

## THE SYSTEM OF THE ORCHIDALES

P. VERMEULEN

(*Hugo de Vries Laboratorium, Amsterdam*)

(received November 3rd, 1965)

### ABSTRACT

After an enumeration of the most characteristic features of the *Orchidales*, the affinities between this order and other monocotyledonous groups are discussed. The *Orchidales* must be placed in the system immediately after the *Commelinales*, chiefly on account of their androecial morphology. For reasons explained in the present paper the *Orchidales* are subdivided into three families, viz. the *Apostasiaceae*, *Cypripediaceae* and *Orchidaceae*. The principal differences between these families are shown in the form of tables.

In the *Orchidaceae* two subfamilies are recognised and amply circumscribed, viz., the *Orchidoideae* and the *Epidendroideae*, the latter again being subdivided into the two tribes *Neottianthae* and *Epidendranthae*.

The androecial morphology is discussed in detail in connection with atavistically developed stamens, with the presence of staminodes (or supernumerary stamens) and with the floral morphology of certain taxa. The auricles are not regarded as staminodes because they persist in flowers with supernumerary (atavistically re-appeared) stamens and also because they lack vascular bundles. The gynostemial wings in some Australian genera (*Diuris*, *Prasophyllum*, and other ones) are considered to be of androecial derivation. The less conspicuously winged but vascularised margins of the gynostemium of many *Epidendroideae* likewise represent androecial elements incorporated in the column.

The suggestion, made by E. Nelson, that the lip is the phylogenetic derivative (the homologue) of the 'missing' stamens  $A_2$ ,  $a_3$  and  $A_3$  (which implies that the median petal has disappeared), is rejected, primarily because Nelson's arguments are based on the morphology of the labellum in the highly specialised genus *Ophrys*. The floral morphology of *Neuwiedia* and of some species of *Herminium*, on the contrary, is indicative of the petaloid nature of the lip which, accordingly, represents the median petal. The vascular anatomy of the orchid flower does not provide arguments in favour of the suggestion made by Lindley (later taken up by Darwin) that the 'missing' stamens  $A_2$  and  $A_3$  are incorporated in the gynostemium.

The orchidalean ovary appears to be compounded of six parts, viz. three broad hyposepalous zones alternating with as many hypopetalous elements bearing the (double) laminal placentae on their inner face. This is considered to be a convergence towards the condition prevailing in *Rhoeadales* (*Brassicales*) (genus *Eschscholzia* etc.).

In the *Orchidoideae* the stigma is locally differentiated into viscid discs which are situated distally of the lateral stigmatic lobes, and the median stigmatic lobe is functional in several genera, but in the *Epidendroideae* the median stigmatic lobe is apically transformed into a mucilaginous substance or a viscid disc, or it is completely replaced by a viscidium. In *Stereosandra* the viscidial element is a derivative of the anther.

### 1. HISTORICAL INTRODUCTION

In his *Systema Naturae* (1735), LINNAEUS distinguishes as Classis XX the *Gynandria* ("Stamina pistillis (non receptaculo) insident"), to which he refers various groups, viz. the *Diandria*, being the orchids

including, e.g., *Orchis* and *Cypripedium*, the *Triandria* with *Sisyrinchium*, the *Tetrandria* with *Nepenthes*, etc. Linnaeus apparently regarded the pollinia as stamens. ADANSON, in his *Familles des Plantes* (II, 1763), described "*Les Orchis*" as having only one stamen, but he also classified *Cypripedium* among this group. Olof SWARTZ (1800) was the first to distinguish "Orchider med en Anthera" and "Orchider med två Anthera", more recently generally referred to as the *Monandrae* and the *Diandrae*. Apparently still under the spell of Linnaeus' views, and not realising that there is a difference between episepalous and epipetalous stamens (in other words that two whorls of stamens may be present), SWARTZ did not raise these groups to family level. This theory goes back to Robert BROWN, after he had studied *Apostasia* (see WALLICH: *Plantae Asiaticae Rariores* (1830), Vol. I, p. 74). BLUME, who described *Apostasia odorata* in 1825, had classified the species among the Orchids Subtrib. III. *Pulvereeae*, B. *Diantherae* (p. 423). LINDLEY is the systematist who has enriched orchidology with his magnum opus *The Genera and Species of Orchidaceous Plants* (1830-1840). In the introduction on p. XVI (1840?) the author writes the following about *Apostasia*: "It may, however, be observed that *Apostasia* has apparently as much claim to be regarded as a diandrous monadelphous Amaryllidaceous plant allied to Hypoxidaceae . . . as it has to be regarded as a trilocular Orchidaceous plant with the gynandrous organization lost." LINDLEY had previously published (1833) his *Nixus Plantarum* where, on p. 22, he gives the following division:

#### Cohors II. GYNANDRAE

Monandrae	233. Orchideae
Diandrae, ovario 1-loculari	234. Cypripedieae m.
Diandrae, ovario 3-loculari	235. Apostasieae m.

He does not mention this booklet in the bibliography of orchids, published in his main work of 1840, but it does occur in 1853 in the third edition of his book: *The vegetable Kingdom* (p. 184) under the heading *Apostasiaceae*, (which are treated as a separate family there, immediately after the *Orchidaceae*). In 1833 Lindley regarded the *Gynandrae* as an order comprising three families, but in his principal work of 1840 he included the *Cypripedieae* again in the *Orchidaceae*.

I do not know the reason why he changed his mind, considering that Darwin and others later pointed out the great difference between the *Monandrae* and the *Diandrae*. In his book: *The various contrivances by which Orchids are fertilised by Insects*, he says about *Cypripedium* (p. 226): "(It) differs from all other Orchids far more than any other two of these do from one another. An enormous amount of extinction must have swept away a multitude of intermediate forms". DARWIN (1890), however, distinguished the *Cypripedeae* only as a tribe.

My personal view is that there are sufficient arguments to distinguish the *Cypripedieae* as a family (and likewise the *Apostasiaceae*).

LINDLEY treats the latter as a separate family, in which he was followed by RIDLEY, HUTCHINSON, GODFERY, SCHLECHTER, SCHWEINFURT and PULLE, whereas others (PFITZER, SMITH, HOLTUM etc.) retain them as a tribe or subfamily of the *Orchidaceae*.

In the following pages I shall attempt to show that the order of the *Orchidales* ought to be considered to comprise three families:

1. *Apostasiaceae* Lindl. (*Apostasieae*)
2. *Cypripediaceae* Lindl. (*Cypripedieae*)
3. *Orchidaceae* s.s. de Juss. (*Orchideae*)

## 2. THE CHARACTERISTICS OF THE ORCHIDALES

The common characteristics of the Order of *Orchidales* are:

1. Herbaceous (rarely suffruticose), perennial plants with a sympodial, less often monopodial, growth, with only adventitious roots. As storage organs rhizomes, tubers, corms or pseudobulbs are present. Rarely hapaxanth (=monocarp, i.e., dying off after having flowered only once).
2. Leaves parallel- or curviveined, in the bud convolute (twisted) or duplicative (infolded from the mid-vein, the margins touching one another) leaves with or without an articulation between sheath and blade, the latter deciduous in the articulated type. Sometimes leaves squamiform in heterotrophic plants: *Orchidaceae* only.
3. Flowers in indeterminate inflorescences, which are terminal (acranth) or lateral (pleuranth); rarely flowers single; or, in the *Cypripediaceae*, inflorescence cymose.
4. Flowers zygomorphic, epigynous, hermaphrodite (rarely unisexual). The ovary has six connate parts, sometimes with a collar (calculus) below the perianth. There are three placenta, on the three parts on which the petals are inserted. The median petal, forming the lip (labellum), differs in shape from the sepals and the two lateral petals.
5. The ovary topped inside the perianth by a column (gynostemium) supporting the androecium and the stigma; this column sometimes hardly developed (rarely missing), mostly distinct, short or more or less elongate.
6. Of the, in the fundamentally regular, trimerous monocotyledonous flower diagram assumed double whorl of 3 stamens, only the abaxial ones ( $A_1 + a_1 + a_2$ ) developed (fig. 1); rarely all three fertile (only in *Neuwiedia* Fig. 2), mostly only  $A_1$  fertile (*Monandrae* Fig. 5.8), and sometimes  $a_1 + a_2$  fertile (*Apostasia* and *Cypripediaceae* Fig. 3).

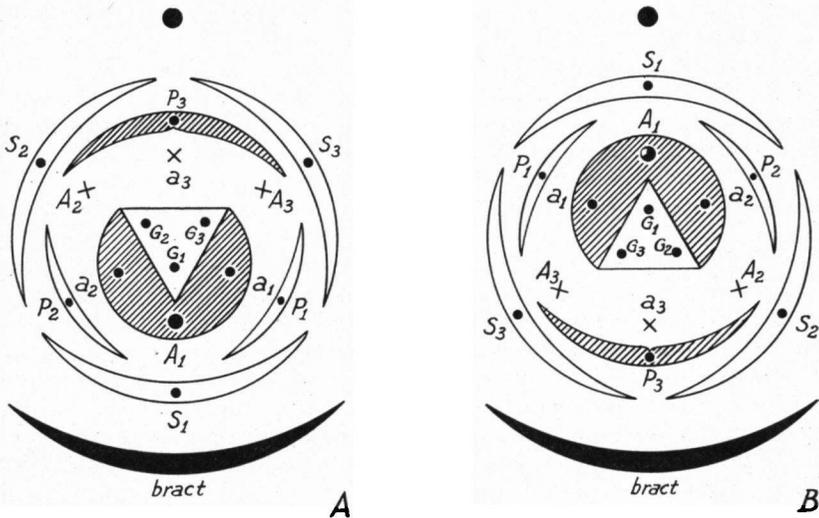


Fig. 1. Two diagrams of the flower of the *Orchidales*. A: not resupinated; B: resupinated.  $S_1, S_2, S_3$ : sepals;  $P_1, P_2$ : lateral petals;  $P_3$ : median petal or lip;  $A_1, A_2, A_3$ : stamens of the outer whorl of which  $A_1$  is fertile or staminodial and  $A_2$  and  $A_3$  are always missing;  $a_1, a_2, a_3$ : stamens of the inner whorl of which  $a_1$  and  $a_2$  are fertile, staminodial or missing and  $a_3$  is always missing;  $G_1, G_2, G_3$ : three vascular strands of the style of which  $G_2$  and  $G_3$  are sometimes missing. The gynostemium is formed by  $A_1 + a_1 + a_2 + G_1 + G_2 + G_3$ .

7. On the gynostemium the sessile stigma with three or two stigmatic lobes.
8. The flowers are entomophilous, sometimes ornithophilous, rarely autogamous.
9. Fruit a unilocular or trilocular capsule, opening with six fissures; sometimes baccate in *Neuwiedia*, *Galeola*.
10. Seeds minute, anatropous, very numerous, and with undifferentiated germ, the latter developing by mycotrophy (fungus symbiosis), into a protocorm with one growing-point. Radicle lacking.

*Ad 1.* In connection with the perennial habit, many orchids have storage organs; these are sometimes rhizomes, sometimes tubers (*Orchis*) or corms (*Gastrodia*). Especially in tropical species, pseudobulbs may occur, i.e., internodes, in which storage food is assembled (in the *Epidendranthae*). Most tropical species live on trees as epiphytes; studies made by Dr. Jacoba RUINEN (1952) have rather convincingly shown that the symbiotic fungus may be parasitic on the supporting tree.

*Ad 2.* Most orchids have convolute leaves in bud, only in the *Cypripediaceae* and the *Epidendranthae* (e.g. *Sarcochilus*) also duplicative

leaves occur. Articulated leaves with deciduous blade are only found in *Epidendranthae*.

*Ad 3.* The inflorescence is indeterminate in the *Monandreae* and the flowers are always inserted in the axil of a bract. In some species the flower is terminal. An adossed bracteole is only found in *Cypripediaceae* (which sometimes have a centrifugal inflorescence). HAGERUP (1959) thinks that in the orchids the bracteolae are represented by sepals.

*Ad 4.* The strong trend towards zygomorphy and specialised insect pollination in this group has caused a considerable diversity of development of the perianth lobes. The labellum is small in *Platanthera* and *Disa*, but strongly developed in *Ophrys*, *Disperis* etc., it is of a relatively simple structure in *Brassavola* and *Cattleya*, but much more complicated in *Stanhopea* and *Coryanthes*. In other families of plants zygomorphy is often also associated with a diversity of development of the floral appendages. For instance, in several genera of the *Lamiales* (*Labiatiflorae*) as in *Anthirrinum*, *Lamium* etc. the lower or anticous lip of the corolla, though homologous with one petal, is bilobed.

In *Linaria* the lip is strongly differentiated ("masked"). Similar phenomena also occur in *Lobelia* and in quite a number of other genera. Among the Monocots, the *Zingiberaceae* possess a labellum, staminodial in origin and homologous with two connate stamens. This labellum lies inside within the petals.

In *Linaria* we find a small rudiment of the median, episepalous stamen inserted opposite and on the superior (posticous) lip. Nowhere, however, do we find an indication of parts of the perianth and the androecium merging into a single organ, which would, in addition, have required an inward or outward shift of either the one element or the other. The shape of the labellum is often particularly adapted to the pollination mechanism, as in *Ophrys*, *Pterostylis*, *Coryanthes*, *Cypripedium* etc. In *Satyrium*, whose flowers are not resupinated, the labellum has two spurs and at the entrance of each spur lies a viscid disc. In *Disa uniflora* the flower is resupinated, but the labellum is small and the median sepal has a spur lying behind the viscid discs of the stamen; this is another adaptation to a specific pollination mechanism. The genotype apparently determines the degree of zygomorphy, sometimes associated with a strongly developed lip, sometimes with a median sepal. This is of course concomitant with different forms of entomophily.

For the ovary, see 10.

*Ad 5.* There are different opinions concerning the nature of the gynostemium. Formerly it was believed to be a coalescence of the style and one or more stamens. Pfitzer defended the opinion that it is an apical extension of the receptacle. It could also be an apical extension of the coalesced parts constituting the ovary. A number of differentiations occurring in the column, such as the chin and the foot, can hardly be regarded as of stylar derivation. Sometimes, as in

*Orchidoideae*, the filament can not be distinguished from the column. Here apparently the filament forms a part of the column. In other cases, viz. in such *Epidendroideae* as *Cephalanthera*, *Epipactis* and *Epipogium*, a short filament is inserted on the column. In the *Apostasiaceae*, where the coalescence into a column is not very pronounced, stamen(s) and style can clearly be distinguished as separate, individual organs. In *Goodyera* and *Spiranthes* the column is also short, and style and stamen are connected by a thin lateral tissue. In particular species of the Australian genera *Diuris*, *Prasophyllum*, *Thelymitra*, etc., style and androecium are quite free and, accordingly, we can not speak of a proper gynostemium in these cases. Sometimes the column attains an appreciable length, as in the South African genus *Satyrium*, in some Australian genera such as *Caladenia*, and in many epiphytes such as *Cattleya*, *Cymbidium*, *Cynoches*, etc. In connection with the development of the androecium, the gynostemium is always clearly zygomorphic and accordingly also the flower, even if the parts of the perianth sometimes differ very little among themselves, as in *Neuwiedia*, *Apostasia*, *Thelymitra*, etc., in whose flowers a whorl of three sepals alternating with a whorl of three petals can clearly be distinguished.

*Ad 6.* The reduction of the adaxial (axis-opposed) stamens ( $A_2 + A_3 + a_3$ ) has left its mark on the development of the orchid flower.

A comparable case of unequal development of adaxial and abaxial stamens is provided by some *Commelinaceae* such as *Commelina*; in their non-resupinated flowers the adaxial stamens are fertile, the abaxial ones sterile. In the *Pontederiaceae* a progressive reduction can be observed, some genera having 6 stamens in two unequally developed groups of three, ( $A_1 + a_1 + a_2$ ) being opposed to ( $A_2 + A_3 + a_3$ ) (e.g., in *Eichhornea* and *Pontederia*), but the genus *Heteranthera* having only  $A_1 + a_1 + a_2$  (a situation we also find in *Neuwiedia*) and the extreme case, *Hydrothrix* from Brazil, only  $A_1$  (see GOEBEL, *Flora* 105, 1913). In the *Philydraceae* only  $A_1$  develops (see HAMANN, 1961). In the *Orchidales* only the abaxial stamens ( $A_1 + a_1 + a_2$ ) are present, whereas the adaxial ones have completely disappeared. We often find only  $A_1$ . One should bear in mind that an extreme reduction of the number of stamens may also have occurred in forms that primarily underwent a reduction of one of the two whorls of stamens, as in the commelinaceous *Palisota* or in *Iridaceae*. If in *Iridaceae*, having only  $A_1 + A_2 + A_3$ , only the abaxial stamen  $A_1$  would remain, a situation comparable to the one in the *Orchidoideae* would result. If in a plant of this group one or both of the normally absent stamens would atavistically develop, it is likely to be  $A_2$  or  $A_3$ , or both of them, and not  $a_1$  or  $a_2$  as one would expect, because these two should be present in the form of the auriculae (see in this connection also 9).

*Ad 7.* The number of stigmatic lobes is three in the *Apostasiaceae* and *Cypripediaceae*. In *Apostasia* the stigmatic lobes are not very distinct. In the *Orchidaceae* s.s. (*Monandrae*) we can sometimes very clearly distinguish three lobes (*Disa*) but in other genera there are only two

(*Pterostylis*) which are also sometimes placed on stigmaphores (*Habenaria*). Upon closer examination, most *Monandrae* appear to have three stigmatic lobes and it is, therefore, highly improbable that, as Darwin suggested, the median stigmatic lobe became the rostellum, but the rostellum sometimes forms a part of this stigmatic lobe, it is true, viz. in the *Epidendroideae*.

*Ad 8.* Many orchid flowers have structures eminently adapted to pollination by certain insects. This particularly holds true for flowers which are pollinated by pseudocopulation of male animals or for those which have a motile labellum. The investigations of the Australian worker Edith COLEMAN (1927) have been epoch-making. In Europe, the work of KULLENBERG (1961) has yielded excellent results. Flowers which are pollinated by humming birds are small and compact as in *Elleanthus* and *Isochilus*. The work of Stefan VOGEL (1959) provides, by inference, fine examples, of insect adaptations in South African species even if the actual pollination process has not been observed. In America, Dodson cooperates in this field with Van der Pijl, The Hague.

*Ad 9.* In *Neuwiedia singaporeana*, *N. javanica*, and *Galeola javanica* baccate fruits occur as in several *Commelinaceae*, but otherwise always capsules are found. *Neuwiedia*, *Apostasia*, *Paphiopedilum*, *Phragmopedium* and *Selenipedium* have trilocular capsules (also *Lecanorchis*?). In all other orchids unilocular capsules occur. The fruit is a so-called replum and opens with six longitudinal fissures, arising on either side of the six parts forming the ovary. The placentae, which are sometimes clearly branched, as in *Epipogium*, are connate with the three broad parts. The narrow parts, which at their top pass into the sepals, bear no placentae but form the stigmas.

*Ad 10.* The germination is in nature consistently associated with the presence of a fungus. After a few weeks the seeds form root hairs, when they are kept in moist surroundings, but the germination only proceeds after an infection with a symbiotic fungus (mostly *Rhizoctonia*) has taken place. An undifferentiated germ subsequently develops which is called the protocorm and possesses only one growing-point. The protocorms are often white and then for their nutrition depend entirely on the digestion of the fungus balls that have penetrated the root cortex (mycotrophy). It is often said that the seedlings live saprophytically, but this is incorrect; they live as parasites at the expense of their root fungus. The protocorms of many *Epidendroideae* soon turn green, and then become partly autotrophic.

*N.B.* It should be noticed that neither the presence of pollinia nor that of a rostellum have been mentioned as features of the order.

### 3. THE PLACE OF THE ORCHIDALES AMONG THE MONOCOTYLEDONS

In the various systems of classification the *Orchidales* or *Gynandrae* are consistently placed among the terminal orders of the Monocots

and that is of course rather obvious, if they are regarded as the most evolved family, which, moreover, contains, in several of its subordinate taxa, genera which are still in speciation (*Orchis*, *Dactylorchis*, *Ophrys* etc.).

Von Wettstein places them after the *Scitamineae*, Takhtajan puts them after the *Haemodorales* in the 'super-order' of the *Liliiflorae*. Hutchinson removes the *Apostasiaceae* to the *Haemodorales* and associates them with *Curculigo* (*Hypoxidaceae*), whilst placing the *Orchidales* behind the *Burmanniaceae*. In the dendrogram proposed by HUTCHINSON (Vol. I, ed. 2, p. 694) the *Apostasiaceae* are considered to be the ancestors of both the *Burmanniaceae* and the *Orchidaceae*. In connection with the development of zygomorphy in the androecium it seems to me more obvious to suppose that the *Orchidales* are more closely related to the *Commelinales* than to the *Liliales*. Both the *Commelinales* (not the *Tradescantia* group) and the *Orchidales* show a tendency towards an unequal development of the adaxial stamens as opposed to the abaxial ones. This feature is, in my opinion, indicative of a close affinity of these two orders, so much so that they form a "natural" group. Considering that not infrequently (see, e.g., *Ophrys*, *Cymbidium*) the *Orchidales* exhibit clearly distinct whorls of sepals and petals (differing in both shape and colour), one could also include them in Hutchinson's *Calyciferae*.

Apart from the *Commelinaceae*, this group would, then, include the *Pontederiaceae*, of which HUTCHINSON says (Vol. I, ed. 2, p. 618): "the Pontederiaceae are a difficult family to place". The order *Commelinales* would then consist of the families *Commelinaceae*, *Pontederiaceae* and *Philydraceae*.

According to this classification, the *Orchidales* would then immediately follow this order. Particularly the *Pontederiaceae* are in some ways reminiscent of the *Apostasiaceae*. The genus *Heteranthera*, for instance, like *Neuwiedia*, has only the three abaxial stamens ( $a_1 + A_1 + a_2$ ) developed, whereas the genus *Hydrothrix* possesses only one fertile stamen,  $A_1$ , like the *Monandreae*. In the *Commelinales* we usually find a well-developed endosperm, but it is lacking in the mycotrophic *Orchidales*. However, the *Commelinales* never possess a gynostemium.

#### 4. THE CLASSIFICATION OF THE ORCHIDALES INTO FAMILIES

Although in 1833 LINDLEY suggested a subdivision of the *Gynandreae* into three families, he did not maintain this classification in his most important publication "The Genera and Species". He still treated the *Apostasiaceae* as a separate family, it is true, but the *Cypripediaceae* are included in the *Orchidaceae* as a tribe. If we consider what criteria are usually applied to delimit families, we must admit that it depends upon the group under consideration (and on the author!), but, generally speaking especially the inflorescences, the construction of the flower and particularly the androecial and gynoecial morphology (stamens and pistils) are taken into account. In the *Zingiberales*, for instance, we see that the reduction of the androecium plays an

important part in the distinction of the *Musaceae* with three + two fertile stamens, the *Zingiberaceae* with one fertile stamen + staminodia, and the *Marantaceae* and *Cannaceae* with half a fertile stamen + staminodia, respectively.

In the *Liliales* the androecium also forms an important characteristic to distinguish various families. In the *Amaryllidaceae* (according to EICHLER, 1875) we find 3 + 3 stamens, in the *Iridaceae* 3 + 0, in the *Haemodoraceae* 0 + 3. These are examples from the Monocots. Among the Dicots the recognised differences between the *Apocynaceae*, the *Periplocaceae* and the *Asclepiadaceae* provide an example. In the *Apocynaceae* there is no gynostemium and no corona, the anthers converge, the pollen grains are free, and the style ends in a stigmatic head; in the *Periplocaceae* there is a gynostemium and sometimes also a corona, the pollen grains are loose or the grains from one theca are so coherent that they are transferred as a whole, and the style has a stigmatic head; in the *Asclepiadaceae* a gynostemium, a corona, pollinia, translators and a stigmatic head are all present. These three families are markedly entomophilous. Similar differences occur in the three groups of the *Orchidales*, so that, in analogy of the examples mentioned, I propose to distinguish three families: *Apostasiaceae*, *Cypripediaceae* and *Orchidaceae* (*sensu stricto*).

Lindley was the first to treat the *Apostasiaceae* as a separate family and many taxonomists have followed him. PFITZER united the *Apostasiinae* and the *Cypripedilinae*, first as *Diandrae* (1887), but later as *Pleonandrae* (1903), on account of the three or two fertile stamens. In the *Orchid Review* 40 (1932) p. 355, Colonel M. J. GODFERY summed up the differences between the *Apostasiaceae* and the *Diandrae* (see also Charles SCHWEINFURTH in WITHNER: *The Orchids* (1959), p. 511). Noteworthy is the statement by J. J. SMITH in: *Nova Guinea*, vol. XII, botanique, livr. III, p. 175 under *Apostasia papuana* Schltr., (translated): "Ridley and Schlechter consider *Apostasia* and *Neuwiedia* to form a natural family, the *Apostasiaceae*. This is partly a matter of opinion; the delimitation of a family can be made more narrowly or more widely. However, if one accepts the *Apostasiaceae* as a family, the recognition of a family *Cypripediaceae* is certainly unavoidable." The differences between *Apostasiaceae* and *Cypripediaceae* are represented in the following table:

	<i>Apostasiaceae</i>	<i>Cypripediaceae</i>
Inflorescence	Flowers small in an indeterminate inflorescence	Flowers large, single or in a cymose inflorescence
Flowers	Uniformly yellow or white	Flowers multi-coloured
Perianth	Somewhat zygomorphic, the labellum slightly differing in shape from the other tepals	Strongly zygomorphic, lateral sepals connate, labellum slipper-shaped
Gynostemium	Very short, style and stamens (almost) completely free	More or less elongate, thick and curved; stamens with very short filaments

	<i>Apostasiaceae</i>	<i>Cypripediaceae</i>
Anthers	Large, oblong, versatile or basifixed and non-motile	Small, ovoid to globose, non-versatile
Pollen	Dry, powdery	Sticky (in <i>Phragmopedium</i> in pollinia)
A <sub>1</sub>	In <i>Neuwiedia</i> fertile, in <i>Apostasia</i> tending towards reduction, thread-like or (in <i>Adactylus</i> ) lacking	Developed as a large staminode at the base of the slipper and reducing its aperture to two small openings
Style	Erect, slender with three small terminal, stigmatic lobes	Thick and recurved into the slipper, with three large, terminal, stigmatic lobes
Resupination	By torsion	The ovary with a sharp bend at the apex

The mode of germination of the *Apostasiaceae* as yet still being unknown, it is not certain that the germ develops as a protocorm. Here, too, the seeds are minute, which suggests mycotrophy. In this family, the roots are hard and course, and thus different from the roots of the *Cypripediaceae*, which, though also thick, are fleshy and soft to the touch instead of woody as in the *Apostasiaceae*.

The differences between the *Cypripediaceae* and *Orchidaceae* s.s. correspond very well with those between the *Apocynaceae* and the *Asclepiadaceae*. The last two families have a clavate pistil, topped with 5 small stigmas. The *Apocynaceae* have loose pollen grains in the converging stamens; but connate stamens, a corona, pollen coherent in pollinia and translators are typical of the *Asclepiadaceae*. Both families are entomophilous, but the *Asclepiadaceae* are more specialized in that the pollinia and the translators play an important part in the process of pollination. In *Cypripediaceae* and *Orchidaceae* a gynostemium is present, but they have a differently developed androecium. The *Cypripediaceae* have sticky but loose pollen grains and no rostellum, the *Orchidaceae* pollinia, and a rostellum as an aid in transport of the pollen during insect pollination. These two families are also entomophilous. Their distinguishing characteristics are represented in the following table:

	<i>Cypripediaceae</i>	<i>Orchidaceae</i> s.s.
Inflorescence	Flowers with adossed bracteole, sometimes aggregated in the shape of a rhipidium, (flower sometimes solitary)	Flowers without bracteole, in racemes, spikes or panicles, (flower occasionally solitary)
Flower	Large; lateral sepals connate, labellum slipper-like	Different in size, lip rarely slipper-shaped
Gynostemium	Thick, recurved	Erect, sometimes with differentiations (foot, chin etc.)

	<i>Cypripediaceae</i>	<i>Orchidaceae s.s.</i>
Androecium	† $A_1 + a_1 + a_2$ ; epipetalous stamens fertile, the epise-palous one staminodial	$A_1 + \dagger a_1 + \dagger a_2$ or $A_1 + 0$ ; epise-palous stamen fertile, the epipetalous ones stami-nodial or missing
Pollen	Sticky, in tetrads (only in <i>Phragmopedium</i> in pollinia)	In pollinia or in tetrads, some-times rather loose, some-times in massulae, occasi-onally waxy or cartilaginous
Rostellum	None	Present, sometimes strongly developed
Stigma	Terminal with three stigmatic lobes	Frontally directed towards the labellum, sometimes secondarily terminal; usually three-lobed, sometimes third lobe with rostellum or this lobe lacking

The *Apostasiaceae* include the Asiatic and Australian genera *Newwiedia* and *Apostasia*. Forms resembling *Apostasia*, but without a staminodial  $A_1$ , are sometimes classified in a separate genus, *Adactylus*.

The *Apostasiaceae* occur in South and East Asia: India, from the Himalayas and Birma to Japan, throughout Indonesia and extending far into North Eastern Australia. The *Cypripediaceae* comprise four genera: *Cypripedium*, occurring in the temperate regions of Eurasia (extending far into the Himalayas) and in North America, *Paphiopedilum* from tropical Asia including Indonesia and extending to New Guinea, *Phragmopedium* found in America from Costa Rica extending into Bolivia and Brazil, and, finally, *Selenipedium*, also American and extending from Panama far into Brazil.

By far the greatest family is that of the *Orchidaceae* with hundreds of genera and thousands of species occurring all over the world, except in permanently snow-and ice-bound regions and in the deserts. This family shows an amazing variety in habit and in floral morphology. As one of the apparently most evolved families in the Monocots it is likely to be a relatively young group. In several genera the speciation is still in progress.

## 5. THE CHARACTERISTICS OF THE RESPECTIVE FAMILIES

### Key to the families

- 1a. Flowers with at least two fertile stamens. Pollinia and rostellum absent. Stigma morphologically situated above the insertion of the stamens. Fruit trilocular or unilocular . . . . . 2
- b. Flowers with only one fertile stamen. Pollinia and rostellum present. Stigma on an erect column below and on the labellar side of the anther, but by resupination of the column (*Satyrium*) sometimes above it. Fruit a unilocular capsule. . . . *Orchidaceae*

- 2a. Flowers less than 3 cm in diameter with approximately regular perianth, uniformly white or yellow. Episepalous stamen fertile or only represented by a thread-like staminode, sometimes entirely lacking. The epipetalous stamens with oblong anthers containing powdery pollen. Style with three small stigmatic lobes. Fruit a trilocular capsule or baccate. . . . . *Apostasiaceae*
- b. Flowers more than 3 cm in diameter, manifestly zygomorphic with the median petal developed as a "slipper", never uniformly coloured. Episepalous stamen sterile, peltate, protruding from the base of the slipper. The epipetalous stamens with subglobose anthers containing sticky pollen. Style short and thick, recurved into the slipper, with three large stigmatic lobes. Fruit a unilocular or trilocular capsule . . . . . *Cypripediaceae*

*Description:*

Fam. *Apostasiaceae* Lindl (Plate I, Figs. 2A and 2B). Terrestrial herbs with a subterraneous rootstock bearing hard adventitious roots. Stem sympodial, with scattered pleated leaves. Inflorescence a simple or ramified terminal raceme. Flowers white or yellow, resupinate by torsion of the pedicel. Perianth scarcely zygomorphic (median petal of approximately the same shape as the other parts). Gynostemium short to very short (not formed by the receptacle), without pollen bed. The episepalous stamen fertile, staminodial or missing. The epipetalous lateral stamens fertile; anthers versatile on filaments or basifixed, erect, always longer than broad, with powdery pollen (no pollinia). No rostellum. Style thin, straight or recurved, with three or two small apical stigmatic lobes, style exceeding or equalling the tops of the anthers, its lobes usually exceeding them. Ovary when ripe with three chambers forming a trilocular capsule or a leathery berry. (See however Plate IV, Fig. 9). Seeds small with sometimes membranaceous testa. Germination not known.

Fam. *Cypripediaceae* Lindl. (Plate I, Figs. 3A and 3B). Terrestrial herbs with short rootstock bearing thick and fleshy adventitious roots. Stem sympodial with scattered leaves along the stem, or leaves densely crowded at the base, convolutive or duplicate. Inflorescence terminal, cymose, with 1-many flowers. Flowers never uniform in colour, resupinate by a sharp bend in the top of the ovary. Perianth zygomorphic; the lateral sepals usually concrescent, situated below the slipper-shaped lip which represents the median petal. Gynostemium thick and recurved into the slipper (with participation of the receptacle?); no pollenbed. Episepalous stamen represented by a more or less peltate staminodium at the base of and partly exerted from the slipper, so that two narrow openings form the exits from the slipper; epipetalous stamens fertile, with short filaments, anthers subglobose, with sticky pollen (no pollinia except in *Phragmopedium*). No rostellum, style short and thick, stigma apical with three large lobes inside the slipper above the fertile stamens. Ovary with one or three chambers

forming a uni- or trilocular capsule. Seeds small with membranaceous testa. Protocorm white and mycotrophic.

Fam. *Orchidaceae* Lindl. (Plate II, Figs. 4A, 4B, 5A, 5B, Plate III, 6, 7, 8A, 8B). Terrestrial or epiphytic herbs, with a rootstock or tubers and a number of thick or thin adventitious roots. Stem monopodial or sympodial, with scattered duplicated or convolute leaves or leaves reduced to scales, sometimes the lower internodia forming pseudobulbs. Inflorescence terminal (acranth) or lateral (pleuranth), racemose, a panicle, raceme or spike (rarely a capitulum, an umbel or a spadix), with few to many flowers of various colours. Flowers nearly always resupinate by torsion or by a bend near the top of the ovary (*Ophrys*). Perianth zygomorphic, the median petal forming a lip (only exceptionally slipper-shaped) and sometimes spurred. Gynostemium of various shapes, sometimes formed with the participation of the receptacle and with differentiations (foot, etc.), short or long (rarely gynostemium lacking: *Thelymitra*, *Diuris*, *Prasophyllum*) straight or curved, sometimes with apical clinandrium (pollen bed). Episepalous stamen fertile (except in unisexual flowers); anther of various shapes, with or without filament, erect or declined over the clinandrium; the pollen always present in the form of pollinia. Epipetalous stamens missing or staminodial (sometimes represented by wings at the sides of the gynostemium); rostellum present (rarely lacking: *Cephalanthera*, *Caladenia*), provided with one or two, sometimes stipitate, retinacula. Style forming a part of the gynostemium, (rarely free: *Goodyera*, *Diuris* (Plate II, Figs. 4A and 4B), *Prasophyllum*) with three or two stigmatic lobes (the latter sometimes with two stigmaphores). Stigma, if the gynostemium is straight on the labellar side, frontal below the anther, in the alternative case, with curved gynostemium (*Satyrium* and allies), apical above the anther. Ovary with one chamber, forming a unilocular fruit (usually a replum). Seeds small with membranaceous testa (very rarely not membranaceous: *Vanilla*). Protocorm white or green, mycotrophic.

## 6. THE SUBDIVISION OF THE ORCHIDACEAE BY DIFFERENT AUTHORS

There is a remarkable difference in the proposed subdivision of the *Orchidaceae* between the Anglo-Saxon and the German groups of authors. Lindley, in his principal work, divided the family into seven tribes (*Apostasiaceae* being treated as a separate family), which tribes he treated as groups of equal rank. Bentham reduced this number to four, likewise equivalent groups. The American author Garay places the five groups which he distinguishes also in juxtaposition as subfamilies of which the *Apostasioideae* and the *Cypripedioideae* are two, apart from the *Neottioideae*, the *Ophrydoideae* and the *Kerosphaeroideae*. Dressler & Dodson approach the German viewpoint in so far that they distinguish two subfamilies, viz. the *Cypripedioideae* with the tribes *Apostasieae* and *Cypripedieae*, and the *Orchidoideae* with the tribes *Neottieae*, *Orchideae* and *Epidendreae*. As opposed to these systems, the Germans prefer a typically

hierarchic system. Apart from the *Cypripedieae* and *Apostasiae*, Reichenbach fil. distinguished the *Ophrydeae* and *Operculatae*, of which the latter are subsequently divided into *Neottiaceae* and *Euoperculatae*, and the latter again subdivided into the *Arethuseae*, *Vandeeae*, *Épidendreae* and *Malaxideae*. Pfitzer also proposed a typically hierarchic system, mainly based on vegetative characteristics. He divided the *Monandrae* into the *Basitonae* as opposed to the *Acrotonae* and the latter were again hierarchically subdivided as follows:

**Acrotonae**, pollinia apically connected with the rostellum

- a. *Acranthae* (inflorescence terminal)
  - 1. *Convolutae* (with convolute leaves)
    - Continentes (lamina not deciduous)
    - Neottiinae
    - Articulatae (lamina deciduous)
  - 2. *Duplicatae* (with conduplicate leaves)
- b. *Pleuranthae* (inflorescence lateral)
  - 1. *Convolutae* (with convolute leaves)
    - Homoblastae (with thin stem or the stem thickened in a series of internodes.)
    - Heteroblastae (with a single internode transformed into a pseudo-bulb)
  - 2. *Duplicatae* (with conduplicate leaves)
    - Sympodiales (with sympodial growth)
    - Monopodiales (with uninterrupted, i.e. monopodial growth)

SCHLECHTER's system, now most current, owing to his well-known publication "Die Orchideen" (1915) corresponds rather closely with that of PFITZER. Unlike Pfitzer, Schlechter distinguishes the *Apostasiaceae* as a separate family and divides the *Orchidaceae* into two sub-families: the *Diandrae* (comprising the *Cypripedilinae*) and the *Monandrae* (subdivided into the *Basitonae* and the *Acrotonae*). The *Acrotonae* are subsequently subdivided into the subdivision 1. *Polychondriae* (having pollen grains lying in tetrads inside the pollinia) and the subdivision 2. *Kerosphaereae* (with waxy or cartilaginous pollinia). Schlechter classifies the *Kerosphaereae* as follows:

- Kerosphaereae* Reihe A. *Acranthae*
- Reihe B. *Pleuranthae*
- Unterreihe I. *Sympodiales*
- Unterreihe II *Monopodiales*.

In my opinion preference should be given to a hierarchic system, because it emphasises the assumed greater or smaller mutual affinity so much better. The recognition of three families not linked by transitions is inevitable if one strives for the conceivable most natural system of classification. In the *Orchidaceae* s.s., two clear-cut groups can be

distinguished by differences in the structure of the gynostemium and the rostellum, without intermediate (transitional) forms, viz. the two subfamilies *Orchidoideae* and *Epidendroideae*. In the latter group, the contriobe of the *Neottianthae* is opposed to the contriobe of the *Epidendranthae* in which the anther is not very persistent and the pollen forms solid pollinia. This system corresponds in broad outlines with that of Reichenbach.

## 7. THE SUBDIVISION OF THE ORCHIDACEAE

In contradistinction to the small and rather uniform families *Apostasiaceae* and *Cypripediaceae*, the *Orchidaceae* excel in an overwhelming polymorphy. The considerable morphological diversity of this group requires a convenient subdivision. In my opinion two subfamilies ought to be distinguished, viz. the *Orchidoideae* (Dressl. & Dods.) Vermln. (= *Ophrydoideae* Garey = *Basitonae* Pfitz.) and the *Epidendroideae* Vermln. nov. subfam. (= *Operculatae* Rchb. fil. (1868) = *Acrotonae* Pfitz.).

The *Orchidoideae* have a broadly inserted stamen, invariably with two pollinia composed of massulae (pollen clumps), and with basitonic caudicles (i.e. their attachment is basitonic in respect of the rostellum). In this group, the rostellum is in principle a strip of tissue, a sometimes very massive tape, with a viscid disc on either side, and in its centre provided with an extension of the vascular bundle running in the median stigmatic lobe. (This is, to my mind, suggestive of the de novo formation of vascular strands in various places where a good translocation of solutes is required). The rostellum exhibits two diverging trends, the one being a progressive infolding of the "tape" which causes the retinacula to approach one another, and the other a tendency towards an appreciable increase in size with long extensions bearing the retinacula at their extreme ends (see VERMEULEN, 1965, p. 237) In the latter case the connective of the anther is often very broad. The rostellum, with in principle always two retinacula, is very characteristic of this subfamily. The basitony is equally characteristic: the pollinia are always basitonically attached to the retinacula of the rostellum by means of the two caudicles.

In *Cephalanthera* and in some Australian representatives of the *Neottieae* the pollinia are also attached near their base to the pollinator by means of viscid matter or a subbasal viscid disc, but in these forms the rostellum is missing or consists of a single and much more simple structure, and, moreover, the attachment is achieved without the intervention of caudicles.

The species of the *Orchidoideae* usually have tubers, much more rarely rhizomes, but never corms or pseudobulbs. The protocorm is white. They exhibit sympodial growth and occur mainly in the temperate regions of the northern and southern hemispheres, but do not constitute an important element in the floras of Australia and South America.

The genus *Habenaria*, recognisable by two stigmatic lobes inserted on

stigmaphores, and allied forms are wide-spread throughout the tropical regions of the Old and the New World with a few species extending to Australia. The main massing centres of the *Orchidoideae* lie in temperate Eurasia, in North America and in South Africa.

The second subfamily, the *Epidendroideae*, comprises all genera not referable to the *Orchidoideae*; in this respect I follow Reichenbach fil. who distinguished this group as early as 1868 under the name of *Operculatae*. Pfitzer dubbed this group the "*Acrotonae*". In many genera belonging to this subfamily the more or less hollow top of the column forms a pollenbed (clinandrium or androclinium), the anther suspended above it, when ripe, depositing its pollinia into this pollenbed. Such a clinandrium never occurs in the *Orchidoideae*. In the majority of the *Epidendroideae* the anther is inserted on a short filament or it is attached only by one point and thus often falls off when the pollinia are removed. A broadly inserted anther occurs much more rarely in this group (*Hammabya*). Although the number of pollinia usually corresponds with the number of loculi, so that there are four, occasionally there are eight, whereas in other cases two of the pollinia are reduced and the remaining two are solitary. Caudicles are not always present and if so, they stretch as far as the top of the pollinia where they are attached, in other words, they are acrotonic. Even if there are no caudicles, the viscid matter or the viscid disc lies on top of the pollinia. In the Eurasian genus *Cephalanthera* the pollinia are carried away by visiting insects, the viscid liquid of the stigma secreted in the proximity of the bases of the pollinia acting as an adhesive.

In several Australian genera (*Acianthus*, *Caladenia*, *Lyperanthus*) the pollinia likewise stick to the pollinator with the aid of an adhesive substance secreted near their base. One could speak of mesotony (sometimes even of basitony) in this case. The sticky matter or the viscid disc consists of a single mass or a solitary body, as a rule, which is excreted at the apex of the median stigmatic lobe, i.e., at its distal end. The viscid disc rarely replaces the lobe entirely as in *Pterostylis*. In the exceptional case of a bilobed or bifid rostellum, there is always a short and broad portion connecting the lobes (in contradistinction to the *Orchidoideae*), the rostellum being fundamentally solitary in this group, even if differentiations do occur. The vegetative development is rather varied in the *Epidendroideae*. This will be discussed under 8. The subfamily is chiefly represented in the tropics but extends to the cold regions.

#### *Key to the subfamilies*

1. Stamen broadly inserted, with two (double) pollinia, each at the base with a caudicle basitonically connected with the retinacula (viscidia) of the rostellum (rarely the two retinacula conerescent); pollen sectile (in massulae). Stigma with three or two lobes, in the last case lobes sometimes inserted on stigmaphores . . . *Orchidoideae*
2. Stamen with filament or basifixed (rarely broadly inserted) with 2-8 pollinia, sometimes with caudicles connected mesotonically

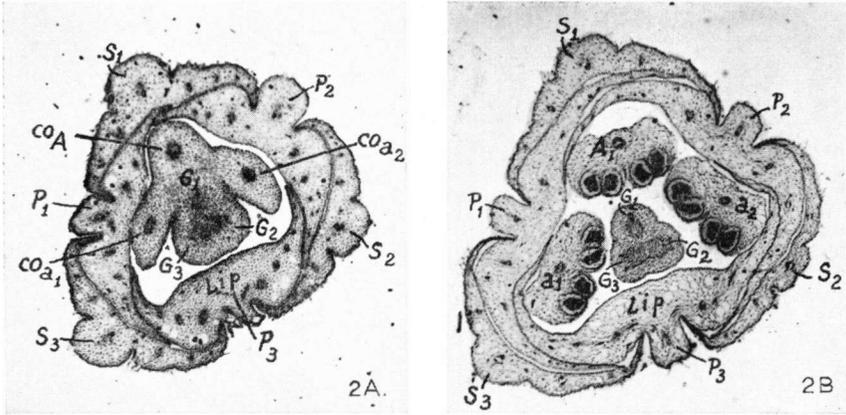
or acrotonically with the viscid matter or the viscidium (rarely split in two); pollen rarely sectile (in massulae). Stigma with three or two lobes never on stigmaphores . . . *Epidendroideae*.

1. Subfam. *Orchidoideae* (Dressl. & Dods.) Vermln. = *Basitoniae* Pfitzer = *Ophrydoideae* Garey (Plate III, Figs. 8A and 8B). Gynostemium never with a pollenbed (androclinium) and anther never opercular. Stamen broadly inserted, usually on each side with an auricle. Anther with two (double) pollinia, each with a caudicle at the base and these caudicles connected with the basal rostellum (basitonic), anther sometimes with broad connective (so that the two thecae are found on the opposite sides of the stigma, as in *Satyrium* and *Disperis* and never deciduous. Pollen always in massulae. No staminodia. Rostellum forming a tape (*Coeloglossum*), or a voluminous body (*Bonatea*), with at each end a viscid disc (retinaculum), sometimes in a bursicula (*Ophrys*, *Orchis*), only in exceptional cases the two retinacula connate into one (*Anacamptis*, *Herschelia*, *Monadenia*). Retinacula always at the base of the pollinia at the caudicular ends, orbicular or oval, rarely oblong. Stipe always lacking. Stigma with three or two lobes, usually frontal (at the labial side) of the gynostemium, sometimes apical if the anther is reflexed (*Disa*, etc.) (If two stigmatic lobes are present sometimes each at the end of a stigmaphore and then always in the neighbourhood of a retinaculum which is found at the end of a thecal tube and rostellum arm, *Habenaria*).

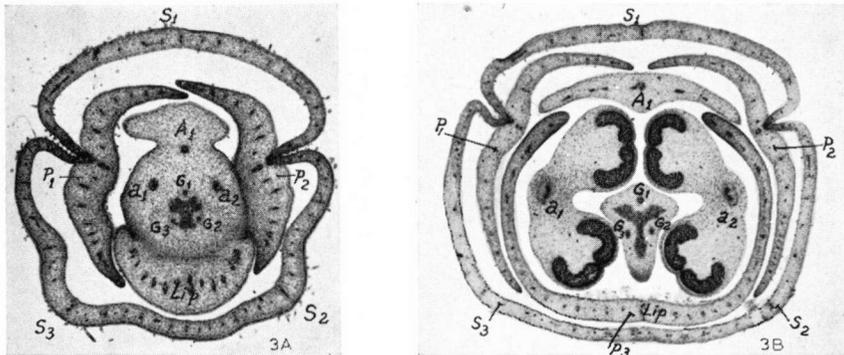
Terrestrial herbs, rarely more than 1 m high, growing sympodially with rootstocks or usually tubers. Stem with convolute inarticulated leaves, usually scattered, rarely opposite. Plants always with chlorophyll. Inflorescence always terminal, spicate or racemose. Flowers from 1–10 cm in diameter. Protocorm white.

2. Subfam. *Epidendroideae* Vermln. nov. subf. (= *Operculatae* Rchb. f. (1868) = *Acrotonae* Pfitz.)

Gynostemium often with an androclinium and anther opercular. Stamen with a short filament or sessile and basifixed (rarely broadly inserted: *Malaxis*), sometimes with an auricle on each side. Anther with two or more pollinia, sometimes with caudicles but these connected at the top of the pollinia, with the rostellum (acrotonic), anther only exceptionally with a broad connective (*Hammarbya*) and in many genera deciduous. Pollen grains in tetrads, rarely loose, or pollen waxy or cartilaginous and strongly coherent, rarely (*Epipogium*, *Stereosandra*) in massulae. Staminodes ( $a_1$ ,  $a_2$ ) sometimes represented by wings (*Diuris*, *Prasophyllum*) or only by vascular strands in the gynostemium, or missing. Rostellum forming a single organ at the apex of the median stigmatic lobe or replacing this lobe (*Pterostylis*) forming viscid matter (*Listera*) or a viscid disc, sometimes secundarily bifid (*Angraecum*, p.p.) Retinaculum acrotonic or mesotonic (in *Stereosandra* a part of the anther (Plate V; Figs. 13A, 13B; Plate VI, Fig. 14), none in *Cephalanthera*. In several genera a stipe, i.e., a part of the gynostemium forming the connection between rostellum and

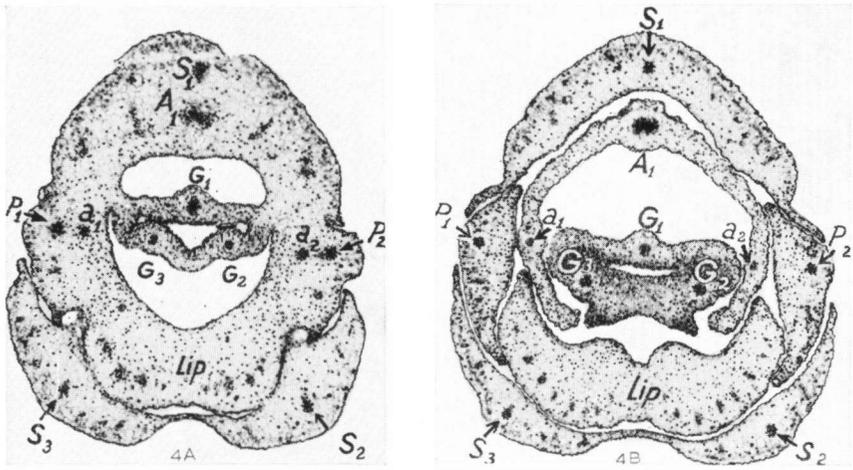


Figs. 2A and 2B. *Neuwiedia veratrifolia* Bl., two cross sections through a young flower bud; A: lower one with gynostemium ( $co_A$  vascular strand of stamen  $A_1$ ;  $co_{a_1}$  and  $co_{a_2}$  vascular strands of the stamens  $a_1$  and  $a_2$  of the inner whorl. B: more distally cut section with the three anthers, each with four loculi, and the style with three vascular bundles.

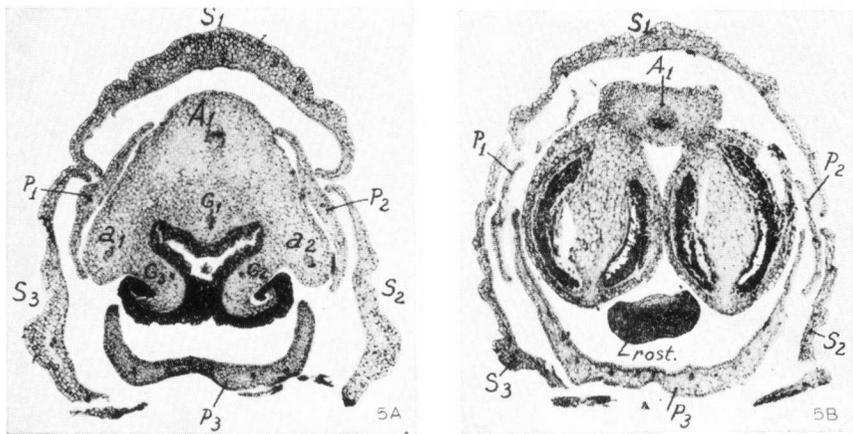


Figs. 3A and 3B. *Phragmopedium schlimii* Rolfe, two cross sections through a flower bud. A: lower one with the lip,  $A_1$ ,  $a_1$  and  $a_2$  still connected with the gynostemium. B: more distally cut section with lip and staminodium  $A_1$  free. The two stamens of the inner whorl ( $a_1$  and  $a_2$ ) each with four loculi.

$S_1$ : median sepal;  $S_2$  and  $S_3$ : lateral sepals;  $P_1$  and  $P_2$ : lateral petals;  $P_3$ : median petal or lip;  $A_1$ : vascular strand of the median stamen of the other whorl;  $a_1$  and  $a_2$ : lateral stamens of the inner whorl;  $G_1$ ,  $G_2$  and  $G_3$ : vascular strands of the style.



Figs. 4A and 4B. *Diuris semilunulata* Messmer, two cross sections through a flower bud; A: lower one with  $a_1$  and  $a_2$  split off from  $P_1$  and  $P_2$ . In B: the three stamens  $A_1$ ,  $a_1$  and  $a_2$  still form a whole and  $G_1$ ,  $G_2$  and  $G_3$  run in the style which is free so that a gynostemium is not realised.  $a_1$  and  $a_2$  become free higher up to form two wings.



Figs. 5A and 5B. *Limodorum abortivum* Sw., two cross sections through a young flower bud; A: lower one with three stigmatic lobes each with a vascular strand ( $G_1$ ,  $G_2$  and  $G_3$ ) and  $a_1$  and  $a_2$  in the margins of the gynostemium. B: more distal one with  $A_1$  with two thecae and each with two loculi.

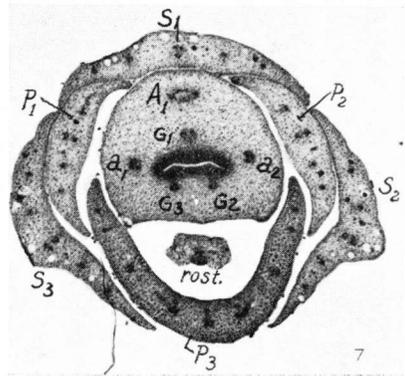
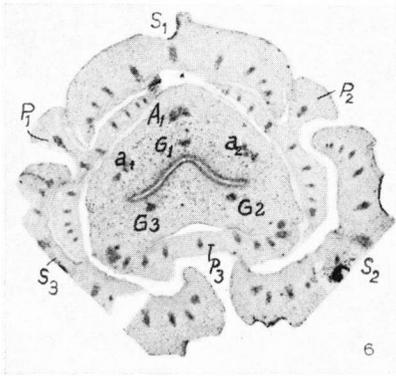
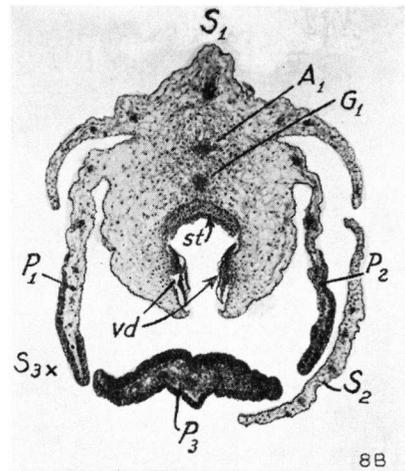
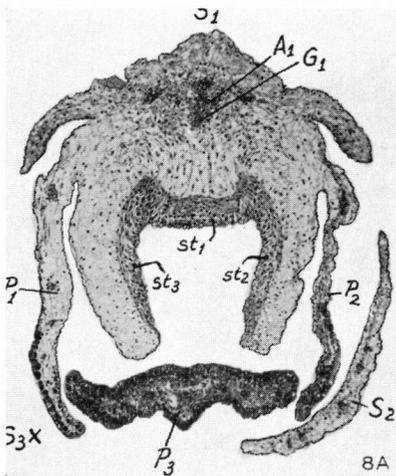
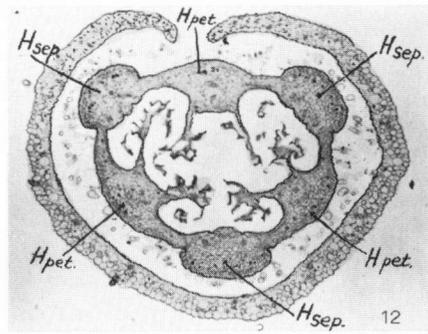
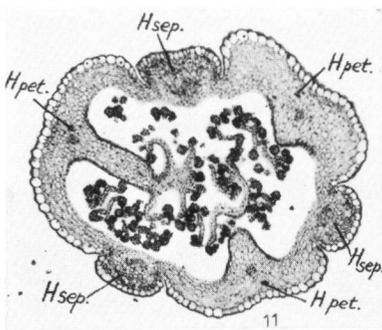
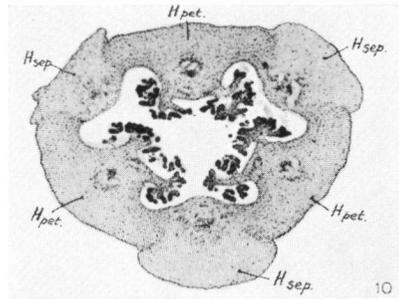
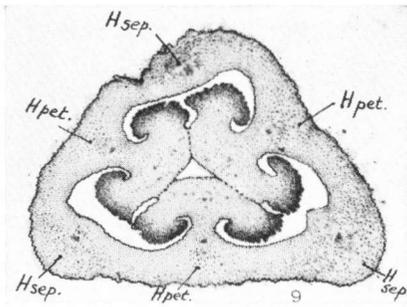


Fig. 6. Cross section through a flower bud of *Vanilla planifolia* Andr., also with vascular strands of  $A_1$ ,  $a_1$  and  $a_2$ .

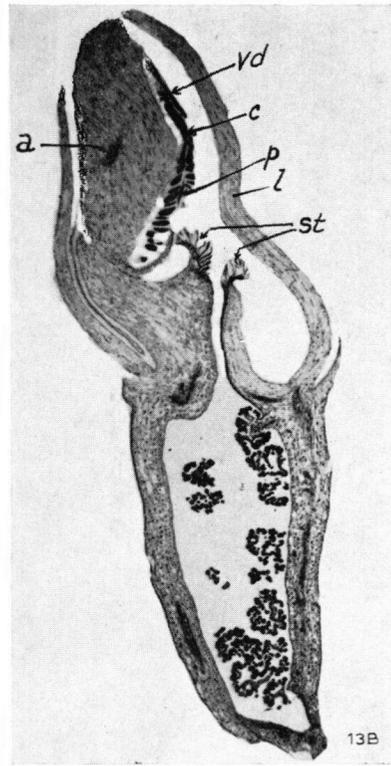
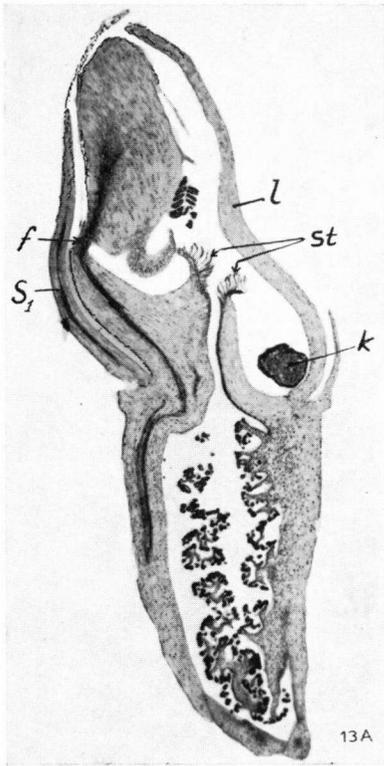
Fig. 7. Cross section through a flower of *Aerangis coriacea* Summerh.



Figs. 8A and 8B. *Platanthera bifolia* (L.) Rich., two cross sections through a young flower bud; A: lower one with three stigmatic lobes ( $st_1$ ,  $st_2$  and  $st_3$ ) and with the vascular strands of the stamen  $A_1$  and the only one of the style still connected; B: more distally cut section with two viscid discs above the two lateral stigmatic lobes;  $A_1$  and  $G_1$  are now separated; only one vascular strand runs into the style.



Figs. 9, 10, 11 and 12. Cross sections through the ovary of the flowers of four different species of orchids. Fig. 9 *Neuwiedia veratrifolia* Blume; Fig. 10 *Disa uniflora* Berg.; Fig. 11 *Schizodium inflexum* Lindl.; Fig. 12 *Caladenia* spec. H<sub>sep</sub>: hyposepalous part of the ovarium; H<sub>pet</sub>: hypopetalous part of the ovarium. In the centre of the figures the placentae are seen with the numerous ovules.



Figs. 13 and 13B. *Stereosandra javanica* Blume, two longitudinal sections through a young flower bud;  $S_1$ : median sepal; f: filament of the anther  $A_1$ ; l: lip; st: two stigmatic lobes at the top of the style canal; K: gland on the lip. B is a section made near the middle of the anther a; vd: viscidium as part of the anther; c: caudicle; p: pollinium; l: lip and st: stigmatic lobes.

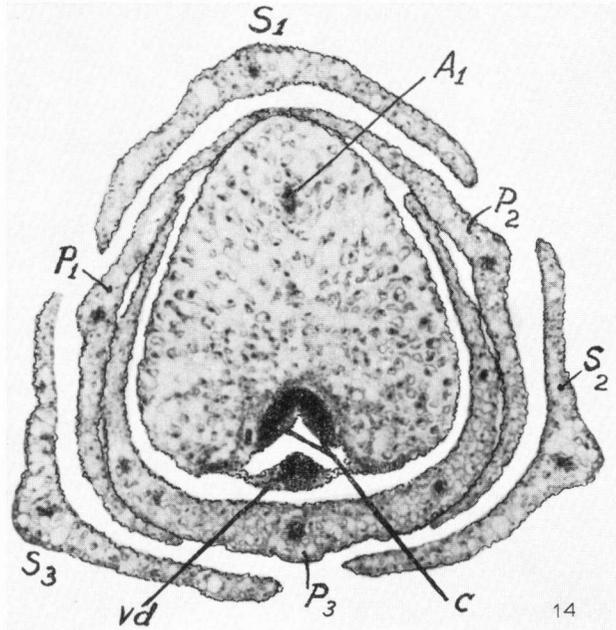


Fig. 14. Cross section through a young flower bud of *Stereosandra* Blume;  $A_1$  is the vascular cord of the fertile stamen of the outer whorl  $c$ : caudicle, composed of two parts;  $vd$ : viscidium as part of the anther.

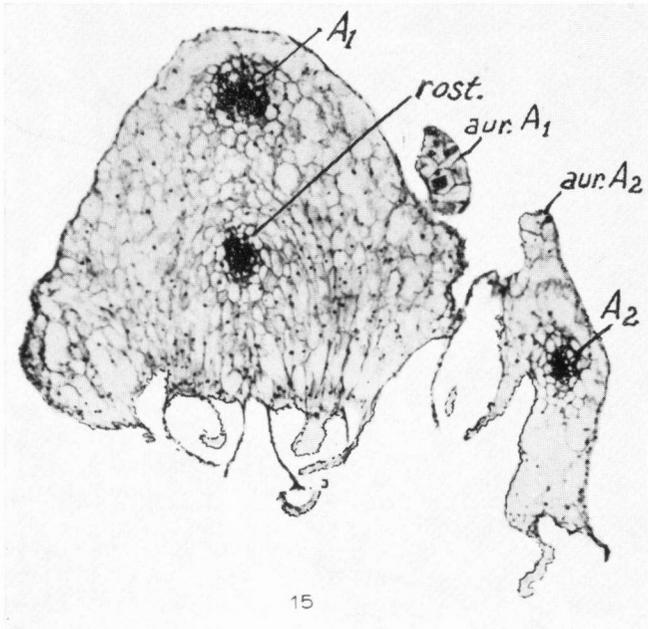


Fig. 15. Cross section of the gynostemium of *Dactylorhiza maculata* (L.) Vermln. with supernumerary developed stamen  $A_2$ . Both the stamens have an auricle (aur.  $A_1$  and aur.  $A_2$ );  $rost$ : vascular strand of the rostellum.

pollinia. Stigma with three or two lobes, frontal (at the labial side) of the gynostemium, its lobes never on stigmaphores.

Terrestrial herbs (rarely suffruticose), or epiphytes, varying from very small to several meters high, growing sympodially or monopodially, with rootstocks, tubers, corms or pseudobulbs, in monopods without storage organ (*Vanda*). Stem with convolute or duplicate articulated or inarticulated leaves, scattered or rarely opposite. Several genera without chlorophyll and if so, with reduced leaves. Inflorescence terminal (acranth) or lateral (pleuranth), a panicle, a raceme, a spike or rarely a spadix (*Megaclinium*), an umbel or a capitulum (*Cirrhopetalum*). Flowers varying from very small (*Taeniophyllum*) to 20 cm in diameter.

#### 8. EPIDENDROIDEAE

In contrast to the *Orchidoideae*, the *Epidendroideae* do not form a homogeneous group, as may be concluded from the diagnosis. Two subordinate groups can be distinguished, which I have indicated as two tribes, viz. the *Neottianthae* and the *Epidendranthae*, a distinction made as early as 1868 by Reichenbach fil. who classified the *Neottianthae* as *Neottiaceae* and the *Epidendranthae* under *Euoperculatae*; it should be noted, however, that he also included the *Arehuseae* in the latter group, but I think that most of them are referable to the *Neottianthae*. The *Neottianthae* are mostly small terrestrial orchids, as a rule occurring outside the tropics, whereas the *Epidendranthae* are very often epiphytes with a mainly tropical distribution. Among the *Neottianthae* many forms occur which are practically devoid of chlorophyll and live as parasites on their root fungus (commonly referred to as "saprophytes"). In connection with their epiphytic way of life, it is among the *Epidendranthae* that we find forms with "pseudobulbs", aerial storage organs developing from one or more stem internodes, often containing photosynthetic tissue, rather well-known especially in our cultivated orchids. The pollen grains of the *Neottianthae* occur in tetrads, but sometimes they are quite free, only rarely arranged in massulae as in *Epipogium* and *Stereosandra* (Plate V, Figs. 13A and 13B). In *Acianthus* the pollen is sometimes waxy or cartilaginous, always tightly coherent into a solid mass.

The genera *Sobralia* and *Bletilla* (and some related genera) have granular pollen, but on account of their general habit they are classified among the *Epidendranthae*. Briefly summarized the differences are as follows:

Contribute *Neottianthae*. Pollen grains in tetrads in two double pollinia, anther straight or opercular, rostellum never stipitate. Pseudobulbs never developed, plants often with rhizomes, tubers or corms. Inflorescence terminal (in *Vanilla* and allied forms lateral). Leafblades never early deciduous. Leaves in bud always convolute. Mode of growth sympodial (in *Vanilla* and some allied forms monopodial). Many genera lacking chlorophyll. N.B. *Sobralia*. *Bletilla* and their near-allies do not belong here.

Contribute *Epidendranthae*: Pollen waxy or cartilaginous, in two to eight pollinia, anther opercular, rostellum sometimes stipitate (sometimes the viscidium split in two and each half with an individual stipe). Pseudobulbs often developed, plants sometimes with rhizomes, never with tubers. Inflorescence terminal or lateral. Leaf blades sometimes early deciduous. Leaves in bud convolute or conduplicate. Mode of growth monopodial or sympodial. Plants with green trophophylls, rarely without leaves (*Taeniophyllum*; in the aphyllous epiphytic species belonging to this genus, the assimilatory function is performed by the exposed roots).

Contribus *Neottianthae*: Polline in turmis quaternis in duobus polliniis bipartitis; anthera erecta vel operculata, rostello non stipitato; nunquam pseudobulbis, saepe rhizomatibus vel tuberibus vel rhizocormis. Inflorescentia terminali (in Vanillinis laterali). Laminis non decidentibus. Foliis in gemma semper convolutis. Structura sympodiali (in Vanillinis monopodiali). Multa genera non virentia.

N.B. *Sobraliinae* et *Bletillinae* non huius contribus sunt.

Contribus *Epidendranthae*: Polline cerae vel cartilagini simili in 2—8 polliniis; anthera operculata; rostello interdum stipitato (nonnunquam viscidio bifido, utraque parte stipitata). Saepe pseudobulbis, interdum rhizomatibus, nunquam tuberibus. Inflorescentia terminali vel laterali. Laminis interdum decidentibus. Foliis in gemma convolutis vel complicatis. Structura monopodiali vel sympodiali. Herbae virentes.

The descriptions of the two contribes are as follows:

Contribute *Neottianthae* (Plate II, Figs. 4A, 4B, 5A, 5B; Plate III, Fig. 6): Gynostemium with straight or opercular anther and in the latter case provided with an androclinium. Sometimes gynostemium not developed, because anther and style are not conerescent (*Diuris*, *Prasophyllum elatum*, *Thelymitra rosea*). Stamen usually with an auricle on each side (*Goodyera*, *Epipactis*). Anther either straight and persisting or opercular and often deciduous, never with more than two double pollinia, sometimes with caudiculae (*Epipogium*, *Stereosandra*). Pollen in tetrads rarely loosely granular or waxy (*Acianthus*) or in massulae (*Epipogium*, *Stereosandra*). Staminodia ( $a_1 + a_2$ ) sometimes developed as discrete wings (*Diuris*, *Prasophyllum*) or only represented by vascular cords in the margins of the gynostemium. Rostellum producing viscid matter or a viscid disc. Retinaculum acrotonic or mesotonic (in *Stereosandra* a derivative of the anther, in *Cephalanthera* missing). Stigma with three or two lobes (two in *Pterostylis*).

Terrestrial herbs or vines, green or white to brownish, sympodial (in *Vanilla* and related forms sometimes monopodial) with rootstock, tuber or corm but never with pseudobulbs. Stem with convolute leaves (or with sheaths only), inarticulate. Inflorescence terminal (in *Vanilla* and its near-allies pleuranth). Flowers varying from small to 10 cm in diameter, usually in a spike or raceme. Protocorm white.

Contribute *Epidendranthae* (Plate III, Fig. 7.). Gynostemium with

a usually deciduous and operculate anther and an androclinium. Stamen rarely auriculate. Anther with 2–8 pollinia (sometimes with caudiculae: *Epidendrum*). Pollen waxy or cartilaginous. Staminodia ( $a_1 + a_2$ ) sometimes represented by vascular strands in the gynostemium (*Aerides*, *Cattleya*), rarely developed as appendices (*Bulbophyllum*). Rostellum formed by viscid matter or a viscid disc, sometimes split. Retinaculum acrotonic. Stigma usually three-lobed.

Mostly epiphytic, less often terrestrial herbs, rarely suffruticose, green, sympodial or monopodial (*Vanda*), never with tubers but with rootstocks or with corms; pseudobulbs often occurring. Stem with convolute or conduplicate, sometimes articulate, leaves. Inflorescence terminal or pleuranth. Flowers varying from very small (*Taeniophyllum*) to 20 cm in diameter, in a panicle (*Oncidium*), a raceme or spike, rarely a spadix (*Megaclinium*), an umbel or a capitulum (*Cirrhopetalum*), Protocorm white or green.

Upon closer examination the two tribes appear to contain several natural groups, here treated as tribes. The most obvious ones are the three tribes of the *Neottianthae*: the *Neottieae*, *Arethuseae* and *Vanilleae*, the *Neottieae* being characterised by the erect stamen without a clinandrium (androclinium, pollen pouch), the *Arethuseae* by the presence of a pollen pouch, and the *Vanilleae* by their climbing habit (they are lianas) and their aberrant mode of growth.

The *Epidendranthae* can be divided into the *Epidendreae* (without stipes) and the *Vandaeae* (with stipes).

## 9. THE STAMINODS IN THE ORCHIDALES

Of the abaxial stamens  $A_1 + a_1 + a_2$ , only  $a_1 + a_2$  are fertile in the *Apostasiaceae* and the *Cypripediaceae* (Plate I, Figs. 3A and 3B), whereas  $A_1$  is fertile only in *Neuwiedia* (Plate I, Figs. 2A and 2B), but in their other genera  $A_1$  is staminodial or completely wanting (as in *Adactylus*). That the fertile stamens belong to the inner or epipetalous whorl, follows from the fact that the vascular bundle, present in each of them, arises from the median vascular bundle of a lateral petal. The vascular bundle of  $A_1$  arises from the bundle of the median sepal and so does the bundle of the staminode ( $A_1$ ) in these two families, which element, therefore, belongs to the outer androecial whorl. I do not know if a corresponding (homotopic) vascular bundle occurs in *Adactylus*. The structure of the androecium is fairly clear in these two families, but rather obscure in the *Orchidaceae* s.s., especially if one wishes to maintain the pattern of  $A_1 + a_1 + a_2$ . The column only rarely bears thread-like protrusions reminiscent of stamens. However, laterally inserted organs (opposite the lateral petals) occur in various Australian genera, e.g., in *Diuris* and *Prasophyllum* (lacking a gynostemium, because style and stamen are free (the presence of pollinia and a rostellum determines their place in the *Orchidaceae* s.s.)). A study of the possible relations between these lateral wings and the rudimentary stamens  $a_1 + a_2$  was indicated. To this end I have examined transverse

microtome sections. In both *Diuris* and *Prasophyllum* these wings appear to have a vascular bundle, and when one follows such a vascular bundle downwards, it appears that it is a derivative of the median vascular bundle of the lateral petals (Plate 2, Fig. 3A and 3B). From this one may safely conclude that these wings are the homologues of the stamens  $a_1 + a_2$  and that they are indeed adnate staminodes.

Such distinct wings are very rare. In several other genera protrusions on the gynostemium have been recorded, such as the stelia found in *Bulbophyllum ciliatum* (Bl.) Lindl. and in *Sobralia cataractarum* Hoehne. In certain genera the gynostemium sometimes has laterally protruding margins. An anatomical examination reveals that often these margins contain vascular bundles, also originating from the main vascular bundle of the lateral petals, in other words, these margins apparently represent the lateral stamens  $a_1 + a_2$  and can be regarded as staminodes adnate to the column.

I have never observed corresponding vascular bundles in the *Orchidoideae*, but I did find them in representatives of the *Epidendroideae*, in both the *Neottianthae* and the *Epidendranthae*. In the *Neottianthae* I examined *Limodorum abortivum* (Plate III, Figs. 5A and 5B) and *Vanilla planifolia* (Plate III, Fig. 6). Among the *Epidendranthae* I noticed them in several genera, such as *Oncidium*, *Sophranitis*, *Cattleya*, *Aerangis* (Plate III, Fig. 7) and *Scaphyglottis*. No doubt they occur in a number of other genera as well. This strongly supports the assumption that also in the *Orchidaceae* subfamily *Epidendroideae* the gynostemium corresponds with that of the *Apostasiaceae* and the *Cypripediaceae*, and that, basically, it has incorporated the stamens  $A_1 + a_1 + a_2$ .

In several Eurasian genera of the *Neottianthae*, such as *Epipactis*, *Cephalanthera*, *Spiranthes* and *Goodyera*, neither wings nor thread-like protrusions on the gynostemium occur and only the three vascular bundles of the pistil and the one innervating  $A_1$  are present. This is obviously a case of reduction. The reduction is even more pronounced in the *Orchidoideae* which have only two vascular bundles in the gynostemium, originating as offshoots of the vascular bundles of the median sepal; the one vascular bundle innervates the stamen  $A_1$  and the other one the stigma and the rostellum (Fig. 15). The lateral stigmatic lobes do not contain vascular bundles. In some of the South African genera (*Disa*, *Satyrium* and other ones) there are indeed three vascular bundles in the pistil in addition to the bundle belonging to  $A_1$ . Apparently the gynostemium includes only the androecial element  $A_1$ . In the majority of the *Orchidoideae* and also in many *Neottianthae* the anther bears a small lateral appendage (auricle) on either side towards the base. It is these appendages which are frequently referred to as "staminodes" in taxonomic text books. This goes back to obsolete ideas expressed by Robert Brown and Eichler. These auricles, when anatomically examined, all appear to have a similar anatomical structure; they consist chiefly of large cells filled with crystals (raphides). Animals with a sensitive tongue will not readily eat these organs and that is presumably why also the anthers are protected from being devoured by animals. BROWN later questioned his own theory (1833, p. 697), because

he had found a flower of *Platanthera* (*Habenaria*) *bifolia* with two supernumerary stamens. If the auricles are of staminodial derivation they must disappear as such when they are replaced by normal stamens. However, not only had the normal stamen in the abnormal *Platanthera* flower retained its auricles, but the extra stamens also bore an auricle at the side facing the normal stamen, in other words, these auricles apparently form a normal and integral part of the anther. Auricles also occur in *Allium*, *Ornithogalum* and *Deutzia*, for that matter. Eichler describes the auricles of the *Lauraceae* as "blosse stipulare Anhängsel der Staubblätter" ("mere stipular appendages of the stamens"). E. CAPEDE (1898, p. 42) describes a similar case in a flower with an additional stamen of *Orchis latifolia* and I have also observed a supernumerary stamen in *Dactylorhiza* possessing an auricle,  $A_1$  having retained this organ (Plate VI, Fig. 15) The auricles of the orchidaceous stamen are manifestly emergentia. Compare also VERMEULEN (1953).

The question arises whether any remnants of the stamens  $A_2 + A_3 + a_3$  can possibly be indicated. This seems most unlikely if we consider the style to be conerescent with the whole androecium, in other words, all stamens are likely to be connate as in the actinomorphic flowers of the *Aristolochiaceae*, *Nepenthaceae* and *Asclepiadaceae*. Some morphologists and taxonomists believe to have found the rudiments of the three missing stamens in the labellum (Darwin, Lindley). This seems improbable, because supernumerary stamens are always inserted on the gynostemium. Moreover, we may assume that the law of Dollo also applies to the orchid flower: *evolution is irreversible*. Supposing that the gynostemium was formed with the inclusion of  $A_1 + a_1 + a_2$ , we may assume that the other parts of the androecium had previously become reduced, and will always remain abortive. Elements of the perigone exhibit various differentiations, it is true, such as the lip in *Glossodia* and *Ophrys*, the lateral petals in *Dendrobium* and the median sepal of *Disa*. Brown suggested that the protrusion on the labellum of *Glossodia*, an Australian genus with about five species, would correspond with  $a_3$  (BROWN in WALLICH, 1830, vol. I, p. 74; see also Verm. Botan. Schr., 1834, vol. V, p. 198; see EICHLER, 1875, vol. I, p. 183, wrongly quoted by EICHLER). To my mind this is nothing but a functional differentiation of the motile lip. This is even more evident in *Glossodia brunonis* Endl. = *Elythranthera brunonis* (Endl.) A. S. George, which possesses two similar protrusions on the base of the labellum (not on the column), which can move independently (see A. S. GEORGE, 1963, p. 4). *Epiblema grandiflorum* R. Br. has no less than half a dozen protrusions on the lip. The hypothesis that the lateral stamens ( $A_2 + A_3$ ) are represented by the labellum is equally untenable, on similar grounds. This hypothesis is erroneously ascribed to Brown, both by DARWIN (ed. 2, 1890, p. 237) and by EICHLER l.c. However, BROWN (in WALLICH l.c.) stated: "It may be remarked that indications or rudiments of the two stamens necessary to complete the number in Orchideae of those namely, corresponding with the lateral segments of the outer series of the perianthium, have not yet been observed in the regular structure of any plant of that order". The hypothesis, in fact,

dates back to LINDLEY who, in his work: *The Vegetable Kingdom*, ed. 3, 1853, p. 183, says: "In general the central of the outer whorl is alone perfect; while in *Cypripedium* perfection is confined to the lateral inner stamens. The rest of the stamens are either wholly suppressed, as in many *Dendrobes*, or appear in the form of ears to the column or crests upon the lip; the ears of the column sometimes representing the lateral inner staminodes, and the crests of the lip being made up either of the two lateral outer and one central inner staminode, or of either."

DARWIN, in his book on orchids (ed. 2, 1830, p. 236), shows a diagram to illustrate his contention that the stamens  $A_2$  and  $A_3$  became incorporated in the labellum. He founded his view on the course of the vascular bundle. The anatomical examination was repeated by B. G. L. SWAMY (1948). In his article: *Vascular Anatomy of Orchid Flowers*, this author draws the following conclusion (on p. 93): "The labellum is also shown to receive the same vascular supply as the rest of the perianth members; it is stressed that there is no evidence to consider it to be a compound structure, as was thought by Brown and Darwin." See also NELSON, 1965, p. 190.

In his splendid treatise on *Ophrys* and in his article: *Zur organophyletischen Natur des Orchideenlabellums*, Erich NELSON (1965), defends the view that the labellum of the orchids is compounded of the three stamens  $A_2 + a_3 + A_3$ , the median petal having disappeared. This hypothesis enables Nelson to identify the three lobes so often observed in the *Ophrys* labellum, e.g., in *O. cornuta* Stev. (= *O. scolopax* ssp. *cornuta* Lam.), with the three above mentioned missing stamens. The labellum in the species of the genus *Ophrys* often bears lateral protrusions. Yet, I do not subscribe to this hypothesis. My principal objections are the following:

If we assume that the highly evolved orchid flower, specialized in pollination by insects, can indeed be derived from the actinomorphic pentacyclic and trimerous Monocot flower, we must start from the simplest forms and not from the most specialized ones when assessing the homology of the various parts of the flower. Formerly, when interpreting the morphology of the higher plants, one started from the *Angiosperms* and the concepts of stem and leaf were extrapolated into the morphology of the lower plants. (See MEEUSE (1965): "Angiosperms — Past and Present".) One has since realised that this is the wrong way round and with the help of the telome theory one can now start with the simplest terrestrial plants, *Rhynia* and related genera, gradually to reach the specialized forms of the *Angiosperms*. When one wishes to interpret the most specialized forms of the orchid flower, in casu the flower of *Ophrys*, one should likewise start from the simplest flower, in which the lip differs very little in shape from the lateral petals and the zygomorphy is not yet manifest in the perianth. As soon as the homology of the lip of such a flower is determined, it will be possible gradually to determine the homology of the floral appendages of more specialized forms, starting from the simplest pattern, even if the various intermediate forms are not known.

In the *Apostasiaceae*, whose perianth is still fairly regular, only the elements  $a_1 + A_2 + a_2$  of the androecium develop (Fig. 1A and 1B). The parts of the perianth, three sepaloid and three petaloid, occupy such a regular position that, to my mind, there is no reason whatsoever to consider the median petal a compound organ (see Plate I, Fig. 2A and 2B) of *Neuwiedia*. It follows from this figure that three stamens have not developed:  $A_2 + a_3 + A_3$ . In the *Orchidoideae*, the genus *Herminium*, with many representatives in the Himalayas, also exhibits only a slight zygomorphy in its perianth. The gynostemium contains  $A_1$  as the only fertile stamen. In this case there is, to my mind, not a single reason either to consider the labellum a compound organ. See KING & PANTLING (1898): The Orchids of the Sikkim-Himalaya, part IV, pl. 442, *Herminium orbiculare* Hook. fil. of which the labellum is almost ecalcarate. *Platanthera bifolia* Rich. also seems to provide a good starting point, even if the labellum in that species does have a spur. It is not always true that the labellum is the largest petal. In the South African genus *Disa* the labellum is sometimes very small and instead of the labellum the median sepal has a special form and is prolonged into a spur. It seems improbable that this median sepal could be a compound organ. Apparently zygomorphy can express itself in various directions. The fact that zygomorphy can evoke great differences becomes apparent from the conditions in the *Commelinaceae*, the species of the genus *Tradescantia* still having quite regular flowers, but the species of the genus *Commelina* exhibiting, not only in the androecium, but also in the corolla, a strong trend towards zygomorphy (*C. communis* L. with  $P_3$  very small).

The morphology of flowers with anomalous and atavistic characteristics does not warrant the conclusion that the labellum is a compound organ, or that the median petal would be lacking. A number of cases is known in which supernumerary stamens  $A_2 + A_3$  develop, (see BROWN, 1833) and in which the labellum develops quite normally. It often happens that a double lip develops, but this does not affect the morphology of the flower in any other respect. Being highly evolved *Ophrys* is a genus with many "adaptations", in particular as regards the lip. This may be concluded from the strange shape, the colour and the pubescence, which make the flower look like an insect or a spider. A similar resemblance not only occurs in representatives of the genus *Ophrys*, but also in several representatives of Australian genera. Edith Coleman has recorded the pseudo-copulation by male animals in those species. In Europe KULLENBERG (1961) carried out numerous experiments, from which it appeared that the *Ophrys* flowers by their shape, colour and smell apparently simulate female animals and thus induce the male animals to attempt a (pseudo-) copulation, by which they bring about the pollination. The lip of *Ophrys* is, to my mind, a strongly derived organ and that is why I think it incorrect to start from this form to determine the homology with a "standard" Monocot flower.

The following conclusions can be drawn:

1. In the orchids the labellum is a single organ, homologous

- with the median petal of the *Monocotyledoneae* with regular flowers.
2. Evolutionary adaptations are responsible for the strongly specialized forms of orchid flowers, as in, e.g., *Ophrys*.
  3. Consequently *Ophrys* is not a suitable object to serve as a starting-point for the assessment of the homology of the lip.

## 10. THE OVARY

The ovary in the *Orchidales* always contains three, often split (bifid) placentae and by a fairly general consensus of opinion, it is obvious to suppose that the ovary is composed of three carpels, on which the placentae developed marginally.

In the *Apostasiaceae* and in the genera *Phragmopedium* and *Selenipedium* of the *Cypripediaceae* the fruit is trilocular, in *Cypripedium* and *Paphiopedilum*, and in the *Orchidaceae* s.s. we find "parietal" placentae.

John LINDLEY (1853, p. 175) defended a different opinion; he thought there would be three fertile carpels bearing the placentae and three sterile ones bearing the stigmas apically. The traditional point of view is that there are sterile strips of tissue in the ovary enabling the fruit to open with six fissures (replum) but this does not imply that these three strips represent carpels. Accordingly, three carpels are drawn in the diagrams with marginal placentae (EICHLER, 1875, vol. I, p. 180; PULLE, 1952, ed. 3, p. 199). Nevertheless EICHLER op. cit., p. 182) says: "Yet the wall, as a rule, appears as if consisting of six, alternatingly sterile and fertile, carpels externally divided by grooves and internally by indistinct strips of tender tissue, of which the three fertile ones stand opposite the petals".

On the same page he reproduced some figures, adapted from LE MAOUT et DECAISNE, representing the six parts with the placentae in the middle (laminal) of the three fertile carpels. E. PFITZER in his *Morphologische Studien über die Orchideenblüthe*, 1886, p. 9 etc., discussed the structure of the gynostemium more exhaustively and mentioned a number of examples.

My attention was drawn to the problem of the structure of the ovaries in the *Orchidales* by the study of microscopic slides and by several drawings in the literature of orchids, e.g., those made by Madelle A. CAMUS, 1929: *Iconographie des Orchidées*, texte p. 126 by V. A. PODDUBNAYA-ARNOLDI, 1960: *Akad. S.S.S.R.*, vol. VI, table I: *Cypripedium* insigne; and by Leslie A. GARAY, 1960: On the origin of the *Orchidaceae*, plate IX? figs. 4 and 6, and various figures scattered in the older literature (e.g., in EICHLER, 1875, vol. I, *Bluthendiagramme*, p. 182). In all these figures the ovary is clearly reproduced as composed of six parts. My own observations of microscopic slides repeatedly indicated the same pattern of three parts bearing the (split) placentae alternating with three sterile parts. I saw this structural pattern in e.g. *Disa uniflora* (Plate IV, Fig. 10) *Schizodium inflexum* (Plate IV, Fig. 11), *Traunsteinera globosa*, *Caladenia spec.* (Plate IV, Fig. 12), *Epipogium aphyllum*, *Limodorum abortivum*, *Microtis parviflora*, *Thelymitra rosea* and *Aerangis coreacea*.

I was much astonished to see in the ovary of *Neuwiedia veratrifolia* also three laminal placentae and not a trilocular ovary as expected. Here too, especially in the young flower bud, I found six parts. The three hypopetalous parts have double placentae which are so large that they touch each other. This gives the impression as if the ovary is trilocular (Plate IV, Fig. 9) and later on this is, indeed, the case (in older flowers and in the fruit). I suppose that in the genera *Apostasia* and *Adactylus* we may find the same development. It also struck me that in the ovary of a *Cymbidium* hybrid, which I examined some time ago, six parts could so clearly be distinguished on the outside: three zones of the ovary wall converge apically and bear the sepals and these hyposepalous parts alternate with narrower hypopetalous zones bearing the placentae in their median portions and lying below the petals. This is rather suggestive of stachyospermy and would imply that the narrow placentae acquired foliaceous lateral outgrowths.

Lindley, the principal opponent of Robert Brown, was the first to submit the thesis that the ovary of the orchids consists of six parts. Brown, under the spell of the conception that the basic structural pattern of the orchid flower consists of regularly alternating trimerous whorls, opposed this idea. Brown's conception became almost universally accepted, but this is rather unfortunate in my opinion. In all modern hand books in which a floral diagram of the orchid flower is shown, the flower is always drawn as if there are only three carpels with marginal placentae.

An analogous problem occurs in those *Brassicales* (*Rhoeadales*) which have fruits dehiscing by means of two valves. In *Eschscholzia californica* we find a collar under the calyx (later under the fruit) and more distally a deciduous bipartite calyx, two dimerous whorls of petals, numerous stamens, and a tetramerous superior ovary with two long stigmas and two slighter shorter ones. There are only two placentae, so that also half of the component parts of the ovary are sterile. In *Glaucium flavum* and in *Chelidonium majus* (*Papaveraceae*) two valves fall off when the fruit ripens, and a frame formed by the two extremely narrow placentae remains. Similar cases are found in the *Fumariaceae*, e.g., in *Corydalis*. In the *Cruciferae* the valves are sterile and the narrow placental zones connected by the partition-wall persist (See HANNIG, Untersuchungen über die Scheidewände der Cruciferenfrüchte, Bot. Zeitung (1901) p. 207 et seq.)

The *Orchidales* exhibit a similar structure in their ovaries as we have seen but the gynoeceum being trimerous, it has three sterile and three fertile parts. As in *Brassicales*, the placentae are split (bifid) and often even branched. The collar in *Eschscholzia*, present under the superior ovary, has an analogon in the calyculus found in some orchidaceous genera (*Epistephium*, *Lecanorchis*, *Neobenthamia* (Fig. 16) near the top of the ovary below the calyx and apparently associated with epigyny. We may accept, at least theoretically, that the receptacle extends to the top of the ovary, even if it is impossible clearly to distinguish the receptacle from the other component parts of the ovary. I think that the placentae of the *Orchidales*, unlike those of the *Cruciferae* (which grow

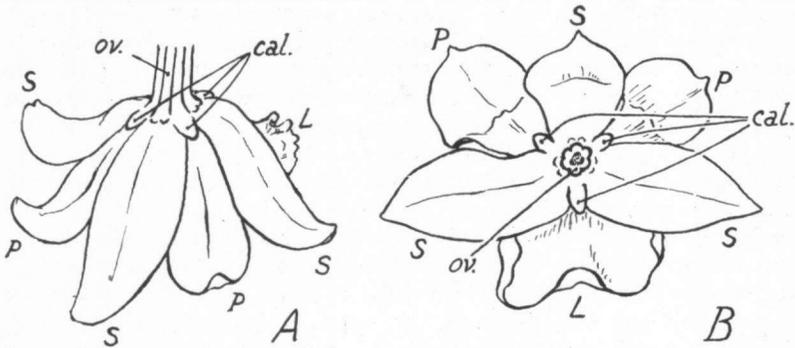


Fig. 16. Flower of *Neobenthamia gracilis* Rolfe to show the calyx on top of the ovary below the sepals. cal.: calyx; ov: ovary; s: sepals; p: petals; l: lip.

centripetally to form the “false” septum), extended laterally to form the epipetalous zones of the ovarial wall. In addition one must assume that the receptacle is trifid, the fundamentally stachyospermous but secondarily foliaceously enlarged placentae having squeezed themselves in between the lobes of the receptacle as it were. The ovaries of several species of orchids indeed suggest that the hypopetalous zones are situated slightly below and between the hyposepalous portions. Sometimes the hyposepalous areas are apically connivent to form a ring-shaped structure overlying the intervening apical portions of the placentiferous zones. This assumption is also quite compatible with the occurrence of a rim-like calyx in the zone of insertion of the sepals (a condition which is the perfect parallelism of the development of a collar-like calyx in *Eschscholzia*). In the face of so much factual evidence, the conventional interpretation of the orchidaceous ovary as a tricarpellate structure with marginal placentation is untenable. The orchidaceous gynoecium consists of three sterile elements supporting the sepals and the pollen-receiving organs (the functional stigmas) alternating with the ovuliferous elements bearing the laminal double placentae (which are strongly ramified, apparently as a secondary adaptation associated with the very numerous ovules). Accordingly, the ovary must be interpreted as a hexamerous aggregate of two alternating whorls of three elements. This structure is suggestive of a stachyosporous condition, the ovules being produced on seed-bearing cauline organs secondarily connate with enveloping foliar elements. It may be significant in this connection that according to Payer the ovules do not develop simultaneously but successively on the placenta. Conceivably this mode of development is attributable to stachyospermy.

## 11. STIGMA AND ROSTELLUM

The *Apostasiaceae* have three small stigmatic lobes, the *Cypripediaceae* have three large, distinct stigmas, alternating with the ovuliferous placentae. It has repeatedly been suggested that in the *Orchidaceae* the

third stigmatic lobe became transformed into the rostellum, in other words, that only two stigmatic lobes are present. However, the examination of microscopic cross sections of the style and the stigma proves this view to be wrong: see the report of my lecture delivered during the I.B.C. in Paris (1954). In the *Orchidoideae* three stigmatic lobes can be frequently distinguished (*Dactylorhiza*, *Disa*, *Himantoglossum*, *Orchis*, *Platanthera* (Plate III, Fig. 8A)), of which the median lobe is well developed. In various genera a reduction of the median stigmatic lobe took place (in *Gymnadenia*, *Anacamptis*) and in some genera the median stigmatic lobe has even disappeared altogether (in *Bonatea*, *Habenaria* s.s.) which is concomitant with an increase in size of the rostellum, which may even become quite large. As regards the connection between the rostellum and the stigma the reader should consult my earlier paper on the subject (VERMEULEN, 1959). In the last two genera the functional stigmatic lobes are born on a pair of stigmaphores.

The *Epidendroideae* often also possess three stigmatic lobes of which the median one not rarely bears the rostellum apically, the latter becoming secondarily attached to the stipe. In the *Neottianthae* the rostellum sometimes takes the place of the entire median stigmatic lobe, e.g., in the Australian genus *Pterostylis* and in *Zeuxine* from Africa and S. E. Asia. In most genera, however, there are three stigmatic lobes although it is often difficult to distinguish them in the maturing stigma because of an excessive secretion of a mucilaginous substance. The presence of three lobes is often indicated by the situation of the stylar canal, viz. in the centre of the stigma and not immediately beneath the rostellum as one would expect in the alternative case.

In the *Orchidoideae* the rostellum develops as a strap-shaped body with at either end a viscid disc, originally situated above the lateral stigmatic lobes (Plate III, Fig. 8B). In the *Epidendroideae* the rostellum develops as a single compact organ representing a part of the third stigmatic lobe (Plate II, Fig. 5B), or even replacing it entirely. In the group of the *Vandaeae*, an important part of the rostellum is formed by the so-called stipe. This organ is always considered to be a derivative of the rostellum. It is often developed as a rather bulky organ and if this is the case it does not only form a part of the third stigma lobe, but also contributes largely to the tissue situated above the clinandrium. The polymorphous and functionally diversified stipe connects the rostellum proper with the pollinia. It gives the impression of being a separate piece of tissue derived from the gynostemium.

A remarkable form of rostellum, derived from the anther, I discovered in the Asiatic genus *Stereosandra*, of which spirit material from Thailand had been put at my disposition by Mr. G. Seidenfaden, Copenhagen. In this genus the stigma does not at all participate in the formation of the rostellum, the latter being formed by a protruding part of the anther which subsequently excretes viscid matter (Plate VI, Fig. 14). The caudicles lie beneath this rostellum. Each caudicle consists of two converging strands, each of which forming a part, situated in the partition wall between the two loculi. The caudicle

being formed by two such strands, it can not possible be a derivation of one of the pollen masses, even though it is ultimately located on top of the pollinia. As in *Epipogium*, the androecial bundle divides itself into three branches of which the middle one innervates the "rostellum" (See VERMEULEN, 1965).

#### ACKNOWLEDGEMENTS

I am much indebted to Prof. Dr. A. D. J. Meeuse for his assistance with the formulation and corrections of the English text and to Miss N. M. Koster for her help. I thank Miss Dr. A. Jaarsveld for the translation in latin of the diagnoses of *Neottianthae* and *Epidendranthae*. The following persons provided me material for which I wish to thank them: Mr. J. Delamain, Jarnac, sent me *Limodorum* buds, the Director of the Botanic Gardens in Singapore a plant of *Newwiedia veratrifolia*, Mr. A. D. Dockrill, Cairns, Australian material and Mr. G. Seidenfaden flower buds of *Stereosandra* from Thailand. Mr. J. Vuijk made the drawings, Mr. D. Boesewinkel the photographs and Miss H. N. v. d. Steenhoven and Mr. J. Houthuesen the microscopical slides. I wish to express my gratitude to them all.

#### REFERENCES

- ADANSON, M. 1763. Familles des Plantes 2. Paris.  
 BLUME, C. L. 1825. Bijdragen tot de Flora van Nederlandsch Indië, 8e stuk. Batavia.  
 BOLUS, H. 1896. Icones Orchidearum Austro Africanum (Orchids of South Africa) 1. London.  
 BROWN, Robert. 1830 in WALLICH: Plantae Asiaticae Rariores 1.  
 ————. 1833. On the Organs and Mode of Fecundation in Orchideae and Asclepiadeae in Transactions of Linnean Society of London 16.  
 CAPEDEK, E. 1898. Beiträge zur Entwicklungsgeschichte einiger Orchideen in Flora, 1898.  
 COLEMAN, Edith. 1927. Pollination of *Cryptostylis leptochila* F. v. M. in Vict. Naturalist.  
 DARWIN, Ch. 1890. The various Contrivances by which Orchids are fertilised by Insects, 2nd ed. London.  
 DRESSLER, Robert L. and DODSON, Calaway. 1960. Classification and Phylogeny in the Orchidaceae in Ann. Missouri Bot. Garden 47.  
 EICHLER, A. W. 1875. Blüthendiagramme. Leipzig.  
 ERICKSON, Rica. 1951. Orchids of the West. Perth, W. A.  
 GAREY, Leslie A. 1960. On the Origin of the Orchidaceae in Botan. Museum Leaflets, Harvard University 19. Cambridge, Mass.  
 GEORGE, A. S. 1963. Notes on Western Australian Orchidaceae in the Western Australian Naturalist 9.  
 GODFERY, M. J. 1932. Apostasiaceae in the Orchid Review 40.  
 GOEBEL, K. 1913. Morphologische und biologische Bemerkungen: 22 Hydrothrix Gardneri. Flora 105 (N.F.Bd. 5).  
 HAGERUP, O. 1959. Prophylls as Sepals in Orchidaceae. Bull. Research Council of Israël. Sect. D. Botany.  
 HAMANN, Ulrich. 1961. Merkmalsbestand und Verwandtschaftsbeziehungen der Farinosae: Philydraceae. Willdenowia 2, Berlin-Dahlem.  
 ————. 1962. Über Bau und Entwicklung des Endosperms der Philydraceae etc. Botan. Jahrb. 81. Stuttgart.  
 HANNIG, E. 1901. Untersuchungen über die Scheidewände der Cruciferenfrüchte in Botan. Zeitung. Leipzig.  
 HOLTUM, R. E. 1953. A revised Flora of Malaya 1. Orchids of Malaya. Singapore.  
 HUTCHINSON, J. 1959. The Families of Flowering Plants 2. Monocotyledons, 2nd ed. Oxford.  
 KULENBERG, Betil. 1961. Studies in Ophrys Pollination. Zool. Bidrag från Uppsala 34.

- KING, George and PANTLING, Robert. 1898. The Orchids of the Sikkim Himalaya. London.
- LINDLEY, J. 1830-1840. The Genera and Species of Orchidaceous Plants. London.
- . 1833. Nixus Plantarum. London.
- . 1853. The Vegetable Kingdom. 3rd ed. London.
- LINNAEUS, C. 1735. Systema Naturae. Leyden.
- MANSFELD, R. 1954. Über die Verteilung der Merkmale innerhalb der Orchidaceae-Monandreae. *Flora* **142**.
- MEEUSE, A. D. J. 1965. Angiosperms – Past and Present. New Delhi.
- NELSON, Erich. 1962. Gestaltwandel und Artbildung erörtert am Beispiel der Orchidaceen. *Chernex-Montreux*.
- . 1965. Zur organophyletischen Natur des Orchideenlabellums. *Botan. Jahrb.* **84**.
- PAYER, J. B. 1857. *Traité d'Organogénie comparée de la Fleur*. Paris.
- PFITZER, E. 1886. Morphologische Studien über die Orchideenblüte in *Festschr. Ruperto-Carola*. Heidelberg.
- . 1887. Entwurf einer natürlichen Anordnung der Orchideen. Heidelberg.
- . 1903. Orchidaceae-Pleonandreae in *Das Pflanzenreich* no. **IV**. **50**. Leipzig.
- PODDUBNAYA-ARNOLDI, V. A. 1960. Study of Fertilisation in the living Material of some Angiosperms. *Phytomorphology* **10**.
- PRILLIEUX, ED. 1857. Observations sur la Déhiscence du Fruit des Orchidées. *Bull. de la Société Botanique de France*. **4**.
- PULLE, A. A. 1952. *Compendium*. 3e druk. Utrecht.
- REICHENBACH, H. G. 1884. Ueber das System der Orchideen in *Bulletin Congres intern. de botanique et d'horticulture à St. Petersburg*.
- ROLFE, R. Allan. 1888. A Morphological Study and systematic Review of the Apostasiaceae. *Linn. Journal-Botany* **25**.
- RUINEN, J. 1952. Epiphytosis. A second View on Epiphytism in *Annales Bogoriensis* **1**. (Bogor 1950-1954).
- SCHLECHTER, R. 1914. Die Orchidaceen von Deutsch-Neu-Guinea in *Rep. spec. nov. regn. veg. Beihefte* **1**. Berlin.
- . 1915. Die Orchideen. Berlin.
- SCHWEINFURTH, Charles. 1959 **1**. Classification of Orchids in Carl L. Withner: *The Orchids*. New York.
- SEIDENFADEN, Gunnar and SMITINAND, Tem. 1959. The Orchids of Thailand. Part. 1. Bangkok.
- SMITH, J. J. 1905. Die Orchideen von Java-Flora von Buitenzorg **6**. Leiden.
- . 1915. *Nova Guinea* **12**, livr. 3. Die Orchideen von Niederländisch-Neu-Guinea. Leiden.
- SWAMY, B. G. L. 1948. Vascular Anatomy of Orchid Flowers in *Botan. Museum Leaflets, Harvard University* **13**. Cambridge, Mass.
- SWARTZ, Olof. 1800. *Afhandl. om Orchid Slägter etc. and Orchidernes Slägter etc. in Kongl. Vetensk. Acad. nya Handl.* **21**. Stockholm.
- TAKHTAJAN, A. 1959. Die Evolution der Angiospermen. Jena.
- VERMEULEN, P. 1953. The vanished Stamens in Amer. *Orchid Soc. Bull.* **22**. Cambridge, Mass.
- . 1954. Le rostellum des Ophrydées. *Comptes rendus des séances du 8ième Congrès intern. de Botanique, sect. 7 et 8*: 233.
- . 1959. The different Structure of the Rostellum in Ophrydeae and Neottieae in *Acta Bot. Neerlandica* **8**.
- . 1965. The Place of Epipogium in the System of Orchidales in *Acta Bot. Neerlandica* **14**.
- VOGEL, Stefan. 1959. Organographie der Blüten Kapländischer Orchideen. *Disinae und Satyrinae. Abh. d. Akad. v. Wiss. u. Lit. Math.-nat.* Wiesbaden.
- WETTSTEIN, R. VON. 1935. *Handbuch der Systematischen Botanik*. Leipzig und Wien.