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THE PLACE OF *EPIPOGIUM* IN THE SYSTEM OF *ORCHIDALES*

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ABSTRACT

The stamen (A_1) of *Epipogium* has a discrete filament and there is no broad in sertion of the large anther. In the anther the pollinia and the caudicles develop differently from those of the *Orchioideae* in a way characteristic of the genus.

The rostellum consists of a simple gland crowning the top of the median stigmatic lobe. This gland lies on top (is acrotonic) of the pollinia (and not basitonic). The common characteristics make it clear that the genus *Epipogium* should be referred to the contribe of the *Neottianthae* (subfamilia *Epidendroideae*).

1. THE SYSTEM OF ORCHIDALES

Before assigning *Epipogium* a place in the system of orchidaceous plants, one has to choose the system one prefers to follow. My personal opinion being at variance with that of other modern taxonomists (MANSFELD, DRESSLER & DODSON, GARAY and MELCHIOR), it seems best to outline here the system I prefer.

Ordo: *ORCHIDALES*, flowers zygomorphic, usually resupinate, epigynous, a gynostemium with only the abaxial stamens present ($A_1 + a_1 + a_2$) and these fertile or partly staminodial. Seeds dust-fine (usually) and after germination mycotrophic. (Fig. 1)

Familia 1. *Apostasiaceae* Lindl.: perianth nearly regular, gynostemium short with A_1 fertile or staminodial, $a_1 + a_2$ fertile, style and stamens partly free, anthers oblong; pollen powdery. No rostellum. Stigma terminal.

Familia 2. *Cypripediaceae* Lindl.: median petal (lip) forming the labellum slipper-like; gynostemium longer and bent with A_1 represented by a staminod, $a_1 + a_2$ fertile, anther orbicular to oblong; pollen sticky, no pollinia. No rostellum. Stigma terminal and deflexed into the slippershaped petal.

Familia 3. *Orchidaceae* Lindl.: median petal forming a labellum, gynostemium straight or reflexed with anther terminal; A_1 fertile, $a_1 + a_2$ staminodial or missing, pollen in pollinia. Rostellum present. Stigma frontal, adaxial.

Subfamilia I. Orchi(d)oideae (Dressl. & Dods.) Vermln. Anther broadly inserted, caudicles at the base of the pollinia, their attachment basitonic to the rostellum; pollinia in massulae; rostellum

in principle with two terminal retinacula (rarely intergrown); no staminodia. Tribes including, e.g., *Orchideae* (*Ophrydeae*).

Subfamilia II. Epidendroideae Vermln. Anther fixed with a filament or attached by one point, rarely broadly inserted; caudicles sometimes present, pollinia rarely built up from massulae; pollinia mesotonically or acrotonically attached to the rostellum; rostellum in principle a single organ or rarely with two secondary developed retinacula; sometimes staminodia.

Contribus A. *Neottianthae* Vermln.: Pollinia composed of tetrads, mesotonic or acrotonic; anther deciduous or persistent, rostellum single, stipe very rare. Tribes including, e.g., *Neottieae.*

Contribus B. *Epidendranthae* Vermln.: Pollinia waxy or cartilaginous; acrotonic; anther usually deciduous; rostellum single (or rarely with two retinacula); in several groups with stipe. Tribes including, e.g., *Epidendreae.*

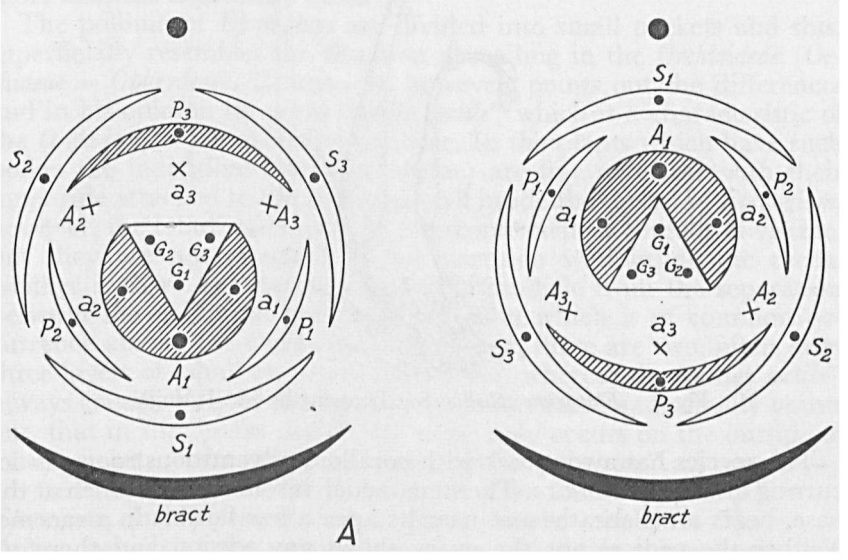

Fig. 1. Two diagrams of the flower of the *Orchidales*. A: not resupinated; B: resupinated. S_1, S_2, S_3: sepals; P_1, P_2: lateral petals; P_3: median petal or lip; A_1, A_2, A_3: stamens of the outer whorl of which A_1 is fertile or staminodial and A_2 and A_3 are always missing; a_1, a_2, a_3: stamens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

2. Epipogium aphyllum Sw. (*E. gmelinii* Rich.)

The genus *Epipogium* R. Br. consists of species without chlorophyll; they are yellowish to pale-pink suffused with purple and heterotrophic. The plants are parasites on their root fungus like *Neottia*, *Gastrodia*, etc. They are parasites having a fungus as their host and usually such plants are erroneously referred to as "saprophytes" in the literature.

The best-known species of this genus is *E. aphyllum* Sw., fig. 2, which is a rare plant in Central and Northern Europe and temperate Asia growing in shady forests. Like other species lacking chlorophyll it occurs in fluctuating numbers; although always remaining rare, in some years it occurs in rather large numbers in its localities, whereas in other years only some scattered individuals are found or none at all.

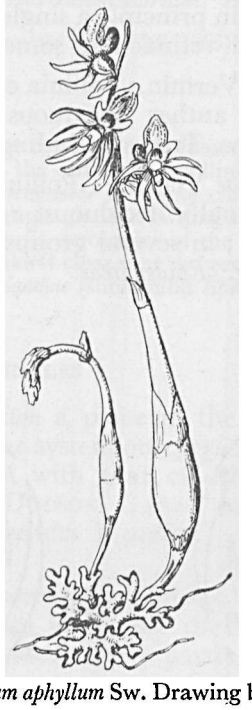

Fig. 2. *Epipogium aphyllum* Sw. Drawing by Mr. J. Vuijk.

The species has a rootstock with coralloid adventitious roots, as occurring also in *Corallorhiza*. The stem, which is sometimes swollen at the base, bears some sheaths and near its apex a few flowers in a raceme. Neither the pedicel nor the ovary shows any torsion and therefore the flowers are not resupinated and have the lip pointing upwards. The lamina of the lip is reflexed and that is the reason why this part touches the spur. The rather long gynostemium is directed downwards; the stamen A_1 is in the young flower straight on the column, but later it bends forward, so that its top comes near the viscid disk. Above this anther lies the pollinium bed, the so-called androclinium or clinandrium. Because the margins of the anther curl up, the pollinia in normal cases are pressed upwards in the androclinium.

3. The Work of Irmisch and Rohrbach

Two detailed studies are devoted to *Epipogium aphyllum*. The eminent German morphologist Thilo Irmisch was the first to describe the

plant accurately in his "Beiträge zur Biologie und Morphologie der Orchideen" (1853), the underground parts as well as stem and flowers. In 1866 (after the appearance of Darwin's book on the fertilisation of orchids) a study by PAUL ROHRBACH was published as a "gekrönte Preisschrift" of the University of Göttingen under the title "Über den Blüthenbau und die Befruchtung von *Epipogium gmelini*", which gives an extension to the work of IRMISCH.

On account of his observations ROHRBACH draws the conclusion that *Epipogium* must be classified among the *Neottieae* in spite of the fact that the stamen, which bends forward, provides a characteristic agreeing with *Arethuseae* (anther terminal, opercular) rather then *Neottieae*, to which the systematists before him referred the plant. Only REICHENBACH FIL., in his "De Pollinis Orchidearum" (1852) on p. 27 (note), came to the same conclusion as ROHRBACH. The anther lies prone and is attached in a single point at the top of the gynostemium it is true, but it does not fall off and is not opercular (even a short filament is present, VERM.).

The pollinia of *Epipogium* are divided into small packets and this, superficially resembles the situation prevailing in the *Orchioideae* (*Orchideae* = *Ophrydeae*). ROHRBACH, however, points out the differences and in his opinion the term "*pollen sectile*" which is a characteristic of the *Orchideae*, is erroneously used here. In the plants which have such pollen the individual lobuli (massulae) are free and only with their inner side attached to the partition wall inside the theca. In *Epipogium*, however, the lobuli are mutually interconnected by threads of viscine, but they are not attached to the partition wall inside the theca. Neither is there any development of a caudicle from the separation between the pollinium halves, a condition which is of common occurrence among the *Orchideae*. In *Epipogium* there are two, often even three layers of lobuli on top of each other, whereas the "*pollen sectile*" always consists only of one layer of massulae. ROHRBACH finally points out, that in the "*pollen sectile*" the exine only occurs on the outside of every packet, whereas in plants with "*pollen pulvereum*" all tetrads are covered with exine. This situation is also found in the pollen of *Epipogium*. In *Epipogium* the caudicles consist wholly of threads of viscine, which at the same time bring about the contact with the lobuli. In the *Orchideae* a caudicle develops from the partition between the two locules of each theca (from the tapetum or sometimes from the pollen itself).

IRMISCH gives a clear description of the origin of the viscid disk (p. 53), which can be translated as follows: "Initially the stylus is formed a little later than the anther; in young buds it is clearly compounded of three parts, viz., one broad part situated near the front of the anther and two small foremost parts. The single larger part grows more quickly and forms the front margin of the androclinium (pollen bed). In the middle of the margin we notice fairly soon the origin of the elegant cordate viscid disk. The two remaining parts soon fuse with the single part. Where the fusion takes place, the papillous stigma develops on the surface of all three parts. In the middle of the stigma

grooves can be recognized as traces of the original structure. This papillate stigma covering is originally separated from the smooth parts of the stylus by certain lines. Soon, however, that layer disintegrates into a homogeneous viscid matter and the surface of the stigma is completely smoothed out to form a narrow, triangular and slightly slanting flat area.

Summarizing we can state that:

1. The pollinia of *Epipogium* have a completely different structure from those of the *Orchioideae* (*Orchideae*) and that also the caudicles are different.

2. The rostellum is a simple organ, which develops as a part of the third, median stigmatic lobe.

By systematists after LINDLEY, *Epipogium* was classified among the *Neottieae* or *Polychondriae*, e.g., by REICHENBACH, BENTHAM, PFITZER, SCHLECHTER, MANSFELD.

4. THE VIEWS OF LATER WORKERS

In the article by DRESSLER and DODSON "Classification in Orchidaceae" (1960) the subtribe of the *Epipogiinae* Schltr. is referred to the tribe of the *Orchideae* (*Ophrydeae*) with the argument: "but the persistent anther and the sectile pollinia with basal caudicles indicate a much closer affinity with the Orchideae" (p. 35).

This view appears to be incorrect to me. To make this clear it will be necessary to oppose the differences between *Neottieae* and the *Orchideae* (*Ophrydeae*) once more (see also VERMEULEN, 1959).

The most striking difference between the two groups is the attachment of the stamen. In the *Orchioideae*, tribe *Orchideae*, as in the other tribes, the stamen is broadly inserted or connected with the gynostemium, the stamen forming as it were its continuation and there is no trace of a filament. Although in the *Epidendroideae* (the *Operculatae* in the sense of REICHENBACH FIL., i.e., all *Monandrae* not included in the *Orchioideae*), a filament can usually be distinguished, it is sometimes, as in *Spiranthes*, very short, whilst in other cases the anther is only attached in one point, so that frequently the anther is early deciduous, apart from being operculate. In the *Epipogiinae* there is no doubt that the anther belongs to the type of the *Epidendroideae*: the anther is attached with a short but manifest filament.

A persistent anther is characteristic of the *Orchideae* it is true, but also in the *Neottieae* there are several genera with persistent anthers, such as *Listera*, *Diuris* etc.

The attachment of the pollinia to the rostellum is also connected with the difference in the attachment of the stamen. In the *Orchioideae* the pollinia are invariably connected basitonically (towards the base) with the rostellum, by means of short or long caudicles, which means that the rostellum is aligned with the caudiculae. In the *Epidendroideae*

this is, generally speaking, not the case, but instead mesotony (pleurotony) prevails, the viscid disk becoming fastened in the middle of the pollinium, as in some *Neottieae*, or (more often) acrotony, the rostellum becoming situated at the apex of the pollinium. DRESSLER & DODSON say (p. 58): "The distinction which has been drawn between "Acrotonae" and "Basitonae" is thus an artificial one", after they have remarked: "Distinct caudicles are not formed in the Neottieae. In the Spiranthinae and some other subtribes the viscid disk is attached to the apices of the pollinia, but in the Australian Neottieae one finds a complete series from basal attachment through ventral to terminal attachment like that of the Spiranthinae." However, basitony is only exceptionally found in the *Neottieae*, this in contrast to the group of the *Orchioideae* (*Ophrydeae*), which are always basitonic. In conjunction with the characteristic of the broad insertion of the stamen, the basitony of the caudicles of the pollinia forms a clear characterisation of the group of the *Orchioideae*.

5. PERSONAL INVESTIGATION OF THE STRUCTURE OF THE STAMEN

As material I had at my disposal young flower buds, collected by Mr. WILHELM FREIBERG (Munich) in Die Baar in Southern Germany in 1964. I am much obliged to Mr. FREIBERG for his kind co-operation.

From the longitudinal section (Fig. 3) made through the middle of the stamen, it appears that a discrete filament is present bearing the

Fig. 5. Pollinia, caudiculae and retinaculum of *Epipogium aphyllum* Sw. on a needle.

anther on top. This anther is relatively large and apart from the two ventral thecae, it consists of a rather voluminous dorsal part. In figure 3 A the viscid disk can be seen lying on the top of the median stigmatic lobe. In the young bud that has been cut here, the viscid disk does not quite reach as far as the top of the anther. In the other section shown (fig. 3 B) only a small part of the viscid disk can be seen: this section goes through the median plane of a theca. Here we see as a continuation of the vascular cord a strand, a "caudicle", beginning at the top of the anther and running along the adaxial, ventral side of the pollinium, without forming a part of that pollinium (fig. 5). The viscid disk here quite clearly lies at the top of the pollinia, in other words, it is acrotonic. The anther has a very remarkable structure, which so far I have not found in any other anther. In the *Orchidales* an anther normally has a solitary median vascular cord, even if both thecae are far apart as in *Satyrium* and *Disperis*. In *Epipogium*, however, this small vascular cord is split into three parts, so that exceptionally

three vascular cords can be distinguished (fig. 4). The lateral ones recline on top of the anther and pass into the caudicles, which are present in the form of two discrete strands. They are in a ventral position in respect of the pollinia. When the viscid disk of an open flower sticks to the top of the caudicles, they are pulled out of the tissue. It appears that they are attached to the base of the pollinia, more or less as in *Epidendrum* ("caudiculis totidem replicatis") (fig. 5). ROHRBACH stated that these caudicles consist of threads of viscine, with which they are also attached to the various pollen packets (lobuli) of the pollinia. It is also remarkable that the partition wall between the pollinia is not quite continuous but is only present in the lower half of the theca. The anther indeed shows many particularities.

Characteristic features are: (1) the presence of a discrete filament (there is no broad insertion of the stamen), (2) the formation of two caudicles in a very special way (they are analogous with the caudicles of the *Orchioideae*, (not their homologues!), and (3) the presence of a single viscid disk distally inserted on the pollinia (i.e., acrotonic). The viscid disk can be clearly distinguished as a simple organ on top of the median stigmatic lobe.

6. THE ROSTELLUM: DISCUSSION

From the quotation of the work of IRMISCH it is clear that the rostellum in *Epipogium* originates as a part of the third stigmatic lobe. It is a simple, somewhat cordate disk. We generally find the rostellum in the form of a simple organ in the *Epidendroideae*, very often as a part of the median stigmatic lobe, sometimes without any remains of this lobe. Consequently, in both cases we may consider the rostellum to represent a differentiation of this stigmatic lobe, i.e., a formation *de novo*. Among other things, the situation in *Epipactis*, as IRMISCH describes it, pleads for this assumption; see: Linnaea 16 (1842) p. 458. He says that in the ordinary orchid flower the style is formed out of three leaves. "For very often in *Epipactis* we find in the corresponding places three rostella, even though the middle one is consistently better developed, and they can not be anything else but the weakened tops of the carpels".

This is reminiscent of the situation in *Epipactis gigantea* I described in my previous article (1959, p. 351), in which the lateral stigmatic lobes form no rostellum it is true, but at least protruding lumps with mucus secretion. In *Epipactis* the median stigmatic lobe is still developed as a stigma and capable of holding pollen. As appears from the figures, *Epipogium* corresponds with *Epipactis*, and also in this respect the genus belongs to *Epidendroideae*.

In the *Orchioideae* (*Orchideae*) the rostellum is of an altogether different structure. In principle we always find two viscidia here and it is only in exceptional, derived conditons that but one viscid disk is present, as in *Anacamptis*, *Holothrix*, *Herschelia* etc. In the *Orchioideae* the retinacula are connected by a strip of tissue, a tape. In the genus *Platanthera*, presenting one of the most primitive conditions, this tape

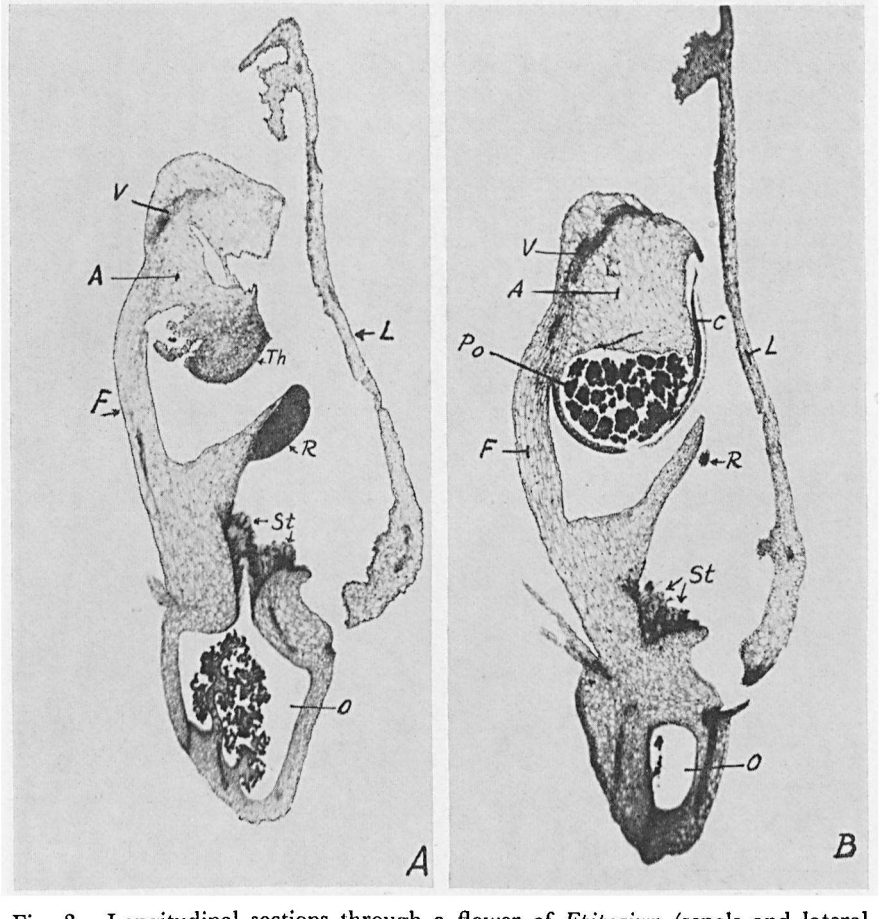

Fig. 3. Longitudinal sections through a flower of *Epipogium* (sepals and lateral petals are removed). A: through the middle of the ovarium, the style canal and of the anther. Th is the outside of a theca; B: through the middle of a theca in which the pollinium is cut. O: ovarium; St: stigma; R: rostellum; L: lip; F: filament; A: anther; V: vascular cord; Th: theca; c: caudicula.

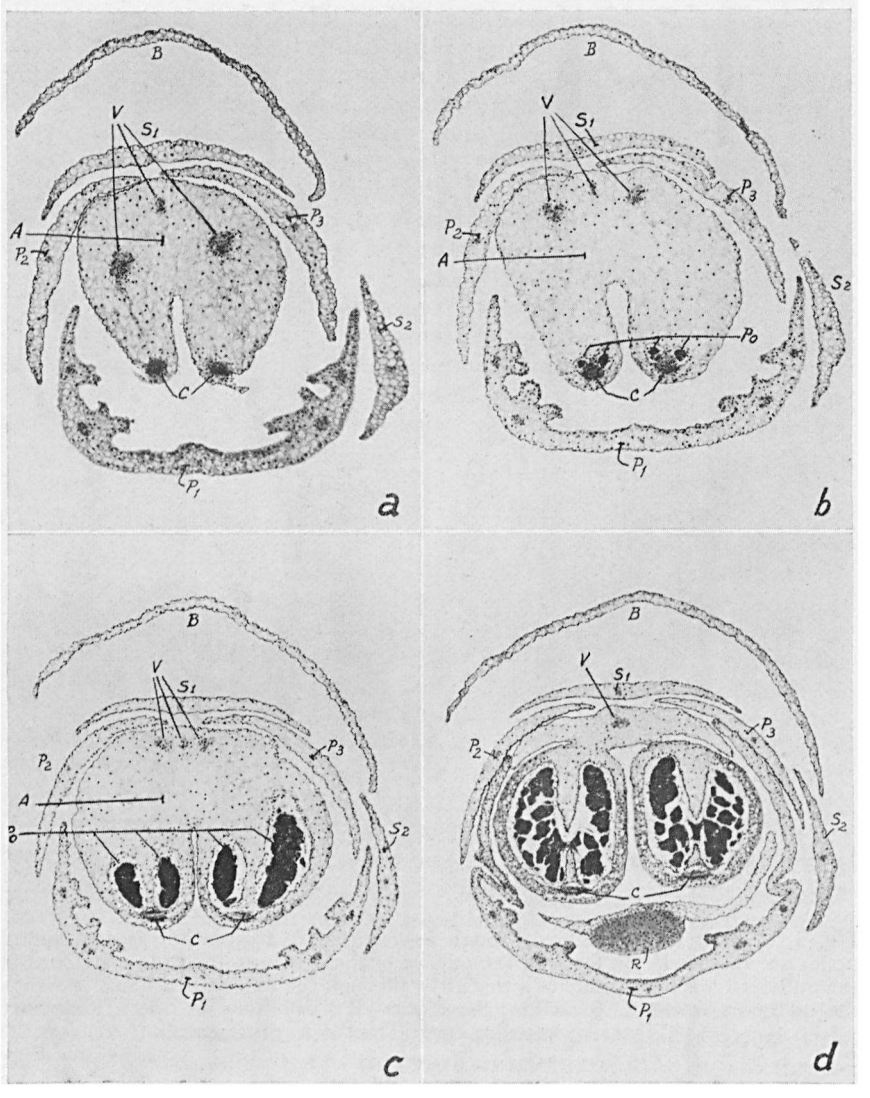

Fig. 4. Cross sections through the anther of *Epipogium*. a: through the top; b, c and d: in each case a lower section. B: bract; S_1, S_2: sepals (S_3 is missing); P_2, P_3: lateral petals; P_1: lip; V: vascular cords; c: caudiculae; R: rostellum; P_0(♀): pollinia.

forms a strip, running from the left viscid disk to the right one above the third stigmatic lobe (see VERMEULEN, 1959. p. 344, plate II, fig.5 c). In one group of genera (*Orchis*, *Dactylorchis*) both glands approach each other, because the communicating tape bends double; in the other group this tape shows vigorous growth and develops into a voluminous organ, as occurs in *Bonatea*, *Habenaria* and related genera (VERMEULEN, p. 347). In this group the development of the tape keeps abreast of that of both stigmas. These stigmas are manifestly prolonged, which is also the case with both rostellum arms. Both viscid disks situated at the end of these arms, now approach the stigmas, which in their turn, develop at the end of the stigmaphores (fig. 6).

In their criticism of my view, DRESSLER & DODSON (p. 56) assume

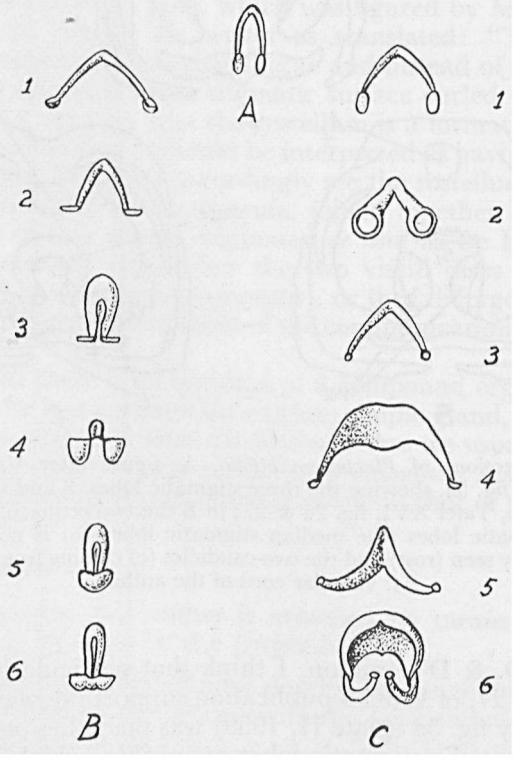

Fig. 6. Two series of rostella in the *Orchioideae*. A is the basic form lying in a horizontal level; series B is more and more vertical; series C is much more horizontal. A: *Platanthera bifolia* (L.) Rich.; B 1: *Coeloglossum viride* (L.) Hartm.; B 2: *Limnorchis dilatata* (Pursh) Rydb.; B 3: *Gymnadenia conopsea* (L.) R. Br.; B 4: *Ophrys insectifera* L., each retinaculum in a pouch (bursicula); B 5: *Dactylorchis majalis* (Rchb.) Verm., both retinacula in one pouch; B 6: *Anacamptis pyramidalis* (L.) Rich., two retinacula intergrown and in one bursicula; C 1: *Platanthera chlorantha* (Custor) Rchb.; C 2: *Limnorchis sparsiflora* (S. Wats.) Rydb.; C 3: *Blephariglottis ciliaris* (L.) Rydb., the two arms loose, not connected with the stigma; C 4: *Platanthera susannae* (L.) Lndl., id; C 5: *Habenaria macroceratitis* Willd., the long arms of the rostellum come near the tops of the stigmaphores; C 6: *Bonatea speciosa* Willd. id. N.B. In *Platanthera* the stigmatic lobes form a whole, in *Habenaria* there are two lobes each on a stigmaphore.

that WOLF's work (1866) pleads against my observation that in the primitive genera of the *Orchioideae* the viscid disks are attached to the lateral stigma lobes. However, they give no arguments. This is why I have carefully reread WOLF's publication and studied his figures anew.

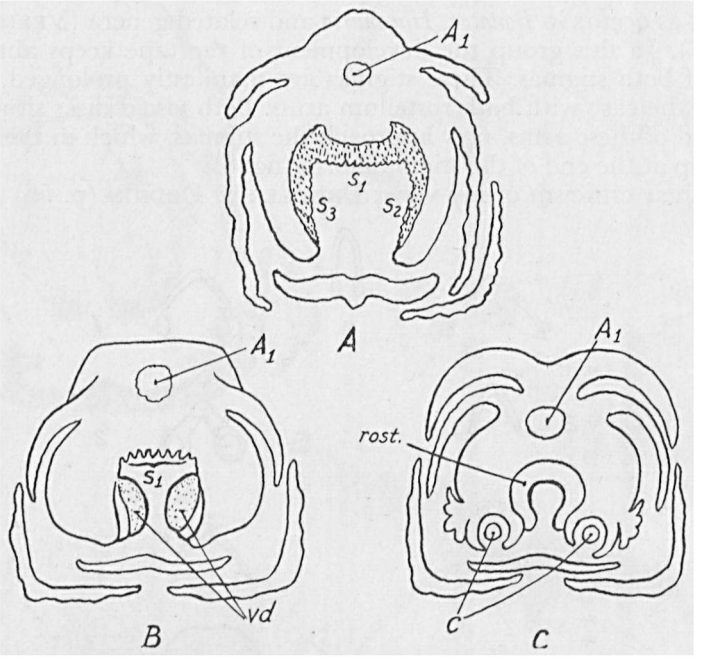

Fig. 7. Cross sections of *Platanthera bifolia*. A. figure after VERMEULEN, 1959, p. 344. Plate II, fig. 5a, showing the three stigmatic lobes. B and C drawings made after WOLF, 1866, Tafel XVI, fig. 26 & 27; in B the two retinacula (vd) are above the lateral stigmatic lobes (the median stigmatic lobe (S_1) is normal); in C the rostellum is partly seen (rost) and the two caudicles (c) coming from the viscid discs; A_1: vascular cord of the anther.

Contrary to D. & D's opinion, I think that particularly Table XVI, figures 26 and 27, of WOLF's publication support my view. The section from which my fig. 5a (plate II, 1959) was made lies on a lower level, however, so that the stigmatic lobes are visible, which is not the case in WOLF's work, (fig. 7). The median stigmatic lobe, however, is very distinct in his fig. 26.

When GARAY (1960) in his work (p. 75) says: "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 anther" we can object to this by pointing out, that in *Platanthera* the "connective" lies between the two retinacula in the continuation of the stigma, not between the thecae, and is even quite separate from the anther (VERMEULEN, plate II, fig. 5 c and WOLF, fig. 27). That this so-called

"connective" lies between the retinacula also follows from the fact that this "connective tape" bends double, when the retinacula, as is the case in *Orchis*, approach one another closely. There would not be any apparent reason for this, if it were merely a question of a tape between both thecae.

In most *Orchioideae-Orchideae* we no longer find vascular cords in the stigmatic lobes. Apparently they are organs which do not need a substantial amount of nutrients. This in contrast to the rostellum: the stronger the development, the more important the vascular cord, which always originates from the same strand, that also gives off abaxial branches to the median sepal and to the stamen (A_1).

Let me point out in this connection the description of a tetramerous flower of *Orchis palustris* Jacq. which was figured by MORITZ SEUBERT in Linnaea 16 (1842). He writes as translated: "The anther has basipetally somewhat diverging thecae and instead of a bursicle there is a petal-like appendix of the stigmatic surface curled upwards." This pleads both for my idea that the rostellum is a formation *de novo*, and for the assumption that it should be interpreted as having a connection with the stigma. We must accordingly see the rostellum in the *Orchioideae* as consisting of two retinacula, joined together by a tape. The development of this organ, originated *de novo* as we have seen, went into two directions, viz., either the two viscid disks approach each other (*Orchis*) or even fuse (*Anacamptis*), or they diverge further, which results in a stronger development of the communication tape (*Bonatea*); see fig. 6.

In *Epipogium* there is no question of a compound organ forming the rostellum. Here it is a somewhat cordate simple gland, forming a part of the median stigmatic lobe. In *Epidendroideae* we usually find such a rostellum, more particularly so in the *Neottianthae*. Also the structure of the rostellum of *Epipogium* corresponds with that of the *Neottianthae*.

7. CONCLUSIONS

1. In *Epipogium* the anther is attached by means of a filament, which is never the case in the *Orchioideae*.

2. In *Epipogium* the caudiculae develop in a very curious way; they are analogous—not homologous—with the caudicles of the *Orchioideae*.

3. In *Epipogium* the lobuli are attached in the thecae in a fashion different from the way in which the massulae are attached in the *Orchioideae*.

4. The lobuli correspond with the tetrads of the *Neottianthae* in being covered with exine. The lobuli are analogous with the massulae of the *Orchioideae*.

5. In *Epipogium* the viscid disk is simple and formed on top of the median stigmatic lobe, in contrast to the viscid disc in *Orchioideae* which is double.

6. The viscid disk lies at the top of the pollinia, acrotonically, but

because the long caudicles run ventrally along the pollinia to their bases and are attached there, the pollinia are seemingly secondarily basitonic as in *Epidendrum.*

7. In its characteristic features (apart from some specific particularities) *Epipogium* corresponds completely with the *Neottianthae* and it should, accordingly, be placed in the contribe of the *Neottianthae.*

Survey of the Characteristics

	Orchioideae *Orchideae* (= *Ophrydeae*)	*Epipogium*	Neottianthae *Neottieae* (*Neottieae* + *Arethuseae*)
Stamen	Broadly attached	Attached with short filament	Attached with filament or point.
Anther	upright or reflexed	upright or prone	upright or prone
Pollinia	divided into massulae connected to partition wall of the loculi (pollen sectile)	divided into lobuli connected by threads of viscine.	pollen in tetrads, not coherent in massulae (pollen pulvereum)
Pectine	only on the outside of the massulae	covering all loculi	covering all tetrads
Caudicles	formed out of the tapetum of the loculi in the theca or from pollen.	originated from threads of viscine, in the sterile tissue of the anther	usually no caudicles
Rostellum	usually consists of two viscid disks and a connecting fold or tape	a simple viscid disk without a fold.	a simple viscid disk or margin without a fold
Attachment of pollinia to the viscid disk	attachment always basitonic by means of caudicles on viscid disks at their base	viscid disk on top of the pollinia (acrotonic) the long caudicles run from that point to the base of the pollinia	pollinia usually without appendices, mesotonic or acrotonic

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