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THE DIFFERENT STRUCTURE OF THE ROSTELLUM IN OPHRYDEAE AND NEOTTIEAE

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The rostellum in orchids is the organ that forms the viscid liquid which makes it possible for the pollinia to stick to the bodies of visiting insects. The pollinia are then taken along and may be deposited wholly or partly on the stigma of another flower. The rostellum, however, does not occur in all orchids, viz. not in the *Cypripedioideae (Diandrae)*, which do not possess pollinia. It is present in practically all the *Orchioideae (Monandrae)*, on the other hand, but often has very different structures. In the group including *Ophrys*, *Platanthera*, *Habenaria* etc., it forms the viscid discs (viscidia), and in the other groups it usually consists of one single gland (viscidium), such as in *Goodyera*, *Spiranthes* and *Epidendrum*, whereas the simple gland, as we find it in *Vanda* and related genera, is moreover, characterized by a stipes, i.e. a tissue tape of the column formin ghe connection between the viscid disc and the pollinia.

§ 1. The division in the Orchioideae

When gradually a great number of orchids became known and when little by little, the pioneering work of Lindley (1853) made it possible to compile a survey of the *Orchidaceae* Reichenbach (1868) was the first to stress the differences between the *Ophrydeae* (Anthera cum columna connata) on the one hand, where the anther is intergrown with the column, and the *Operculatae* (Anthera demum a columna libera, secedens saltem) on the other hand, in which the anther is completely free or is fixed only at the base (1868 p. 293). Pfitzer (1889) distinguished the same two groups, be it under different names, viz. as *Basitonae* versus the *Acrotonae*, according to the place where the viscid liquid comes into contact with the pollinia. With the *Basitonae* (Fig. 1) the viscid liquid is at the base of the vertical or reclining anther, so that the pollinia contact the viscid liquid at their bases. In the great majority of the *Acrotonae* (Fig. 2), on the other hand, the anther is prone and on top of the column, and then the pollinia touch the rostellum with their top and they consequently stick with their top to the viscidia; sometimes there is a stipes between the viscid liquid and the pollinia. The *Basitonae* include only the tribus *Ophrydeae*, whereas the *Acrotonae* consist of the tribus *Neottieae*, *Epidendreae* and *Vandeae*, as they were distinguished by Bentham and Hooker (1883). Mansfeld (1954) made another division, viz. in the contribus *Thrauosphaereae* with loosely constructed pollinia, to which the *Ophrydeae*

and the *Neottieae* belong, and the contribus *Kerosphaereae* with the tribus *Epidendreae* and *Vandeae* with waxy or cartilaginous pollinia. It has been found that the *Neottieae*, which, according to PFITZER, belong to the *Acrotonae-Polychondreae* are not by far all of them acrotonic:

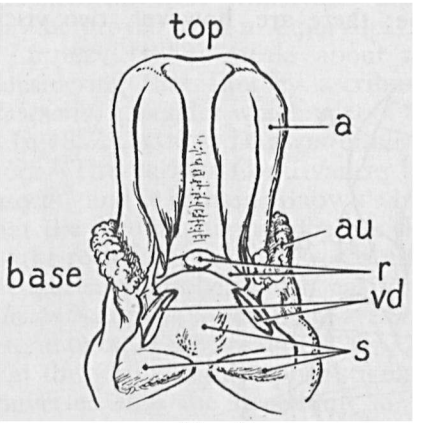

Fig. 1.

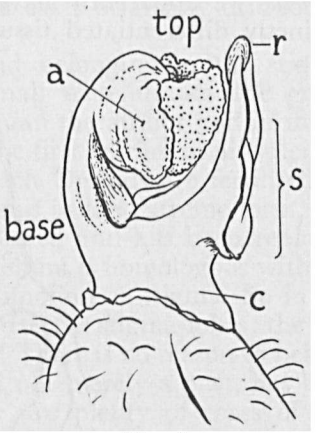

Fig. 2.

Fig. 1. Column of *Platanthera bifolia* (L.) Rich. as an example of a basitonic orchid: the bases of the pollinia are attached to the viscid discs of the rostellum; s: three stigma-lobes; vd: viscid discs; r: tape of the rostellum connecting the viscidia; au: auricle; a: theca of the anther.

Fig. 2. Column of *Goodyera repens* (L.) R. Br. as an example of an acrotonic orchid: the top of the pollinia is attached to the viscid disc(r) of the rostellum; c: column; s: stigma; a: anther; r: rostellum on the backside of which the pollinia are seen (dotted).

some genera, e.g. *Cephalanthera*, have vertical anthers, others are slightly prone, e.g. in the Australian genera *Leptoceras* and *Pterostylis;* in these cases the viscid liquid is deposited in the middle of the pollinia (pleurotonic). Mansfeld, consequently holds that the nature of the pollinia prevails over the attachment of the stamen and the clinging to the viscid discs, in my opinion unjustly, although it is true that in the *Neottieae* there exist all kinds of transitions between basitonic and acrotonic orchids.

§ 2. THE ROSTELLUM

The rostellum, as a technical term, was first introduced in orchidology by RICHARD (1818), who defined the term as follows: "Supernus stigmatis processus ultra gynizus (= areo stigmatis viscoso-madida) plerumque ad epicam angustatus . . ." Apparently this definition was inspired by the genus *Orchis* and related genera, where the rostellum is situated between the bases of the thecae (Fig, 3, r), so above the stigma, as a fold with at its base the bursicle, containing the viscidia. In cases where the rostellum does not consist of such a vertical part, it is sometimes hard to recognize. RICHARD states, that the genus *Platanthera* has no rostellum. Here it is difficult to observe it as a separate

organ, but it must be considered as the tissue tape above the stigma, which on either side ends in a viscid disc (plate II, 5 c). For according to the present conception the viscidia should be considered as parts of the rostellum. If RICHARD says that there is no rostellum in *Platanthera*, we apparently have to conclude from it, that there is no distinctly differentiated tissue tape; there are, however, two viscid discs.

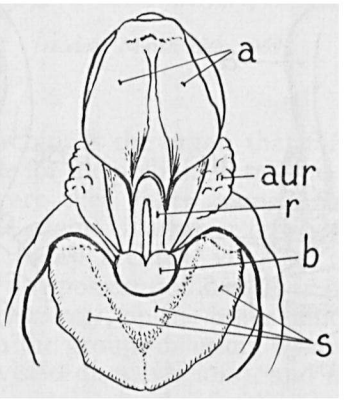

Fig. 3. Column of *Dactylorchis majalis* (Rchb.) Vermln. (= *Orchis latifolia* auct.); s: three stigma-lobes; b: bursicle containing the two viscid discs; r: tape of the rostellum connecting the viscid-discs; aur: auricle; a: two thecae of the anther.

Sometimes, such as in *Orchis*, *Dactylorchis* etc., the viscidia are moreover covered with a bursicle, an enveloping tissue; these bursicles too belong to the rostellum.

In *Epipactis*, *Goodyera* etc., as representatives of the *Neottieae*, the rostellum is much simpler and consists of one single gland centrally situated on top of the stigma. Sometimes this rostellum is a viscid disc, which sticks to visiting insects, sometimes the rostellum forms viscid liquid, which is pressed out on being touched and which ensures the attachment of the pollinia, as in *Listera* and *Neottia*.

§ 3. THE HOMOLOGY OF THE ROSTELLUM. ROBERT BROWN, DARWIN, EICHLER

The first author who occupied himself with the homology of the rostellum was ROBERT BROWN. He mentions the result of his research in 1833, as usual, in very prudently formulated terms. From this it appears that in the opinion of BROWN the viscid discs belong to the median stigma-lobe, though it is not definitely stated that they are homologous with it.

R. BROWN (1833 p. 699) said: "The result of my examination of this point satisfied me that *Orchidaceae* have in reality three stigmata, generally more or less confluent, but in some cases manifestly distinct, and two of which are in several instances even furnished with styles of considerable length" and (p. 701) "In most other cases (in which the lateral stamina are *not* perfect) the anterior lobe, or that placed

opposite to the perfect stamen, and deriving its vessels from the same cord, manifestly differs both in form and texture from the other two. To this anterior, or upper lobe, as it generally becomes in the expanded flower, the glands always belong to which the pollen masses become attached, but from which they are in all cases originally distinct, as may be proved even in Ophrydeae."

LINDLEY (1853) speaks about a gland belonging to the stigma. Considering that Lindley ascribes a small rostellum to the genus *Habenaria*, I wonder which part of this organ the author had in mind.

In 1882 CHARLES DARWIN published the first edition of his splendid work "The various Contrivances by which Orchids are fertilised by insects" and it contains BROWN's hypothesis in the extreme form, viz. that the median stigma-lobe has disappeared and has been replaced by the rostellum, in other words, the rostellum is homologous with the median stigma-lobe, which has lost its function as stigma. So in the *Monandrae* or *Orchioideae* there are only two fertile stigma-lobes: the two lateral ones. DARWIN said (1890 p. 248): "There is no reason to believe that the whole of this upper stigma, and not merely a part, has been converted into the rostellum; for there are plenty of cases of two stigmas, but not one of three stigmatic surfaces being present in those Orchids which have a rostellum." We find the same hypothesis in the Blütendiagramme by EICHLER, and owing to the work of those two brillant scientific workers this became the generally accepted conception of the rostellum, found in all textbooks (Fig. 4).

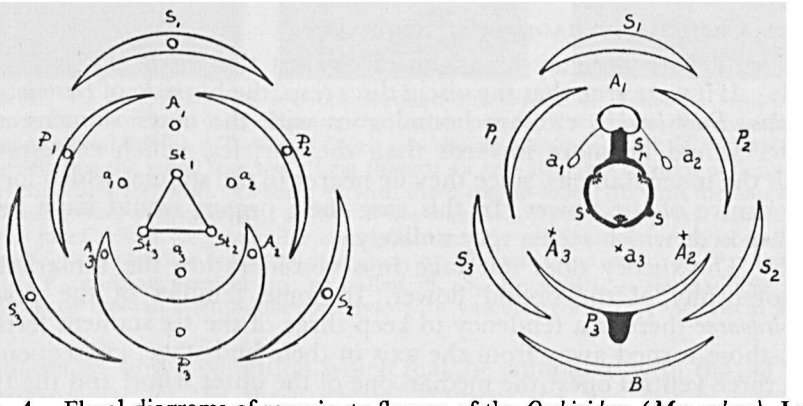

Fig. 4. Floral diagrams of resupinate flowers of the *Orchioideae (Monandrae)*. Left figure by Darwin as suggested by John Lindley; right one by Eichler as suggested by Robert Brown. B: bract; S_1, S_2, S_3: sepals; P_1, P_2: lateral petals; P_3: lip; A_1, A_2, A_3: stamens of the outer whorl; a_1, a_2, a_3: stamens of the inner whorl; s: lateral stigma-lobes; s_r: rostellum; st_1, st_2, st_3: stigma-lobes. In Darwins diagram the stamens A_2 and A_3 of the outer whorl form part of the lip; a_1 and a_2 are staminodes.

§ 4. THE HOMOLOGY OF THE ROSTELLUM ACCORDING TO HAGERUP

HAGERUP (1952, p. 134) posited a different theory; he started from the prototype of the Monocotyledon-flower, which possesses two whorls of three stamens: an outer whorl opposite the sepals and an inner whorl opposite the petals. Hagerup, who examined the flower of

Herminium monorchis (L.) R. Br., was of the opinion that the viscid discs were homologous with the lateral stamens of the outer whorl, while there was, moreover, a gland instead of the median stigma-lobe: so there would be "two different kinds of viscid organs". In *Dactylorchis maculata* (L.) Vermln (= *Orchis maculatus* L.) he considered the bursicle homologous with the two lateral outer stamens and the auricles with the two lateral inner stamens. HAGERUP is therefore trying to find an explanation for the two glands of the Ophrydeae. (Fig. 5).

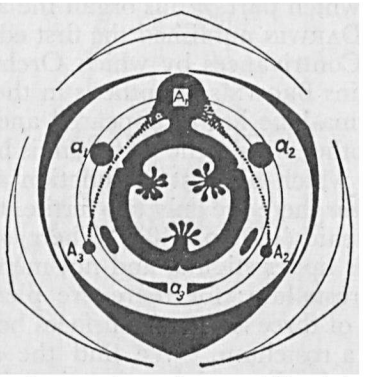

Fig. 5. Floral diagram of a resupinate flower of *Herminium* as suggested by Hagerup. A_2 and A_3 form the viscid discs; a_1 and a_2 are staminodes; A_1 is the fertile stamen.

§ 5. CRITICISM OF HAGERUP'S THEORY

Two arguments may be advanced against this theory:

1. If it were true that the viscid discs resp. the bursicle of *Herminium*, *Orchis*, *Dactylorchis*, etc. are homologous with the outer stamens, the latter would lie more inwards than the auricles, which correspond with the inner stamens, since they lie nearer to the stigma, which forms the centre of the flower. In this case these organs would have been transposed, which seems very unlikely.

2. The theory does not take into consideration the remarkable zygomorphy of the orchid flower. In some families of the *Monocotyledoneae* there is a tendency to keep three of the six stamens fertile, viz. those turned away from the axis in their bud-stage, consequently the three ventral ones: the median one of the outer whorl and the two lateral ones of the inner whorl; the three dorsal ones either become smaller or sterile or they disappear altogether. This tendency is apparent in the *Commelinaceae*, in the *Pontederiaceae*, in the *Apostasiaceae* and finally, in the most extreme form, in the *Orchidaceae*. The *Commelinaceae* show all the transitions between six fertile stamens and three dorsal sterile and three ventral fertile stamens. Some genera of the *Pontederiaceae* have three long and three shorter stamens as a result of their trimorphy, but there too, the dorsal ones are unlike the ventral ones. The *Apostasiaceae* have only the ventral stamens developed, the others have completely disappeared. This is seen best in *Nieuwedia* (plate I, 1a & 1b), where all three ventral stamens are fertile. In the genus

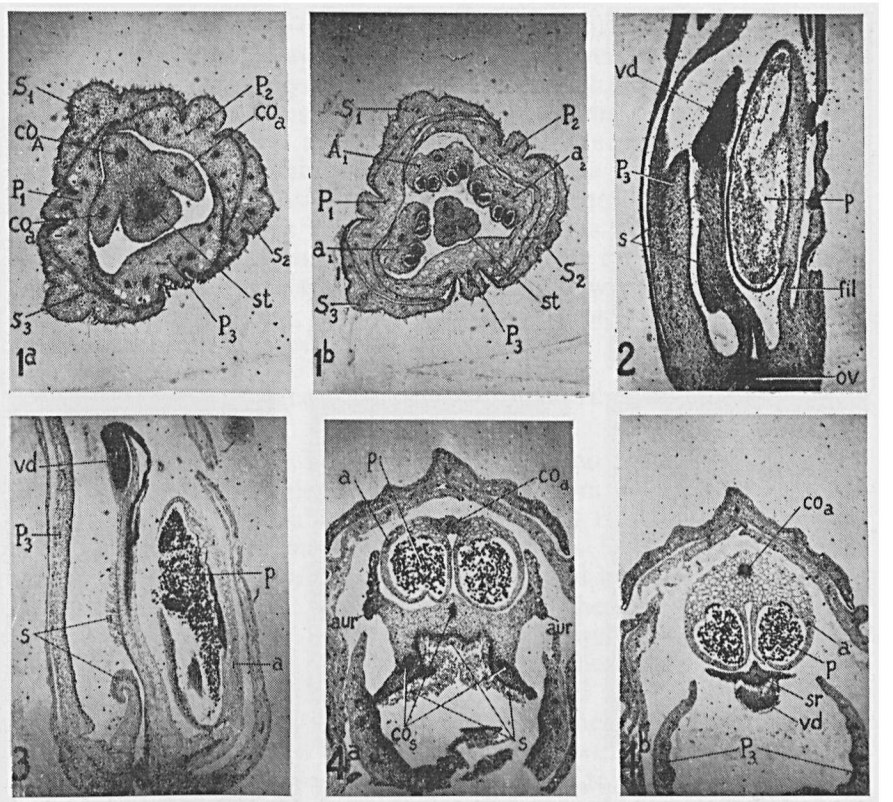

Plate I. 1a and 1b: Cross sections through the flower of *Neuwiedia veratrifolia* Blume; 1a: lower one with column; 1b: higher one with style and three anthers; 2: longitudinal section of flower of *Diuris semilunulata* Messmer; 3: id. of *Prasophyllum elatum* R. Br., the viscid disc has a long thread; 4a and 4b: cross sections of flower of *Epipactis helleborine* (Mill.) Crantz; 4a with three stigma-lobes; 4b with median lobe and viscid disc. a: anther; A_1: anther of the outer whorl; a_1 and a_2: lateral anthers of the inner whorl; co_A: vascular cord of anther A_1; co_a: vascular cord of anthers a_1 and a_2; co_s vascular cords (3) of stigma; fil: filament; ov: ovary; P_1, P_2: lateral petals; P_3: median petal or lip; p: pollen; S_1, S_2, S_3: sepals; s: stigma-lobes (3); s_r: third or median stigma-lobe; st: style with vascular cords (3); vd: viscid disc.

Apostasia we find a condition which may be compared with that of the *Cypripedioideae:* of the three ventral stamens the two lateral ones of the inner whorl are fertile, the median one of the outer whorl is sterile. In the *Orchioideae* only the median ventral stamen of the outer whorl is fertile; the lateral stamens have either disappeared altogether or they have remained only as staminodes.

One sometimes wonders if perhaps in the *Ophrydeae* this state has developed from a flower with only three outer stamens (as in the *Iridaceae);* in that case the median stamen would remain if there were a tendency to promote the ventral part of the androecium. In my opinion an argument for this theory is that if there is an extra stamen, as happens sometimes, it is always a lateral one of the outer whorl.

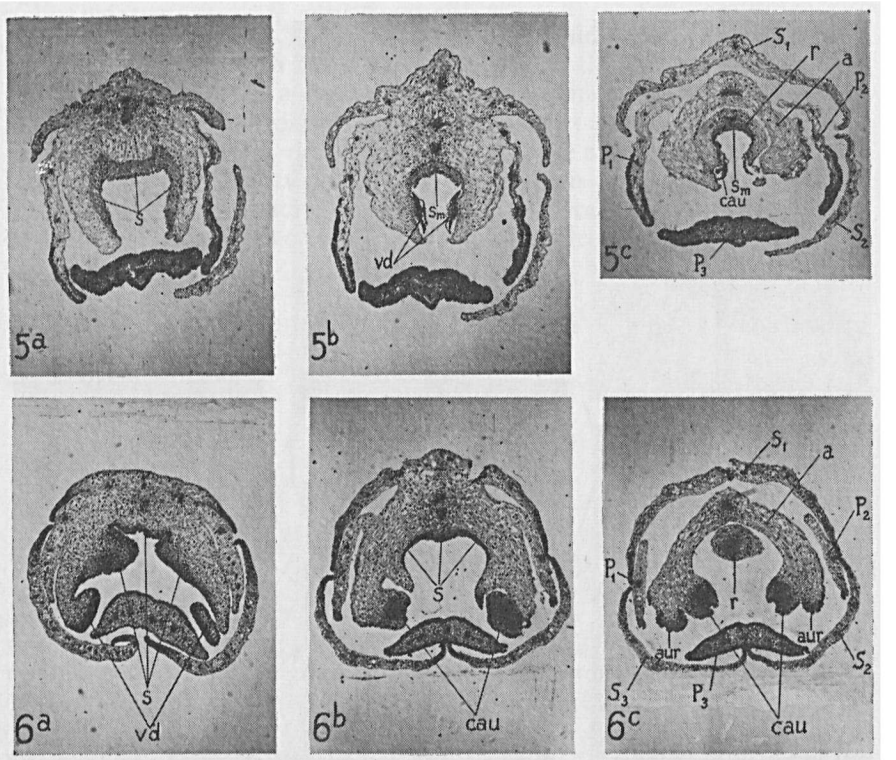

Plate II. 5: Three cross sections of a flowerbud of *Platanthera bifolia* (L.) Rich. 5a: lowest section with three stigma-lobes; 5b: somewhat higher with viscid discs on the place of the lateral stigma-lobes, third stigma-lobe still present; 5c: still higher, rostellum separated from the anther and still with the third stigma-lobe. 6: Three cross sections of a flowerbud of *Platanthera chloranha* (Cust.) Rchb. 6a lowest section: column with three stigma-lobes and viscid discs at the end of the lateral lobes; 6b higher section showing caudicles separated from the stigma tissue; 6c still higher with rostellum and anther with auricles and caudicles. a: anther; aur: auricle; cau: caudicle; P_1, P_2: lateral petals; P_3: lip; r: rostellum with top of median stigma-lobe (s_m); s: stigma-lobes; s_m; median stigma-lobe; S_1, S_2, S_3: sepals; vd: viscid discs.

If the conception of zygomorphy, as here presented, is true, it seems extremely unlikely that the lateral (dorsal) stamens off the outer whorl should develop as viscid discs.

The order of the *Zingiberales* differs from the families mentioned, in that of the two whorls of stamens all the four lateral ones are either fertile or staminodes; one of the median stamens is usually sterile and one fertile, but the tendency: promotion of the ventral opposite the dorsal ones *in both whorls* is lacking.

§ 6. Criticism of Darwin-Eichler's hypothesis

If the hypothesis of Darwin-Eichler were true, the *Orchioideae* or *Monandrae* would include no species, which possess three stigma-lobes, since the median stigma-lobe has become a rostellum. In my previous

article, The Rostellum of the Ophrydeae (1955), I showed, however, by means of photographs of sections of flowerbuds of the genera *Orchis*, *Galeorchis*, *Ophrys* and *Himantoglossum*, that these have indeed three stigma-lobes. This also applies to the genera *Dactylorchis*, *Coeloglossum* and *Platanthera* and several more. Moreover all these genera possess a rostellum, which proves therefore, that rostellum and third stigma-lobe cannot possibly be homologous. The rostellum, I argued, must be considered as a new organ, which is characteristic of the *Orchioideae*, just as the corona is a new organ for the *Asclepiadaceae*. It is remarkable that in the two families where a new organ has appeared, there are also pollinia, and small transport organs, retinacula and translators resp., are developed.

§ 7. Series of developments of the rostellum according to Darwin

In Chapter IX of his book, under "Gradation of Organs", Darwin (1890) deals with a series of developments from *Anacamptis* with only one single viscid disc to *Coeloglossum viride* (L.) Hartm. (= *Platanthera viridis* (L.) Lindl. = *Habenaria viridis* (L.) R. Br. = *Peristylus viridis* (L.) Lindl.) with two separate discs, connected by a roof-shaped tape of the rostellum (Fig. 6). Darwin then says: "These facts are intelligible only on the view, that, whilst the two discs were gradually brought together, during a long series of generations, the intermediate portion or summit of the rostellum became more and more arched, until a folded crest, and finally a solid ridge was formed" (Darwin, 1890 p. 256). I completely agree with this view of Darwin's. The development of bursicles particularly in the genera with a folded crest is another indication of the truth of the conception that this state is a derived one and not primitive.

It is then obvious to assume, however, that the roof-shaped tape is not the most primitive state, but that we should look for this among those genera where this tape is almost straight and lies immediately above the stigma. I think I have found an example of this in the genus *Platanthera*. In some species of that genus, which is distinguished from *Habenaria* in that the stigma forms a whole, has three lobes and not two, both thecae diverge considerably and the connective is very broad, as in *P. chlorantha* (Cust.) Rchb., *P. hookeri* Torr. ex Gray and *P. orbiculata* (Pursh) Torr. (the latter two are American species); this state must be considered as derivative. The European species *P. bifolia*, on the other hand, has a practically normal connective and, here, where the rostellum does not form an arched ridge above the stigma, I suppose to have found a primitive species. *P. blumei* Lindl. from Indonesia has already a somewhat diverging connective but a primitive rostellum as shown in fig. 11.

§ 8. Two series of development

In the genus *Platanthera* we find a rostellum consisting of a narrow tissue tape above the stigma, with on either side a terminal naked viscid disc (plate II, 5). In *P. bifolia* the viscid discs lie quite near and

opposite each other, at the foot of the thecae at the end of the caudicles of the pollinia. In the frogorchid *(Coeloglossum viride = Peristylus viridis* , which distinctly possesses three stigma-lobes (See SCHLECHTER, 1928 Tafel 30 nr. 117 and VERMEULEN, 1958 I, 5 fig. 22 p. 49) the rostellum begins to detach itself from the stigma so to say: the rostellum takes on a roof-shape and the viscidia get a little closer to each other (Fig. 6). In *Herminium* the tape of the rostellum has the shape of a horse-shoe. In the genera *Gymnadenia* and *Nigritella* the arching has developed to such an extent that both halves of the tape have come so near to each other that there remains only a narrow interstice in between, which shows how this crest has come about.

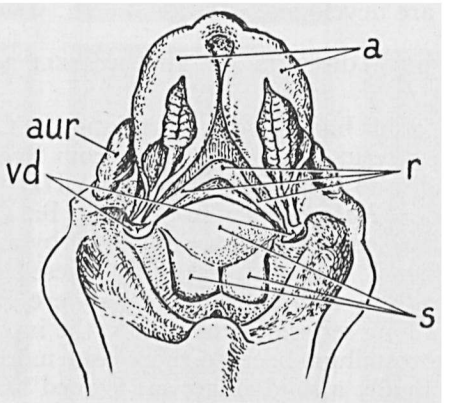

Fig. 6. Column of *Coeloglossum viride* (L.) Hartm. (= *Peristylus viridis* (L.) Lindl.); s: three stigma-lobes; vd: viscid discs; r: tape of the rostellum connecting the viscid discs; aur: auricle; a: thecae of the anther.

RICHARD (1818) speaks of a "rostellum fissum". We find a similar rostellum in *Orchis*, *Dactylorchis* (Fig. 3), *Galeorchis*, but here a bursicle has developed around the viscidia. In the genus *Anacamptis* the viscid discs are connate and ringshaped and both halves of the tape of the rostellum have become a simple ridge between the thecae. This genus forms the end of the series on the one side. For the series on the other side, we can start again with *Platanthera*, but now with *P. chlorantha:* here the connective has become broad and the thecae are separated from each other. The viscid discs lie at the ends of the caudicles of the pollinia: so the rostellum has become longer. We find a similar state in *Blephariglottis ciliaris* (L.) Rydb. (= *Habenaria ciliaris* (L.) R. Br.) from North America, but here the ends of the two thecae project from the column. The tendency of the thecae to become longer also communicates itself to the arms of the rostellum, which is necessary to bring the two viscidia near the ends of the caudicles. We see a similar symptom in the genus *Pecteilis*, e.g. in *P. susannae* (L.) Raf. (= *Platanthera susannae* (L.) Lindl. = *Habenaria susannae* (L.) R. Br.) from Indonesia. In the genera *Blephariglottis* and *Pecteilis* the stigma has remained simple, i.e. it has three lobes. In the genus *Habenaria* sensu stricto there are two stigma-lobes in which, in some species, have

hardly become longer, but which, in other species, have clearly developed into separate stigmaphores. The median stigma-lobe has not been developed. In the species *Habenaria arietina* Hook. f. the projecting parts of the thecae are very long, but the ends approach each other very closely, just as the ends of the rostellum and the two viscid discs, so that a visiting insect will easily take along both pollinia. We find a similar state in the South African genus *Bonatea* (Fig. 7 en 8); here there are also two long stigmaphores; the rostellum has become crest-shaped (this crest is perhaps part of the *receptacle* grown upwards) and completely clear of the anther, but yet the two rostellum arms develop to such an extend that the viscid discs come to lie near the end of the caudicles of the pollinia.

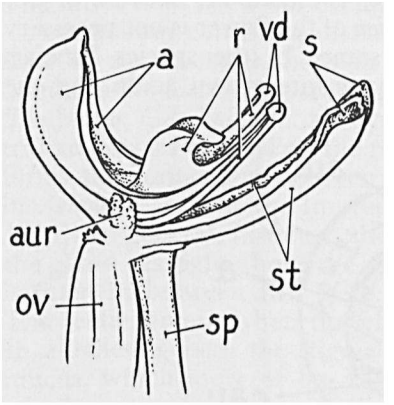

Fig. 7.

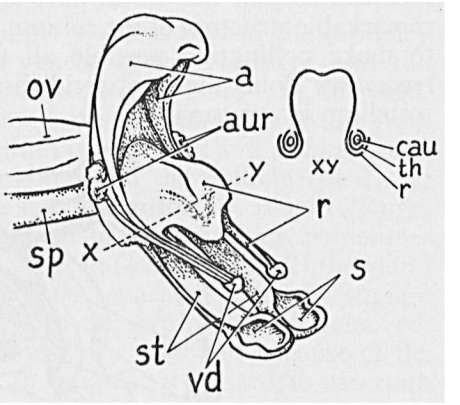

Fig. 8.

Fig. 7. Side view of the column of *Bonatea speciosa* (L. f.) Willd.; ov: ovary; sp: spur of the lip; st: stigmaphores; s: two stigma-lobes; vd: viscid discs; r: parts of the rostellum; aur: auricle; a: thecae of the anther.

Fig. 8. Column of *Bonatea speciosa* (L. f.) Willd. seen slantingly from above; the letters are the same as in fig. 7. The small figure on the right gives a cross section through line x-y; r: rostellum; th: theca; cau: caudicle of the pollinium.

In the genus *Platanthera* the rostellum completely surrounds the upper part of the stigma. In other genera, however, on the one hand the rostellum detaches itself entirely and forms a fold, the two discs intergrowing, on the other hand the arms of the rostellum become considerably longer, and finally approach each other, because of which the viscidia also come to lie near each other.

§ 9. Ophrydeae of the southern hemisphere. their rostellum

South Africa is a centre for the development of the *Ophrydeae* in the Southern Hemisphere. Here we find the genus *Disa* with more than a hundred species, which is characterized by a distinct three-lobed stigma. Bolus (1918 p. 67 and p. 68), who accepts Darwin's theory, nevertheless mentions that in *Disa maculata* L. f. and in *Disa uniflora* Berg. the stigma is three-lobed. The most striking feature of the column

in this genus is that the stigma is indeed right above the ovary, so that the rest of the column must consist of the receptacle with the anther; otherwise we should have to assume that the column above the stigma were the filament; usually the rostellum is a more or less *curved tape* here, but clearly separated from the stigma. In some species, however, there is only one viscidium (sections *Monadenia* & *Herschelia* – LINDLEY considered these two as separate genera).

In the genus *Satyrium* the flower is not resupinate and the labellum, bearing two spurs, is turned upwards. The column splits in two parts at the top, one part bearing the stigma, the other part, turned downwards, is considered to be the rostellum (Fig. 9); it bears two viscidia at the sides, with which the caudicles combine. Here the anther is reclined, so that the dorsal part touches the column. Because of this remarkable structure of the column *torsion* of the flower is not necessary to make pollination possible all the same. In the species *Satyrium ryncanthum* Bolus the two viscid discs have intergrown again and the rostellum is very small.

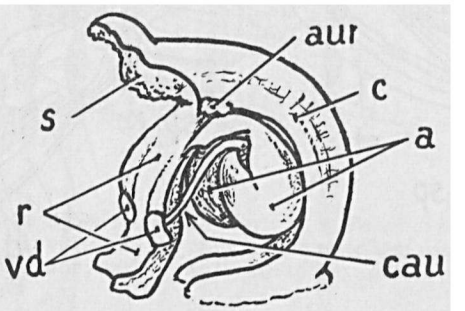

Fig. 9. Side view of the column of *Satyrium nepalense* Don; vd: viscid discs; r: rostellum; s: stigma; aur: auricle; c: column; a: thecae of the anther; cau: caudicle of the pollinium.

In the genus *Holothrix* there is only one viscid disc, but it seems as if here the whole rostellum is taken along, for between the places where the pollinia are connected there is a projecting part, corresponding with the "crest" in *Anacamptis*. Also in the other South African genera *Pterygodium*, *Ceratandra*, *Disperis*, it gives the impression that again and again the rostellum is a crest with the viscidia at the ends; where there is only one viscid disc, this seems a derived condition. In these last mentioned genera, one also finds — just as in *Habenaria* s.s. — two distinct stigma-lobes. Apart from *Satyrium* there is a similar condition in the South African genera as in the Northern Hemisphere ones: a rostellum consisting of a tissue tape with two viscid discs at the ends.

§ 10. THE ROSTELLUM IN THE NEOTTIEAE

The rostellum in the *Neottieae* is completely different. Here is no question of a tissue tape nor of two viscid discs. On the contrary, here the rostellum, the organ producing the viscid liquid, consists of one

simple gland. In the most primitive representatives of the tribus, e.g. in the genus *Cephalanthera*, the rostellum is lacking; perhaps the upper ridge of the stigma, rich in viscid liquid, may be regarded as a rostellum. The stigma here is very rich in viscid liquid and with the help of this sticky secretion the pollinia are indeed stuck to the visiting insects. So this is apparently a primitive state. In the related genus *Epipactis* we find a number of species which possess a rostellum, lying in the middle above the median stigma-lobe and which looks like a simple gland. In some *Epipactis*-species, however, there seems to be no rostellum, e.g. in *E. leptochila* (Godf.) Godf., *E. muelleri* Godf., *E. confusa* Young etc., and one wonders whether here we have to deal with a case of reduction or with a primitive state reminiscent of *Cephalanthera*. The latter does not seem excluded.

A rostellum consisting of one simple gland is indeed the ordinary state in the *Neottieae*, both in the genera of the Northern and the Southern Hemisphere. *Goodyera*, *Spiranthes*, *Diuris* (plate I, 2), *Glossodia*, *Thelymitra*, *Caladenia* etc. always show a simple rostellum. In the Australian genus *Prasophyllum* the rostellum is very long and a thin thread forms the connection between the gland and the pollinia (pl. I, 3); in *Acianthus* it gives the impression that the rostellum is split (RUPP, 1943). In general, however, these appear to be exceptions. Sometimes the gland lies right above the stigma, but in *Goodyera* (Fig. 2) the gland is fitted in between two teeth, distinctly separated from the stigma. The teeth remain when the gland with the two pollinia is removed. In all these genera the stigma always forms a whole; because of the mucus, which more or less covers the stigma, it is hard to ascertain whether there are two or three lobes. I think that there are sometimes three, as in *Cephalanthera*, *Epipactis*, *Spiranthes*. Were there is no distinct separation between the stigma and the viscid disc, it seems as if the disc is more or less a continuation of the stigma, often only separated from it by means of a slight interruption (plate I, 4b). In *Listera* and related genera the rostellum consists of partitions, from which, when touched, viscid liquid is pressed out.

§ 11. THE VASCULAR CORDS IN THE COLUMN

DARWIN gives an accurate description of the number of the vascular cords in the column of several orchids (1890, p. 239 note etc.).

In the *Neottieae* we often find at the column small projecting parts, which are looked upon as staminodes. In most cases they contain no vascular cords and the supposition that we have to do with remnants of the lateral stamina of the inner whorl cannot be proved. In some genera, however, the lateral projecting parts are large, as in the Australian genera *Pterostylis*, *Diuris*, where the anther lies apart from the rest of the column (plate I, 2), *Caladenia* and *Thelymitra*, and they form wings at the column. It appears that these projecting parts contain vascular cords, which arise from the cords of the lateral petals, in which case they would be homologous with the lateral stamina of the inner whorl. Besides the vascular cords for the stamen and staminodes the column usually contains three cords. These cords are found

opposite the sepals. The median cord, which also provides for the rostellum, is well developed, apparently in connection with the double task which the cord has to fulfill.

In the *Ophrydeae* the gynostemium often has only one single vascular cord, which lies in front of that of the median sepal. This cord splits into two parts: one branch enters the connective and provides for the anther; the other branch apparently has to cater for the rest of the column and usually this branch leads to the rostellum. If the rostellum is broad as in *Platanthera chlorantha*, there yet remains one simple and that is the median vascular cord. I consider this state (one vascular cord) as a derived one, that of the *Neottieae* (three vascular cords) as more primitive.

In *Habenaria arietina* with two long stigmaphores, each of these also contains a vascular cord. (Is this also the case with *Bonatea?)*. An exception is the genus *Satyrium* from Africa, with one single species, *S. nepalense* Don., occurring as far north as in the Himalayas. Here we find a long column, containing three vascular cords, of which the median one again provides for the rostellum and the stigma. Wether the same is the case in the other South African genera, I have not been able to investigate.

In the *Ophrydeae* the anther nearly always has auricles, which BROWN, DARWIN and EICHLER consider to be staminodes. BROWN (1833), however, is in doubt, because in a flower of a *Platanthera*, which had an extra stamen, the latter also had an auricle at the side of the median, normal stamen. I have found a similar case in *Dactylorchis maculata*. These auricles are in my opinion to be considered as appendices of the stamen, as they are also found in the stamens of *Allium* (see my article "The vanished stamens" (1953)). In the *Ophrydeae* these auricles always contain raphides. They never have a vascular cord. The *Neottieae* have more often staminodes but *Epipactis* (plate I, 4) and *Cephalanthera* have auricles.

§ 12. THE DIFFERENCES BETWEEN OPHRYDEAE AND NEOTTIEAE

Comparing these two tribes, we find the following differences in the column:

OPHRYDEAE	NEOTTIEAE
Anther intergrown with its backside with the column.	Anther connected with a broad base or only by means of the filament with the column.
Column with anther with auricles, no staminodes.	Column often with wings, which are probably staminodes; anther seldom with auricles.
Pollinia with caudicles at their bases and basitonic.	Pollinia never with caudicles; pollinia pleurotonic or acrotonic.
Rostellum more or less in the shape of a tape with a viscid disc on either end; sometimes one or two bursicles.	Rostellum a simple viscid disc above the median stigma-lobe, consisting only of viscid matter or of a gland, forming viscid liquid, never bursicles.
Stigma one whole, with three lobes, or stigma with two separate lobes.	Stigma more or less clearly provided with three lobes or with two lobes, which always form a whole.

Besides other differences especially the one in the structure of the rostellum is apparent. DARWIN concluded that the rostellum in the *Ophrydeae* was originally an organ with two viscid discs. Gradually a simple rostellum may have developed from this. In the §§ 8, 9 and 10 I have tried to prove that these differences between the rostellum of *Ophrydeae* and *Neottieae* are essential and not accidental. How is one to imagine the original state in the *Ophrydeae?*

§ 13. EPIPACTIS GIGANTEA DOUGL. EX HOOK

Accidentally my attention was drawn by the gynostemium of *Epipactis gigantea* Dougl. ex Hook., which was blossoming in the Amsterdam Hortus Botanicus in 1958. This species, which has a movable epichilium at the hypochilium, like *E. palustris* (Mill.) Crantz, shows a peculiarity. For this point I have consulted CORRELL's book "Native Orchids of North America", 1950, page 129 of which gives a reproduction of this species. The column, however, is not reproduced. Also in the case of *Habenaria* Correll's book continually fails us. The American authors take as general a view of this genus as do BENTHAM and HOOKER (1883), but they do not pay attention to the structure of the column, consequently they neither deal with the peculiarities of the stigma, nor with that of the rostellum. It is true that the structure of the perigone, in particular that of the labellum, is sufficient to determine the name of the species, but this does not give us sufficient insight into the relationship between the species, and that should be considered as one of the most important aims of systematics.

The gynostemium of *E. gigantea* shows a stigma with three lobes, and near or above these lobes three spots occur, which secrete viscid matter. Most viscid liquid is above the median lobe, close below the

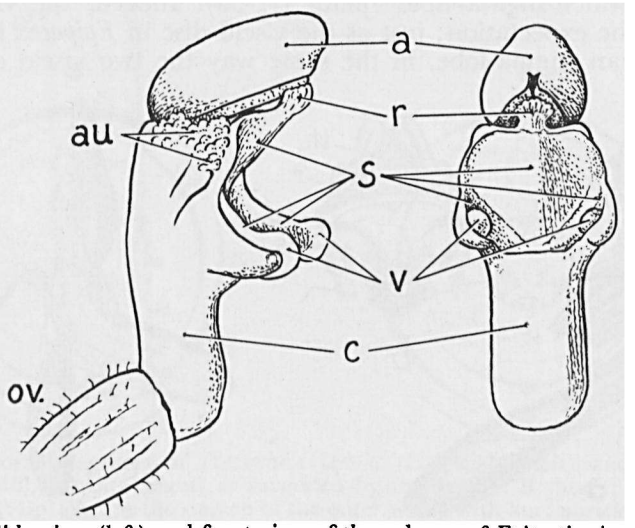

Fig. 10. Side view (left) and front view of the column of *Epipactis gigantea* Dougl. ex Hook.; ov: ovary; c: column; v: sticking fluid on the side lobes of the stigma; s: three stigma-lobes; aur: auricle; r: rostellum; a: anther.

top of the anther and it is this which forms the rostellum. There is only a slight separation between the median stigma-lobe and this rostellum. With the help of the viscid liquid, formed by this small organ, the pollinia are stuck with their tops to the head of a visiting insect. The organ forming this viscid fluid is simple, as is always the case in the *Neottieae*. The two other spots forming viscid liquid are on short arms on the lateral stigma-lobes (Fig. 10). It does not seem probable that this viscid fluid plays a part in the transportation of the pollinia. In this connection it appears important to me, however, that not only above the median stigma-lobe a gland with viscid fluid can be formed, but that it seems probable that such glands can also arise above the lateral stigma-lobes. It seems important that this ability to form lateral glands is formed in the genus *Epipactis*, which shows primitive properties also in another respect: a rostellum is lacking in some species.

§ 14. The rostellum in Platanthera bifolia (L.) Rich

The fact that viscid fluid is secreted also through the lateral lobes of the stigma in *Epipactis gigantea* suggested the idea to me that the two viscid discs of the *Ophrydeae* might have arisen or formed by and above the lateral stigma-lobes, whereas in this group viscid liquid would not be formed by or above the median stigma-lobe. If this thought should contain a substratum of truth, this state would have to be verified in primitive *Ophrydeae*, consequently in such species where the rostellum still lies above and against the stigma, and is not or hardly differentiated, such as in the genus *Platanthera*. Then the species with hardly broadened connective, *P. bifolia*, would have to show this the most clearly. A cross-section of the gynostemium has three distinct stigma-lobes (plate II, 5a). Indeed, the viscid discs answer the expectation; just as the viscid disc in *Epipactis* lays above the median stigma-lobe, in the same way the two viscid discs of *P.*

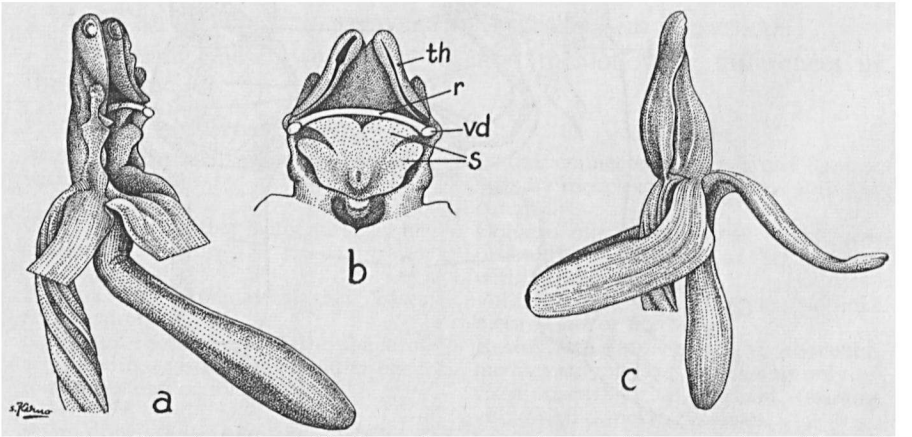

Fig. 11. *Platanthera blumei* Lindl. c: flower; a: flower without sepals and lateral petals, the lamina of the lip is cut away; b: column with; s: stigma; vd: viscid disc; r: tape of the rostellum; th: theca of the anther.

bifolia lay right above the lateral stigma-lobes and with *P. blumei* it is the same (Fig. 11).

In *P. chlorantha*, where the connective is already broadened considerably, the viscid discs lie beside the lateral stigma-lobes (plate II, 6a). If in these three *Platanthera* species, we speak of a rostellum, we can regard the two viscid discs as such and we can speak of a separate tissue tape, which connects them (plate II, 5c, 6c). It is true that the tissue on which the stigma is situated, continues for a small distance and there is even a separation between this tissue and the stamen. In my opinion this tape must be regarded as the primitive origin of the connecting tape between the viscidia, which, in other genera, forms an integral part of the rostellum.

§ 15. Gradation of the rostellum. Criticism of Brown

The rostellum would consequently have developed from this primitive organ, hardly to be distinguished, into a separate tissue tape, which appears to be a separate organ. In one series there seem to be a tendency to detach this organ from the stigma. In *Coeloglossum* it can be distinguished as a roof-shaped ridge with at the ends the viscidia, which have approached each other but they are still in connection with and lying above the lateral stigma-lobes (Fig. 6). In *Herminium* the connecting tape is curved in the shape of a horse-shoe; in *Galeorchis* and *Ophrys* the two halves come closer until finally both touch each other in the genera *Gymnadenia*, *Orchis*, *Dactylorchis* (Fig. 3) etc. In the other series *(Pecteilis, Habenaria, Bonatea)* the connecting ridge between the viscid discs shows the tendency to lengthen and the viscidia are more separated; there is no question of a rising ridge. Both ends of the rostellum keep pace with the lengthening of the thecae, as a result of which the viscid discs always remain at the ends of the pollinia (Fig. 7 & 8).

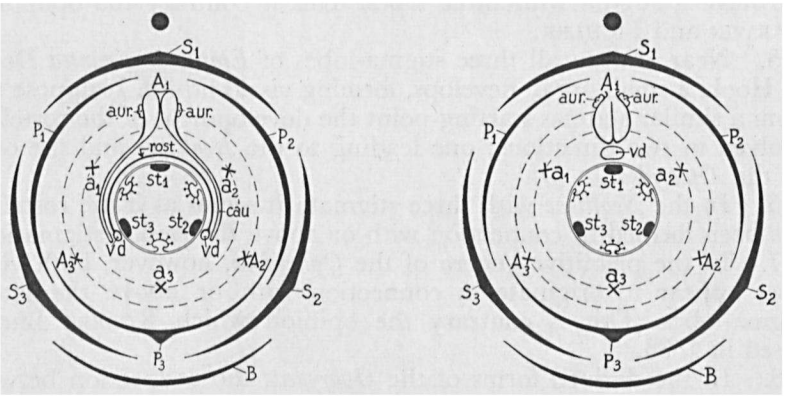

Fig. 12. Floral diagrams of *Platanthera bifolia* (L.) Rich. (left) and *Epipactis helleborine* (Mill.) Crantz (right) as suggested by the author. B: bract; S: sepals; P: petals (P_3: lip); A_1: fertile stamen of the outer whorl with aur: auricle and cau: caudicle; A_2 and A_3: place of the lateral outer stamens which are suppressed; $_1a$, a_2, a_3: stamens of the inner whorl which are all suppressed; rost: rostellum; vd: viscid discs of it; st_1, st_2, st_3: fertile stigma-lobes. Flowers resupinate.

In several genera of the *Ophrydeae* there is a tendency to reduce the median stigma-lobe so as in *Gymnadenia* and *Anacamptis* (VERMEULEN, 1958 p. 31 fig. 10, 4 and p. 51 fig. 23, 5). This lobe is situated opposite the anther which is normal. In *Habenaria* s.s., *Bonatea* and several other South African genera the third stigma-lobe has totally disappeared, whereas the thecae of the anther are more or less lengthened at their base. The rostellum ridge is lengthened in the same way. This may be an indication the more that the ridge does not belong to the third lobe but behaves as an independant organ (VERMEULEN, 1954). Sometimes the middle part of the rostellum becomes very broad as in *Bonatea, Cynorchis, Platycorne* etc. All these cases seem to be derived and it is impossible to establish here if the viscid discs originally are situated above and near the lateral stigma-lobes. Therefore it is necessary to look for primitive genera like *Platanthera.* However, it must be possible to verify the original state of the rostellum with other primitive genera in the *Ophrydeae* too.

The hypothesis: the glands in the *Ophrydeae* are originally formed near and in contact with the lateral stigma-lobes, is contrary to the hypothesis, which ROBERT BROWN posed in 1833, viz. that the glands would always belong to the upper lobe of the stigma. Fig. 12 gives the differences between *Platanthera* and *Epipactis* in diagrams.

§ 16. CONCLUSIONS

From the foregoing I think I may draw the following conclusions:

1. There is an essential difference between the rostellum in the *Ophrydeae* and the *Neottieae.*
2. In the *Ophrydeae* it consists of a tape or ridge with a viscid disc at each of its ends.
3. In the *Neottieae* the rostellum consists of a simple organ.
4. In many *Ophrydeae* the stigma has three lobes. Several *Neottieae* too have a stigma with three lobes. This is contrary the opinion of DARWIN and EICHLER.
5. Near and on all three stigma-lobes of *Epipactis gigantea* Dougl. ex Hook. a small organ develops, forming viscid liquid. I suppose that from a similar state as starting-point the development of the rostellum evolved in two directions: one leading to the *Neottieae* and the other to the *Ophrydeae.*
6. In the *Neottieae* with three stigmata it seems as if the rostellum has been formed in connection with or above the *median* stigma-lobe.
7. In the primitive genera of the *Ophrydeae,* however, both viscid discs appear to originate in connection with or above the lateral stigma-lobes. This is contrary the opinion which ROBERT BROWN posed in 1833.
8. In the derived forms of the *Ophrydeae* the connection between the viscid discs and the lateral stigma-lobes may be completely broken. This is to be described to the independent development which the rostellum, as a new organ, can apparently go through.

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