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AN ASPECT OF ORCHID ANATOMY AND ADAPTATIONISM

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THE DESCRIPTIVE anatomy within Orchidaceae — as elsewhere — is greatly influenced by the adaptationistic way of thinking. The tendency toward judging characters in terms of adaptive value stems partly from the idea that such considerations may be a guideline toward the polarization of character states in phylogenetic reconstruction. However, in many cases it is indeed very difficult to point out any adaptive significance of a particular character or any of its states. The silica cells (stegmata) in orchids are such a case. There is no indication that the different, species-specific expressions of stegmata are in any way connected with habit or life form of the species in which they occur. Although their access to natural silicon is believed to be very low, the epiphytic species often have stegmata. However, terrestrial species very often lack them. Although the adaptational importance of this feature is doubtful, the character states can nevertheless be used in phylogenetic considerations on the basis of their distribution within the orchids.

Usually, we split up the phenotype of a plant into a number of traits, in order to describe it to the detail needed in each particular case. It is important to remember that most traits making up a description of a species are inherited from ancestors of that species. Only very few — perhaps only a single one — have been acquired recently by that particular species. These few traits are the ones that could be used in a diagnostic key. Only such traits can be estimated in relation to recent conditions, and can with some degree of certainty be viewed as adaptive. The other traits may have kept their adaptive importance, or they may have lost it through changes in conditions. Most often we cannot make a determination.

Therefore it is important to try to clarify the phylogeny of a character, so that the character states can be evaluated at the level where they were established. This fact has been emphasized many times (e.g. Gould and Lewontin, 1979; Wanntorp, 1983), but it is often overlooked even in modern works on plant morphology and anatomy.

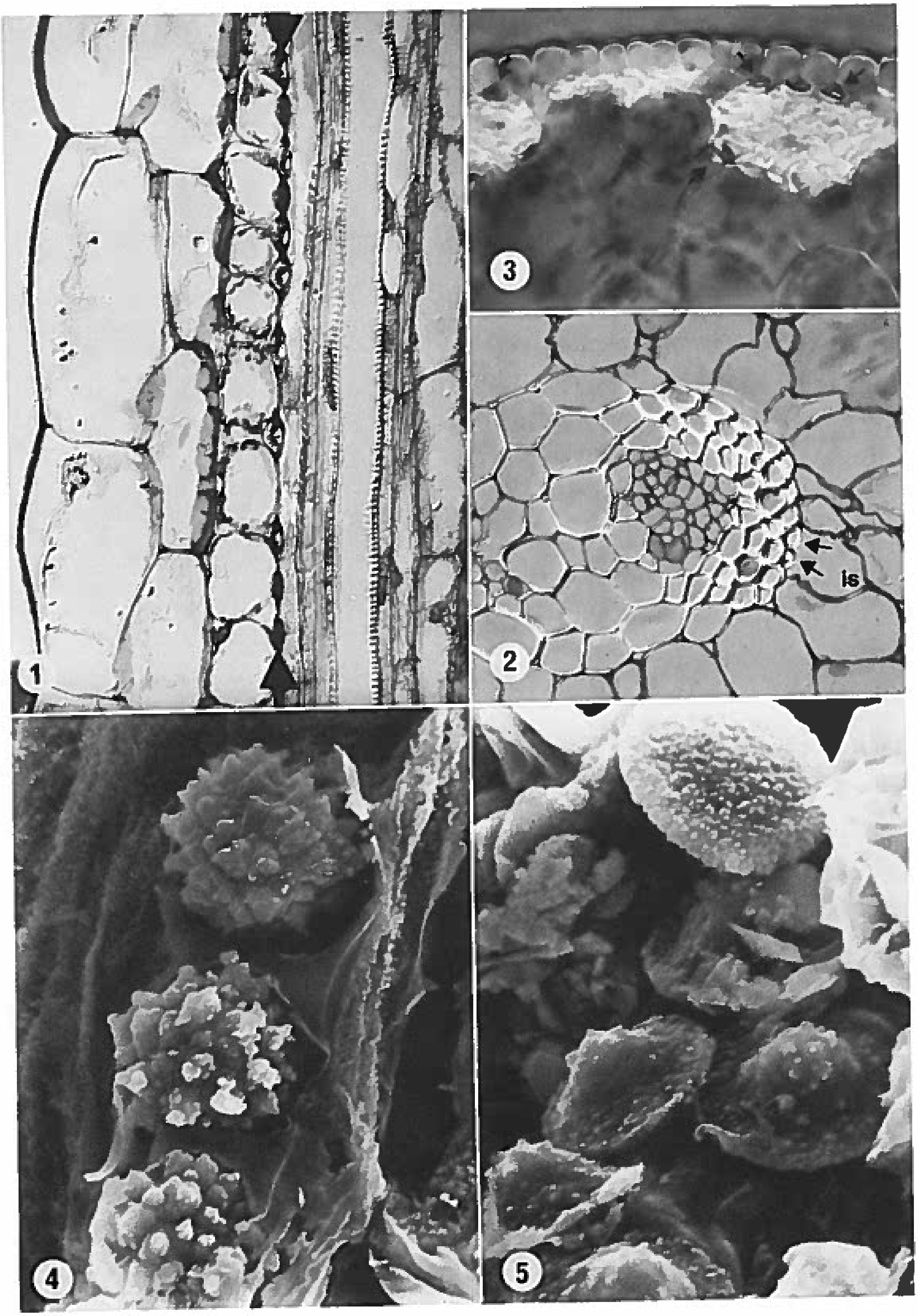
I will illustrate this by one aspect of orchid anatomy, the silica cells. One advantage of these cells is that their function seems so entirely obscure that we can approach them without preconceived ideas. Nevertheless, their history in orchids can be outlined, and by doing this, adaptational speculations can be tested.

The silica cells of orchids have been much neglected except in the older German literature (e.g. Kohl, 1889; Siebe, 1903; Molisch, 1920). Several more recent anatomical papers in English mention these structures in orchids without realizing that they are silica cells (Rosso, 1966; Withner, Nelson, and Wejksnora, 1974). However, other recent papers correctly state the presence of silica cells in orchids (Pridgeon and Williams, 1979; Pridgeon and Stern, 1982).

The silica cells occur as longitudinal files of protrusions from a vascular strand. At maturity, they are very small compared with cells of other tissues (Fig. 1). They always occur in association with supporting tissue and often adjacent to an intercellular space (Fig. 2).

When mature, the cells are filled with a silicious body that may take either of two shapes. One type is spherical, with a spiny surface (Fig. 4). In incinerated material we still see the remains of the surrounding cell walls of the silica cells. The silica bodies are intact, since they are resistant to high

Fig. 1-5. Silica cells (stegmata) in orchids. **1.** At maturity, silica cells (arrows) are very small compared with other kinds of cells. Epidermis to left, a vascular strand in longitudinal section to the right. Glycolmethacrylate section, toluidine blue O, *Thunia alba* Reichb. f. (GT 9244), leaf. Interference contrast microscopy. ×347. **2.** Silica cells (arrows) occurring at the interface between a sclerenchymatous cap of a vascular strand and an intercellular space (is). Transverse section. Glycolmethacrylate section, toluidine blue O, *Pholidota* sp. (GT 7665), stem. Interference contrast microscopy. ×337. **3.** Silica cells by fibrous strands at the surface of a leaf. Most of them are developed on the side of the strand facing the epidermis, but silica bodies are not produced at fibrous strands which are immediately adjacent to the epidermal cells, such as the one in the middle. Hand section, safranin-light green, *Cymbidium aloifolium* Rolfe (GT 1553), leaf transverse section. Interference contrast microscopy. ×415. **4.** Spherical silica bodies. Glowed material of leaves, *Cleisostoma subulatum* Blume (GT 5525). SEM. ×7,800. **5.** Conical silica bodies. Incinerated material of leaves, *Agrostophyllum stipulatum* J. J. Smith (GT 6011). SEM. ×7,800.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temperatures. A second type of silica body, also seen in incinerated material, is conical with a flat side appressed to the side of the vascular strand (Fig. 5).

The silica cells, or stegmata, as they are properly called, occur in all organs except roots. They line the interface between sclerified tissue and parenchyma. They are found in sclerenchymatous sheaths of a rhizome, always on the outer surface toward the cortex and they occur along fibrous strands and fibrous caps of vascular bundles, most numerously toward the epidermis (Fig. 3). It may be noted that the epidermis never produces silica bodies, not even if a fibrous strand or a fibrous bundle sheeth is adjacent to it.

Together with one of my colleagues in Copenhagen I have surveyed about 130 species of orchids for the presence of silica cells (Dahl Møller and Rasmussen, 1984). Only some orchid species investigated have stegmata. Among species possessing them, both kinds of stegmata do not occur in the same species, and we have observed no intermediate forms.

Many orchids lack stegmata and this condition is sometimes accompanied by a general lack of supporting tissue. That observed stegmata always occur in association with supporting tissue suggests a developmental connection between the supporting tissue and stegmata. In species with very little such tissue, the ability to form stegmata might remain latent. The species in question must be referred to an undecided category. The existence of species with abundant supporting tissue but without stegmata indicates that the ability to form stegmata in some species is effectively absent.

Hence we recognize three character states and an undecided group:

- Conical bodies in silica cells.
- Spherical bodies in silica cells.
- Supporting tissues present — silica cells lacking.
- Supporting tissues lacking.

Preliminary observations of the ontogeny show that in species lacking stegmata neither the silica bodies nor their specialized cells are formed (Fig. 6).

In species containing stegmata the initial stages appear very early in leaf development. The lines of small, densely cytoplasmic cells elongate during numerous transverse mitoses (Fig. 7). At the outset, no silica bodies are found in the cells, forming instead at a more advanced stage (Fig. 8). The silica cells increase very little in size, so when the other tissues stretch, they are pulled apart (Fig. 9). There is little difference between the two kinds of silica bodies in early ontogeny. Eventually the stegmatal cell dies.

Although much of our material was drawn from field-collected herbarium specimens, a large part was from greenhouse-grown specimens. There is no indication that our greenhouse conditions affect the presence of silica. Beside each other under the same cultural conditions we can find species with conical silica bodies, other species with spherical bodies, and yet other species without stegmata. This contradicts any suggestion of an immediate environmental cause for the various character states. The character states are inherited and largely independent of the immediate environment.

It is tempting to consider the silica cells in relation to the epiphytic life form. The matter in which the epiphytes grow is mainly of organic origin and often very, very sparse. One would expect that for epiphytes the silicon level in the substrate is much lower than for ground orchids. If the accumulation of silicon in stegmata is simply a storage of a waste substance, a predominance of ground orchids would be expected among those containing stegmata.

We have tried to classify our plant material with respect to epiphytism. This is very difficult, since many species that grow in trees in established forest will thrive on the ground in clearings. In many cases it is almost impossible to decide where a particular species is naturally at home. Figure 10 should be regarded with due reservations.

By coincidence, there is an almost equal number of terrestrials and epiphytes in our material. The figures do not indicate that epiphytes are poor in silica cells. On the contrary, the special bodies are found exclusively in epiphytic species. When the two kinds of silica cells are considered together, there are about twice as many epiphytes as ground orchids containing stegmata. On this basis, could it be that stegmata are of adaptive significance in relation to epiphytism? No such suggestion has been made so far, but silicification of tissues in other plant groups is known to occur in places where there is a strong transpiration stream such as root endodermis (Bennett, 1982), supporting tissues of rhizomes (Sangster, 1983), etc. and has been connected with increased drought resistance. The form of silicon in these bodies is thought to be a silica-gel (e.g., Kaufman, Petering, and Smith, 1970; Perry, Hodson, and Sangster, 1984), which is a substance known for its capacity to absorb water. It is thus reasonable to suggest that stegmata have a role in the water economy of the plant. Considering that epiphytic orchids in many respects are xerophytic, could stegmata perhaps be considered as a xerophytic specialization?

It is impossible to evaluate this idea without clarifying the evolutionary history of stegmata. Fortunately, this can be done without resorting to adaptational argumentation, because there is already a clear-cut framework of orchid phylogeny

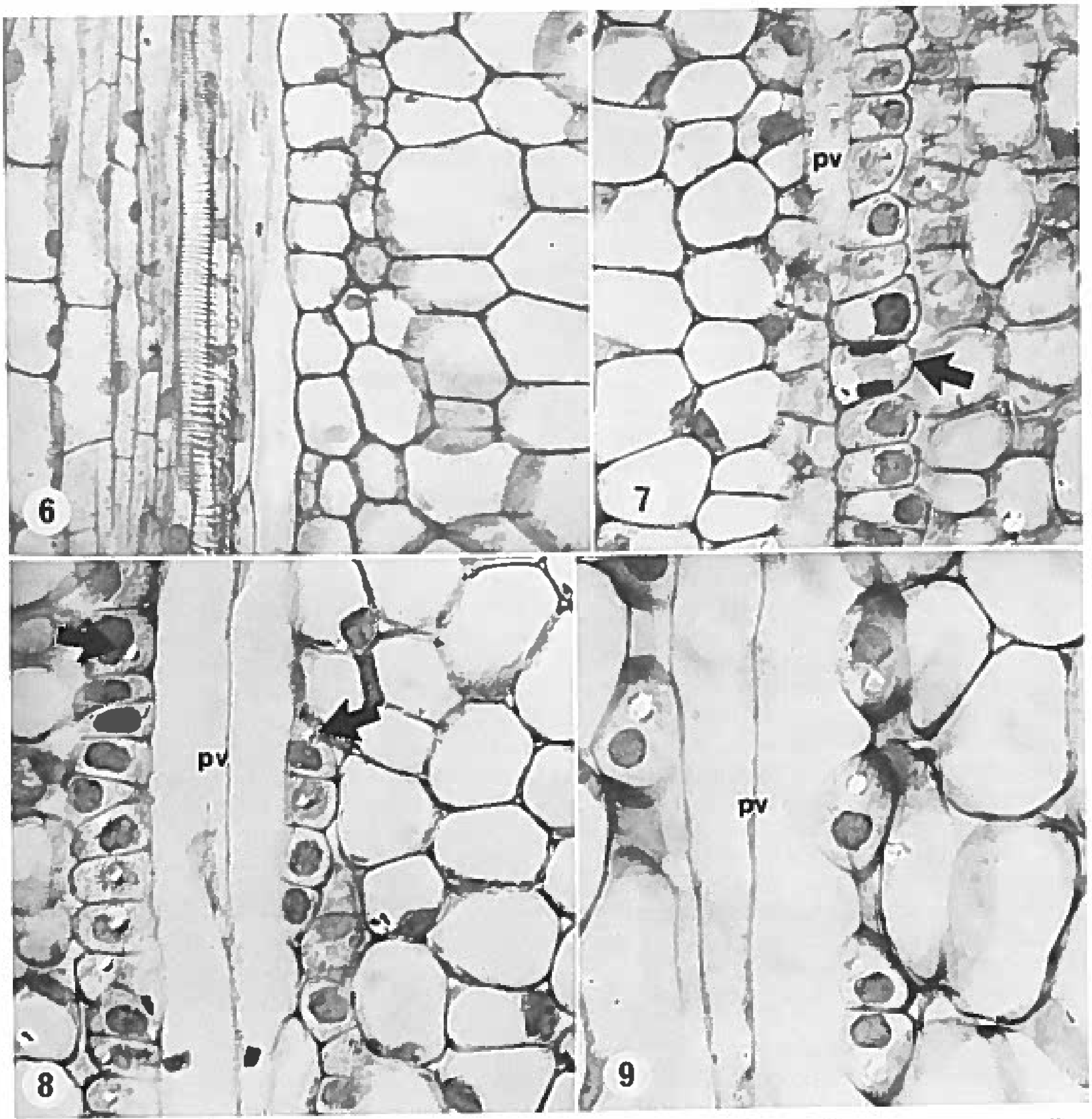

Fig. 6-9. Orchids without and with development of stegmata. 6. Vascular strand in a species without stegmata. Adjacent parenchyma not specialized. Longitudinal glycolmethacrylate sections of leaf, toluidine blue O, *Bulbophyllum ecornutum* (J. J. Smith) J. J. Smith (GT 5528). Interference contrast microscopy. ×347. 7. Early stage in stegmatal development. Parenchyma adjacent to a provascular element (pv) divides transversely (arrow) into a file of small cells. No silica present. Crystals seen in other cells are calcium oxalate. Longitudinal glycolmethacrylate section of leaf, toluidine blue O, *Flickingeria pallens* (Ridley) Hawkes (GT 6461). Interference contrast microscopy. ×872. 8. Same as Fig. 7. Later in development, small silica bodies form in the stegmata (arrows). 9. Same as Fig. 7-8. While other tissues elongate extensively, the small stegmata become separated.

based on characters of the flower. The adnation of stamens and styles into a compound organ, the column, is considered a uniquely derived condition defining all orchids as a monophyletic group.

We have a well-defined, minor group with two functional stamens, the Cypripediaceae (subfamily Cypripedioideae of Dressler, 1981), or slipper orchids. The majority of orchids have only one stamen, the monandrous orchids, sometimes referred to as Orchidaceae in the strict sense. The two groups do not share any stamen, so both must be derived from a group with at least three functional stamens. This condition is found in a single genus of extant orchids, *Neuwiedia*. The assumed trend is toward a reduction in the number of stamens, in accordance with Dollo's law which states that a lost organ is unlikely to reappear in the same form. The unlikely possibility that monandrous orchids or diandrous orchids have developed more than once is disregarded in this hypothesis.

Figure 11 shows the monophyletic groups as nested sets, one within the other. The cones depict-

	terrestrial	epiphytic
▲	16	18
★	0	20
○	15	16
—	27	8
total	58	62

Fig. 10. A tentative distribution of 120 investigated orchid species with respect to habitat preference, compared with their content of silica cells. ▲ = conical silica bodies. ★ = spherical silica bodies. ○ = supporting tissues present and silica cells lacking. — = supporting tissues lacking.

ed should be imagined as wrapped around a branch of the phylogenetic tree, and containing all descendants of a single phyletic line, that is, containing a clade. The monandrous and the cypripedioid orchids are both considered clades, derived from triandrous ancestors. Present day triandrous orchids have no uniquely derived character states. They simply comprise the orchids remaining after the two distinct clades are segregated. On the basis of this phylogenetic hypothesis an out-group comparison is possible in the Orchidales. The Orchidaceae can be in-group with Cypripediaceae and the "rest-group," Apostasiaceae, as out-group. Accordingly, the character states of stegmata are distributed as indicated (Fig.11). It is immediately seen that conical bodies are present in in-group as well as out-group, an indication that conical silica bodies represent the ancestral character state. Lack of stegmata is a character condition noted in the two clades but not in the rest-group. Again according to Dollo's law, it is more likely that the silica cells have been lost twice than that conical bodies have been acquired several times. So lack of stegmata must be considered derived compared to conical stegmata. The spherical bodies comprise another derived state, acquired within the clade of the monandrous orchids (Fig. 11). In view of the similar ontogeny of the two kinds of silica cells, it is most likely that a direct evolution from conical to spherical shape has taken place, rather than assuming an intermediate stage without stegmata.

Further information can be gained by viewing in more detail the phylogeny of the monandrous orchids as outlined in Rasmussen (1983, Figure 2), but it is not very different from most recent classifications (e.g. Garay, 1960; Dressler, 1981). Without entering too much into the details of this hypothesis of orchid phylogeny, the distribution of stegmatal character states can be visualized in a very informative manner (Fig. 12).

On the assumption that the scheme is true, there is nothing in it to contradict the hypothesis that the conical state is ancestral and convex. In other words, every species with conical silica bodies may well descend from other species with conical silica bodies.

The spherical bodies show a surprising pattern of distribution. The orchid groups that contain them are Vandeae and Eriinae, Dendrobiinae, and part of Podochilinae in the Epidendreae (Dahl Møller and Rasmussen, 1984). On the basis of this phylogenetic diagram (Fig. 12), the condition must have arisen twice. The characters on which the diagram is constructed and the distribution data about stegmata give conflicting evidence at this point. If instead the spherical silica bodies were presupposed to be monophyletic, this would entail a hypothesis involving parallel evolution in a number of other characters. Until further is known, diphyletic origin of the spherical silica bodies appears most likely (Fig. 13).

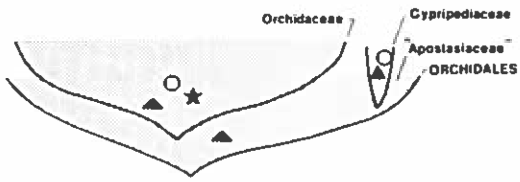

Fig. 11. Diagram of the major orchid groups, reflecting their supposed phylogenetic relationships. The relevant character states of silica cells are indicated by symbols in each clade. Symbols as in Fig. 10.

The most likely conclusion from this study is that stegmata with conical bodies occurred in the most recent ancestor of orchids, an ancestor which in all likelihood was terrestrial. Stegmata have been lost during the evolution of some orchid groups but changed into a different, spherical shape in one or perhaps two groups of advanced, epiphytic orchids. The history of stegmata does not indicate any connection with epiphytism or xerophytism that could not be accidental.

It has often been pointed out, for instance by Gould and Lewontin (1979), that it makes little sense to discuss ancestral character states with respect to their adaptive importance under actual conditions. The conditions under which they have become established may be very different from those of the present. In view of this, further speculations about the origin of the conical bodies may be dismissed, and effort concentrated on the spherical silica bodies and the level where they became established.

The fact that spherical bodies may have arisen twice makes it reasonable to search for indications

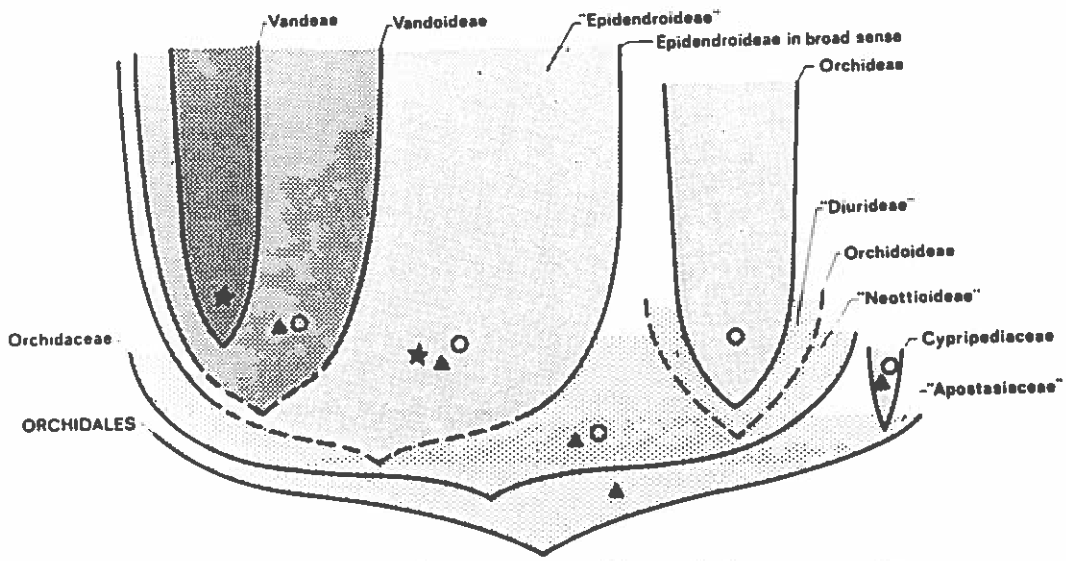

Fig. 12. More detailed diagram as in Fig. 11, with character states of silica cells indicated. Symbols as in Fig. 10. Phylogenetic diagram from Rasmussen, 1985.

of parallel evolution, for instance revealed by small differences in structure or ontogeny. A confirmation of parallel evolution would markedly support a view of silica cells as a trait under selection pressure.

The function of stegmata is not yet clarified. However, this study of the distribution of character states has helped to clarify the questions that should be considered in future research of that structure.

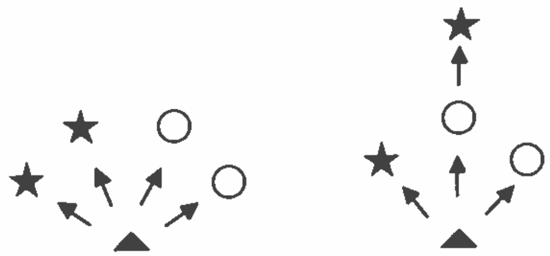

Fig. 13. Two hypotheses for the evolution of silica cells within Orchidaceae. In view of the apparently similar ontogeny of the two kinds of silica cells, it is most likely that a direct evolution from conical to spherical shape has taken place (left) rather than assuming an intermediate state without stegmata (right). Symbols as in Fig. 10.

LITERATURE CITED

BENNETT, D. M. 1982. Silicon deposition in the roots of *Hordeum sativum* Jess., *Avena sativa* L., and *Triticum aestivum* L. *Ann. Bot. (London)* 50: 239-245.

DAHL MØLLER, J., AND H. RASMUSSEN. 1984. Stegmata in Orchidales: character state distribution and polarity. *Bot. J. Linn. Soc.* 89: 53-76.

DRESSLER, R. L. 1981. *The orchids: natural history and classification.* Harvard University Press, Cambridge, Massachusetts.

GARAY, L. A. 1960. On the origin of the Orchidaceae. *Bot. Mus. Leafl.* 19: 57-96.

GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 205: 581-598.

KAUFMAN, P. B., L. B. PETERING, AND J. G. SMITH. 1970. Ultrastructural development of cork-silica cell pairs in *Avena* internodal epidermis. *Bot. Gaz. (Crawfordsville)* 131: 173-185.

KOHL, F. G. 1889. *Anatomisch-Physiologische Untersuchung der Kalksalze und Kiselsaüre in der Pflanze.* Elwert, Marburg.

MOLISCH, H. 1920. Aschenbild und Pflanzenverwandtschaft. *Akad. Wiss. Wien Sitzungsber., Math.-Naturwiss. Kl.*, Abt. 1 129: 261-294, tables I-III.

PARRY, D. W., M. J. HODSON, AND A. G. SANGSTER. 1984. Some recent advances in studies of silicon in higher plants. *Philos. Trans.*, Ser. B 304: 537-549.

PRIDGEON, A. M., AND W. L. STERN. 1982. Vegetative anatomy of *Myoxanthus* (Orchidaceae). *Selbyana* 7: 55-63.

———, AND N. H. WILLIAMS. 1979. Anatomical aspects of *Dresslerella* (Orchidaceae). *Selbyana* 5: 120-134.

RASMUSSEN, F. N. 1985. Orchids. Pages 249-274 *in* R. M. T. Dahlgren, H. T. Clifford, and P. F. Yeo [eds.], *The families of the monocotyledons: structure, evolution, and taxonomy.* Springer Verlag, Berlin.

ROSSO, S. W. 1966. The vegetative anatomy of the Cypripedioideae (Orchidaceae). *Bot. J. Linn. Soc.* 59: 309-341.

SANGSTER, A. G. 1983. Anatomical features and silica depositional patterns in the rhizomes of the grasses *Sorghastrum nutans* and *Phragmites australis*. *Canad. J. Bot.* 61: 752-761.

SIEBE, M. 1903. *Über den anatomischen Bau der Apostasiinae.* Heidelberger Verlagsanstalt, Heidelberg.

WANNTORP, H.-E. 1983. Historical constraints in adaptation theory: traits and non-traits. *Oikos* 41: 157-160.

WITHNER, C. L., P. K. NELSON, AND P. J. WEJKSNORA. 1974. The anatomy of orchids. Pages 267-347 *in* C. L. Withner [ed.], *The orchids: scientific studies.* John Wiley & Sons, New York.