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POLLINIA-PRESENTATION IN DENDROBIUM SECTION PEDILONUM

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ABSTRACT. The rostellum of *Dendrobium* is normally covered by a membrane that must be broken to expose the glue. In section *Pedilonum* the anther beak covers and becomes attached to the rostellar membrane, so that moving the anther exposes the glue, pushes it downward toward a potential pollinator and then deposits the pollinia on the fresh glue. Some species of other sections have similar mechanisms.

In botanical terms, the pollinia of *Dendrobium* are "naked," meaning only that the pollinia have no appendages. In most orchids there is some kind of stalk that attaches or positions the pollinia on a pollinator, and in many cases the pollinia and their accessory structures are quite complicated. *Dendrobium,* however, achieves pollination without the same sort of complexity we find in many other orchids.

Rasmussen (1982) reports that the rostellum of *Dendrobium* "explodes" when touched, implying that the rostellar glue is under pressure, like that of *Listera* or *Neottia* (see Schick et al., 1987, for photographs of *Listera* in action). Rasmussen's article stimulated me to survey the *Dendrobium* species in flower at the Marie Selby Botanical Gardens on my irregular visits there.

While botanical descriptions give the impression that the column of *Dendrobium* is quite uniform in structure, there is a good deal of variation, and some species have quite elegant mechanisms for attaching their pollinia to pollinators. As Rasmussen indicates (1986, figure 19), the rostellar glue of *Dendrobium* is covered by a membrane. This membrane is usually thick above the glue, and the thick portion may extent onto the lower (ventral) surface, where it becomes much thinner toward the receptive stigma. The thin membrane may be delicate and easily broken, or there may be a definite line where breakage usually occurs.

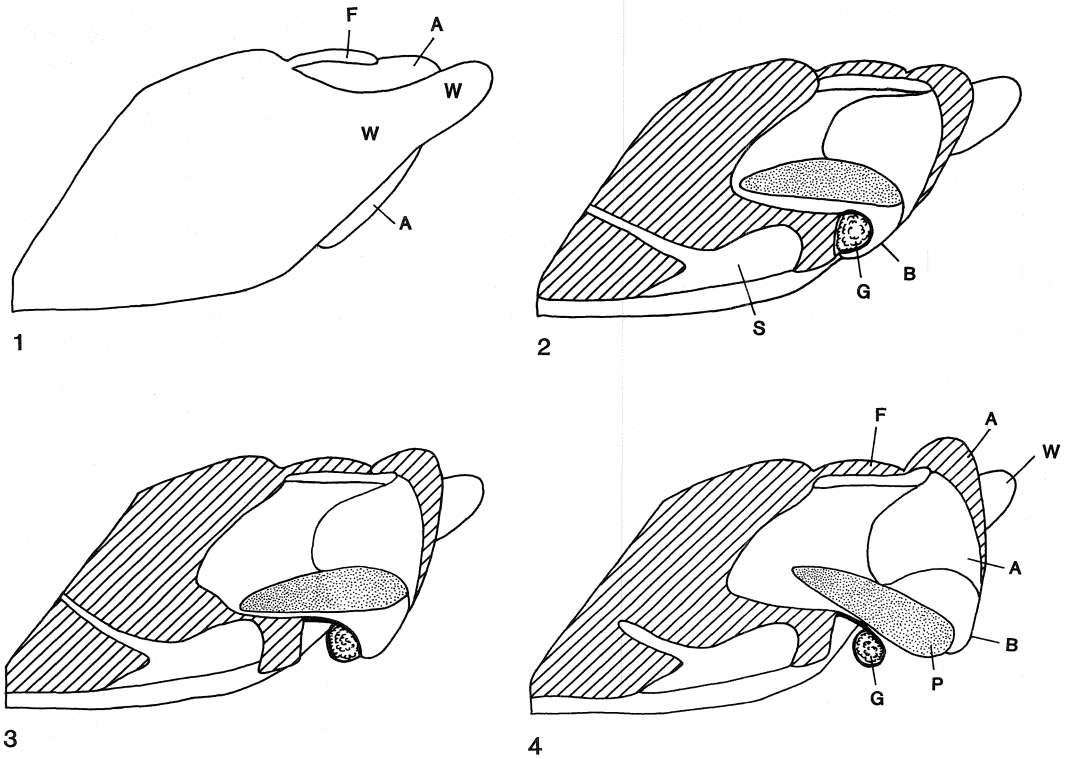
In some species of *Dendrobium* the anther and the membrane-covered rostellum work together very smoothly. One need only brush the tip of the anther to uncover the rostellar glue, push it out onto the would-be pollinator, and then drop or push the pollinia onto the fresh glue (see FIGURES 1–8). In these species, the beak of the anther covers the rostellar membrane, and the tip of the beak normally becomes attached to the edge of the membrane. Thus, when any object withdraws from the flower and brushes the beak of the anther, the anther swivels out and pulls back the membrane, exposing the glue. At the same time, the pollinia are pushed against the upper side of the rostellum, forcing the glue toward the object. Finally, the anther swings farther out, dropping the pollinia onto the freshly applied glue. In these species there is an unusually prominent filament at the base of the anther. This slender filament appears to function as a spring, holding the anther down so that it pushes against the rostellum as it swings forward.

This mechanism occurs so quickly that it could be taken for "glue under pressure," even under a dissecting microscope. However, the anther beak fails to become attached to the membrane in a small percentage of the flowers; in these cases one may remove the anther without breaking the membrane, and the glue is clearly not under pressure. In reality, as the anther swivels forward, it simply pushes the rostellum (and thus the glue) outward from the surface of the column.

While one may observe rostellar function under a dissecting microscope, it is difficult to obtain good drawings or photographs. Cutting through the rostellum releases the glue and changes its shape. The rostellar membrane may rupture even in liquid preservative, and the rostellum shrinks and becomes distorted if flowers are stored in liquid. The accompanying drawings are necessarily somewhat diagrammatic.

So far, I have found similar mechanisms in eight species of section *Pedilonum* (see Appendix). The tip of the anther beak may bear large bristles, as in *D. victoriae-reginae,* or it may be smooth and turned in toward the rostellum, as in *D. epidendropsis* and *D. platygastrium. Dendrobium amethystoglossum* is intermediate, with the anther beak incurved at the tip, but with small marginal bristles. When large and spreading bristles are present, some of them are attached to the rostellar membrane, while others catch on any object that brushes the anther beak.

The rostellar glue may be thick and paste-like and it becomes solid soon after exposure to air. I had described a plate of solid tissue in the glue of *D. secundum* (Dressler, 1981), and I also noted solid material in the rostellar glue of *D. victoriae-reginae.* Re-examination shows that the glue of



FIGURES 1–4. Pollinia presentation in *Dendrobium amethystoglossum.* 1. Lateral view of column. 2. Longitudinal section through column (diagrammatic), with anther and pollinia undisturbed. 3. The anther moved slightly, so that the rostellar membrane is broken. 4. The anther moved farther out so that the anther beak has separated from the membrane and the pollinia are pushed against the rostellum; the pollinia are being forced out. A, anther. B, anther beak. F, filament. G, rostellar glue. P, pollinia. W, column wing.

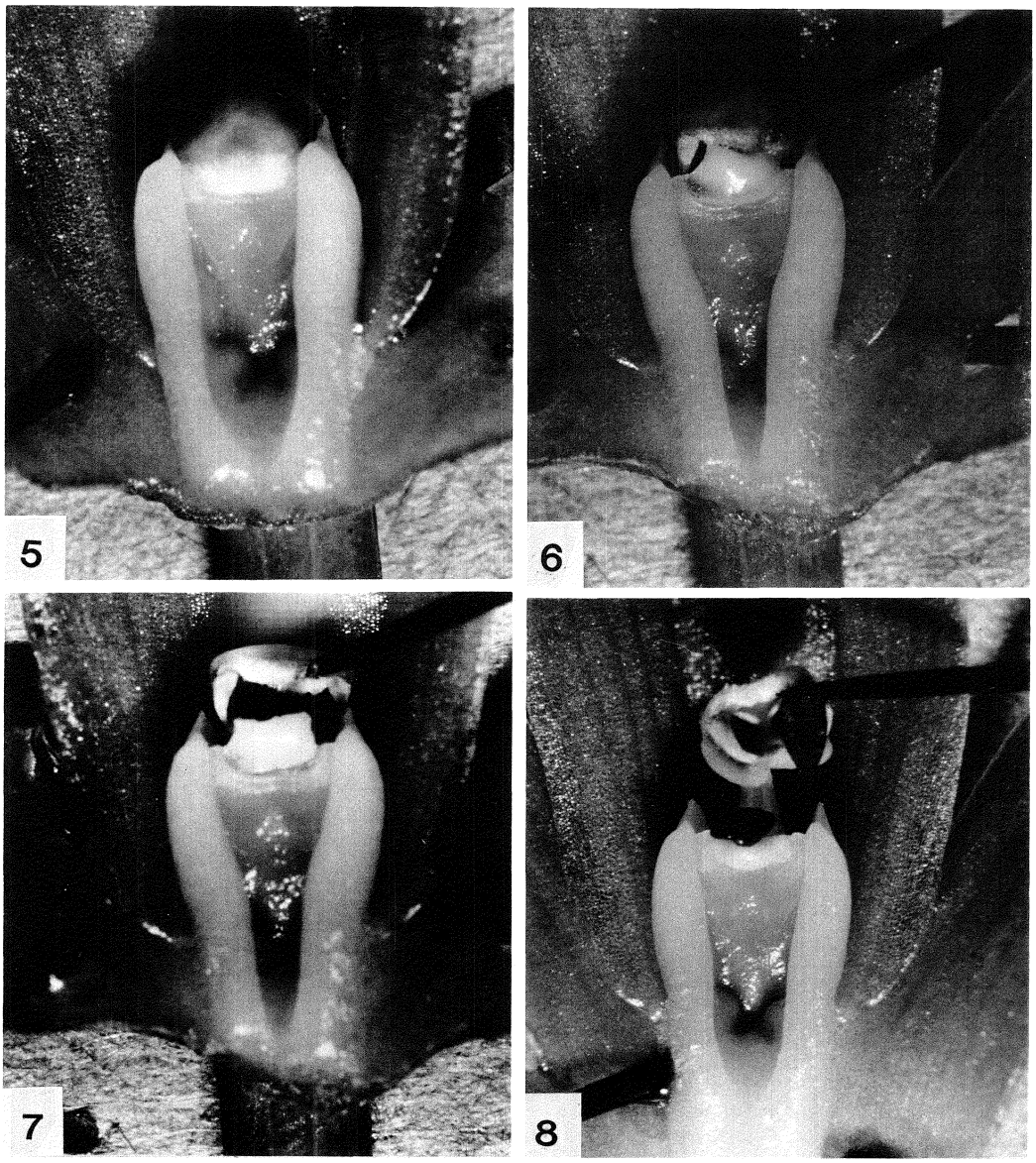
these species is not solid when first exposed, but solidifies very quickly. In most cases, the pollinia appear to fall out when the anther swivels outward, but in *D. amethystoglossum* the long, tapering pollinia are caught between the rostellum and anther and forced outward (FIGURE 4).

Structure similar to that of sect. *Pedilonum* has been found in three other sections. In these cases, the anther beak usually becomes attached to the rostellar membrane, though the anther may exert no pressure on the rostellum. Since the anther beak is adjacent to the rostellum in many species of *Dendrobium,* the stage is set for the independent (or parallel) evolution of this mechanism. Each of the sections mentioned below includes species without this mechanism, so parallelism is the most probable explanation (though some sections of the genus may prove to be unnatural, or polyphyletic).

In section *Latouria,* the anther beak becomes attached to the rostellar membrane in *D. atroviolaceum, D. bifalce* and *D. johnsoniae,* but not in *D. alexandrae.* In the first three species the rostellum protrudes somewhat from the column and has a small area of rostellar glue near the apex. The beak of the anther is folded inward near the tip and becomes attached to the rostellar membrane, so that the glue is exposed when the anther is tipped back.

Of the species in section *Formosae* that were examined, only *D. dearei* shows attachment of the anther beak to the rostellar membrane. In the other five species examined (see Appendix) the anther beak covers the rostellar membrane, but does not become attached to it. That portion of the rostellum, however, projects below the column surface, and anything that brushes the area will probably break the membrane as it touches the anther beak and causes the anther to swing out.

In sect. *Aporum, D. rosellum* shows structure very much like that of sect. *Pedilonum* in all respects. These two sections are vegetatively quite different, but the flower of *D. rosellum* is narrow and tubular with a nectary at the base, very like a miniscule flower of sect. *Pedilonum.* In *D. aloi-*



FIGURES 5–8. Pollinia presentation in *Dendrobium secundum*. 5. Ventral view of column, with anther undisturbed. 6. Anther moved slightly with a pin; the membrane is broken and the glue exposed and pushed outward. 7. Anther moved farther; the dark pollinia are seen in the anther. 8. One pair of pollinia is attached to the pin, while the other pair is attached to the remaining rostellar glue.

folium the anther beak bends over the bulging rostellum without becoming attached to it. When the anther is moved it grips the rostellum long enough to break the membrane (on the side near the receptive stigma), but the membrane is not straightened by the movement of the anther. The rostellum already projects downward from the surface of the column, so the glue is then exposed and ready to be removed by a pollinator. No such mechanism was observed in *D. acerosum, D. anceps,* or *D. indivisum* var. *lampangense.* In these species the anther beak does not clasp or become attached to the rostellar membrane.

Another elegant mechanism in *Dendrobium* is the "scraper" (Kerr, 1909; Rasmussen, 1982). In many species, the rostellum forms a shelf be-

tween the rostellar glue and the receptive stigma. This shelf points back toward the stigma and probably scrapes the pollinia off of the pollinator. The edge of the scraper may be either straight or notched, or the scraper may form a triangular tooth. Even when there is no real scraper, there is usually an area of firm, non-receptive tissue between the rostellar glue and the receptive stigma. The scraper appears to be a development of this non-receptive area, and is thus part of the rostellum.

Though the pollinia lack appendages of any sort, their form and color are quite variable. The pollinia often cohere in pairs, and in some species all four pollinia are strongly coherent, so that they function as a single structure.

We find, then, that column structure in *Dendrobium* is not as monotonously uniform as botanical descriptions imply. Most of these complications involve the rostellum and the anther, rather than the pollinia, and would be difficult to see in pressed and dried specimens. For the botanist, the variation in the column of *Dendrobium* offers another set of details that may help understand the relationships in this and allied genera. *Dendrobium cincinnatum* F. Mueller, of New Guinea, shows unusually primitive column structure, with no scraper and no membrane over the rostellar glue (or a membrane so thin that I could not see it). I have seen no scraper in *Diplocaulobium, Cadetia* or *Epigeneium.*

Traditionally, orchid classification has been based on details of the pollinia. Groups such as *Bulbophyllum, Dendrobium, Liparis* and *Malaxis,* that have (or appear to have) "naked" pollinia have thus remained undivided, with the sections or subgenera weakly delimited and often unnatural. I must stress that breaking large genera into many small ones does not necessarily bring either natural groups or better understanding. Still, a careful survey of the structural details of the column may contribute valuable information toward a better understanding of the *Dendrobium* alliance.

The observations offered here are, at best, just a beginning. I have examined only a small percentage of the *Dendrobium* species, and representatives of less than half of the sections. While glue under pressure was not observed, this may well occur in other species. A rostellar membrane like that of *Dendrobium* is probably a necessary first step for the evolution of glue under pressure, the mechanism described here, or quick-setting glue.

Acknowledgments

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Schick, B., K.-H. Seack, and J. Kaeding. 1987. Rostelldifferenzierung und Pollinarienbildung europäischer Orchideen IV. Kinematographische Dokumentation der Extrusion des Rostellklebstoffs von *Listera ovata* (L.) R. BR. Die Orchidee 38: 251–255.

Appendix

Materials mentioned in text, with Marie Selby Botanical Gardens (MS) or Florida Museum of Natural History Greenhouse (FM) accession numbers, where applicable.

Section *Aporum* (Bl.) Lindley
- *D. acerosum* Lindley, MS#81-2216
- *D. anceps* Sw., MS#81-156
- *D. aloifolium* (Bl.) Reichb. f., MS#78-179
- *D. indivisum* var. *lampangense* Rolfe, FM#88-007
- *D. rosellum* Ridley, MS#78-200

Section *Formosae* (Benth. & Hook. f.) Hook. f.
- *D. dearei* Reichb. f., MS#87-184
- *D. draconis* Reichb. f., Motes
- *D. formosum* Roxb. ex Lindley, Motes
- *D. sanderae* Rolfe, MS#87-187
- *D. scabrilingue* Lindley, Motes
- *D. virgineum* Reichb. f., Motes

Section *Latouria* (Blume) Miquel
- *D. alexandrae* Schltr., MS#77-2786
- *D. atroviolaceum* Rolfe, MS#74-15-12
- *D. bifalce* Lindley, MS#77-2803
- *D. johnsoniae* F. Muell., MS#74-23-1059

Section *Pedilonum* (Blume) Lindley
- *D. amethystoglossum* Reichb. f., MS#87-182
- *D. bullenianum* Reichb. f., Motes
- *D. epidendropsis* Kraenzlin, MS#87-149
- *D. miyakei* Schltr., MS#79-1703
- *D. platygastrium* Reichb. f., MS#75-89-51
- *D. purpureum* Roxb., MS#76-146-7, MS#81-2252
- *D. secundum* (Bl.) Lindley, Motes
- *D. victoriae-reginae* Loher., MS#87-187

Section *Trachyrhizum* Schltr.
- *D. cincinnatum* F. Mueller, MS#81-22-61