THE SUBFAMILIES OF THE ORCHIDACEAE

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There have been a number of attempts to divide the Orchidaceae into major phyletic units, or subfamilies, but none of them has been wholly satisfactory. The many parallelisms within the family make it difficult to delineate natural groups by simple key features. Further, in most systems some groups have been defined solely on the basis of one or two shared primitive features. The systems of Pfitzer (1887) and Schlechter (1926) were both rather artificial, and often inconsistent with the key features used. Garay (1960) has divided the family into five subfamilies, but his system is largely based on Schlechter's and retains most of its defects. Brieger (in Brieger, Maatsch & Senghas, 1970-1978 ff.) offers a rather different system of classification. This, too, is based on arbitrarily chosen unit features, and the features chosen are, in too many cases, discordant with the classification. In the present paper I will review some features of special systematic importance, offer a revised subfamily classification, and provide valid names for a few taxa. These names are needed for a forthcoming book, in which the features and the classification discussed here are to be treated at greater length.

FEATURES OF SPECIAL IMPORTANCE

1. Pollen

A few orchids have powdery, unconnected pollen grains, but most have the grains at least lightly aggregated into pollinia. Soft pollinia are considered primitive as compared to hard pollinia, but there is a complete spectrum from very soft to very hard. Thus, the texture of the pollinia is of little systematic value unless correlated with other features. Sectile pollinia, in which each pollen mass is made up of several or many smaller packets, or massulae, are known in a number of groups and have undoubtedly evolved independently several times. This condition is not to be considered as an intermediate between soft and hard pollinia.

The structures associated with the pollinia are also of some importance. Caudicles are appendages that are formed within the anther and may be parts of the pollen masses themselves. These appendages vary in shape and may be either granular (primarily formed by pollen grains) or hyaline (primarily formed by clear, elastic "viscin," apparently tapetal in origin). Caudicles may be developed at either the base or the apex of the anther and may be developed within the anther cells or between adjacent cells. In many orchids a portion of the rostellum forms a sticky pad, or viscidium, which is removed with the pollinia. This structure has evolved independently in many groups. Among the vandoid tribes one commonly finds a stipe, or a strap of non-sticky tissue, which connects the caudicles of the pollinia with the viscidium. The stipe is a cellular tissue derived from the column, and is thus quite different from the caudicles. Stipes appear to have evolved independently a few times.

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2. Anther

Features of the anther are important in orchid classification, but more work on the development and structure of the anther is clearly needed. The primitive condition would seem to be an elongate, four-celled anther that is erect, or parallel with the axis of the column. In more advanced orchids the anther may have almost any orientation, and it is sometimes not clear just what is base and what is apex.

Among the epidendroid orchids the anther is commonly operculate, that is, it sits like a cap on or near the apex of the column. Hirmer (1920) has shown that the anther is at first erect in these orchids and later bends down over the apex of the column (see Figure 1). We may restrict the term incumbent to this condition. The anther of the vandoid orchids is also operculate, but Hirmer found no sign of bending in the anther development of these orchids (see Figure 1). He interpreted this as the anther being already bent from its earliest stages. My own impression is, rather, that the vandoid anther is short and remains erect, opening basally rather than ventrally. This is just the opposite of Garay's interpretation (1972), in which he characterizes the vandoid orchids as having incumbent anthers and the epidendroid orchids as having erect anthers. It is quite clear, though, that many epidendroid orchids have the anther incumbent at anthesis. Whatever the morphological interpretation may be, there is an important developmental difference between these two groups.

In most orchid groups the anther partitions are longitudinal and the cells or pollinia are laterally flattened, that is, the partitions are perpendicular to the (ventral) opening of the anther, and, in many cases, to the underlying surface of the column (clinandrium). In the vandoid orchids the partitions are much reduced and may be oriented more or less parallel to the opening of the anther. In these groups the pollinia, if four, are superposed, or dorsoventrally flattened, that is, flattened parallel to the clinandrial surface. This distinguishes the vandoid orchids from most other groups, but in *Coelogyne* and in some species of *Sobralia* one finds a very similar condition.

3. Rostellum

In most monandrous orchids a part of the stigma, the rostellum, aids in transferring pollen from one flower to another. In the simplest case, the rostellum is a projection of the stigma which is brushed by an insect leaving the flower, so that some stigmatic fluid is placed on the insect and serves to glue the pollinia, or their caudicles, to the pollinator. In many orchids the rostellum forms a clearly defined viscidium, to which the pollinia or their caudicles are attached, so that the viscidium and all pollinia are removed as a unit. The rostellum is commonly defined as the third, or median, stigma lobe, following Darwin, but in most cases it is only a part of the median stigma lobe. Indeed, the median stigma lobe may make up most of the receptive stigmatic surface.

In the tribes Orchideae and Diseae the viscidium is basically two-parted, a condition occasionally found in other groups. This has led Vermeulen (1959) to suggest that the rostellum of the Orchideae and Diseae is derived not from the median stigma lobe but from the two lateral lobes. However, developmental studies show that the viscidia of the Orchideae and Diseae are derived from the median stigma lobe (see Figure 2; also figure 2 in Vogel,

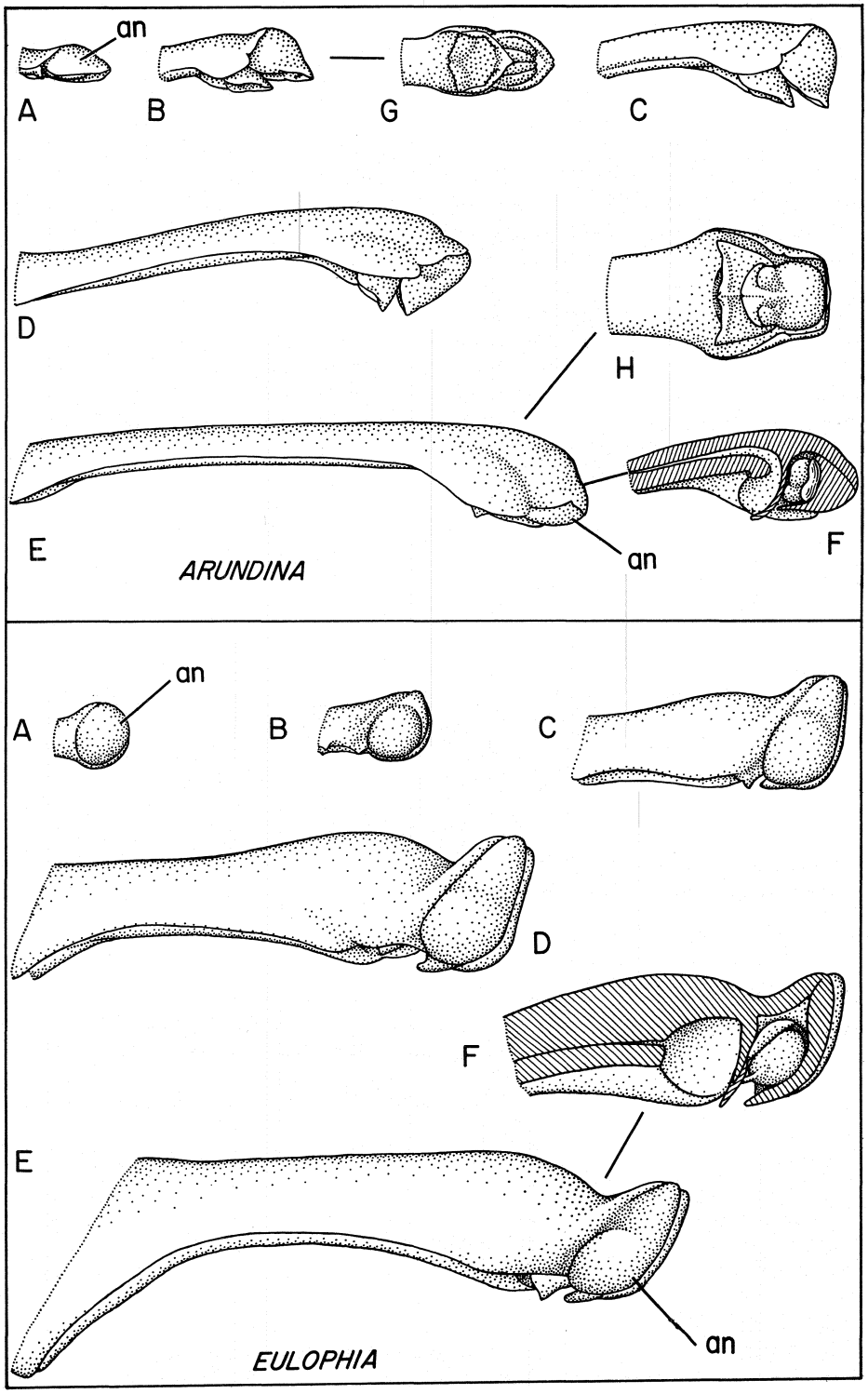

Figure 1: Column development in *Arundina graminifolia* (Epidendroideae) and *Eulophia petersii* (Vandoideae). Note that the anther of *Arundina* is erect in the early stages and bends downward over the apex of the column, while no such bending is shown by *Eulophia*. An = anther.

1959). Vermeulen's drawings of *Coeloglossum* and *Platanthera* show that when the viscidia are far apart the median stigma lobe is extended to them. When the viscidia are together, as in *Dactylorhiza*, there is no corresponding extension of the lateral stigma lobes. Further, the "tape" which connects the viscidia of the Orchideae (the rostellum) would be very difficult to explain if the viscidia were derived from the lateral stigma lobes as two separate structures. Garay (1960) says simply that the Orchideae do not have a rostellum, and that the viscidia are derived from the connective. However, no evidence is offered in support of this curious hypothesis.

The relationships between the anther and the rostellum offer some useful taxonomic features. In the Orchideae the caudicles are formed at the base of the anther and are attached to the viscidia at the base. In the spiranthoid orchids, on the other hand, the rostellum is subequal to the anther, the viscidium is attached at the apex of the anther, and the caudicles, when present, are terminal. Pfitzer, indeed, characterized the Orchideae as the Basitonae, and treated all other monandrous orchids as the Acrotonae. In the Diurideae one finds every condition from extreme basitony to acrotony, with most members of the tribe being intermediate or rather closer to basitony. It is quite possible, too, that the vandoid orchids are, in fact, basitonic rather than acrotonic.

4. Subsidiary Cells

The nature of subsidiary cells of the stomata of leaves may prove to be a very useful feature, though more study is clearly needed. Subsidiary cells may be lacking in some members of any orchid group, but, contrary to some recent papers, they are present in many orchids. Among the monandrous orchids, the members of the spiranthoid complex often have mesoperigenous subsidiary cells (Williams, 1975), while the orchidoid complex lacks subsidiary cells in all cases. Trapezoid (perigenous) subsidiary cells are found in many epidendroid and vandoid orchids (Williams, 1979), and subsidiary cells are reported in both the Apostasioideae and the Cypripedioideae, though developmental studies are lacking.

SUBFAMILIES

The tribes referred to in the following pages are those of Dressler (1974), with some revision in a few cases. Butzin (1971) gives a useful listing of the names which have been used for subfamilies, tribes and subtribes.

1. **Apostasioideae** Reichenbach, Repert. herb. 56. 1841. (*Apostasia, Neuwiedia*).

This is a relic group with two or three elongate, fertile anthers, free pollen grains and a slightly zygomorphic perianth. In older classifications they were often grouped with the Cypripedioideae, but the fertile lateral anthers, a primitive feature, are clearly not evidence of close relationship. Some authors would exclude the Apostasioideae from the Orchidaceae, largely because they "don't look like orchids," or because they are not closely allied to the ladyslippers. The apostasioids have free pollen grains and a slender style with equal and similar stigma lobes, and they clearly differ from other orchids in these features. Most other features which have been cited as arguments for their exclusion from the Orchidadeae do not

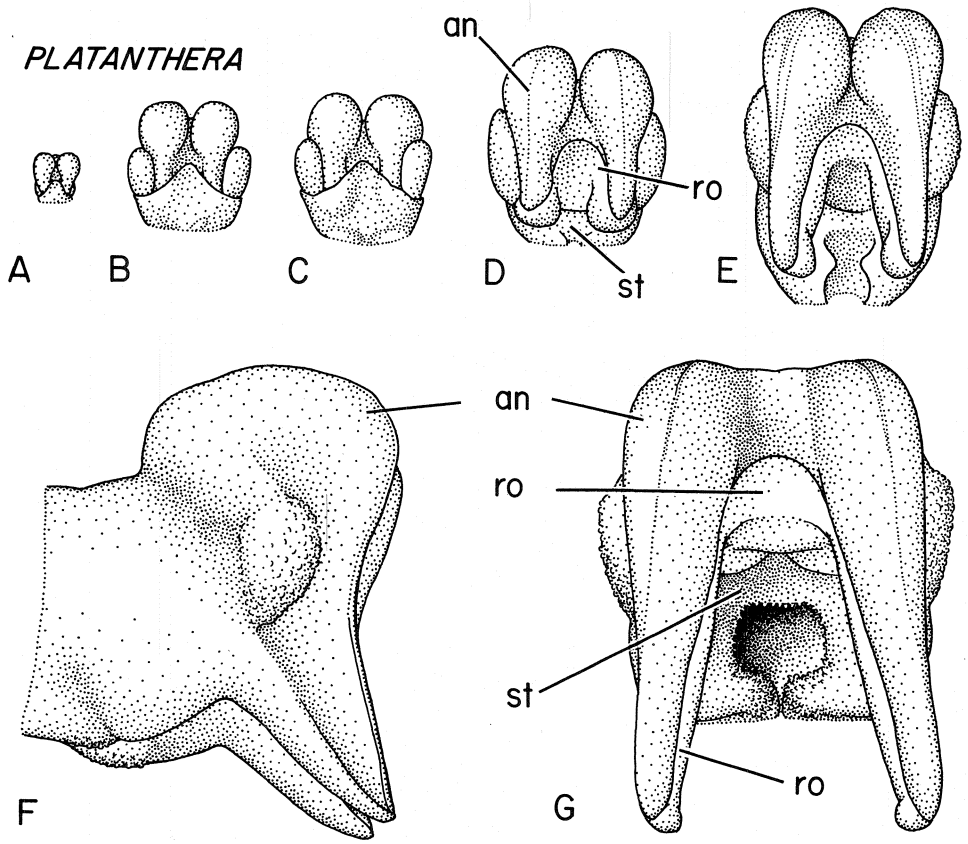

Figure 2: Column development in *Platanthera ciliaris* (Orchidoideae - Orchideae). Note that the rostellum arises as a single lobe (the median stigma lobe) and elongates to form two separate viscidia. An = anther, ro = rostellum, st = stigma.

hold up under close scrutiny. There is considerable union between the style and filaments, the anthers are not basically different from those of other orchid groups, and the flowers are resupinate and do have a definite lip in *Neuwiedia*. Barthlott (1976) suggests that their seed structure supports their exclusion from the Orchidaceae, but seed structure is also rather aberrant in *Selenipedium* and in the Vanillinae. Most authors who would exclude the apostasioids from the Orchidaceae still treat them as ancestral to the orchids.

2. **Cypripedioideae** Lindley, Coll. bot., App. 1821. (*Cypripedium*, *Paphiopedilum*, *Phragmipedium*, *Selenipedium*).

These genera share fertile lateral anthers, a shield-like, sterile median anther and a deeply saccate lip. Though the fertile lateral anthers must be considered a primitive feature, this subfamily shows definite relationships with the monandrous Neottieae, and especially with *Epipactis*, which resembles *Cypripedium* closely in habit, seed structure and large chromosomes.

3. **Spiranthoideae** Dressler (see appendix). (Cranichideae, Erythrodeae).

This group is characterized by having the rostellum erect and subequal to the anther, thus having terminal viscidia, by the presence of mesoperigenous subsidiary cells, and usually by relatively small chromosomes. These tribes, with the Neottieae and Diurideae, were included in the Neottieae of Pfitzer, the Polychondreae of Schlechter and the Neottioideae of Garay, but the soft pollinia, being a primitive feature, do not necessarily imply a close relationship. In fact, the Cranichideae and Erythrodeae show no close relationship with the Neottieae or the Diurideae (both here included in the Orchidoideae). If the Spiranthoideae have a close relationship with any other subfamily, it is likely to be with the Apostasioideae.

4. **Orchidoideae** (Diseae, Diurideae, Neottieae, Orchideae).

This subfamily is characterized by having the anther project beyond the stigma or rostellum, by the absence of subsidiary cells, and, in the Diseae, Diurideae and Orchideae, by the presence of root-stem tuberoids. Most systems have exaggerated the isolation of the Orchideae and Diseae. In fact, the unique root-stem tuberoids are strong evidence of a relationship between these tribes and the Diurideae. Virtually all features of the Orchideae are to be found in the Diurideae, as well. The Neottieae are less specialized than either the Diurideae or the Orchideae, but they may well share a close common ancestry with both.

5. **Epidendroideae** Lindley, Coll. bot., App., 1821. (Arethuseae, Calypsoeae, Coelogyneae, Cryptarrheneae, Epidendreae, Epipogieae, Gastrodieae, Malaxideae, Vanilleae).

This group is characterized primarily by the ontogenetic bending of the anther (see Figure 1). The primitive members of this subfamily have soft pollinia, and there is no clear line between them and the more advanced members with hard pollinia, which may have caudicles or be quite naked (most Malaxideae, Bulbophyllinae, Dendrobiinae). Viscidia occur in many groups, but stipes are lacking, with few exceptions (*Calypso*, *Monomeria*, *Sunipia*, some *Bulbophyllum* species). In advanced members with viscidia, such as Podochilinae and some Pleurothallidinae, the anther may remain erect through the development of the flower, but these will not be confused with the members of the Vandoideae. In terms of species diversity, the Epidendroideae form much the largest of the orchid subfamilies.

6. **Vandoideae** Endlicher, Gen. pl. 196. 1837. (Cymbidieae, Maxillarieae, Polystachyeae, Vandeae).

This subfamily is characterized by stipes, dorsoventrally flattened pollinia, reduced anther partitions, and by operculate anthers that do not bend during their development. The vandoid orchids have been considered to be derived from epidendroid ancestors. The development of the anthers, however, suggests independent origins for the two groups. The vandoid orchids are generally considered as the most highly evolved group in the family. Parallelisms make the tribal classification of this group difficult. For the present, I include all groups with four pollinia, except the Polystachyeae and Vandeae, in the Maxillarieae, and all groups with two pollinia, except the Vandeae, in the Cymbidieae. The reduction from four to two pollinia may have occurred independently in some of the groups that are tentatively assigned to the Cymbidieae, but there is no conclusive evidence either way.

Figures 3 and 4 show the suggested relationships of the major orchid tribes in the six subfamilies.

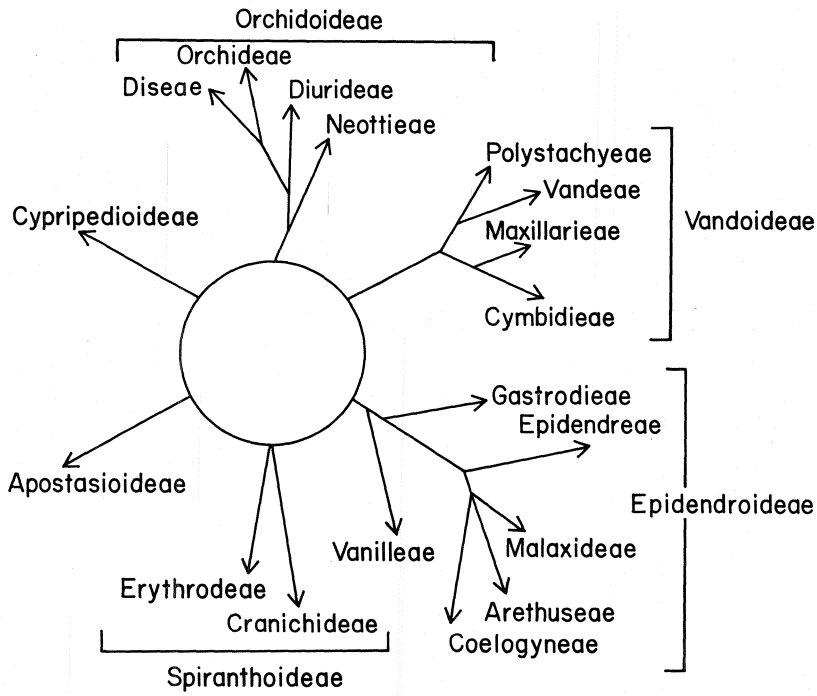

Figure 3: A scheme showing the suggested relationships of the major orchid tribes.

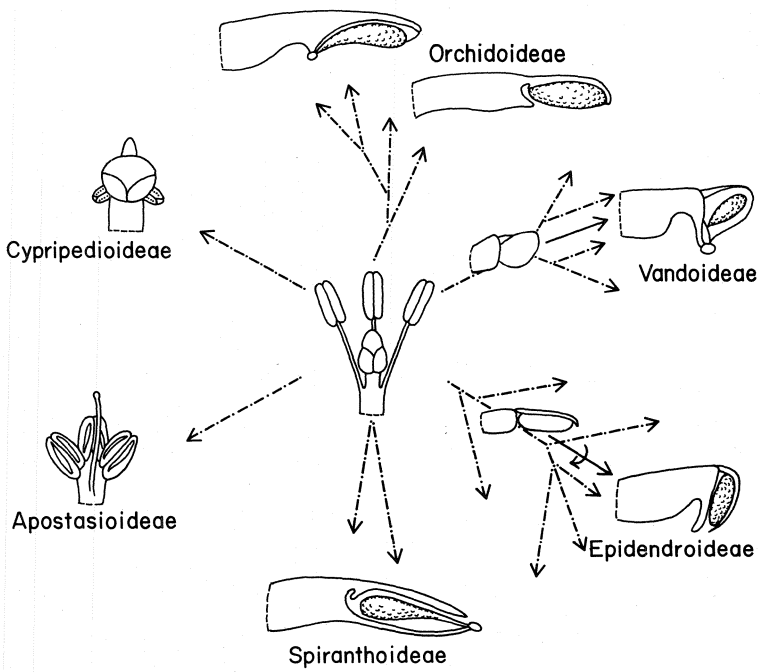

Figure 4: A diagrammatic representation of the orchid subfamilies. A hypothetical ancestor is shown in the center. Compare with Figure 3.

APPENDIX - NEW TAXA

Spiranthoideae Dressler, subfam. nov. plantis herbaceis; foliis convolutis pedunculo terminali; rostello recto anthera subaequilongo; anthera dorsali; glandula terminali.

TYPE. *Spiranthes* L. C. Richard.

Tribe **Calypsoeae** (Camus) Dressler, stat. nov., subtribe Calypsoinae Camus, Monogr. orchid. 376. 1908.

TYPE: *Calypso* Salisbury.

In the new edition of Schlechter's Die Orchideen, Brieger assigns the subtribe Calypsoinae to the Epidendroideae because of the supposed lack of a stipe. In fact, *Calypso* has a very well developed stipe, but Brieger's placement of this genus seems to be correct, in spite of this. The developmental stages that I have been able to study show that *Calypso* has an incumbent anther, very like that of *Coelogyne*, and I believe, thus, that this represents the independent evolution of a stipe in the epidendroid line of evolution. As *Calypso* does not fit well in the Arethuseae, the Coelogyneae, or any other tribe of the Epidendroideae, tribal status seems appropriate.

Diseae Dressler, trib. nov. tribui Orchideis similis sed anthera reclinata vel resupinata.

TYPE: *Disa* Bergius.

The tribal name Diseae has been used by several authors, and credited to Bentham, however, Bentham used this group as a division of a tribe, and thus the tribal name must be treated as new. One may make a good case for separating the Disinae, Satyriinae and Coryciinae from the Orchideae as a distinct tribe.

Triphoreae Dressler, trib. nov. plantis herbaceis; foliis convolutis; pedunculo terminali; anthera recta, terminali, carnosa.

TYPE: *Triphora* Nuttall.

These genera (*Monophyllorchis*, *Psilochilus*, *Triphora*) have been placed in the Pogoniinae by most authors, but the Pogoniinae are characterized by a clearly incumbent anther, markedly sinuous epidermal cell walls, and an abcission layer between ovary and perianth, all features that are lacking in the Triphoreae. Superficially, at least, the Triphoreae would fit reasonably well in the subfamily Orchidoideae, but *Monophyllorchis* and *Psilochilus*, at least, have subsidiary cells, which seem quite out of place in the Orchidoideae. The Triphoreae show no close alliance to any member of the Orchidoideae, and I suspect that this is a relict group, somewhat closer to the common ancestor of the Epidendroideae and the Vandoideae than to any living group. For the present, I consider this an anomalous tribe, and I do not place it in a subfamily.

Acriopsidinae Dressler, subtrib. nov., pseudobulbis ovatis, paucifoliatis; foliis conduplicatis; pedunculis lateralibus, multifloris; columna labello adnata; clinandrio cucullato; polliniis 2, complanatis, stipiti anguste affixis.

TYPE: *Acriopsis* Reinward ex Blume.

The genus *Acriopsis* is usually included in the Thecostelinae, but *Acriopsis* and *Thecostele* are very different in almost every feature. *Acriopsis* is rather isolated, and the thin, laterally flattened pollinia are quite unlike those of any other Asiatic orchid.

Bifrenariinae, Dressler, subtrib. nov. caulibus pseudobulbosis, paucifoliatis; foliis plicatis vel conduplicatis; pedunculis lateralibus; polliniis 4, superpositis, stipitatis vel glandulis sessilibus.

TYPE: *Bifrenaria* Lindley

Bifrenaria and *Xylobium* have been placed in the Lycastinae or the Zygopetalinae, but they fit poorly in either subtribe, and their inclusion in either one makes any distinction between these two subtribes difficult. If all these groups are united, then the distinction between the inclusive Zygopetalinae and the Maxillariinae becomes rather tenuous. Creating a separate subtribe for *Bifrenaria*, *Horvatia*, *Rudolfiella*, *Teuscheria* and *Xylobium* seems the best alternative.

Lecanorchidinae Dressler, subtrib. nov. plantis saprophyticis, tenuibus; floribus calyculatis; labello columnae basi adnato, trilobato; columna tenui; polliniis pulvereis; seminibus minutis.

TYPE: *Lecanorchis* Blume.

In overall flower structure, in the calyculus borne at the base of the perianth, and in its pollen structure, *Lecanorchis* shows a close alliance with the Vanillinae. At the same time, its small seeds are quite aberrant for that subtribe. A separate subtribe within the Vanilleae seems the best status for this genus.

Palmorchidinae Dressler, subtrib. nov., caulibus tenuibus; folia plicata; pedunculis terminalibus vel lateralibus; labello columnae adnato; anthera incumbenti; polliniis 4, coherentis, nudis; stigmate projecta.

TYPE: *Palmorchis* Barb. Rodr.

Schweinfurth & Correll (1940) suggest subtribal status for *Palmorchis*, but fail to supply a valid description. In fact, the *Vanilla*-like flower structure and the compact, naked pollinia suggest that *Palmorchis* and *Diceratostele* form a very distinct subtribe.

Sunipiinae Dressler, subtrib. nov. pseudobulbis ovatis, unifoliatis; foliis conduplicatis; pedunculis lateralibus; labello simplici; columna brevi; anthera extrorsa dehiscenti; polliniis 4, leviter complanatis, stipitibus 2 et glandulis 2.

TYPE: *Sunipia* Lindley.

The *Bulbophyllum*-like genera with stipes (the Genyorchidinae in the sense of Schlechter) have caused problems in all systems of classification. *Genyorchis* proves to be a vandoid genus, referable to the Cymbidieae. *Monomeria* has a single stipe, but seems otherwise very close to *Bulbophyllum*. Though *Drymoda* has been classed with these genera, it has only a well developed viscidium, not a stipe. Since viscidia occur in some species of *Bulbophyllum*, and stipes are reported for species of *Bulbophyllum* section *Cestrochilus* (Seidenfaden, pers. comm.), neither *Drymoda* nor *Monomeria* can be clearly separated from the Bulbophyllinae. *Sunipia*, on the other hand, is much more distinctive. Each flower has two distinct stipes, and the persistent anther dehisces on its outer (adaxial?) surface, exposing the pollinia.

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