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ON THE ORIGIN OF THE ORCHIDACEAE¹

BY

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INTRODUCTION

To discourse on the origin of the Orchid family, which represents the culmination of one of the evolutionary lines of the Monocotyledons, is a rather formidable task. Its existing members display such a high degree of complexity of organization in their structures that the primitive characters or simple elements, which might have shed light on ancestral origins, are either lost or well masked. When we take into consideration that the Orchid family, comprising at present some 30,000 species distributed in 800 genera, is devoid of paleobotanical documentation, save *Protorchis monorchis* Massal. from the Eocene of Monte Bolca, it is impossible to explain or even state the manner in which the various evolutionary forces have acted upon the primordial organism that served as the prototype for modern species. In addition to these difficulties, information on the anatomy, embryology, genetics, cytology, fertilization, ecology, etc., of today's species is too fragmentary to give us a reliable and coherent picture.

In spite of these deficiencies, I shall attempt to present an outline of the Orchid family and its origin, as I

¹This paper will be read on May 31, 1960 during the 3rd World Orchid Conference in London, England.

understand it, from an interpretation of the evidence now available, as well as to point out the gaps where intensive research is required for further clarification. It is my hope that this effort may stimulate the students of evolution to turn some of their attention to this intricate and perplexing group of plants.

The problem of the origin and phylogeny of various plant groups and families has occupied the minds and interest of a number of outstanding botanists from Linnaeus to our time. All have recognized that in nature a system prevails within which everything seems to follow a pattern of progressive differentiation from simplicity to complexity. While Linnaeus' sexual system can hardly be associated with progressive differentiation, the systems of Bentham and Hooker or of Engler and Prantl, to mention but two, in essence convey this idea. However, progressive differentiation in the light of our modern species-concept assumes an entirely different role and meaning from that which was understood and employed by the earlier workers. A glance at any of the proposed "natural" systems is sufficient to make us recognize that they are based on a continuous modification along a straight line of descent. We are informed today, however, that species could also have been derived simultaneously or consecutively from a common ancestor or from the fusion of one or more common ancestors. Progressive differentiation in the light of these latter principles assumes an entirely new and far reaching significance.

If we wish to understand the origin or phylogeny of any group, regardless of its taxonomic status (genus, subfamily, family, etc.), we must first understand the basic unit: THE SPECIES. A lengthy discussion about the nature of species does not, however, lie within the scope of this paper, and I must assume that the reader is fully acquainted with the subject. It is sufficient, there-

fore, if we merely state that the species represents a dynamic, adaptive peak in evolution. Any taxonomic group above this level, in order to express a meaningful expansion, must represent further dynamic macro-units or enlarged adaptive peaks (which are the results of the coaction and coaptation of the basic units), because if these higher units are merely categories of convenience (as most of them are today) they will hinder rather than broaden our perspective and comprehension of the evolutionary makeup of our object of study.

We have to keep constantly in mind that living species are scanty representations of all the possible modifications and combinations that may have occurred in nature, although those types which have been eliminated by selective pressures still contributed to the formation of present species. Therefore, when we study a group of plants, we find that its basic units (i.e. species) are connected by a series of trends which are radiating in various directions, forming a reticulate pattern. In visualizing this reticulate pattern in a three-dimensional perspective, we find that the connective trends progressively decrease as we advance towards higher levels, but that this decrease never terminates in complete elimination.

Such a dynamic and 3-dimensional structure (vaguely resembling the molecular structure of a crystal) cannot be projected into a 2-dimensional perspective without destroying, or at best distorting, its salient features.

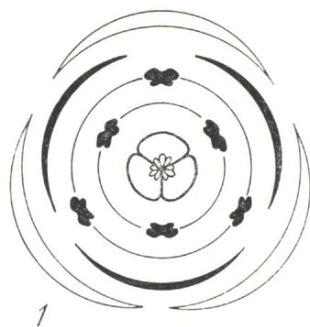
All of us, from time to time, have felt and recognized the presence of such a system, but our conventional mind with its categorizing instinct continuously interferes with and obscures our vision. I wish to make it clear that I fully recognize the necessity of categories of convenience, but I strongly object when these categories of convenience are employed as the basis of a so-called "natural" system; and this is what has happened in the case of the Orchid family

Keeping constantly in mind the dynamic structure of nature, I shall attempt to examine the Orchid family and its origin against this background.

FLORAL DIAGRAMS AND BASIC GROUPS

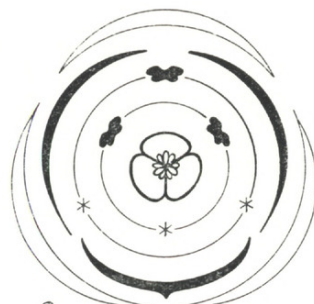
The Orchid family is an extremely heterogeneous unit with respect to its external and internal composition. The vast array of types of modified structures, many of which combine simultaneously characters of both a primitive and advanced nature, are, however, tied together by a few definite characteristics: 1, the inferior ovary; 2, the production of a large number of seeds without endosperm; and 3, the various degrees of fusion between the style and stamens.

Notwithstanding the large number of species in the family, it is possible to outline and express the arrangement of floral parts by means of three or four basic floral diagrams (Plate VIII). From an inspection of these floral diagrams, it is evident that orchid flowers are built on a trimerous pattern and that they are merely modifications of the liliaceous type. The essential deviation from the liliaceous pattern is to be seen in the staminal circles. In the first diagram (Pl. VIII, fig. 1), which may equally serve for *Ornithogalum* of the *Liliaceae* or *Hypoxis* of the *Hypoxidaceae* (*Amarillidaceae* sens. lat.), both staminal circles are fertile and fully developed, i.e., all six anthers are functional. In the *Orchidaceae* (Pl. VIII, figs. 2–4) the anthers opposite the lateral sepals and the median petal are completely suppressed (with the exception of *Satyrium*, about which more will be said later). The reduction in number of fertile anthers is always paralleled by a fusion of the stamens and of the stamens with the style. Developmental and anatomical investigations with respect to the origin of these fertile circles indicate that the existing species must have evolved along at least two different lines from an already modified ancestral type,



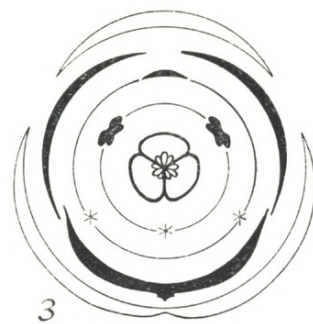
1

HYPOXIS



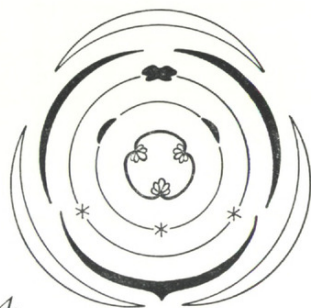
2

NEUWIEDIA



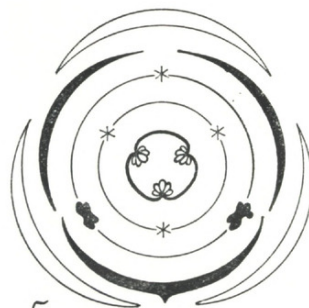
3

SELENIPEDIUM
APOSTASIA



4

NEOTTIOIDEAE
OPHRYDOIDEAE
KEROSPHAEROIDEAE



5

SATYRIUM

because each of these lines, although still sharing detectable characters, displays an unequal rate of differentiation. These functional circles, or the number of functional anthers present in these circles, are still employed today to characterize the two major subdivisions of the family.

In *Neuwiedia* (Pl. VIII, fig. 2), there are three fertile anthers, one dorsal and two ventral. This is the only genus in the family *Orchidaceae* where fertile anthers are present simultaneously in both staminal circles. In this respect *Neuwiedia*, one of the three genera of the *Apostasioideae*, is perhaps the most primitive orchid: the other two genera, *Apostasia* and *Adactylus* are merely modifications of the *Neuwiedia*-pattern. In *Apostasia* (Pl. VIII, fig. 3), we observe a transformation of the dorsal anther into a staminode, while in *Adactylus* a further suppression completely eliminates this structure. *Apostasioideae* are set apart from the rest of the orchids by an additional series of correlated characteristics which will be discussed in further paragraphs.

Although the floral diagram of *Apostasia* is identical with *Selenipedium* (Pl. VIII, fig. 3) of the group *Cypripedioideae*, this identity is restricted to diagrammatical representation. The vegetative appearance, as well as the floral morphology in both of these groups, is very dissimilar. In *Apostasioideae*, the filaments of the anthers are usually still present and recognizable; while in *Cypripedioideae* these structures are completely fused with the style. Furthermore, in *Cypripedioideae*, the shape of the staminode and the median petal exhibit a major deviation from *Apostasioideae*, to such an extent that these two groups can hardly be interpreted as representing two subsequent stages of one evolutionary trend.

The discontinuity between *Neuwiedia* and the monandrous orchids is even greater. The floral diagram (Pl. VIII, fig. 4) brings into focus a single criterion only: the

suppression of a different staminal circle. This suppression seemingly conveys the idea that *Neuwiedia* gave rise simultaneously to both *Cypripedioideae* and to the monandrous orchids. However, the sum total of characteristics which make up the monandrous orchids suggests that during the course of evolution there were other lines besides that of *Neuwiedia* which fed into the complex. Although the general pattern of the monandrous orchids (which include 90% of the known species) can be expressed by a single diagram, the group itself is composed of three distinct units, depending on the manner and degree by which the individual pollen grains adhere to each other to form the pollinia. These three groups are: *Neottioideae*, *Ophrydoideae* and *Kerosphaeroideae*.

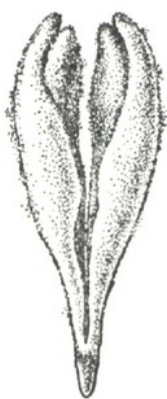
In *Neottioideae* and *Ophrydoideae* (text fig. 1) the pollen grains are of a soft consistency and cohere into massulae in a relatively loose manner; in the former unit they easily separate into a fine powdery mass (sectile pollinia), while in the latter they form large granules (granular pollinia). In *Kerosphaeroideae* the cohesion of the individual grains is so compact that the pollinium may be broken only through the exertion of considerable force.

The presence of pollinia is characteristic of the three units of monandrous orchids only. In the *Apostasioideae*

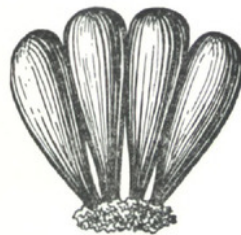
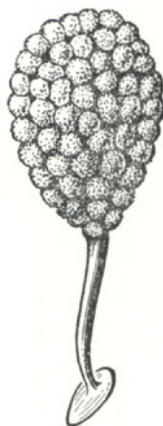
NEOTTIOIDEAE

OPHRYDOIDEAE

KEROSPHAEROIDEAE



massulae



pollinia

Text fig. 1

and *Cypripedioideae*, no pollinia are formed; the anthers contain single pollen grains either dry or embedded in a viscid secretion respectively.

ENDOMORPHIC AND EXOMORPHIC FEATURES

Vascularization. The distribution of vascular bundles in the stem and inflorescence-axis of orchids exhibits the same more or less scattered arrangement as is generally observable in the vegetative axis of other Monocotyledons. The bundles are enclosed within a sclerenchyma-like ring of perivascular fibers, either in a circular manner (similar to the primitive *Aristolochia* type in Dicotyledons) or in a scattered pattern. A preliminary investigation indicates that the circular pattern is always associated with other primitive characters. Those species which exhibit this characteristic have a more or less well developed horizontal rhizome (e.g. *Apostasia*, *Cypripedium*, *Zeuxine*, etc.). Nevertheless, more information is needed before the significance of this association may be fully and definitely evaluated.

In the vascular supply of the flower, the bundles which enter the floral axis vary in number, and this variation is correlated with the primitive or advanced stage of the group. Swamy reports the number of vascular bundles in the *Cypripedioideae* as six; in the *Neottioideae* and *Ophrydoideae* and the less specialized members of the *Kerosphaeroideae* three; while in the advanced types of the *Kerosphaeroideae* there is a further reduction in number to two. Our investigation of the *Apostasioideae* reveals six vascular bundles, as is the case in the *Cypripedioideae*.

In *Apostasioideae* and *Cypripedioideae*, the six bundles constitute the main traces of the ovary without further differentiation. In both of these groups, there is an additional seventh bundle which gives rise to the midrib of the bract.

In the remaining groups (*Neottioideae*, *Ophrydoideae* and *Kerosphaeroideae*) the entering three or two bundles already differentiate in the pedicel to supply the ovary with its six main traces. The pattern by which these six traces of the ovary proliferate in passing to the floral and sex organs is uniform throughout the family. The three dorsal bundles of the ovary enter directly into the three sepals, with a trace leading from each of them to the gynostemium; an additional branch deviates from the main bundle which supports the dorsal sepal to the anther of the outer whorl. The three ventral bundles of the ovary enter directly into the petals, the two lateral ones giving rise to a trace which supports the anthers in the inner whorl. The main trace of the bract is also derived from one of the three incoming bundles.

The presence of six undifferentiated bundles in the *Apostasioideae* and *Cypripedioideae*, as contrasted with three or two in the monandrous orchids, is a further indication of the relative primitiveness of these two groups.

Placentation. The ovary in the Orchid family is syncarpous, either three- or one-carpellate (Plate IX). The three-carpellate condition, i.e. with axile placentation, is present in all species and genera of the *Apostasioideae*, in *Selenipedium* and *Phragmipedium* of the *Cypripedioideae* and in a few genera of the *Neottioideae* (*Lecanorchis*, *Eriaxis*, etc.). The remaining genera of the *Cypripedioideae* and the monandrous orchids exhibit a monocarpellate ovary, i.e. the placentae are parietal in origin.

It is generally accepted that axile placentation is a more primitive condition than parietal, and its occurrence in the Orchid family is limited to groups of respectively primitive status.

Our knowledge with regard to the manner of transition from axile placentation to the parietal type is very meager. Two seemingly aberrant types, i.e. *Phragmi-*

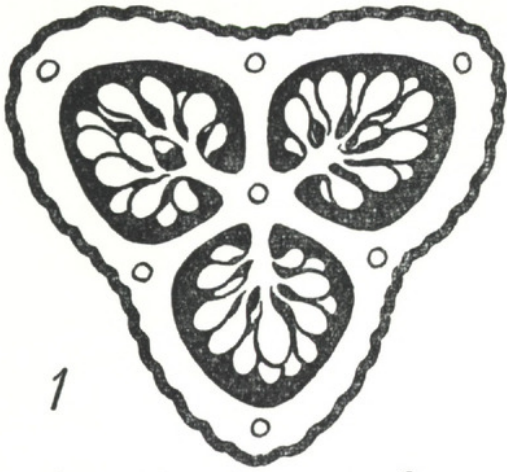
pedium longifolium (*Cypripedioideae*) (Pl. IX, fig. 3) and *Lecanorchis javanica* (*Neottioideae*) (Pl. IX, fig. 4), however, may possibly represent independent steps in the reduction process. Theoretically, the placentae in *Phragmipedium longifolium* are parietal in origin because each of the two placental lamellae, although situated in adjacent locules, are vascularized by a common strand (note the connecting dotted arrow). The placentation itself is intermediate between the axile and parietal positions. In *Lecanorchis javanica*, we find another type of modification of axile placentation. The septa are broken down into separate placental lamellae, and the torus is completely eliminated. The individual lamellae facing the adjacent ventral bundles are united by the margin, thus leaving a Y-shaped empty cavity in the center of the ovary, and the ovules are borne in two rows at the point of junction of the lamellae.

These intermediary steps suggest that the reduction from a tricarpellate to a monocarpellate condition might have come about by a longitudinal division of the septa which eliminated the torus, followed by a gradual shortening of the lamellae (*Limodorum abortivum*, Pl. IX, fig. 5), until merely traces are found along the inner wall (*Cephalanthera alba*, Pl. IX, fig. 6).

Embryogeny. No other plant family exhibits such an inconsistent embryogeny as the *Orchidaceae*. Only the first and second cell generations of the zygote are consistent; the subsequent divisions apparently take place in a random manner.

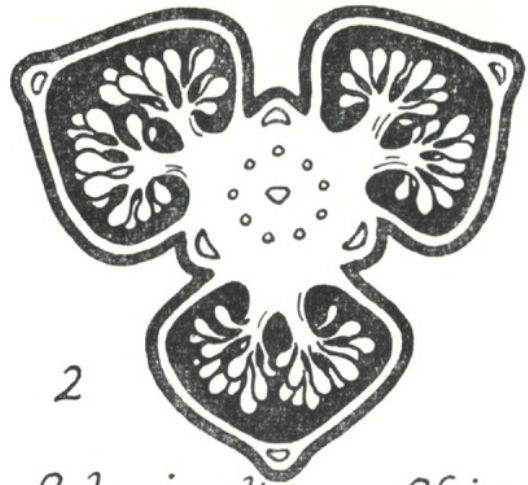
In the first cell generation (Pl. X, fig. 1), the zygote divides into a basal and terminal cell. During the second cell generation, the basal cell differentiates into a suspensor initial cell and middle cell, while the terminal cell divides by a vertical wall. From this step onward, the further divisions are without any definite sequence, but

PLATE IX



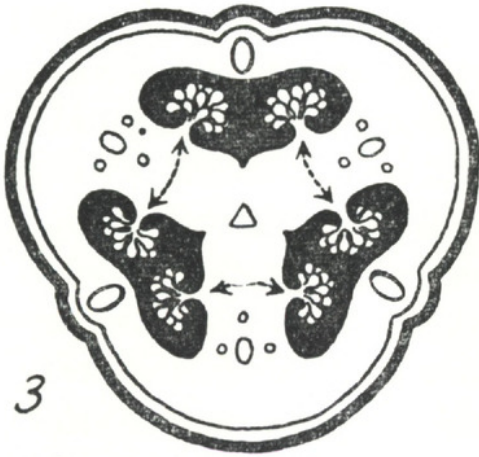
1

Apostasia nuda



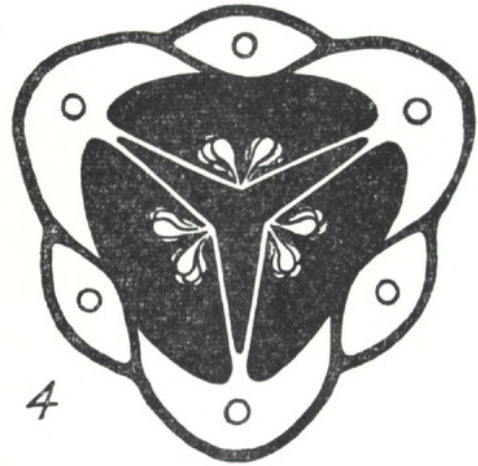
2

Selenipedium Chica



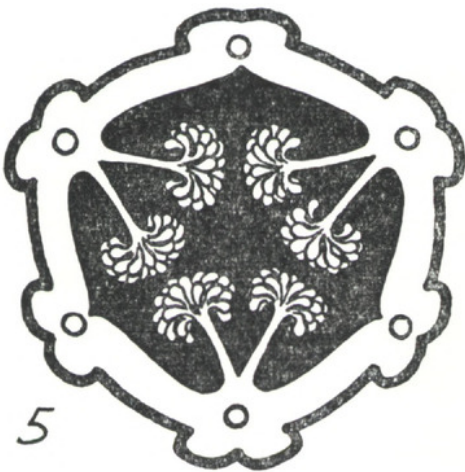
3

Phragmipedium longifolium



4

Lecanorchis javanica



5

Limodorum abortivum



6

Cephalanthera alba

the development may be oriented in two directions: 1. (Pl. X, fig. 1A) all cells including the suspensor initial cell enter into the formation of the embryo, and the mature embryo is suspensorless; 2. (Pl. X, fig. 1B) the suspensor initial cell appears as a distinct structure, either simple or modified.

The suspensorless type of embryo is primitive and is to be found in *Cypripedium* of the *Cypripedioideae* and some members of the *Neottioideae* (*Spiranthes*, *Listera*, *Neottia*, etc.), while those with a suspensor are distributed among the rest of the groups. Swamy, after having studied the embryogeny of a number of species, recognized five different types of suspensors (Pl. X, fig. 2): TYPE I, with a single-celled suspensor, occurring in *Cypripedioideae* (*Paphiopedilum*) and also in the *Neottioideae* (*Vanilla*, *Epipactis*, *Goodyera*, etc.); TYPE II, which is unique in the family in developing a haustorium, is limited, so far as is known, to the *Ophrydoideae*. TYPES III to V are found in various representatives of the *Kerosphaeroideae*.

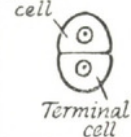
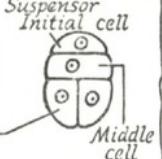
There is a striking parallelism or correlation between the various types of suspensors and the relatively primitive or advanced stage of the main groups of the family.

The mature embryo is an ovoid mass of cells without any definite differentiation of the tissues; thus, there is no endosperm in orchids. With respect to the method by which the undifferentiated mass of cells becomes organized into the several organs of the embryo, no information is available as yet. In a few instances, endosperm development has been reported, but in all of these this development is not consistent. Whenever it occurs, the tissue is of the nuclear type. This rare and casual occurrence is noted in the *Cypripedioideae* and *Neottioideae*.

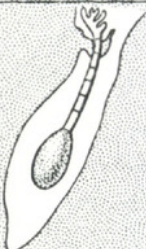
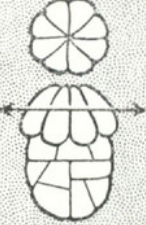
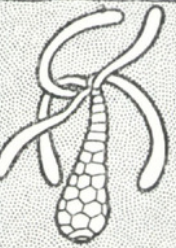
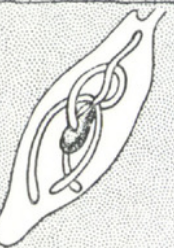
Seeds. The mature embryo is enclosed in a loose, air-filled, reticulate testa which is characteristic of the *Micro-*

PLATE X

1

	Zygote	1 st Cell Generation	2 nd Cell Generation	(Intermediate step)	Adult Organization
GROUP A					
GROUP B					

2

TYPE I				
TYPE II				
TYPE III				
TYPE IV				
TYPE V				

spermae (Pl. XI, A). At maturity the cells of the outermost layer of the integument lose their protoplast, and the seed coat becomes transparent. This type of seed is observable in every genus of the family, except in *Apostasia*, *Adactylus*, *Selenipedium* and *Vanilla* (Pl. XI, B). In these four genera, all layers of the outer integument and most of the inner integument enter into the formation of the seed coat which tightly surrounds the embryo; the testa becomes highly sclerotic, opaque and sculptured.

It is rather remarkable that the presence of a primitive type of seed in *Apostasioideae*, *Cypripedioideae* and *Neottioideae* corresponds to the respective status of these groups.¹

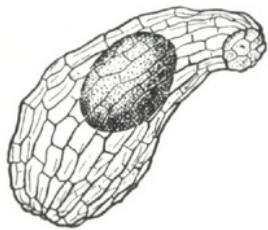
Gynostemium. One of the most distinct features of the *Orchidaceae* is the fusion of the stamens and style into a central organ, the column. This structure has generally been interpreted as an extension of the floral axis, thus being axial in origin. Recent studies, however, have shown it to be only an appendicular structure, since the morphological apex of the flower does not extend to the apex of the gynostemium, but only to the level of insertion of the perianth; the ovary contains all traces of the floral whorls and the gynostemium of the reproductive whorls.

Even today there is a constant debate about the meaning and application of the terms "column" or "gynostemium." The group *Apostasioideae*, from time to time, has been kept apart from the *Orchidaceae* as a distinct

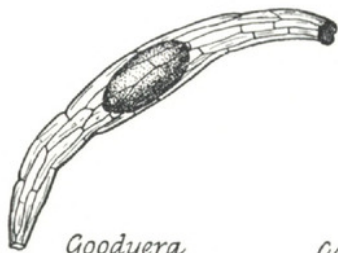
¹ It is noteworthy that, in addition to *Vanilla*, both *Selenipedium* and *Apostasia* possess aromatic substances. *Epistephium* and *Galeola* (Plate XI, A) of *Neottioideae* have also been reported to have essential oils in the fruits, but in lesser quantity. *Epistephium* and *Galeola* have the seeds provided with a prominent, transparent wing (probably a dispersal mechanism), but the embryo itself is enclosed by a sclerotic testa. *Vanilla*, *Epistephium* and *Galeola* p. pt. have been recognized as constituting a distinct family, *Vanillaceae*, on account of the characteristics mentioned above.

PLATE XI

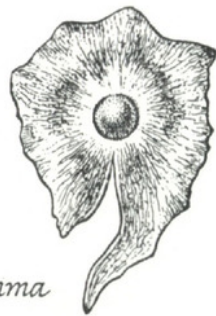
A



*Calopogon
pulchellus*

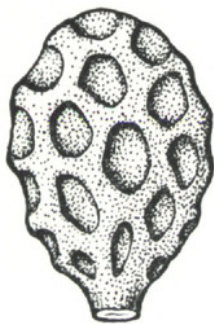


*Goodyera
pubescens*

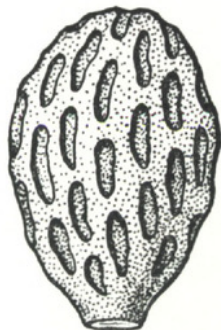


*Galeola
altissima*

B



*Apostasia
nuda*



*Selenipedium
Chica*



*Vanilla
planifolia*

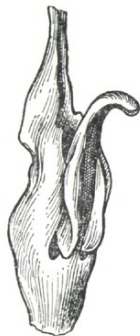
family, because in some of its members the fusion between stamens and style is only partial and the length of the adnation is relatively short. Indeed, in some species of *Neuwiedia* and *Apostasia*, the filaments of the anthers are partially recognizable, but this character is not even constant within a given genus. In *Apostasia papuana* (Plate XII), for instance, the filaments are completely obliterated or reduced to a mere connective tissue. In this respect *Cranichis crumenifera* (Plate XII) or any species of the genus *Spiranthes* or *Erythroides* of the *Neottioideae* might likewise be removed from the Orchid family, because structurally the column is quite homologous in these taxa. Should we express the differences between families by a degree of adnation of these organs in millimeters?

The same incomplete fusion is also observable in *Vanilla anomala* (Plate XII) (*Neottioideae*) where the structure of the column is comparable to that of *Neuwiedia*, although only one anther is fertile, while the other two are expressed by the traces of the filaments as staminodes. *Vanilla anomala* exhibits a further important feature, viz., the versatile anther. This character, along with others, has also been marshalled to support the separation of the *Apostasioideae* into a distinct family. The occurrence of a versatile anther is not limited to this single species in the *Neottioideae*; there are a number of other genera and species which possess the same characteristic: e.g. *Cephalanthera*, *Psilochilus*, *Limodorum*, *Galeola*, *Didymoplexiella*, etc. In other instances, the anther is basifixed and attached rigidly to the column. *Vanilla Griffithii* var. *formosana* (Plate XII) clearly illustrates this situation, but a similar method of attachment is also present in several species of *Apostasioideae*.

In viewing the other columnar structures as depicted on Plate XII, our attention is focused on another point of



*Apostasia
papuana*



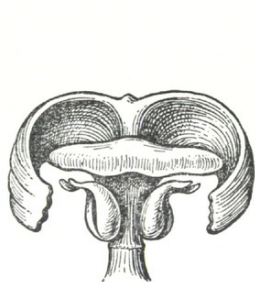
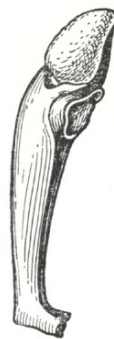
*Cranichis
crumenifera*



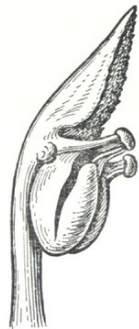
*Vanilla
anomala*



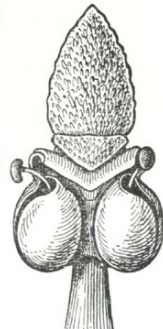
*Cephalanthera
alba*



*Corycium
crispum*



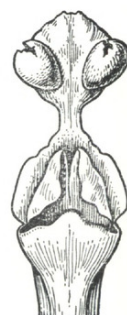
*Satyrium
saxicolum*



*Cypripedium
Calceolus*



*Vanilla Griffithii
var. formosana*



significance, the position of the anthers in relation to the stigmas. Both *Apostasioideae* and *Cypripedioideae* have been distinguished from the monandrous orchids by the adnation of the anthers to the style at a level below the stigma. This criterion, however, may not be applied as an absolute rule, as it has been in the past, because, in addition to these groups, an extensive number of genera (ca. 50) in the *Neottioideae*, as well as the whole *Satyrium*-complex of the *Ophrydoideae*, exhibit a position of substigmatic insertion of the anthers. Therefore, the criterion of the occurrence of such an insertion, which was also applied to justify the removal of *Apostasioideae* from the Orchid family, is invalidated.

The striking structural similarity of the column in both *Satyrium* and *Cypripedium* points to the convergent nature of the respective branches of the main lines of *Ophrydoideae* and *Cypripedioideae*. *Satyrium* itself represents a departure from the general monandrous orchid type in having two distinct anthers developed in the outer whorl of stamens (Pl. VIII, fig. 5). The fact that it is referred constantly to the monandrous orchids is, however, due to the nature of its pollinia.

Rostellum. One of the most significant features in the organogenesis of the column is the formation of a new or modified structure, the rostellum. The theoretical explanation of the origin of this organ, as postulated by Brown and Darwin, is widely discussed in various textbooks; therefore, it is sufficient if we merely state that the median stigma during the reorganization of the flower has evolved into a new organ, the rostellum, with a specific function. It is the controlling and ensuring device for fertilization, since its position is located between the anther and the remaining stigmas; the pollinia are attached by a viscid secretion to the tip of this structure. Although this general situation is observable in the great

majority of orchids, transitional stages, as well as complete absence of it, are also well documented. In *Apostasioideae* and *Cypripedioideae* all three stigmas are fertile; therefore no rostellum is produced. In the remaining groups (*Neottioideae*, *Ophrydoideae* and *Kerosphaeroidae*) it is assumed that a rostellum must be present.

In some members of the *Neottioideae* (e.g. in the genera *Spiranthes*, *Goodyera*, *Erythrodes*, etc.) the style is modified into a wedge-shaped structure with the two separate stigmas situated laterally, while the third one is transformed into an elongate rostellum, all on the same plane. In this situation the nether surface of the rostellum is, however, still a functional stigma, as has been demonstrated by experimentation. We may look upon this condition as an intermediate step in the reduction or modification process, because in the more evolved members of the *Neottioideae* the rostellum ceases to be a functional stigma.

There are also a number of species in the *Ophrydoideae* without any reduction in number of stigmas. Several attempts have been made recently to explain the presence and origin in the *Ophrydoideae* of a so-called "rostellum" in addition to the three fertile stigmas. Since in the other groups (*Neottioideae* and *Kerospheroideae*) the gland of the pollinia is attached to the tip of the rostellum, it is believed that *Ophrydoideae* must also possess such a structure. Vermeulen postulated that the rostellum in the *Ophrydoideae* has an independent origin when all three stigmas are fertile, while Hagerup would derive the glands of the pollinia from the aborted lateral stamens of the outer whorl. I am unable to find a rostellum in the *Ophrydoideae* (comparable to that of the other groups); the structure which is generally called "rostellum" is merely a connective tissue between the two thecae of the anthers. Swamy in his studies of vascularization, has

shown that in *Habenaria* (*Ophrydoideae*) the compound stigma is supported by three vascular strands and in those species where the dorsal stigma is aborted, the supporting strand is obliterated simultaneously. Vermeulen's suggestion that the rostellum in *Bonatea* (*Ophrydoideae*) represents an elongation of the receptacle is hardly convincing, because of the appendicular nature of the column. To derive the viscid gland from the rostellum as a separate organ, or as a modified stigma, and the pollinia from the anther poses a situation rather difficult to comprehend. In my opinion, the whole structure of the pollinium originates as a unit from the anther; the gland itself is a transportation mechanism only. Furthermore, the nature of the anther and the pollinia in the *Ophrydoideae* is such that self fertilization is hardly possible. In those few species which are known to be autogamous, the presence of the connective tissue (whether or not representing a rostellum in reality) does not prevent self fertilization. Much research must yet be done with respect to developmental anatomy before a final conclusion as to the origin of the rostellum and the viscid gland may be drawn.

Indeed, at this point, it makes no difference which of the proposed theories is correct, because each of them bears out the same conclusion: the column of the *Ophrydoideae* is not derived from that of any of the other groups, but it is the product of an independent evolutionary line emerging from a polyphyletic complex.

Pollen. The pollen grains in orchids, at the time of shedding, are either single or more commonly united into tetrads, with or without aggregation into pollinia. In *Apostasioideae* and *Cypripedioideae*, as mentioned above, no pollinia are formed, but the sulcate or monocolpate microspores (similar to other Monocotyledons, e.g. *Hyppoxis*) are always single at maturity.

In *Neottioideae*, the pollen grains cohere loosely into sectile pollinia (first step in specialization); in the advanced species, these are composed of microspores which are united into tetrads, while in the less evolved members (e.g. *Cephalanthera*, *Aphyllorchis*, *Lecanorchis*, *Gal-eola*, *Pogonia*, *Cleistes*, *Epistephium*, *Vanilla*, etc.), the pollinia are formed by single, either monocolpate, ulcerate or porate grains.

In the *Ophrydoideae*, with granular pollinia (second step in specialization) and *Kerosphaeroideae*, with hard, compact pollinia (final step in specialization), the pollinia are always composed of tetrads, which, depending on the position they occupy — whether along the periphery or towards the center — may be one of the five basic types: 1. tetrahedral; 2. isobilateral; 3. decussate; 4. T-shaped, or 5. linear.

The occurrence of single pollen grains and their aggregation into pollinia are in accord with the primitive or advanced status of the five main groups.

DISCUSSION

I have attempted to demonstrate, in the diagram on Plate XIII, the correlation of the majority of criteria discussed in the foregoing paragraphs. The numbers beneath each name summarize, out of the 16 selected characteristics, the essential constitution of each group, and the numbers along the lines connecting these groups are those of characters shared.

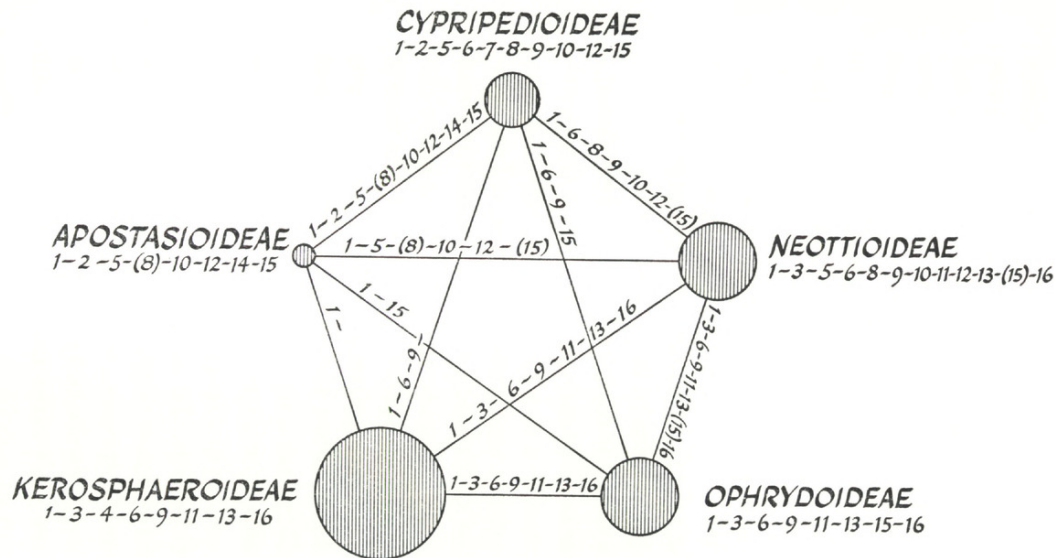
It has previously been stated that the dynamic and 3-dimensional structure of nature cannot be projected into a 2-dimensional perspective without destroying, or at best distorting, its salient features. This statement is relevant also to the diagram on Plate XIII. For the proper interpretation of this projection, we have to visualize each group (shaded circles) as a 3-dimensional unit

and the numbers, connecting each of these groups, as representing independent trends which originate from and link the groups at different points.

The sundry orchid systems proposed in the past were based essentially on progressive differentiation in a linear sequence, which assumes that the family is monophyletic in origin. Indeed, one's first impression is of a linear sequence from *Apostasioideae* to *Kerosphaeroideae*, especially when the groups are evaluated individually. When we attempt to assign a definite position and sequence to each of these groups, however, after studying their alliances, we find the linear arrangement to be rather absurd and unrealistic, since the groups are constantly in juxtaposition with each other. The pattern expressed by these interrelationships is reticulate and indicate that the family, as a unit, is polyphyletic in origin.

The general belief that, during the course of evolution, *Neuwiedia* (*Apostasioideae*) gave rise to both *Cypripedioideae* and the monandrous orchids, is hardly tenable. The so-called "clear cut" differentiation between *Diandrae* (*Apostasioideae* and *Cypripedioideae* together) and *Monandrae* is obliterated, as was mentioned earlier, by the presence of two anthers in the outer staminal circle of the *Satyrium*-complex in *Ophrydoideae*. In addition to this criterion, there are a number of characteristics common to both *Diandrae* and *Monandrae* which have been discussed above as well as documented on Plate XIII. I look upon each group as having an equal standing with respect to its adjacent group, and, for the purpose of classification, I am recognizing each as a distinct subfamily.¹ Perhaps some phylogeneticists may object to such a conclusion, but we have to bear in mind that each group is rather well circumscribed in spite of the close interrelationship.

¹ For the descriptions of these subfamilies see Appendix.



- | | |
|---|---|
| 1. Inferior ovary; $\pm$ fusion of σ and ρ organs | 9. Embryo with a suspensor (types I-V) |
| 2. 6 vascular bundles entering floral axis | 10. 3 stigmas fertile |
| 3. 3 vascular bundles entering floral axis | 11. 2 stigmas fertile, and rostellum formed |
| 4. 2 vascular bundles entering floral axis | 12. Pollen grain simple |
| 5. Axile placentation | 13. Pollen grain compound |
| 6. Parietal placentation | 14. 3 fertile anthers |
| 7. Intermediate placentation | 15. 2 fertile anthers |
| 8. Embryo without a suspensor | 16. 1 fertile anther |

As was stated earlier, *Apostasioideae* is considered by most recent phylogeneticists to represent a distinct family and has consequently been removed to distant alliances, such as *Haemodorales* and *Liliales* by Hutchinson and Takhtajan respectively. It is obvious that if *Apostasioideae* is removed from the Orchid family, this procedure automatically demands also the separation of *Cypripedioideae*, as was suggested by Mansfeld, because of the absence of pollinia formation, different fertile staminal circles, etc. If *Apostasioideae* and *Cypripedioideae* are removed from this interrelated complex, the remaining groups, *Neottioideae*, *Ophrydoideae* and *Kerosphaeroidae*, would also require a new family status, because the equilibrium between these five groups is destroyed. On the other hand, the relationship between *Cypripedium* (*Cypripedioideae*) and *Cephalanthera* (*Neottioideae*) is so close that to regard them as members of distinct families would defy our whole evolutionary approach to systematics.

When we study the origin and phylogeny of the Orchid family devoid of paleobotanical documentation, our analysis is strictly limited to the uncovering of primitive features in living species. Since our approach is based *a priori* on such terms as genus and subfamily, these higher categories will aid our investigation only if they represent expanded dynamic units, although it is almost impossible to visualize the occurrence of such units in nature. The various evolutionary forces which have shaped and brought about the present-day orchids obviously did not act upon the family or even on a given genus, but rather on the species, because a species is the only tangible unit in nature with potentialities to mutate or evolve. Therefore, it would not be surprising if an absolute delimitation of a family becomes impossible.

The structure of an orchid flower is definitively a de-

rived one, and several attempts have been made by sundry workers to visualize its prototype as having three free segments in each of the five whorls. This arrangement by itself suggests but one course of evolution: progressive differentiation in a linear sequence. The evolutionary makeup of the Orchid family, on the contrary, is indicative of a rather complicated origin, because in certain species characters of a primitive and advanced nature occur simultaneously. A striking example is *Vanilla* (*Neottioideae*). The plant itself starts out as a terrestrial (primitive), but soon climbs up to the tree-tops where it leads an epiphytic mode of life (advanced); its ovary has a parietal placentation (advanced) yet the seeds possess a heavy sclerotic seed coat (primitive) and the embryo is sometimes known to develop an endosperm (primitive). *Vanilla* itself may be considered an advanced type with respect to other members of the *Neottioideae*.

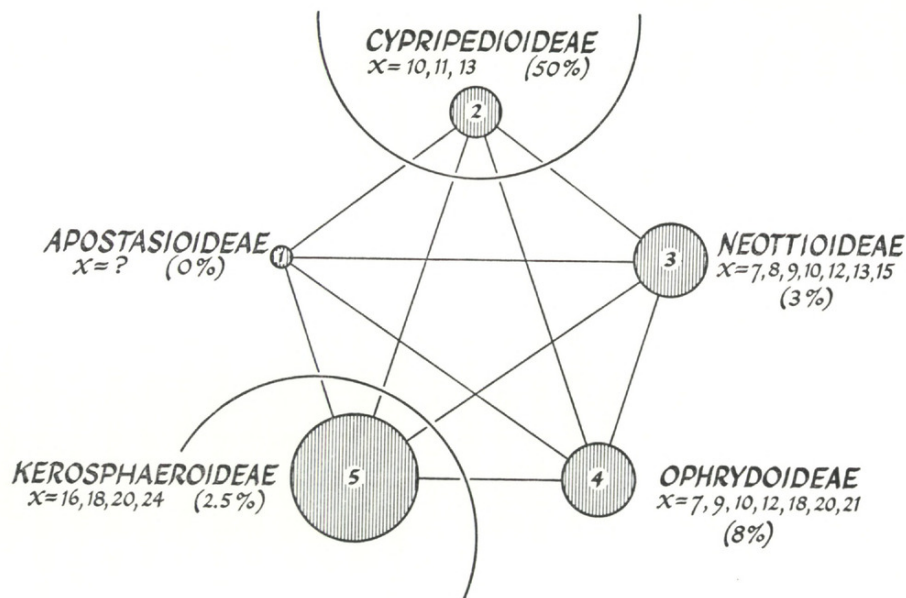
The association of primitive with advanced characters, which is to be found in each of the five groups, speaks rather clearly in favor of considering the Orchid family as one of those groups established relatively early during the evolution of the Angiosperms. Stebbins places its origin in the early Cretaceous Epoch and, on the basis of other evidence, I am inclined to agree with him. My studies of distribution, for example, based on deductive reasoning, lead to the same conclusion. The presence of the phenomenon termed pseudocopulation, noted in the *Ophrydoideae* and *Neottioideae*, may be mentioned here as further supporting evidence of age. If the Orchid family has evolved relatively recently, as some scientists postulate, such a precarious adjustment between the flowering time and the emergence of the fertilizing agents, as we find in the case of pseudocopulation, could hardly have come about. Nevertheless, I consider that the Orchid family is still in a state of evolutionary flux, and am in-

clined to believe that it has also undergone a rather sudden expansion during post Pleistocene time.

The manner through which the five main groups acquired their characteristics is impossible to determine without fossil evidence. The presence of primitive and advanced characters in the same species may, however, be an indication of fusion of independent evolutionary trends which very probably date back to a remote past, since cytological investigations and genetical experiments have demonstrated an absolute incompatibility of the groups. Whether or not this statement can be upheld without alteration in the future is hard to predict, inasmuch as the presently available information is very meager and unsatisfactory. Unfortunately, with respect to experimental genetics, only successful crosses are reported, while those which failed to "take" are carefully guarded from public possession and scientific scrutiny.

On Plate XIV, I have shown the results of a few crosses between *Cypripedioideae* and *Kerosphaeroideae*. Also I have on file certain data about attempted crosses between *Disa uniflora* (*Neottioideae*) and members of other groups, but since I am unable to ascertain the source of this data, I have omitted them in the diagram. The fact that the pollen is apparently unable to induce even parthenogenesis in the reported crosses between *Cypripedioideae* and *Kerosphaeroideae* may be a further indication of a remote origin of the respective groups.

The cytological coverage of the family is exceedingly poor. The known percentage of the chromosome counts of the species in each group is shown on Plate XIV. *Cypripedioideae* has a 50% coverage, due to the extensive studies in the genus *Paphiopedilum* by Duncan. The next highest is *Ophrydoideae*, a group almost exclusively of temperate regions, with 8% coverage based for the most part on European and Japanese species. Informa-



- 2 x 5 *Paphiopedilum* x *Cattleya* — pollen dried, flower fresh
 2 x 5 *Paphiopedilum* x *Dendrobium* — pollen rotted stigma away
 5 x 2 *Epidendrum* x *Paphiopedilum* — column withered, pollen decayed
 2 x 5 *Paphiopedilum* x *Odontoglossum* — a few chaffy ovules

x = basic chromosome numbers
 (%) = percent of species counted

tion about *Neottioideae* and *Kerosphaeroideae* is virtually lacking.

The known basic chromosome numbers for genera within each group are also included on Plate XIV. Hoffman, Duncan and Blumenschein have given the basic number of the Orchid family as $x=20$, calculated on the occurrence of this number in the majority of species of horticultural importance (*Ophrydoideae* and *Kerosphaeroideae*). Such a conclusion is, however, unwarranted, because the best we can hope for, with our present knowledge, is to suggest only the basic number for each of the groups.

The presence of an uninterrupted aneuploid series from $n=10$ to $n=22$ in the *Neottioideae*, and extensive polyploidy in the *Ophrydoideae* and to a lesser extent in *Kerosphaeroideae*, as well as the occurrence of euploid polyembryony in various groups, indicate a great genetic complexity in the family and, if this be fully exploited through further investigation and experimentation, it will contribute materially to our understanding of the origin and phylogeny of the *Orchidaceae* and probably go far towards full clarification of the many attendant problems.

CONCLUSION

The picture of the *Orchidaceae* which I have tried to present clearly demonstrates the great complexity of this family. The various degrees of specialization observable within each of the five groups make it rather difficult to trace the possible course of evolution. In the whole orchidaceous complex, *Neuwiedia* is, perhaps, the most primitive member, but even this taxon has to be considered as derived from more than one ancestor. In many respects, *Neuwiedia* is closely allied to the *Hypoxidaceae* and *Burmanniaceae*, with both of which it shares a pos-

sible origin, on the one hand with *Curculigo* and *Hypoxis*, and on the other with the leafy species of *Burmannia* (e.g. *B. longifolia*). *Apostasia* is hardly to be considered as a descendant of *Neuwiedia*, since its floral aspects and other morphological characters suggest rather a parallel course of development for both taxa. *Curculigo* and *Hypoxis* both have globular seeds with a sclerotic seed coat, as does *Apostasia*; *Neuwiedia* is characterized by an advanced type of seed with a loose testa. In addition to this characteristic, the non-saprophytic members of the *Burmanniaceae* show other primitive characters, such as axile placentation, monocolpate microspores, etc., which are also present in the *Apostasioideae*, *Cypripedioideae* and, to some degree, in the *Neottioideae*.

The presence of connecting trends between the *Orchidaceae* and its allies indicates that the family has been derived from other similarly complex groups and not, as often proposed, from any given family.

It is safe to assume that the Orchid family originated somewhere in the Asiatic tropics, possibly in Malaysia, because those species which possess primitive characteristics, and also the allied families, are native to that area.

The prototype of orchids, as Rolfe aptly wrote, may be visualized as ‘terrestrial monocotyledons, with an inferior ovary, numerous minute seeds having a reticulate seed coat and rudimentary embryo; the stamens and pistils are not yet aggregated into a column. The flowers were doubtless fertilized by insects, which on visiting the former, would become dusted with the pollen grains from the anthers as in the case of other entomophilous monocotyledons. We may also infer that the ancestral orchids were natives of great tropical region. The characters mentioned are found in the Malayan genus *Neuwiedia*, the most primitive of the existing orchids. The species of *Neuwiedia* have short, erect stems with a tuft of plicate,

Curculigo-like leaves and an erect spike of yellow flowers with nearly regular, connivent perianth, and three linear or oblong anthers borne on one side of the flower, free pollen grains and a slender nearly free style.”

APPENDIX

The following descriptions of the five subfamilies mentioned in the text are herewith presented, according to the requirements set forth by the rules of the International Code of Botanical Nomenclature. The accompanying plates illustrate representatives of these groups.

Subfamilia **Apostasioideae** *Garay subfam. nov.*

(Plate XV). Flores zygomorphi; perianthii partes consimiles; filamenta antherarum stylo sive pro parte sive fere omnino connata, ergo columnam brevem formantia; antherae 2 vel 3, erectae, basi- vel dorsofixae interdum versatiles; pollen siccum granulosum; microsporaе semper monocolpatae numquam in pollinium aggregatae; stigmata 3.

TYPUS: *Apostasia odorata* Bl.

Subfamilia **Cypripedioideae** *Garay subfam. nov.*

(Plate XVI). Flores zygomorphi; perianthii partes dissimiles; antherae stylo omnino adnatae, semper 2, tertia ex circulo exteriori staminodium formans; pollen viscosum, granulosum; microsporaе semper monocolpatae, numquam, in pollinium aggregatae; stigmata 3.

TYPUS: *Cypripedium Calceolus* L.

Subfamilia **Neottioideae** *Garay subfam. nov.*

(Plate XVII). Flores zygomorphi; perianthii partes dissimiles (raro in *Thelymitra* fere consimiles); columna saepe abbreviata; anthera erecta, semper singula, basi- vel dorsofixa, interdum versatilis; microsporaе sive mono-

colpatae vel ulceratae vel poratae sive tetradae in pollinia farinosa aggregatae; stigmata 2 vel 3, separata vel confluentia, tertium rostellum formans.

TYPUS: *Ophrys Nidus-avis* L.

Subfamilia **Ophrydoideae** *Garay subfam. nov.*

(Plate XVIII). Flores zygomorphi; perianthii partes dissimiles; columna saepe parva, cylindrica; antherae vulgo singulae, raro duae, thecis parallelis; microsporaе tetradae semper in pollinia grosse granulosa aggregatae; stigmata 2 vel 3, semper confluentia, tertium saepe oblitteratum, nunquam rostellum formans.

TYPUS: *Orchis morio* L.

Subfamilia **Kerosphaeroideae** *Garay subfam. nov.*

(Plate XIX). Flores zygomorphi; perianthii partes dissimiles; columna valde evoluta; anthera incumbens vel dorsaliter reclinata, singula; microsporaе tetradae in pollinia valde compacta aggregatae; stigmata 2, confluentia, tertium semper in rostellum modificatum.

TYPUS: *Epidendrum ciliare* L.

ACKNOWLEDGMENT

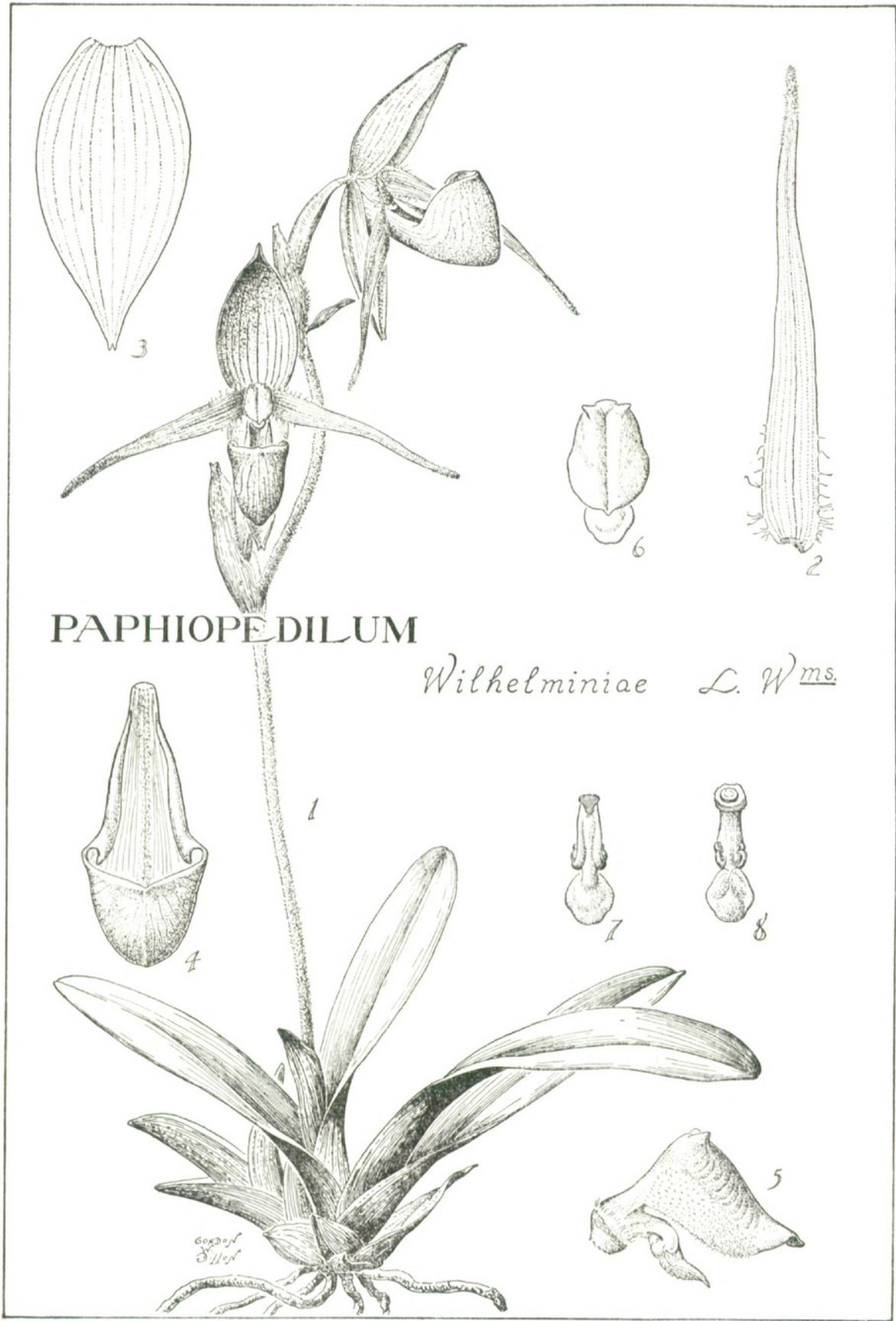
Part of the research upon which this paper is based was made possible through a grant from the National Science Foundation which is gratefully acknowledged.



APOSTASIA
nuda

R. Br. ex Wallich

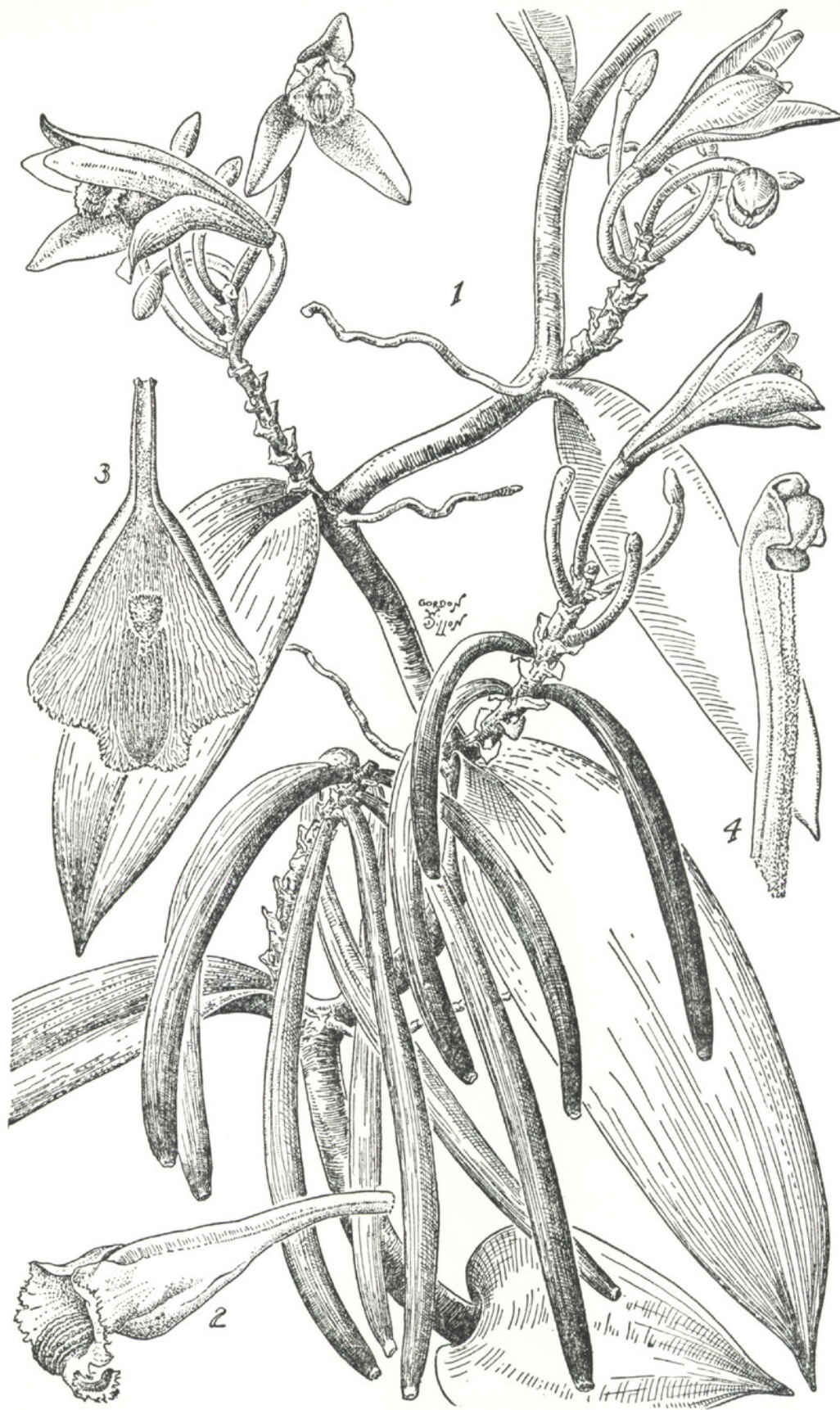
APOSTASIOIDEAE



PAPHIOPEDILUM

Wilhelminiae L. W^{ms.}

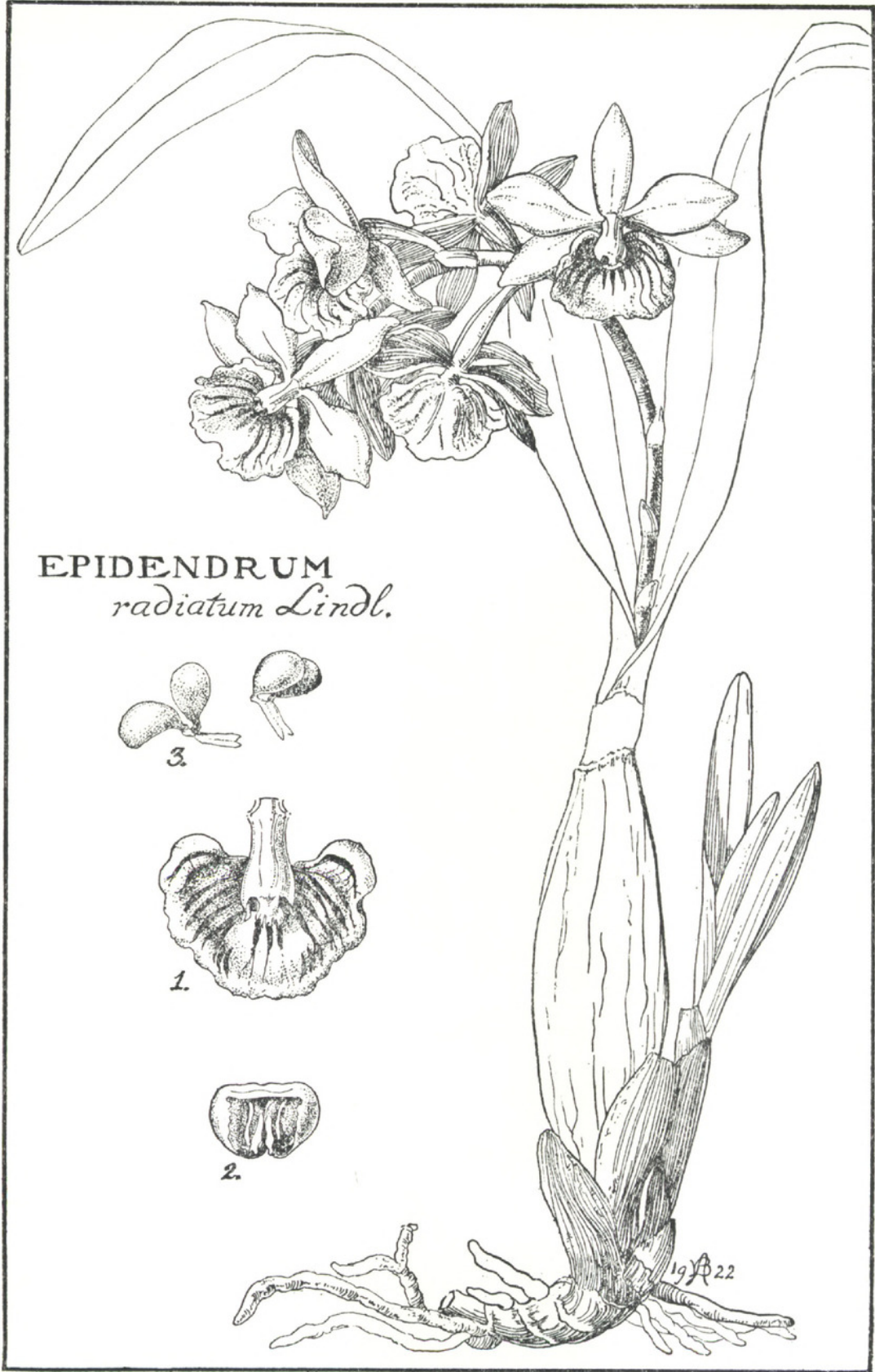
CYPRIPEDIOIDEAE



Vanilla planifolia Andr.
NEOTTIOIDEAE



Habenaria distans Griseb.
OPHRYDOIDEAE



EPIDENDRUM
radiatum Lindl.

KEROSPHAEROIDEAE

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ILLUSTRATION CREDITS

All plates and figures were drawn by Mr. Elmer W. Smith.

Plates VIII, XI, XIII, XIV, originals.

Plate IX, fig. 1, fig. 6, after Bauer & Lindley, Illustrations of Orchidaceous Plants.

fig. 2, fig. 3, after Pfitzer, Orchidaceae-Pleonandrae.

fig. 4, original.

fig. 5, after Müller and Kränzlin, Abbildungen der in Deutschland und den angrenzenden Gebieten vorkommenden Grundformen der Orchideen.

Plate X after Swamy, Embryological Studies in the Orchidaceae II.

Plate XII: *Apostasia papuana* after Smith, Nova Guinea XII, Orchidaceae.

Cranichis crumenifera and *Vanilla anomala*, originals.

Cephalanthera alba after Bauer and Lindley l.c.

Corycium crispum and *Satyrium saxicolum* after Vogel, Organographie d. Blüten Kapländischer Ophrydeen.

Vanilla Griffithii var. *formosana* after Ito, Icon. Jap. 1: t. 1, 1911.

Cypripedium Calceolus after Hegi, Ill. Fl. Mitteleuropas.



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