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THE PHLOEM SUPPLY TO THE NECTARIES

BY

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The physiological work on nectaries done in this Laboratory (Frey-Wyssling, 1933; Frey-Wyssling und Agthe, 1950; M. Zimmermann, 1952, 1953, 1954) has shown that *nectar is secreted phloem sap*. Although its composition is modified by the activity of the glands (Frey-Wyssling, Zimmermann und Maurizio, 1954), there exists a direct connection with the sugar translocation in the phloem. Therefore, an extensive study has been undertaken with the aim of elucidating whether there is any anatomical evidence of an association of the nectaries with phloem strands. For this purpose extrafloral (Agthe, 1951) and floral nectaries (E. Frei, 1955) have been investigated. The result is that every nectary is provided with a direct phloem supply either by neighbouring vascular strands or by special glandular traces.

Glandular traces

It has been known for a long time that highly differentiated nectaries contain some kind of a translocation tissue, but its true nature has never been identified. Bonnier (1879, p. 119. 134) speaks of a 'faisceau peu différencié', Stadler (1886) of 'cambiform' cells, Radtke (1926) of 'langgestreckte leitparenchymatische Elemente', Fisher (1928) of 'suggestive tissue', Daumann (1935) of 'xylem parenchyma" and Moore (1936) of 'provascular strands'. The view of some authors (Schniewind-Thies, 1897; Böhmker, 1917; Arber, 1936), that phloem might be involved, is refuted by Sperlich (1939, p. 66): 'Die Annahme, die teilweise Leptomelemente der betreffen den Gefässbündel in Anspruch nimmt, wird sich kaum befriedigend begründen lassen'.

In many extrafloral nectaries (*Ricinus*, *Pithecolobium*, *Cassia* etc., J. G. Zimmermann, 1932) and in some floral nectaries (*Ranunculus*, Arber 1936; *Fritillaria*, Agthe 1951) the glandular trace is a complete vascular strand with phloem and xylem. As compared with such a vascular supply the glandular traces without tracheids seem to be reduced, so that in general they are thought of as degenerated vascular strands. This view fits into the endeavour to interpret the nectaries morphologically wherever possible as abortive floral organs or rudimentary leaves. But an accurate study of the vascularization problem of the nectaries suggests other possibilities of interpretation.

Evidence of phloem

Along the stalk of the leaves of *Impatiens roylei* small teeth are found which represent extra-floral nectaries. Below the secretory tissue there are groups of sieve tubes and companion cells (Fig. 1). Similar

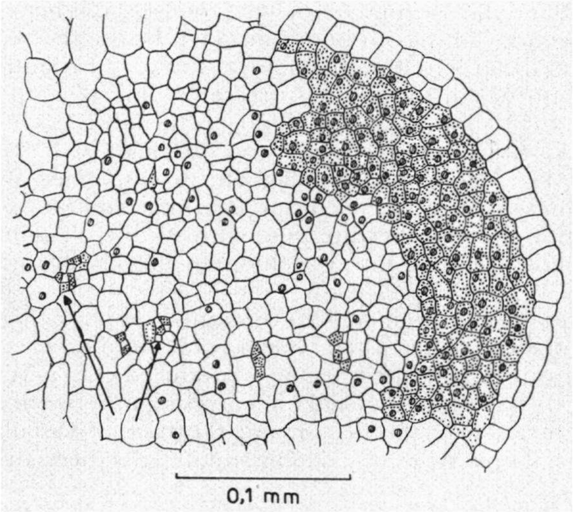

Fig. 1. Nectary of the leaf of *Impatiens roylei.* Phloem groups below the secretory tissue; → companion cells and sieve tubes. (Agthe, 1951).

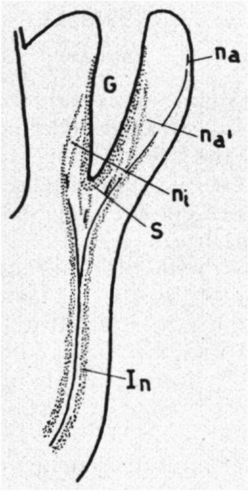

Fig. 2. Nectary in the cyathium of *Euphorbia pulcherrima.* The xylem (continous line) of the glandular trace does not reach the secretory tissue (S) which is supplied only by phloem (dotted). n_a, $n_{a'}$ outer strand; n_i inner strand; G cavity containing nectar; I_n glandular trace. (Agthe, 1951).

pictures have been found in many floral nectaries and reproduced by photomicrographs which even show sieve plates (Plate I, Fig. 1 and 2). Therefore, the nectaries contain phloem elements in a similar way as hydathodes are provided with tracheids.

The big nectaries in the cyathium of *Euphorbia pulcherrima* show a very conspicuous glandular trace consisting of xylem and phloem. But the xylem does not enter into contact with the secretory tissue, which is only reached by phloem bundles. The outer xylary strand avoids the glandular region completely, whilst the inner one becomes interrupted and vanishes at some distance below the secretory parenchyma; on the other hand, the phloem strands surround and enclose the cavity into which the nectar is secreted (Fig. 2).

E. FREI (1955) finds that the floral nectaries of 91 out of 160 investigated dicotyledonous species are supplied with pure phloem strands. In 12 cases only is the phloem accompanied by xylem. In the remaining 57 cases the nectaries are small and without a special vascularization because they are in touch with the phloem of adjacent vascular bundles leading into the different flower organs.

Physiology

These anatomical statements are sustained by physiological investigations: In the rare cases where xylem comes into direct contact with the excretory tissue a diluted nectar is produced. FREY-WYSSLING and AGTHE (1950) have found a striking correlation between the average sugar concentration of the nectar and the type of vascularization of the nectaries. Three types of vascular supply have been distinguished:

Vascular supply to the nectary	*Examples*
1) exclusively by phloem	*Euphorbia pulcherrima* (cyathium) *Abutilon striatum* (sepals) *Impatiens roylei* (leaf stalk)
2) by phloem and xylem	*Ranunculus spec. div.* (petals) *Ricinus communis* (cotyledo, leaf)
3) predominantly by xylem	*Fritillaria imperialis* (perigone)

In the first group nectars with up to 50 % sugar are produced, whereas in the third group nectar with only 8 % sugar is secreted, which is so diluted, that it is not even accepted by the bees. The second group holds an intermediate position between those two extreme cases. This relationship shows that the glandular trace represents no 'suggestive tissue' nor a 'provascular strand', but active phloem.

The established correlation is further proved by the fact that foreign substances introduced into the phloem are secreted by the nectaries (fluorochromes, AGTHE 1951; pentoses, M. ZIMMERMANN 1953; radioglucose, FREY-WYSSLING, ZIMMERMANN und MAURIZIO 1954). The function of these glands consists, therefore, in the elimination of substances from the phloem.

Ontogeny of the glandular phloem

The nectaries with special phloem strands (in German: drüseneigenes Phloem) deserve careful interpretation.

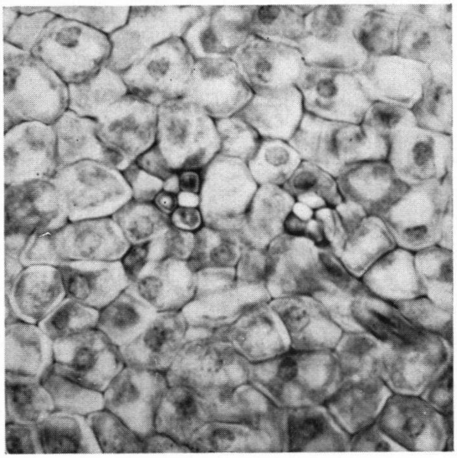

Plate I, Fig. 1. Phloem in the lateral floral nectary of *Brassica arvensis*. Cross section of sieve tubes and companion cells.
(× 600, phot. E. FREI).

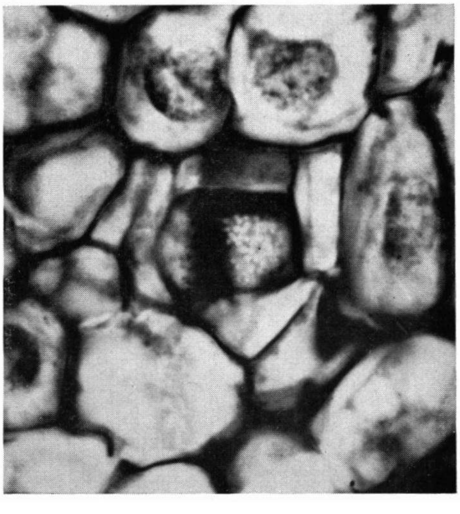

Plate I, Fig. 2. Phloem in the floral nectary of *Knautia arvensis*. Sieve plate.
(× 1400, phot. E. FREI).

In many instances the glandular traces of floral nectaries branch off from vascular strands supplying sepals (Malvaceae, Fig. 3) or stamens (Fumariaceae; Leguminosae, Fig. 4). Even more frequently, the glandular phloem is given off from vascular bundles of the carpels (*Calluna vulgaris*, Fig. 5; *Convolvulus sepium*, Fig. 6), although a great deal of the flat or ringshaped nectaries of the receptacle, the so called discs, show no special phloem strands (e.g. Cornaceae, Araliaceae), because their secretory tissue is in contact with the phloem of vascular bundles passing in their vicinity.

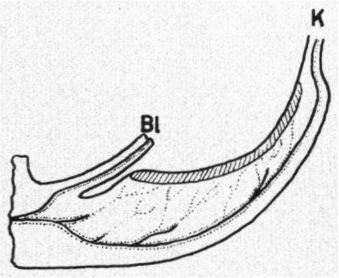

Fig. 3. Nectary on the sepals of *Abutilon striatum*. Bl petal, K sepal. (AGTHE, 1951).

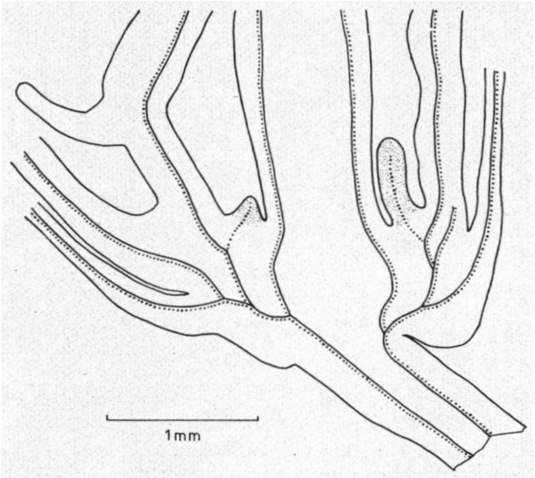

Fig. 4. Floral nectary of *Phaseolus vulgaris*. The glandular traces are phloem ramifications of the staminal vascular strands. (E. FREI, 1955).

Only in some Umbelliferae (e.g. *Heracleum*) are glandular strands observed which branch off from bundles in the axis; as a rule the phloem strands do represent ramifications of vascular bundles which belong to the flower organs. In this respect the term 'glandular trace' is perhaps not very satisfactory, but it is much better than such erroneous designations as 'suggestive tissue' or 'provascular strands'.

As a matter of fact these traces are neither degenerated 'suggestive', nor undifferentiated 'provascular' bundles, because there is a fully developed phloem with active sieve tubes. Provascular strands can, it is true, be observed during the development of the nectaries; but in full-grown glands the meristematic provascular cells differentiate into sieve tubes, companion cells and phloem parenchyma. In general the sieve tube members are short and rather broad. There is an uninterrupted series of phloem cells on the longitudinal section. If, by way of exceptions, it is accompanied by xylem, the strand of tracheids appears to be interrupted towards its end (Fig. 2) and the phloem strand progresses much further in the direction of the secretory tissue.

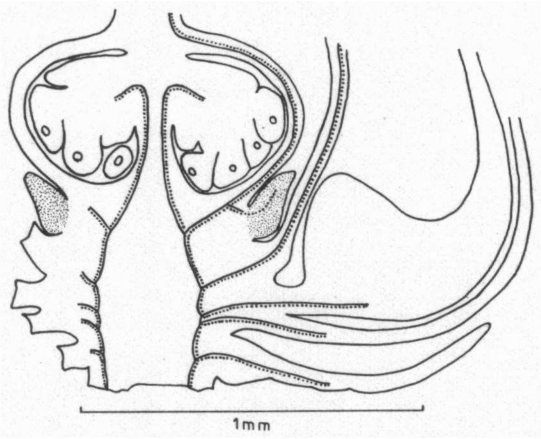

Fig. 5. Floral nectary of *Calluna vulgaris*. The glandular trace derives from the phloem of a carpellary bundle. (E. Frei, 1955).

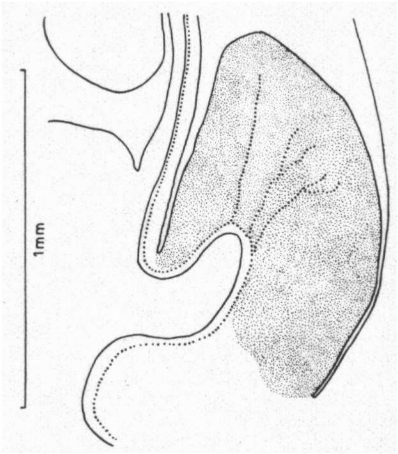

Fig. 6. Floral nectary of *Convolvulus sepium*. Phloem supply deriving from a carpellary bundle. (E. Frei, 1955).

These facts recall the origin and development of the primary vascular tissue in the leaf (Esau, 1943); the shortening of the sieve tube elements also is a characteristic of the ending of the veins in leaves. As long as the xylem does not form an uninterrupted series of tracheids, it cannot function. Therefore, even if there are some isolated vascular cells in the glandular strand, the differentiation of the xylem remains incomplete, whilst the phloem evolves into functioning proto- and metaphloem.

PHYLOGENETIC CONSIDERATIONS

The fact that the glandular trace is a tissue for active sugar translocation rules out the possibility that it represents an abortive vascular strand. On the contrary it must be considered as a progressively evolving phloem bundle, because it is a common feature in the derived and complicated glands, whilst the more primitive nectaries have no such traces.

Although nectaries already occur in certain ferns (e.g. *Pteridium aquilinum*) they are not in every case phylogenetically very old organs. J. G. Zimmermann (1932) states that extrafloral nectaries are much more frequent in the Sympetalae than in the corresponding ancestral Choripetalae. He concludes, therefore, that extrafloral nectaries have appeared independently in different families, so that they are of a polyphyletic origin.

As to the floral nectaries, various progressive series can be observed. In the Umbelliflores the flowers of the more primitive families (Cornaceae and Araliaceae) investigated by E. Frei (1955) have glands without traces, whilst in the evolved family of the Umbelliferae there are conspicuous strands, already described by Bonnier (1879) as 'poorly differentiated bundles.'

A similar series exists within the Papilionaceous Leguminosae: In many genera the glands are flat and supplied by the phloem of the vascular strands of the stamens (*Robinia*, *Astragalus*). In other genera the glands are characterized by a zygomorphous swelling of the glandular ring and a predominance of the phloem in the neighbouring vascular strands (*Trifolium*, *Medicago*, *Melilotus*, *Hippocrepis*). In *Onobrychis* and *Hedysarum* short phloem traces branch off from the vascular strand (Fig. 7). These glandular traces grow longer in

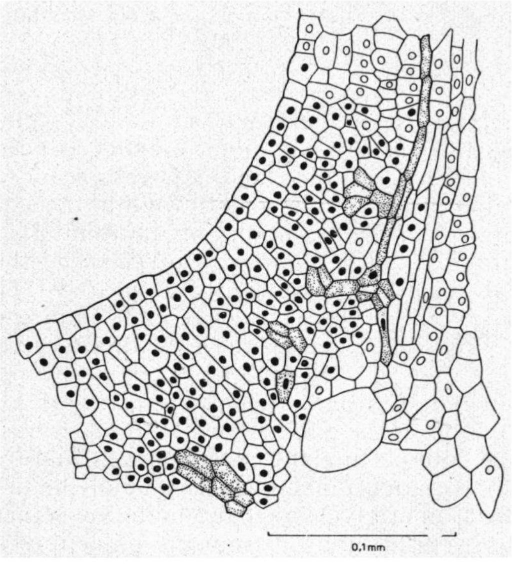

Fig. 7. Floral nectary of *Onobrychis vicifolia*. Phloem supply by a proliferation of the staminal phloem. (E. Frei, 1955).

Anthyllis, *Phaca*, *Lathyrus* and *Vicia*. The highest specialisation is reached in the nectary of *Phaseolus*; there is a beautiful glandular ring with ten lobose tips, each supplied by a phloem trace. These phloem strands derive from the ten staminal vascular bundles (Fig. 4 and 8). The trace differentiation of these nectaries is so conspicuous that they have been interpreted as the rudiment of a second staminal ring lost in the course of the phylogenetic evolution (MOORE, 1936). Since the strands of the two rings belong to the same vascular bundle and, therefore, do not alternate, such an interpretation seems, however, rather unlikely. Instead of a regressive rudimentary organ, the nectaries of *Phaseolus* seem rather to represent the terminal stage of the evolution by which dependent disc-shaped nectaries have been transformed into large and independent secretion organs.

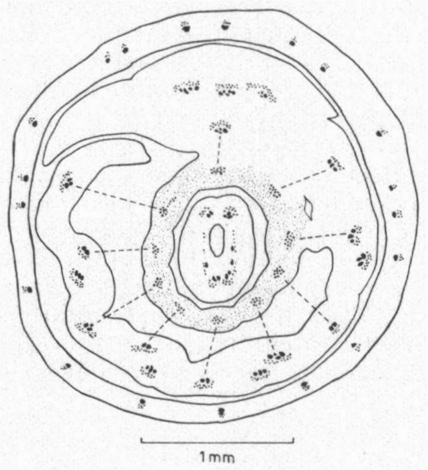

Fig. 8. Section cut across the base of the flower of *Phaseolus vulgaris* showing the correspondence (----) of the staminal and the glandular traces (cf. Fig 4). (E. FREI, 1955).

Highly evolved nectaries are organs in their own right, and it seems to me that they do not necessarily represent staminodia or other reduced flower organs. It is true that in many cases the glands are really reduced stamens as in *Parnassia*. But then the traces descend down into the axis of the flower where they branch off from bundles of the stem. It is of special interest that in the glandular staminodia of *Parnassia* the xylem of the original vascular strand has completely disappeared. The same is true for the nectary of *Salix*, whose trace ascends from the pedicel, so that this gland is said to be a rudiment of the disappeared perianth (Fig. 9).

So it is evident that the function of the glandular trace as a path for the translocation of sugar solutions is the only decisive feature we must take into consideration when interpreting the morphological nature of nectaries. For the functioning of such a gland it is irrevelant whether the phloem trace is derived from an original vascular bundle or whether it has evolved neoplastically by branching off from the phloem of a neighbouring vascular bundle. The study of E. Frei (1955) shows that the second case is the common way of supplying the nectaries with phloem strands whilst the first possibility is rather rare.

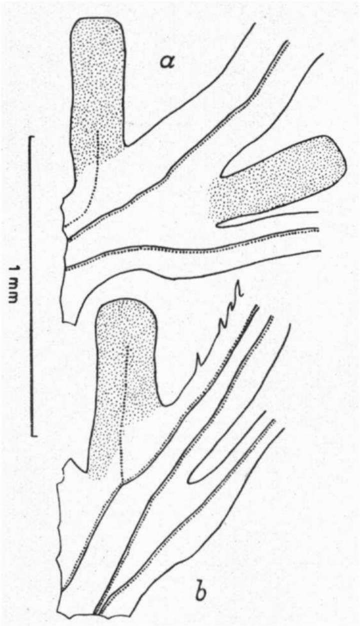

Fig. 9. Floral nectaries of *a. Salix alba* ♂ and *b. Salix caprea* ♂. The phloem strand descends below the flower base. (del. E. Frei).

In this connection the theories on the nature of the Cruciferous flower deserve reconsideration. In the genera *Brassica*, *Cardamine*, *Barbaraea* and others, there are four nectaries. The two lateral ones display a beautiful phloem supply, whilst the median ones show no translocation tissue whatsoever. As a result, only the lateral glands secrete nectar profusely whereas the median nectaries remain almost dry (E. Frei, 1955).

Motte (1946) has found teratological transformations of these nectaries into small sterile carpels. Based on this observation he concludes that the nectaries represent reduced buds, and as a consequence the Cruciferous flower is interpreted as a reduced inflorescence. Chaudefaud (1953) accepts this view of an 'intra-inflorescence'. In *Brassica arvensis* the phloem traces of the lateral nectaries branch off from the vascular strands of the petals and stamens. At the bottom of the median glands there are some phloem strands coming from the vascular bundle of the sepals, but they do not penetrate into the nectary and terminate at some distance from the secretory tissue. It is difficult to attribute the rank of buds to these nectaries by virtue of such a 'vascularization'. Since in many genera of the Cruciferae there is only a ringshaped disc, the nectaries of *Brassica* etc. must be considered as segments of that ring which have evolved to such a size that a special phloem supply has become necessary. In one pair of the glands ramified phloem strands have grown into the enlarged tissue and guarantee an abundant secretion, whilst the other pair has been left without such a supply so that its function is defective.

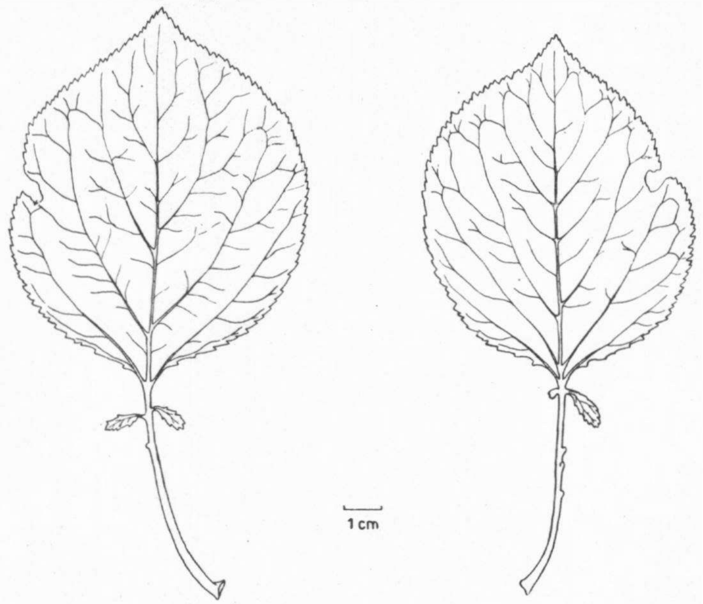

Fig. 10. Virescence of the extrafloral nectaries of *Prunus armeniaca* clone Luizet (del. E. ANNEN).

The virescence of these nectaries and their proliferation to small sterile carpels is no proof that they are buds. Similar transformations of extrafloral nectaries into small leaves are frequent. In the case of *Prunus armeniaca* such teratological formations might be interpreted as leaflets of an originally pinnate leaf (Fig. 10). But we know examples where such an interpretation is impossible. The trifoliolate leaf of *Hevea brasiliensis* bears three nectaries at the end of the leaf stalk (Fig. 11*a*); in a certain clone the median gland is rather often transformed into a small leaflet (Fig. 11*b*) with an orientation opposite

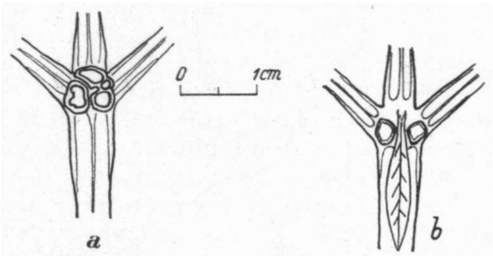

Fig. 11. *a*. Extrafloral nectaries at the insertion of the three leaflets on the petiole of *Hevea brasiliensis*. *b*. Virescence of the median nectary in clone Avros 163. (FREY-WYSSLING, 1933).

to that of the normal leaflets. In this case, there is no possibility of associating the additional leaflet with any lost member of the leaf. It is true that sometimes quadrifoliolate *Hevea* leaves occur; but then the fourth leaflet originates as a lateral outgrowth of the end of the leaf stalk (Frey-Wyssling, 1931). So the additional leaflet in Fig. 11*b* must be considered as a real monstrosity caused by some wrong hormonal impulse applied to the meristeme which normally evolves to a crateriform nectary.

Therefore, one must be careful in using teratological features of nectaries for phylogenetic considerations. In the special case of the Cruciferous flower it seems rather unlikely that the nectaries correspond to reduced buds.

Conclusion

Primitive nectaries consist of a flat glandular region which is supplied with sugar sap by the phloem of a neighbouring vascular strand. The distance between the phloem and the secretory cells is small.

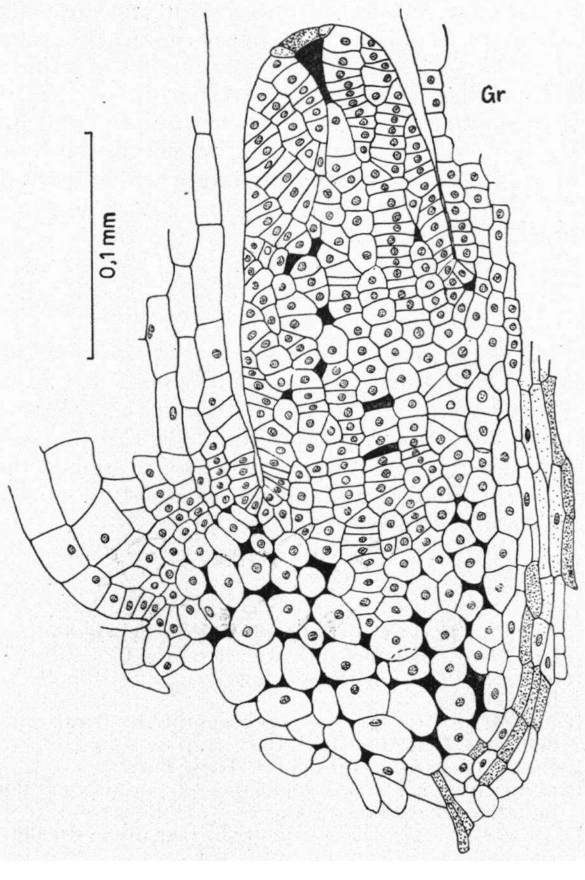

Fig. 12. Floral nectary of *Taraxacum officinale*. Black spaces = intercellular system which is in connection with the apical pore (del. E. Frei).

However, there seems to be a tendency—which is manifest in many families—to enlarge the glands. In this way eminences or even protuberances are formed. Such an evolution increases the distance between the phloem and the secretory tissue so that the sugar sap supply is impeded. This unfavourable effect is counterbalanced by a proliferation of the phloem into the glandular area whereby the sieve tubes come near to the secretory tissue or even penetrate it. This process is a general feature so that almost every big nectary displays a special phloem supply. In this way the nectaries become self-reliant organs with their own glandular trace. This phloem trace must be considered as a functional necessity and it is wrong to attribute it to rudimentary or provascular strands.

Yet there are some exceptions of large-sized nectaries without a special phloem supply, such as the median nectaries in the Cruciferous flowers and the—for a flower of the Compositae—exceptionally large glands of *Taraxacum officinale*. In those cases the secretion is poor, or there is an extensive intercellular system by which the nectar reaches the stomata-like pores of the epidermis (Fig. 12). Seemingly, the number of cells between the sieve tubes and the surface of the secretory tissue cannot exceed a certain figure if an abundant secretion has to be guaranteed. In many cases this figure is found to be about ten cells. If it increases considerably, so that the way for the sugar translocation through the parenchyma of the fundamental and the secretory tissue becomes unduly lengthened, the secretion is hampered. It would be of interest to know the limiting factor which slows down the physiological sap translocation from cell to cell in such a way that it becomes impracticable across a series of too many cells.

SUMMARY

Large nectaries, whose secretory tissue is developed at some distance from neighbouring vascular strands, are usually provided with a glandular trace. Very often this strand consists of pure phloem with active sieve tubes, companion cells and phloem parenchyma. Therefore, the glandular trace cught to be looked upon, in the first place, as a functional tissue and not as a rudimentary vascular bundle or an undeveloped provascular strand.

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