but it is doubtful that this is a natural group. *Maxillaria valenzuelana*, for example, is extremely closely related to *M. crassifolia* (a sympodial species) in all floral features, and seedlings of *M. crassifolia* have the habit of *M. valenzuelana*.

Chrysocynis, *Cyrtidium*, *Maxillaria*, *Mormolyca*, *Pityphyllum*, *Scuticaria*, *Sepalosaccus*, *Trigonidium*.

c. ZYGOPETALUM ALLIANCE

The *Huntleyinae* are traditionally separated from the *Zygopetalinae* by the conduplicate leaves, but this distinction is not usable. The leaves are subplicate in most species. We have observed cases in both *Zygopetalum mackayi* and *Cochleanthes flabelliformis* in which young growths with conduplicate vernation were seen in the same plant with growths of distinctly convolute vernation. The genera assigned to the *Zygopetalinae* usually have pseudobulbs, while those assigned to the *Huntleyinae* usually have the pseudobulbs inconspicuous or none. Some genera of this alliance, such as *Otostylis*, strongly resemble the *Cyrtopodiinae*, and suggest the origin of this subtribe from *Eulophia*-like ancestors.

Aganisia, *Batemannia*, *Bollea*, *Cheiradenia*, *Chondrorhyncha*, *Cochleanthes*, *Colax*, *Galeottia*, *Huntleya*, *Koellensteinia*, *Menadenium*, *Neogardneria*, *Otostylis*, *Paradisiantbus*, *Pescatoria*, *Promenaea*, *Stenia*, *Wareella*, *Zygopetalum*.

ONCIDIINAE Benth. (*Notyliinae* Benth., *Adinae* Pfitz., *Aspasiinae* Pfitz., *Ionopsidinae* Pfitz., *Odontoglossinae* Pfitz., *Trichopiliinae* Pfitz., *Bractiinae* Schltr., *Campanemiinae* Schltr., *Cochliodinae* Schltr., *Comparettiinae* Schltr., *Dichaeinae* Schltr., *Lockhartiinae* Schltr., *Macradeniinae* [Mansf.] Schltr., *Ornithocephalinae* Schltr., *Papperitziinae* Schltr., *Pterostemmiinae* Schltr., *Saundersiinae* Schltr., *Telipogoninae* Schltr., *Trichocentrinae* Schltr.)

It is in this group that we have committed the most wholesale reduction of subtribes. These changes, however, are required not only by the rapidly accumulating evidence of intergeneric fertility (see Moir, 1959), but by the patterns of morphological variation as well. Some of the "genera" placed in separate subtribes by Schlechter can not be distinguished by any feature known to us.

KEY TO ALLIANCES

1. Pollinia 2.....*Oncidium* alliance
 1. Pollinia 4.....2
 2(1). Column with elongate, beak-like rostellum; lip not anchor-shaped...*Ornithocephalus* alliance
 2. Column with a short rostellum, not beak-like; lip usually anchor-shaped.....*Dichaea* alliance

a. DICHAEA ALLIANCE

This genus is distinctive in habit and aspect, but closely related to the *Ornithocephalus* alliance. The pilose column with a "ligule" on the ventral surface is also found in *Telipogon* and allied genera.

Dichaea.

b. ONCIDIUM ALLIANCE

It might seem, from a survey of Schlechter's classification, that there would be a valid break within this group into two major alliances, those with spurs and those without. The presence or absence of a spur, however, is not consistent within the genera, and these groups are nearly all interfertile. We have successfully crossed *Comparettia* with *Oncidium*, *Trichocentrum*, *Trichopilia* and *Ionopsis*. *Rodriguezia*, similarly, is interfertile with a wide range of genera. *Trichopilia* is superficially distinct, in that the base of the lip enfolds the column, but this same feature is found in some species of *Miltonia*. *Notylia* is unusual in the dorsal position of the anther, but this, too, is inconsistent. *Lockhartia* is distinctive in habit, but has no other consistent feature to distinguish it from the other genera of this group. *Pterostemma* is poorly known, but its monopodial habit can not be taken to exclude it from this subtribe.

Ada, *Amparoa*, *Aspasia*, *Bractia*, *Brassia*, *Capanemia*, *Caucaea*, *Chaenanthæ*, *Cochlioda*, *Cobniella*, *Comparettia*, *Diadenium*, *Erycina*, *Gomesa*, *Hybochilus*, *Ionopsis*, *Leochilus*, *Lockhartia*, *Macradenia*, *Mesospinidium*, *Miltonia*, *Neodryas*, *Neokoebleria*, *Notylia*, *Odontoglossum*, *Oncidium*, *Pappperitzia*, *Petalocentrum*, *Polyotidium*, *Plectrophora*, *Pterostemma*, *Quekettia*, *Rodriguezia*, *Rodrigueziopsis*, *Roetzliella*, *Rusbyella*, *Sanderella*, *Saundersia*, *Scelochilus*, *Sigmatostalix*, *Solenidium*, *Systeloglossum*, *Sutrina*, *Theodorea*, *Trichocentrum*, *Trichopilia*, *Trizeuxis*, *Warmingia*.

c. ORNITHOCEPHALUS ALLIANCE

These genera are distinguished from the *Oncidium* alliance only by the number of pollinia, but they do form a somewhat distinctive group. There is no way, however, to separate the *Telipogoninae* and the *Ornithocephalinae*. Many of the *Telipogoninae* are distinctive in that they apparently mimic insects (as in many species of *Ophrys*), and in the pilose column and hooked viscidium, but these latter features are matched by *Cordanthera* and some species of *Dipteranthus*.

Centroglossa, *Chytroglossa*, *Cordanthera*, *Cryptarrhena*, *Dipteranthus*, *Dipterosteles*, *Hintonella*, *Hofmeisterella*, *Oakes-amesia*, *Ornithocephalus*, *Phymatidium*, *Platyrhiza*, *Sodirolella*, *Sphyrastylis*, *Stellilabium*, *Telipogon*, *Thysanoglossa*, *Trichoceros*, *Zygostates*.

PACHYPHYLLINAE Pfitzer

Though distinguished by the differently shaped column and consistently monopodial habit, these genera seem closely allied to the *Maxillariinae*. *Pachyphyllum*

and *Chrysocynis*, especially, appear to be closely allied, and resemble each other in habit, inflorescence and 3-winged ovary.

Centropetalum, *Pachyphyllum*.

PLEUROTHALLIDINAE Benth

These genera form a distinctive American group most closely allied to the Epidendrinae, especially to the *Arpophyllum* alliance.

Acostaea, *Barbosella*, *Brachionidium*, *Cryptophoranthus*, *Lepanthes*, *Lepanthopsis*, *Masdevallia*, *Octomeria*, *Physoisiphon*, *Platystele*, *Pleurothallis*, *Pleurothallopsis*, *Porroglossum*, *Restrepia*, *Scaphosepalum*, *Stelis*, *Yolanda*.

POGONIINAE Pfitzer (Nerviliinae Schltr.)

We follow Mansfeld in separating the Vanillinae and the Pogoniinae, and including *Nervilia* in the Pogoniinae. The flower structure of *Nervilia* is quite comparable to that of the other Pogoniinae, and most species were first described under *Pogonia*. The habit is somewhat distinctive. These genera are similar in floral structure to both the Vanillinae and the Sobraliinae. The pollen is quite mealy, but they lack the distinctive seed structure of the Vanillinae.

Cleistes, *Isotria*, *Lecanorchis*, *Monophyllorchis*, *Nervilia*, *Pogonia*, *Pogoniopsis*, *Psilochilus*, *Triphora*.

RIDLEYELLINAE Schltr.

The habit of this genus is suggestive of *Bulbophyllum*, and the pollinia are said to be naked, though the floral structure is otherwise more reminiscent of the Thelasiinae.

Ridleyella.

SARCANTHINAE Benth (Aeridinae Pfitzer)

This is the great group of primarily Old World monopodial orchids. In floral specialization and complexity they parallel the American Oncidiinae and are not easily "keyed" from the monopodial Oncidiinae, though there is probably no close relationship. Note that this group must be known as the Vandinae if the tribe Vandae is maintained. Hawkes and Heller (1959) list the "subtribe Campylocentrinae." This name is listed by Hoehne in *Flora Brasiliica* (12¹:23, 39), but we cannot find that it has ever been formally proposed, nor can we find any reason that it should be.

Abdominea, *Acampe*, *Adenoncos*, *Aerangis*, *Aeranthus*, *Aerides*, *Ambrella*, *Ancistrorhynchus*, *Angraecopsis*, *Angraecum*, *Ankylocheilus*, *Arachnis*, *Armadorum*, *Ascozentrum*, *Ascochilopsis*, *Ascoglossum*, *Barombia*, *Bathia*, *Beclardia*, *Bogoria*, *Bolusiella*, *Bonnieria*, *Calymanthera*, *Calyptrochilus*, *Camarotis*, *Campylocentrum*, *Ceratochilus*, *Chamaeangis*, *Chamaeanthus*, *Chauliodon*, *Cheirorchis*, *Chiloschista*, *Chroniochilus*, *Cottonia*, *Crossangis*, *Cryptopus*, *Cyrtorchis*, *Dendrophylax*, *Diaphanantbe*, *Dinklageella*, *Diplocentrum*, *Diploproa*, *Dryadorchis*, *Eggelingia*, *Encheiridion*, *Esmeralda*, *Eurychone*, *Finetia*, *Fitzgeraldiella*, *Gastrochilus*, *Holcoglossum*, *Hymenorchis*, *Jumellea*, *Lemurella*, *Lemurorchis*, *Listrostachys*, *Luisia*, *Macropodanthus*, *Malleola*, *Microcoelia*, *Microsaccus*, *Microtatorchis*, *Mystacidium*, *Nephrangis*, *Neobathia*, *Oeonia*, *Oeoniella*, *Omoea*, *Ornithochilus*, *Pelatantheria*, *Pennilabium*, *Perrierella*, *Phalaenopsis*, *Phormangis*, *Phragmorchis*, *Plectrelminthes*, *Podangis*, *Polyrhiza*, *Pomatocalpa*, *Porphyrodesme*, *Rangaeris*, *Renanthera*,

Renantherella, *Rhipidoglossum*, *Rhynchosstylis*, *Robiquetia*, *Saccolabiopsis*, *Saccolabium*, *Sarcanthus*, *Sarcochilus*, *Sarcorrhynchus*, *Schoenorchis*, *Solenangis*, *Sphyrarhynchus*, *Staurochilus*, *Stauroopsis*, *Taeniophyllum*, *Taeniorrhiza*, *Thrixspermum*, *Triceratorhynchus*, *Trichoglottis*, *Tridactyle*, *Uncifera*, *Vanda*, *Vandopsis*, *Ypsilopus*.

SOBRALIINAE Schltr. (Palmorchidinae Schweinf. & Correll [not validly published])

These genera were included in the Neottieae by Schlechter, but the pollinia are more or less waxy in many species, and the flower structure agrees well with that of the Epidendrinae and Thuniinae. Mansfeld actually assigns the Thuniinae to this subtribe, though we believe this action to be questionable, at least without more detailed knowledge of the Thuniinae. Schweinfurth has evidently abandoned the use of the subtribe Palmorchidinae, which was proposed without description. In no case did Schweinfurth and Correll assign *Corymborchis* to the Palmorchidinae, an action which would scarcely have been defensible (see, however, Hawkes & Heller, 1959).

Diceratostele, *Elleanthus*, *Palmorchis*, *Sertifera*, *Sobralia*, *Xerorchis*.

STANHOPEINAE Bentham (Gongorinae Schltr.)

This group is not clearly distinguished from the Maxillariinae (*Lycaste* alliance), though the more bizarre genera (*Stanhopea*, *Coryanthes*, etc.) are easily distinguished. More study of this group is needed.

Acineta, *Chaubardia*?, *Cirrhaea*, *Coeliopsis*, *Coryanthes*, *Endresiella*, *Gongora*, *Gorgoglossum*, *Houlletia*, *Kegeliella*, *Lacaena*, *Lueddemannia*, *Lycormorium*, *Paphinia*, *Peristeria*, *Polycycnis*, *Schlimia*, *Sievekingia*, *Stanhopea*, *Trevoria*.

THECOSTELINAE Schltr.

The flower structure of *Thecostele* is quite bizarre, but adequate knowledge of all species may indicate that it should be included in the Genyorchidinae.

Thecostele.

THELASIINAE Schltr.

The Thelasiinae are small Asiatic plants which are distinctive in habit and inflorescence. The pollinia have been described as having a stipe, but this appears to be an unusually long caudicle (Mansfeld, 1937b).

Chitonanthera, *Octarrhena*, *Oxyanthera*, *Phreatia*, *Rhynchosphreatia*, *Thelasis*.

THUNIINAE Schltr. (Claderiinae Mansf. [not validly published])

Tall Asiatic plants with slender stems and rather showy flowers, in habit these plants (especially *Arundina*) closely resemble the Epidendrinae. In the structure of the column, however, they more closely resemble *Coelogyne* and *Phajus*. *Brombeadia* was placed in the Polystachyinae by Schlechter, but is surely out of place there (see Ridley, 1891). It resembles *Dilochia* in habit and appears to resemble *Claderia* in flower structure. Unfortunately, we have seen too little of all these genera. The group is unusually diverse in the structure of the pollinia, and it is possible that further study will show it to be unnatural. The subtribe Claderiinae was proposed without description.

Arundina, *Brombeadia*?, *Claderia*, *Dilochia*, *Thunia*.

VANILLINAE Bentham

These genera are, in several features, among the most primitive in the sub-family. They are included in the Pogoniinae by Schlechter, but the habit and distinctive seed structure would seem to justify their separation, as indicated by Mansfeld. They also show some affinity to the Sobraliinae, but there is little evidence of close alliance with the Neottieae.

Duckeella, Epistephium, Eriaxis, Galeola, Vanilla.

SUBTRIBES OF UNCERTAIN AFFINITY

GROBYINAE Schltr.

This genus has been placed near the Cymbidiinae in most systems, but this seems to be questionable. We have not seen adequate material, but a comparison with the Maxillariinae may be in order.

Grobya.

PACHYPLECTRINAE Schltr.

This genus is known only from New Caledonia. It apparently belongs to the Neottieae, but Schlechter's description is not adequate for more exact placement. It may be allied to the Diuridinae and Cryptostylidinae.

Pachyplectron.

PHYLOGENY

There are two extremes in the variation patterns shown by living plant groups, depending apparently on rates of evolution and amount of extinction. At one end of the spectrum stand such families as the Magnoliaceae, Annonaceae and Nymphaeaceae. These families have the appearance of being "old" groups, in which evolution is proceeding at a leisurely pace and extinction has greatly affected the pattern of variation. Such groups as the cacti and the Euphorbiaceae-Euphorbieae represent the other extreme. They show little evidence of great age, show signs of relatively rapid diversification in geologically recent time, and give much less evidence of extinction. Our classification of genera and higher groups is in large measure based on extinction, and so we have very different problems with these two types. The delimitation of genera and tribes within the Magnoliaceae or the Nymphaeaceae is not difficult. We are often at a loss, though, to understand their relationships or phylogeny.

As should now be clear, the orchids are near the other end of our spectrum in these features. Genera are often difficult to define, and higher categories within the family seem even worse. These hazy boundaries between tribes and subtribes, however, may give clues to the patterns of phylogeny within the family. We do not mean to imply that living groups can often be derived from other living groups, but one can find excellent evolutionary series for nearly every morphological feature within the orchids. In recent years there has been a healthy skepticism concerning phylogenetic schemes (see especially Sporne, 1959). Even

when one can find a good morphological series in some feature, it is often difficult to decide in which direction or directions evolution has occurred. This problem is not so serious in a highly derived group such as the Orchidaceae. In comparing *Cephalanthera* and *Oncidium* there can be little doubt as to which is derived and which is primitive. In nearly every feature in which these two differ, it is *Cephalanthera* which is the ordinary monocot, easily comparable with other monocot families, while *Oncidium* can scarcely be understood without comparing it with the less specialized members of the family. One would scarcely expect to derive whorls of separate stamens and pistils from the column of the advanced Epidendreae, but the evolution of the column from primitively free parts is easily understood and partially documented among the living orchids. As an actively evolving group in which the patterns of evolution are unusually clear, the orchids are especially appropriate for evolutionary study and may throw a good deal of light on parallelism, polyphyletic and other problems which plague the biologist dealing with apparently more ancient groups.

When one studies the relationships of the subtribes, a pattern takes shape, and one may form a rather clear idea of the over-all evolutionary patterns for the family. The pattern of relationships for the Epidendreae (fig. 1) scarcely provides a classic dendrogram, but there are clear indications of primitive groups and some indications of the patterns of evolution which may have occurred. These may best be considered by discussing evolution in particular features of the plant.

HABIT

As Holttum (1955) has shown, the predominant growth form in a wide range of monocots is the sympodium, and we may reasonably consider this to be the primitive condition in the orchids. The majority of primitive orchids have a rather ordinary monocot habit, as for example *Cephalanthera*, with a short rhizome and erect, non-thickened annual stems with scattered, spiral leaves and a terminal inflorescence. The origin of the majority of other sympodial growth forms by phyletic shortening and/or thickening of the stems is readily envisioned. Of special interest is the monopodial habit, in which the stem has unlimited apical growth and roots are not restricted to the basal portion. In some systems this has been considered to be the distinguishing mark of the Sarcanthinae. We find, however, that the monopodial habit occurs in the Vanillinae, Cymbidiinae, Maxillariinae, Pachyphyllinae, Cryptocentrinae, Thelasiinae and Oncidiinae, and possibly in other groups as well. In some of these groups we have a good graded series from sympodial plants to related monopodial types. Not only does the monopodial habit appear to have evolved independently in many groups, but its evolution seems to have followed somewhat different patterns in different cases. In the Vanillinae and the Sarcanthinae it has apparently been the simple retention of apical growth in the members of a sympodium (with lateral inflorescence). In some of the Maxillariinae and allied groups it appears to be the suppression of pseudobulbs on a leafy rhizome. In other cases, such as *Maxillaria valenzuelana*, and some Oncidiinae (*Oncidium pusillum* complex, *Rodriguezia* spp.), the monopodial habit

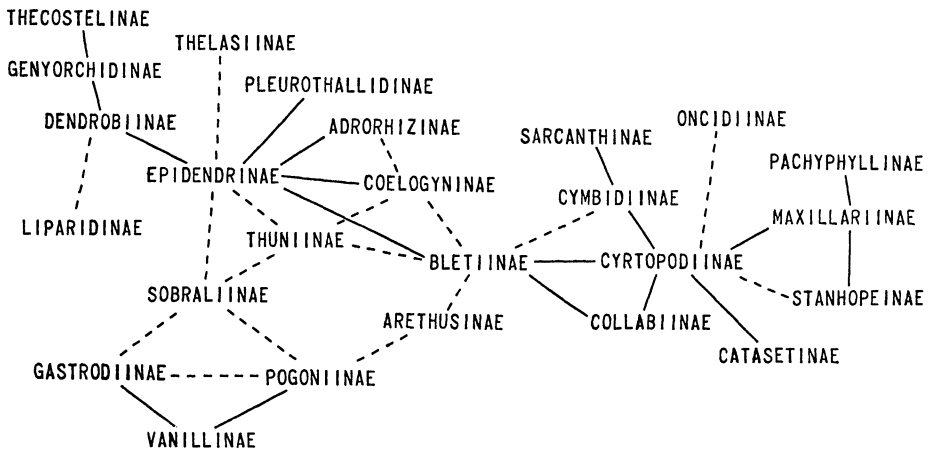


Figure 1. A diagram of suggested relationships within the tribe Epidendreae. Solid lines represent close relationships, while dashed lines represent relationships which are more distant or less clear.

seems to have evolved by the retention of a permanent juvenile form. In hybrid swarms involving *Rodriguezia refracta* (sympodial) and a related monopodial species one may find a complete series ranging from those plants which are monopodial only in the seedling stage to those which are monopodial for the life of the plant.

Kränzlin (1923) attempted to retain the monopodial habit as the distinguishing feature of the Sarcantinae by classing *Dichaea*, *Lockhartia*, *Pterostemma* and the Pachyphyllinae as the heterogeneous "Pseudomonopodiales," pointing out that *Lockhartia* and some species of *Dichaea* are not strictly monopodial, in that the stems are erect, and of more or less limited growth, with roots and branches arising only at the base. While this is true, a very strict definition of the monopodial habit would also disqualify some Sarcantinae (ex. *Mystacidium distichum*), and still leaves some undoubted monopodia in *Oncidium*, *Maxillaria*, and species of *Dichaea*. Though of considerable morphological and evolutionary interest, the monopodial habit has limited value as a taxonomic criterion.

SAPROPHYTISM

Saprophytic orchids are found in all three tribes of the Orchidoideae, and in at least twelve different subtribes. The majority of orchids pass through a saprophytic seedling stage, which may last for months, especially in terrestrial species. Thus, the evolution of a completely saprophytic life cycle in many different groups of orchids is not surprising. The wholly saprophytic orchids pose special taxonomic problems. The adaptations for saprophytism drastically change the vegetative features of the plant, thus obscuring some of the characteristics normally used in determining relationships. It may be that even the reproductive features are affected by these adaptations. In *Corallorhiza*, for example, we find the pollinar

apparatus to be simpler than in the related *Oreorchis* and *Tipularia*. In the absence of these closely allied genera, its relationship to the Cyrtopodiinae would be much less clear. The saprophytes are difficult to cultivate and poorly represented by herbarium specimens, which further complicates their study. Autogamy is frequent, and an autogamous saprophyte is nearly the ultimate in taxonomic difficulty. A special key to the saprophytic genera of orchids is needed.

PSEUDOBULBS AND CORMS

A great many orchids, and especially the epiphytic groups, show variously thickened stems or "pseudobulbs." While these structures are quite diverse in form, they fall into a limited number of morphological types and seem to show some evolutionary trends. One of these seeming trends is from pseudobulbs (or corms) of several or many internodes to pseudobulbs of a single internode (as in *Bulbophyllum*, Maxillariinae and Oncidiinae). Reference to the chart of relationships (fig. 1) suggests that there may be two basic patterns for the origin of pseudobulbs. In the majority of the Blettiinae, Cyrtopodiinae and related groups (the right side of fig. 1), pseudobulbs seem to have been derived phyletically from more or less corm-like structures, as in *Bletia* and *Phajus*. These thickened stem-bases may be found in either terrestrial or epiphytic groups, while the pseudobulbs of a single internode are restricted to primarily epiphytic groups. The other main pattern for the derivation of pseudobulbs appears to be shown by the Epidendrinae and some related groups (left side of fig. 1). In these groups corm-like structures are not found, and the pseudobulbs appear to have evolved by a phyletic thickening of the entire aerial shoot (as in *Dendrobium*, *Barkeria*, etc.). The more derived members of these groups may also possess pseudobulbs of a single internode, which are morphologically indistinguishable from those of the Oncidiinae or Maxillariinae (ex. *Bulbophyllum*, some species of *Dendrobium*).

LEAVES

The evolutionary trends in leaf type seem rather clear, and have already been outlined by Rolfe (1909-1912). The primitive type of orchid leaf is probably non-articulate, wide (more or less elliptic) and plicate, of convolute vernation. The trends toward an articulate leaf which is narrow (more or less ligulate) and conduplicate, have probably occurred independently in several phyletic lines, and appear to be strongly correlated with the epiphytic habit. It is interesting that the monopodial orchids all have strictly conduplicate leaves, with the partial exception of *Vanilla*, which has convolute vernation, but the fleshy leaves of *Vanilla* are by no means plicate, and the mature leaf usually appears conduplicate. This points out the imperfect correlation between conduplicate leaves and duplicate vernation. The correlation is generally good, however. We have used plicate and conduplicate in the present paper, as terms descriptive of the mature leaf and therefore more readily determined. There are, of course, transitional stages, such as the many-veined but conduplicate leaves of most Cymbidiinae, which appear superficially plicate.

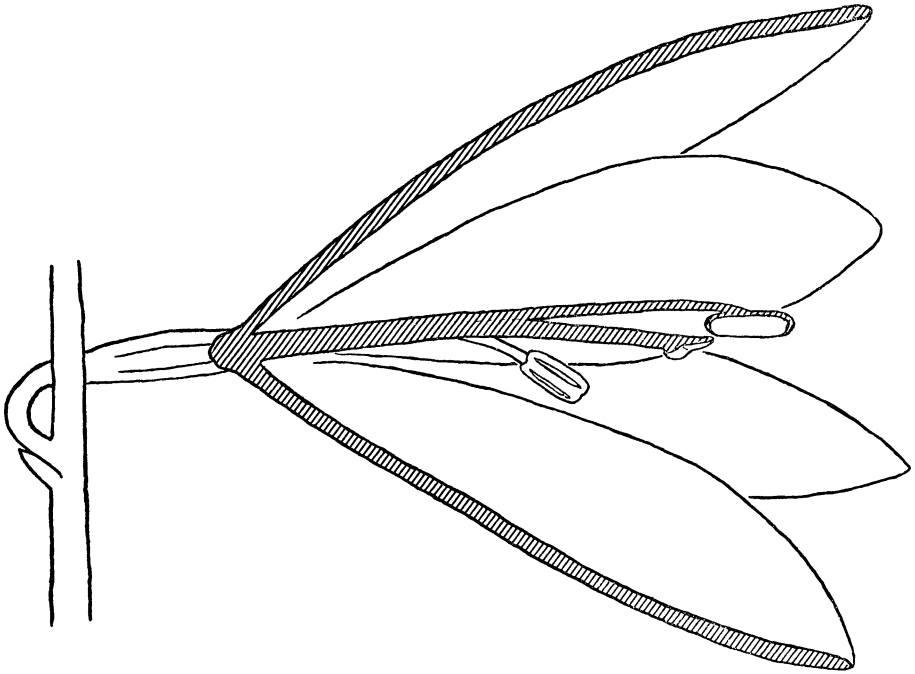


Figure 2. A longitudinal section of a hypothetical primitive orchid flower, highly schematic. In such a flower we would expect the perianth segments to be similar, and we would expect 3 anthers, one of which is borne above the stigma, the other two being lateral in position. Such a flower is closely matched in the living *Apostasiae*. A simple form of resupination is shown.

FLOWER

It is probable that the primitive orchid flower was a relatively unspecialized monocot flower with equal and similar perianth parts, similar to that now found in the *Apostasiae*. Such a hypothetical primitive orchid flower is sketched in fig. 2. The only unusual feature of the simpler orchid flowers is a certain degree of zygomorphy in the androecium. The three anthers which are found in the orchids are all on the abaxial side of the flower and are members of two different whorls. The adaxial stamens were evidently lost at an early stage in orchid evolution. In some groups of ancestral orchids, as in the living *Cephalanthera*, the viscid matter of the relatively unspecialized stigma may have served to glue the pollen masses of the median anther to the pollinating agent on its withdrawal from the flower. Such a relationship was surely the basis for the evolution of those tribes in which only the median anther is functional. A tremendous diversity exists in the form of the column and anther among living orchids. So great is this diversity in form and position that it is very difficult to use a precise terminology for the anther and its parts. The column itself has clear dorsal, ventral and lateral aspects (though morphologically confused by resupination, in which the adaxial side of the flower becomes ventral).

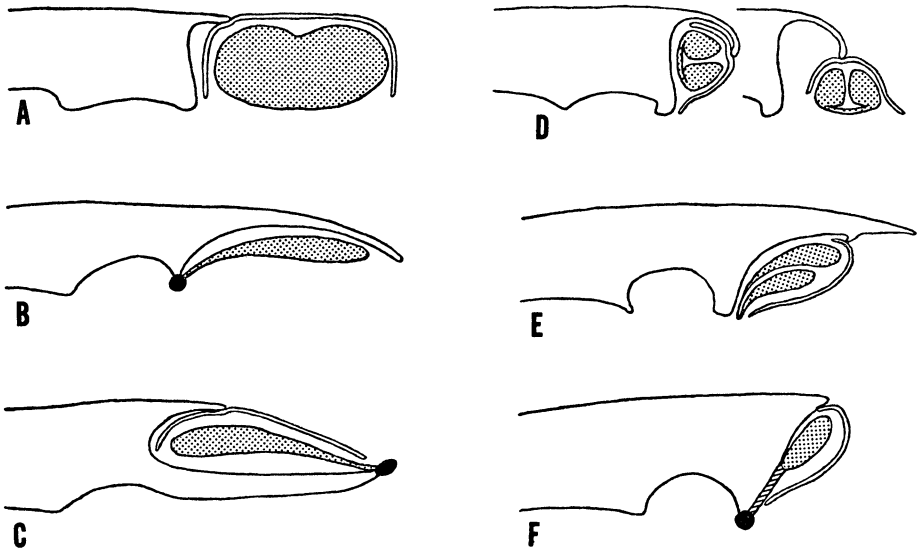


Figure 3. Diagrammatic longitudinal sections of orchid columns, showing the relationships of anther, pollen and stigma. Pollen is stippled; the viscidium, where present, is shown in black. A. A primitive orchid with the anther terminal and erect, the stigma is undifferentiated; *Cephalanthera*. B. A member of the Orchidinae, in which the anther is erect and broadly united to the column. The viscidium (or viscidia) is attached to the base of the pollinia. C. An orchid with dorsal anther; the rostellum is elongate and erect, with the viscidium attached to the apex of the pollinia; Spiranthinae, *Meiracyllium*, *Podochilus*, etc. D. An orchid with operculate, versatile anther; *Dendrobium*, *Cattleya*, *Vanilla*, etc. E. An orchid with ventral anther overtopped by the column, as in *Coelogyne*. F. An orchid with a more or less operculate anther and a distinct stipe (cross-hatched) attaching the pollinia to the viscidium. Typical of Sarcantinae, Maxillariinae, Oncidiinae, etc.

ANTHER

In the subfamily Cyripedioideae three distinct stamens are usually present, though the median anther is represented by a staminode in *Apostasia* and the Cyripedioideae. In the Orchidoideae it is only the median anther which is functional, the lateral anthers being completely absent or represented by staminodia. Three fertile anthers do occur as an occasional abnormality, and are the rule in a few autogamous forms. Vermeulen considers the auricles of *Cephalanthera*, *Epipactis* and the Orchidoideae not to be staminodia. Some other orchids, however, do bear distinct lateral staminodia. *Diuris* is probably the most noteworthy case, for here the staminodia are nearly as long as the style and are free nearly to their bases. Column wings or stelidia occur in a number of genera and are probably staminodia.

It is quite probable that the anther is primitively erect, and the anther is erect in the majority of living Neottieae. In the Spiranthinae, Diuridinae and related subtribes the anther is dorsal, and does not appreciably overtop the apex of the stigma. In these groups the pollinia are associated with the stigma by a terminal rostellum, and it may be that the dorsal anther is primitive for these groups. In this feature they are quite comparable to some of the Apostasiae. In the remaining

Neottieae the anther is normally terminal, usually reaching well beyond the stigma. Thus it is the basal or ventral portion of the pollinia which is usually associated with the rostellum in these subtribes. Such a condition was the probable starting point for the evolution of the Orchideae, for in this tribe the pollinia are attached to the viscidia by basal caudicles. In some members of this tribe the anther is erect and the anther cells fairly close together, the pollinia attaching to a single viscidium or two adjacent viscidia. This is, if not the primitive condition for the tribe, certainly the one most readily understood. In many members of the Orchidinae and Coryciinae the anther cells are widely separated and each pollinium is attached to a separate viscidium, the viscidia often being widely removed from the functional stigma. In the Disinae the anther is usually reclinate, being "bent" backwards from the column. In most species of *Satyrium* the anther actually has the base uppermost.

In the primitive Epidendreae the anther is normally incumbent and operculate on the apex of the column. In these subtribes the anther is actually more or less versatile, the (morphologically) ventral face of the anther resting against the apex of the column until the anther is rotated on the filament, as shown in fig. 3D. The anther is erect in the early floral ontogeny of these groups, and is erect in the mature flower of a few species. This probably represents an ontogenetic "reversion" in these plants, rather than a primitively erect condition, for they are all closely allied to species with fully incumbent anthers. In the more derived members of the Epidendreae the anther may take on almost any position: dorsal, terminal, ventral, or intermediate conditions which render accurate description and categorization difficult (see fig. 3).

ROSTELLUM

The rostellum has been given as one of the family characteristics of the Orchidaceae. In its extreme development it is quite comparable to the situation in the Asclepiadaceae, in which part of the stigma has become associated with the pollen and takes part in the transfer of the pollen from anther to functional stigma. One finds, however, a complete series of gradations in the living orchids from forms with no structure which can be called a rostellum to the markedly complex structures in the advanced Oncidiinae and Sarcanthinae. The rostellum may perhaps be best defined as the structure separating the functional stigma from the anther, a portion of which serves to attach the pollinia to the pollinating agent. It is frequently stated to be the third (median) lobe of the stigma. As Vermeulen (1959) has shown, however, many orchids with a distinct rostellum have three stigma lobes, and the work of Wolf (1866) shows portions of the median lobe to be functionally stigmatic. Indeed, superficial observations suggest that the third stigma lobe may often be much the largest of the three. It would appear that only a portion of the third stigma lobe is involved in the rostellum, and it is not clear that other structures (such as style or filament) are not also involved. In the more highly evolved Orchidaceae the column behaves as a separate organ *sui generis*, the boundaries between the phyletically component parts being lost or

obscured. Vermeulen (1959) believes the rostellum of the Orchideae to be different in origin and nature from that of the Neottieae and Epidendreae, and suggests that it may be derived from the lateral stigma lobes. This does not seem to be supported by the developmental studies of Wolf (1866).

In its most primitive expression, in *Cephalanthera*, the entire stigma is functional as such, and the pollinia are normally attached to insects by a portion of the stigmatic fluid which the insects receive by brushing the stigma in retreating from the flower. In many groups of orchids a special part of the stigma is differentiated to supply the viscid material which attaches the pollinia to the pollinating agent, but the transfer is similar to that in *Cephalanthera*. In *Cattleya*, for example, the rostellum projects beyond the stigma, but the viscid matter and the pollinia do not come into actual contact without action of the pollinating agent. A slight further specialization is seen in *Sophranitis* and some species of *Calanthe*, where a portion of the rostellum is more or less differentiated as a viscid pad which is attached to the pollinia and is removed with them as a unit. This structure is variously known as viscidium, viscid disk or gland; we use the first term, as the structure is not a gland in the usual sense, nor is it usually a disk. In the more highly specialized groups, the viscidium is a sharply delimited structure attached to the pollinia by a strap of rostellar (or columnar) tissue which is not viscid. This connecting tissue is termed the stipe, and is cellular in structure, unlike the translator of the asclepiads. The high degree of diversity in rostellar structure, and the degrees of specialization within taxa suggest that, after the initial action of stigmatic fluid in transfer of pollen, all of the other specializations (viscidium and stipe) have arisen independently several or many times in separate phyletic lines. Early stages in the independent evolution of the viscidium are to be seen in several genera of the Epidendrinae, and the stipe appears to have evolved independently in the Prasophyllinae, Genyorchidinae, Spiranthiniae, and perhaps elsewhere.

POLLINIA

The major systems of orchid classification have focused attention on variation in the pollen and associated features. As in most other features, there is a high degree of diversity in the structure of the pollinia, but this diversity is accompanied by many gradations to a simple and unspecialized pollen. The simplest and surely most primitive condition is that in the Apostasiae. In this tribe we find unspecialized 4-locular anthers with powdery pollen. In the Cypripedieae the pollen grains are not united into larger units, but the pollen is somewhat viscid. In almost all members of the Neottieae and Orchideae the pollen grains are united into tetrads (free grains occur in *Cephalanthera*). Further, this granular pollen is usually loosely united into large masses by elastic threads of tapetal origin. These masses, or pollinia, may be two in number, each representing the contents of one half of the anther; more commonly the two halves are each more or less divided, so that each of four anther cells contains a pollen mass. The pollinia of the Orchideae are divided into many granular packets, interconnected by elastic threads. This is the condition termed sectile. In the Neottieae the pollinia are sectile only in the *Good-*

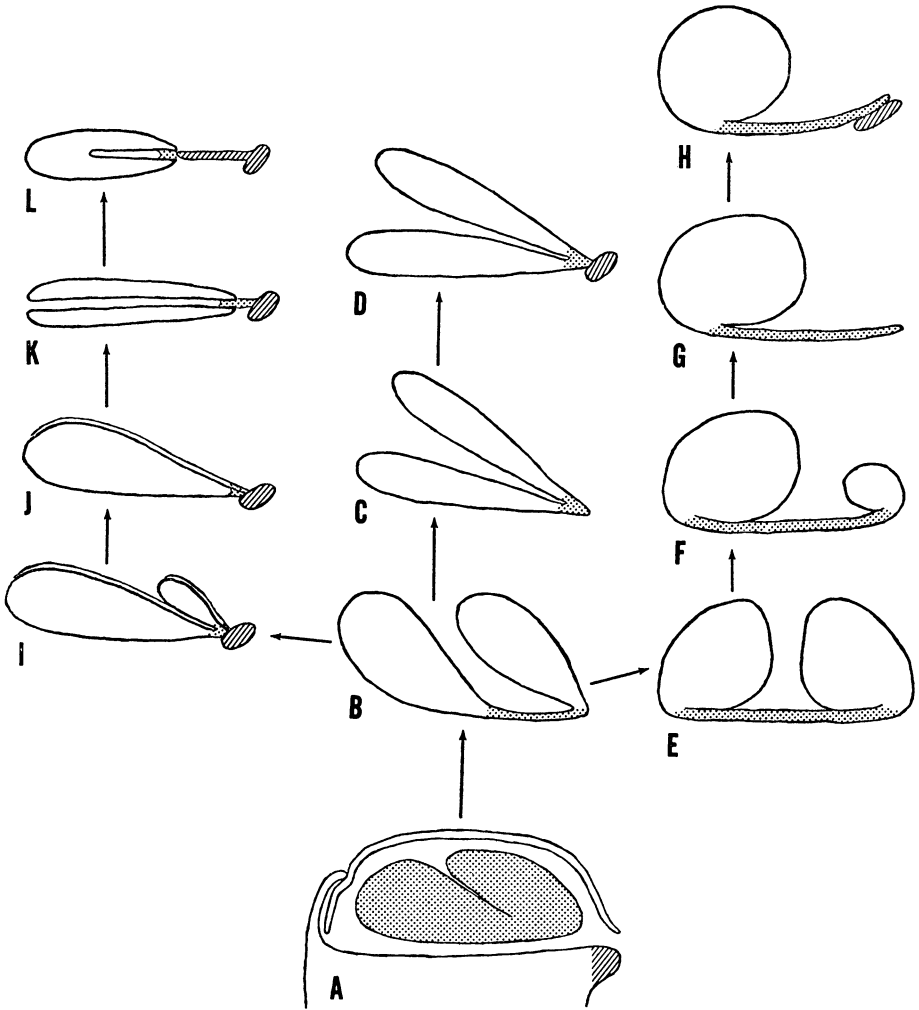
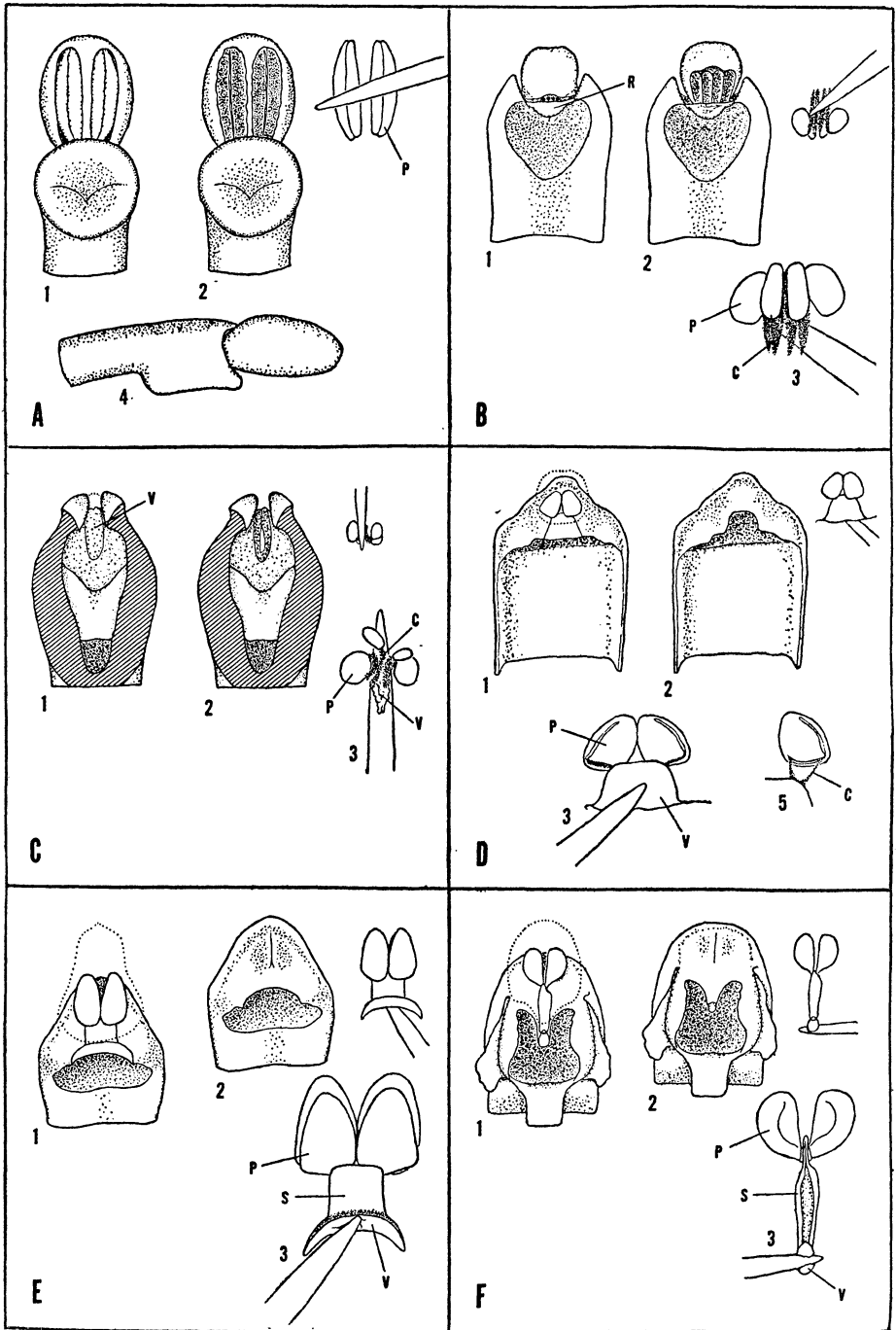


Figure 4. Diagram showing some of the major patterns of evolution in pollinia within the Epidendreae. Mealy pollen (only the caudicles in the higher forms) is stippled; the rostellum in A and the viscidium, where present, are cross-hatched. A. A relatively primitive orchid as in the Arethusinae or Sobraliinae, showing the orientation of the pollen within the anther and the position of the rostellum. In such an orchid there are 4 mealy pollinia, each more or less divided into 2 portions. Highly schematic. B-D. The evolution of clavate pollinia, as in Bletiinae and some sections of *Eria*. A viscidium may be formed (D). E-H. The major pattern of evolution in the *Epidendrum* and *Polystachya* alliances, in which 8 equal pollinia are reduced to 4 (rarely 2). A viscidium may be formed, but is usually attached to the pollinia by caudicles. I-L. The evolution of superposed pollinia, as in Cyrtopodiinae, Sarcanthinae, Maxillariinae and Oncidiinae. In the highly evolved forms the pollinia are frequently reduced to 2 in number and are attached to the viscidium by a stipe.

pera alliance. Sectile pollinia have, by some, been considered an intermediate step between mealy and waxy pollinia, but they represent rather a separate specialization. A single sectile pollinium may pollinate a number of separate flowers, as only a few of the packets are normally left in any one flower. In the Orchideae the basal portions of the pollinia form slender, sterile "caudicles" which attach the pollinia to the viscidia. The caudicles are largely composed of the elastic strands which unite the tetrads of the pollinium, but some tetrads may be found in the caudicles. Distinct caudicles are not formed in the Neottieae. In the Spiranthinae and some other subtribes the viscid disk is attached to the apices of the pollinia, but in the Australian Neottieae one finds a complete series from basal attachment through ventral to terminal attachment like that of the Spiranthinae. The distinction which has been drawn between "Acrotonae" and "Basitonae" is thus an artificial one.

In some of the more primitive groups of the tribe Epidendreae (Vanillinae, Pogoniinae, Arethusinae, some Blettiinae and Sobraliinae) granular or mealy pollinia occur, but the pollinia usually form hard, more or less "waxy" masses. In the more highly specialized groups the pollinia are quite compact and hard. In the Arethusinae and some Sobraliinae each of the four mealy pollinia is partly divided into halves. In most of the more primitive Epidendreae eight waxy pollinia occur. These are subclavate or laterally flattened and occur in two series, each basal pollinium being united to the terminal pollinium of the same anther cell by a band of granular pollinia which is strengthened by elastic strands, as in the caudicles of the Orchideae. These granular bands or caudicles may be united with each other so that the pollinia form two units of four each or a single unit of eight pollinia. In these groups it is the caudicle which is normally attached to the pollinating agent and provides a weak zone which can be stretched and broken when the pollinia contact the stigma of another flower. Reference is frequently made to "a caudicle having a viscid apex" or to "viscid disk arising from the apex of the pollinia." Such statements seem to represent translations from Schlechter's key (1926). As nearly as we can determine, adhesive matter is never derived from the pollinia, but is always rostellar in origin. Bentham (1881) restricted the term

Figure 5. Examples of pollen apparatus found in the orchids. 1. The underside or apex of the column showing the stigma, and the pollinia in place within the anther. The anther is shown by dotted lines in C-F. 2. Same with the pollinia removed by a needle (to the upper right). 3. An enlarged view of the pollinia. c: caudicle; p: pollinia; r: rostellum; s: stipe; v: viscidium. A. *Cephalanthera rubra*: the anther is terminal and erect. Stigmatic fluid serves to attach the pollinia to insects, but no rostellum is differentiated. The pollinia are mealy. 4. Lateral view of column. B. *Cattleya aurantiaca*: the anther is operculate and versatile. A part of the stigma is specialized as the rostellum, but there is no direct connection between the pollinia and the rostellum. Well developed caudicles are present. C. *Epidendrum schlechterianum*: the anther is dorsal (and scarcely visible from beneath). A distinct, though semi-liquid viscidium is formed, and is attached directly to the caudicles of the pollinia. D. *Cymbidium lowianum*: a well developed viscidium is present, but no stipe. The four superposed pollinia are united into two. 5. pollinium slightly separated from viscidium to show the stretched caudicle. E. *Maxillaria elatior*: a short stipe is present but is not sharply differentiated from the viscidium. The four pollinia are superposed. F. *Oncidium antibocrene (powellii)*: a long stipe is present and sharply differentiated from the viscidium (the stipe is translucent at the point of attachment). This last represents a highly evolved pollen apparatus comparable to the structure found in *Asclepias*. All drawn from living material, except A, which is semi-diagrammatic and adapted from Godfrey (1933) and Reichenbach (1851). A: ca. 5.5 \times . B, C & F: ca. 4.5 \times & 9 \times . D: ca. 2 \times & 3.5 \times . E: ca. 3.5 \times & 6.5 \times .



caudicle to the tribe Orchideae, and used "appendage" for the mealy portion of the pollinia of the Epidendreae. This distinction is taxonomic rather than morphological, and generally has not been followed by other botanists. There is a clear morphological distinction, though, between stipe and caudicle.

Several trends of specialization occur in the pollinia of the Epidendreae, and all may be derived from the subclavate pattern found in many Blettiinae (see fig. 4). In the Pleurothallidinae, *Glomera*, *Podochilus* and some sections of *Eria*, the pollinia are strongly clavate. Within these groups reduction to four or even two pollinia occurs in several cases (ex. in the Pleurothallidinae). Viscidia are relatively frequent (*Glomera*, *Podochilus*, some Pleurothallidinae, *Meiracyllium*, etc.). Stipe-like structures are found in the *Podochilus* alliance, but these may be caudicular in nature, as are those of the Thelasiinae, according to Mansfeld (1937b). In *Dendrobium* and *Bulbophyllum* the four pollinia (which are probably derived from a clavate pattern) are quite naked; the versatile anther, however, is well designed to bring the pollinia in contact with the rostellar adhesive. In the Genyorchidinae and Thecostelinae both a viscidium and a stipe-like structure are formed. The close affinity of *Bulbophyllum* suggests that the Genyorchidinae may lack caudicles. If this is the case, the pollinia must be attached to the viscidium by true stipes, as they appear to be.

In the *Epidendrum* and *Polystachya* alliances, some Blettiinae, and some sections of *Eria*, the pollinia are laterally flattened and usually more or less discoid. The primitive pattern here appears to be that found in *Laelia*, *Brassavola*, and some species of *Bletia*. In these genera the pollinia are relatively discoid, and each pair is connected by a conspicuous caudicle, which may be about as long as the anther cell. The simplest modification of this pattern is the reduction or complete loss of the terminal pollinium in each set. Thus the pattern of *Cattleya*, *Epidendrum*, etc. is achieved, in which only four laterally flattened pollinia are formed. In these genera each pollinium bears a well developed caudicle which projects downward to the vicinity of the rostellum. In several genera, such as *Neobenthamia*, *Sophronitis* and *Epidendrum*, a small or ill-defined viscidium is formed, which is attached to the pollinia by means of the caudicles. In *Polystachya* and some species of *Epidendrum* the viscidium is quite well developed. In some species of *Polystachya*, such as *P. masayensis*, a distinct stipe is formed. Some other species, however, lack a stipe, and the close affinity of *Stolzia* and *Neobenthamia* clearly align *Polystachya* with the Epidendrinae. Reduction or fusion to two pollinia is infrequent in this series, but occurs in *Epidanthus* and some species of *Polystachya*. Also infrequent is the formation of superposed rather than laterally flattened pollinia. In some species of *Polystachya*, there appears to be a phyletic torsion which could lead to superposed pollinia. Semi-spherical, non-flattened pollinia occur in some species of *Epidendrum* and closely allied genera.

One of the most important trends is the development of superposed (rather than laterally flattened) pollinia, which are usually attached to a viscidium. While we have suggested that this pattern might be derived from the clavate pattern, further study is needed. The Collabiinae and Coelogyninae would seem to be

especially critical in this respect. Fusion of the four pollinia into two is common in this pattern. Holttum has suggested that division of two into four may occur in the Sarcanthinae. The fusion into four is frequently imperfect, and it is not unlikely that the trend may be reversed in some groups. Superposed pollinia are

PRIMITIVE	ADVANCED
Roots fleshy, without velamen	Roots spongy, with velamen
Rhizome slender, subterranean	Rhizome fleshy, epiphytic, or absent
Growth sympodial	Growth monopodial
Stem slender, elongate	Stem fleshy, or otherwise modified
Corms or pseudobulbs of many internodes	Pseudobulbs of a single internode
Leaves many, scattered, spiral	Leaves few, clustered or distichous
Leaves plicate	Leaves conduplicate
Leaves non-articulate, persistent	Leaves articulate, deciduous
Leaves herbaceous or leathery	Leaves fleshy
Inflorescence terminal	Inflorescence lateral
Lip similar to the other petals	Lip variously modified, unlike the petals
Flower without a spur	Flower with a spur or spurs
Filaments and style only partially united	Filaments and style completely united
Lateral anthers present and fertile	Lateral anthers staminodia or absent
Anther erect	Anther incumbent, or otherwise modified
Pollen soft, granular	Pollen variously united into pollinia, hard
8 waxy pollinia	Pollinia 6, 4 or 2
Rostellum absent, or simple, without a viscidium	A clearly defined portion of the rostellum (viscidium) removed with the pollinia
Pollinia without a distinct rostellar stipe	Pollinia with a distinct stipe
Ovary 3-celled	Ovary 1-celled
Seed with endosperm	Seed without endosperm
Seed with a wing or sclerotic testa	Seed with thin, reticulate coat

A chart comparing some of the primitive and advanced features to be found among the living orchids. A number of other specializations, such as saprophytism, sensitive anther, united sepals, etc., could be added. In some cases generally primitive features, such as non-articulate leaves or a simple lip, may occur among highly specialized groups. These features are not necessarily primitive in such cases, but may be secondary modifications. Some features are taken from Swamy (1949).

nearly always accompanied by a distinct viscidium (not so in *Coelogyne*). In the majority of genera from the Cyrtopodiinae to the Oncidiinae (as listed on p. 29), the rostellar tissues are differentiated into a distinct stipe which connects the viscidium to the pollinia. In *Cymbidium* and some Cyrtopodiinae and Maxillariinae, however, the stipe is absent or very small, so that it is difficult to separate the "Vandae" on the basis of the stipe alone. The stipe may be partially or completely divided into two, as in *Dipodium* or some species of *Angraecum*. Even when a distinct stipe is present in these genera, it is usually connected to the pollinia by small caudicles. In *Oncidium*, *Cymbidium*, and others, the caudicle is concealed within the furrow formed by the incomplete fusion of the pollinia, and is readily seen only when stretched (fig. 5D).

TRIBAL RELATIONSHIPS AND PHYLOGENY

With the possible exception of the Neottieae, the currently recognized tribes of orchids are relatively natural groups, whose genera are closely knit by clear interrelationships. The relationships between the tribes are less obvious; divergence and extinction apparently have been more important at this level. This is not to imply that the relationships between the tribes are extremely distant. The resemblances between *Tropidia*, *Apostasia*, *Palmorchis*, *Selenipedium* and *Cephalanthera* are strong enough that one may seriously doubt the advisability of distinguishing subfamilies within the Orchidaceae.

The relative advancement of the orchid tribes and their presumed relationships are schematically shown in figure 6. Since the relationships within the Neottieae are not altogether clear, we have diagrammed four different groups of this tribe separately. These are the groups as listed on p. 29. The Neottiinae and Spiranthinae are each treated separately, while the Diuridinae, Cryptostylidinae and Prasophyllinae are treated as one series of interrelated subtribes, and the remaining subtribes are grouped with the Limodorinae.

None of the living tribes of orchids could readily be derived from another living tribe, but their derivation from similar or common ancestors is easily visualized. The Cyripedieae are not very closely related to any other group, their relationship to the Limodorinae being perhaps quite as marked as their few resemblances to the Apostasiae. The ladyslippers have clearly diverged early from the main lines of orchid evolution. The Apostasiae more nearly approach the hypothetical ancestral type, the median anther being functional in *Neuwiedia*. They, too, represent a small relic group of somewhat isolated phyletic position, though perhaps closer to the other orchids than are the Cyripedieae. The Orchideae are presumably derived from somewhat *Cephalanthera*-like types, but they would stand quite isolated if it were not for the relic Epigoniinae, which show some relationships to both the Neottieae and the Epidendreae. The Epidendreae might be derived from somewhat Neottieae-like ancestors, but they show more primitive seed structure in the Vanillinae than any living Neottieae, and the two tribes have apparently diverged at an early level in orchid evolution. The subtribes of Neottieae which we group with the Limodorinae are among the more generalized and

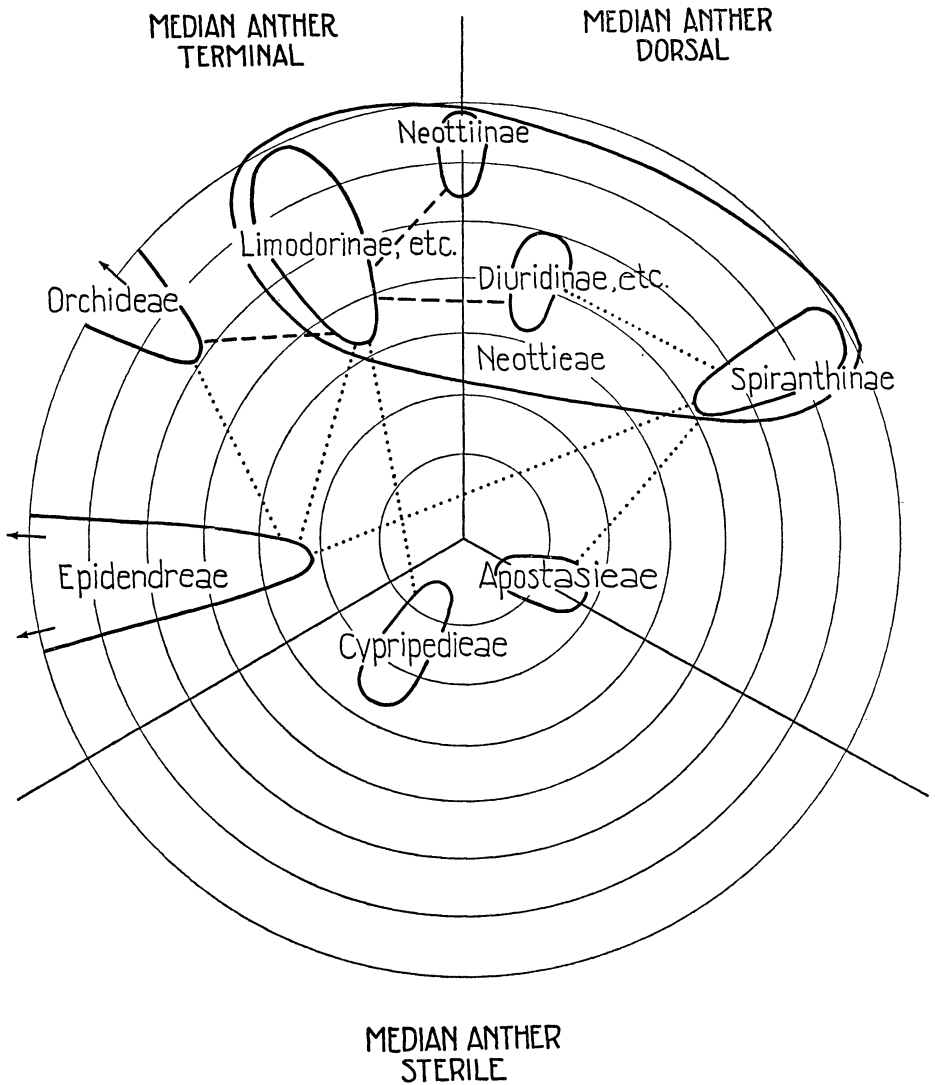


Figure 6. Relative advancement and suggested relationships among the orchid tribes. The less advanced groups have their bases nearer the center, and the ancestral type would fall within the central circle. A more complex advancement index would exclude the Cypripediae from this sector. Dashed lines are meant to represent closer or more obvious relationships than dotted lines. The subtribes Neottiinae and Spiranthinae of the Neottiae are shown separately; the subtribes Diuridinae, Cryptostylidinae and Prasophyllinae are grouped together, while the remaining subtribes are grouped with the Limodorinae. The advancement index is calculated as follows: lateral anthers fertile, column incompletely formed, anther erect, pollinia mealy, ovary 3-celled, and seed with sclerotic coat or wing; each 0. lateral staminodia present, a distinct column formed, anther incumbent or reclinate, pollinia sectile or ceraceous, ovary 1-celled, and seed coat thin and reticulate; each 1 point. lateral stamens completely absent; 2 points.

primitive of the living orchids, and would be a typically relic group if it were not for the great evolution of this group in Australia, where several striking specializations occur. The association of the rostellum and the pollinia is usually basal or ventral (to the pollinia) in this group, but it is subterminal or quite terminal in a few cases. In the genus *Thelymitra* one finds a series from clearly ventral viscidia to some species with the viscidium quite terminal. There are some resemblances between *Thelymitra* and the Prasophyllinae, and these may indicate the derivation of the Prasophyllinae, Diuridinae, etc. from forms with a terminal, erect anther. On the other hand, the conspicuous, nearly free staminodia, and the slight union of filament and style in *Diuris* suggests a highly primitive condition not to be found in *Chloraea*- or *Caladenia*-like plants. The position of the anther in the Neottiinae is somewhat variable, but this subtribe seems most closely allied to the Limodorinae. In the Spiranthinae the anther is distinctly dorsal and does not overtop the stigma. In several genera the column is more theoretical than real, the short filament being only basally attached to the style (see, for example, Vermeulen's recent figure of *Goodyera*, 1959 p. 339). The *Tropidia* alliance, especially, bears a close resemblance to the Apostasiaeae. *Tropidia* has actually been described as a new genus of the Apostasiaeae by Gagnepain (see Mansfeld, 1934). In the absence of clear relationships between the Spiranthinae and other subtribes of the Neottiinae, their position is unclear, and it is possible that they are not derived from forms with a terminal anther, but that the anther is primitively dorsal in this group.

The relationships which we suggest between the primitive members of the several orchid tribes are yet somewhat speculative. This is the level at which relationships are expected to be least clear, and, further, many of these orchids are poorly known. We have no detailed morphological information on the Apostasiaeae, for example. When more information is available on these plants, their interrelationships will surely be better understood, and we will be able to speculate on their origins with a much firmer basis. While the orchids are unusually favorable for a study of relationships within the family, we may never be able to build an exact and detailed family tree for the early evolution of the group.

We have suggested a change in the circumscription of the Epidendreae, which seems to render the group more natural from the phyletic standpoint and more definable from the descriptive standpoint. In a similar fashion it might possibly be desirable to separate the Spiranthinae as a separate tribe, but further study of this complex is needed. With reference to the subfamily Cyripedioideae, it may be that the Apostasiaeae should be given subfamilial rank, as Wettstein has already suggested, or it may be that the subfamilial division should be abandoned altogether. Another possibility which must be considered is the recognition of five subfamilies (as Brieger has already suggested, 1958) and the delineation of 10-12 tribes. Such a system might be more comparable to the classifications used for other major families (such as the Compositae and Gramineae).

In dealing with the primitive orchids and their evolution from groups now extinct, we must bear in mind the bewildering parallelisms to be found in the more

advanced groups. If all the monopodial genera with a distinct pollinar stipe were at hand and their sympodial allies extinct, no one could seriously doubt that he was dealing with a "natural" group. The separate and parallel evolution of the different genera of leafless Sarcanthinae would be inconceivable if we did not have the evidence at hand in their living relatives. It is altogether possible that the subfamily Orchidoideae, as now delimited, has not evolved from a single species which possessed all the features of the modern subfamily: column, single fertile anther and rostellum. Rather, this group has probably evolved from a series of related species or genera with partial union of filaments and style, androecial zygomorphy and a close association of the stigma and the median anther; all features which would predispose the group to parallel patterns of evolution. Some of the ancestral populations may have been quite similar to the Apostasiaeae, while others were similar to *Selenipedium*, and yet others quite unlike either. The orchid family is not "unnatural" or polyphyletic in the strict sense, since the ancestral group was, itself, a natural and closely interrelated group, even though it may have differed from the modern orchids in a number of features. We feel fairly sure that the stipe, sectile pollinia and the viscidium have evolved independently in different groups of orchids. It is quite possible that the rostellum, itself, has evolved independently in two or more separate lines and that the reduction to a single median anther is similarly polyphyletic in the unusually "natural" family Orchidaceae.

The patterns of phylogeny and relationships within the orchid tribes help us to understand the evolution of the tribes themselves. A better understanding of both levels may throw more light on the patterns of origin for families and higher categories.

DISCUSSION AND CONCLUSIONS

Probably the foremost conclusion to be reached from a survey of orchid classification is that there are no infallible "key characters." The habit of growth, the presence or absence of pseudobulbs, the nature of the leaves, the position of the inflorescence, the presence or absence of a column foot, the texture of the pollen, the number of pollinia, and the presence or absence of viscidium or stipe; all have been assigned great importance in orchid classification. Yet in every case one can find closely related species which differ in the feature chosen, or even, in some cases, variation within a species. This lack of hard and fast key characters does not mean that a classification of the orchids is impossible. It does mean that a classification must be based on all features of the plant and that comprehensive keys will often be difficult to prepare. Students of the orchids have often erred in assigning too great importance to a single feature. Both our systems of classification and our concepts of relationship are based on relatively few features. With intensive systematic and morphological study we will be able to base our systems on a much broader and firmer foundation.

Ames (quoted by Schweinfurth, 1959) has suggested that many of the difficulties in orchid classification are due to extinction. We feel, on the contrary, that a relative lack of extinction characterizes the family. Interfertility between

morphologically very distinct genera and close morphological resemblances between subtribes, tribes and even subfamilies point to a rapidly evolving group in which extinction has played a minor role. The groups of orchids are closely interrelated, and clear indications of phylogeny are often to be found. Parallelism also plays a part in rendering orchid classification more difficult. There is every indication that monopodial growth, saprophytism, compact pseudobulbs, conduplicate leaves, lateral inflorescences, spurs, viscidia, stipes, and reduction in number of pollinia have all occurred independently in two to several different groups of orchids. It is difficult to define clearly the several groups of monopodial orchids with highly evolved pollinia, yet there appears to be no direct relationship between them. Both classification and phylogeny must be studied by tracing relationships from group to group.

As a family undergoing relatively rapid evolution, the Orchidaceae provide excellent material for the study of evolution. A chart of primitive and advanced features is given on p. 61; a scheme showing the probable relationships between the tribes in fig. 6. There is a tendency to define the family Orchidaceae in terms of its specializations (such as the column, rostellum or pollinia), but one must not lose sight of the primitive features to be found in living orchids. The style and filament are partially free in both the Apostasiaeae and the Diuridinae; the pollen grains are free in the Vanillinae, and the seeds possess a thick, sclerotic testa in this same subtribe. *Cephalanthera* lacks a rostellum, and several genera bear an erect, relatively unspecialized anther. The patterns of evolution within the family point rather clearly to an ancestor which would be classified in the Lilialean complex of living monocotyledons. Hutchinson has specifically suggested the Hypoxidaceae as a possible close relative of the Orchidaceae. Further morphological study of the primitive orchid genera may greatly clarify this problem. There is no direct relationship between the orchids and the Zingiberales, but rather striking parallelisms, as Hutchinson has suggested. The supposed relationship between the Orchidaceae and Burmanniaceae is based primarily on the tiny seeds; but this type of seed is to be expected in any saprophytic group, and the floral symmetry and inflorescence are basically different in the two groups (Jonker, 1938).

Not only are the fleshy flowers of many orchids crushed in the preparation of herbarium specimens; several of the parts considered important in classification (viscidium, caudicle, pollinia) are frequently dissolved by either alcohol or water. The study of living plants is, thus, especially important. Orchids can, of course, be identified from dried specimens, but a better understanding of relationship is to be obtained from the living plant. Field work by specialists cannot fail to add greatly to our knowledge, while the great variety of orchid genera cultivated by hobbyists can be of great value to botanists.

Finally, we must stress the limitations of the present paper. We have reviewed the nomenclature of orchid tribes and subtribes, following the rules of botanical nomenclature, including priority. We have attempted to evaluate the system of Schlechter, and have offered several changes in arrangement and circumscription, as well as a key to the subtribes which we recognize. We do not consider this a

final, complete system of orchid classification, so much as an evaluation of previous systems, and a working system to be improved and replaced as soon as possible. A discussion of several aspects of orchid phylogeny is presented. Many of the problems which are raised here can best be studied by regional specialists, and it is hoped that the present paper may stimulate such research.

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