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OBSERVATIONS ON THE STOMATAL APPARATUS OF ORONTIUM AQUATICUM (ARACEAE)

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ABSTRACT

The stomatal apparatus of *Orontium aquaticum* is confined to the upper epidermis of the leaf and consists solely of two guard cells, with no accompanying subsidiaries. The guard cells, which possess flangelike thickenings of the wall flanking the stomatal pore, are sunken and largely obscured by the overlapping ordinary epidermal cells. *Lysichitum* and *Symplocarpus*, genera closely related to *Orontium*, also lack subsidiaries. This indicates that the stomatal complex within the Araceae is probably more diverse than was previously thought.

Introduction

In a previous paper by the author (GREAR 1966) devoted primarily to the cytology and migrational history of *Orontium aquaticum* L., mention was made of the need for further studies in this monotypic genus, especially in connection with various aspects of morphology.

STEBBINS and KHUSH (1961), in a pioneering survey of the stomatal complex of a large number of monocots, found that genera and even families are usually constant in having a characteristic stomatal complex and that such morphological data obtained from vegetative portions of a plant could be of use in classification.

WEBBER (1960) surveyed the epidermal structure and stomatal apparatus of representatives of a wide range of terrestrial Araceae; however, neither *Orontium* nor any other member of subfamily Calloideae of the Araceae was included. His survey, based upon representatives of 21 genera, indicated that stomata may be confined to the lower surface of the leaf or may be present on both surfaces. In reference to the subsidiaries surrounding the guard cells, it was found that the number varied from two to four, six, eight, or more. Finding considerable variation in the number and arrangement of subsidiaries associated with stomata, WEBBER concluded that no taxonomically significant conclusions could be drawn from these data.

As mentioned previously, STEBBINS and KHUSH (1961) later surveyed and classified variation in the organization of the stomatal complex in the leaf epidermis of monocotyledons in general and assessed its value in reflecting phylogenetic relationships. These authors did not refer to the work of WEBBER. They indicated the number of subsidiaries surrounding the guard cells for three named genera of Araceae: *Arisaema*, with two, *Dieffenbachia*, with six or seven, and *Scindapsis*, with eight. A repre-

sentative having four subsidiaries was mentioned, although not by name. None of these belongs to the Calloideae of ENGLER, which, in addition to *Orontium*, includes *Calla*, *Symplocarpus*, and *Lysichitum*. *Lysichitum* was described as having large epidermal cells but the number of subsidiaries was not indicated. Three general classes of stomatal apparatus, based upon the number of associated subsidiaries, if any, were recognized: Class I, with no subsidiaries, Class II, with two, and Class III, with more than two. With the exception of *Arisaema*, the Araceae included by STEBBINS and KHUSH belong to Class III. Class III was considered as exemplifying the generalized (primitive) condition, Class I the most specialized (advanced), and Class II an intermediate condition. The Lemnaceae, represented by a species of *Lemna*, was placed in Class I because of the absence of any subsidiaries whatsoever. This is of interest because the Lemnaceae are generally accepted as representing a group derived from the Araceae through reduction and simplification (WILSON 1960), which would appear to have involved not only the vegetative body and floral features, but the epidermis as well. These various considerations prompted the author to undertake a special study of the epidermis of *Orontium*.

Material and methods

Strips of leaf epidermis from both living and dried specimens, as well as plastic peels of cuticular imprints prepared according to the method of SINCLAIR and DUNN (1961), served as sources of information in the analysis of the structure of the epidermis. These materials were supplemented by transverse freehand sections of leaf blades in the final interpretation of the structural organization of the stomatal apparatus.

Results and discussion

The lower epidermis of the leaf is devoid of stomata, lacks chloroplasts, and is composed of long, somewhat irregular, rectangular cells several times longer than they are broad and oriented in the direction of the long axis of the leaf blade. The cells are plain surfaced (nonpapillose).

The stomatal apparatus of the upper leaf epidermis consists solely of two guard cells containing numerous chloroplasts. The guard cells are manifestly depressed below the level of the ordinary epidermal cells, which lack chloroplasts. The surface area of a pair of guard cells essentially equals that of a single ordinary epidermal cell. In plastic impressions, the guard cell wall thickenings, simulating whole guard cells, appear in surface view to be surrounded by two narrow subsidiaries (fig. 1). Examination of actual epidermal strips, however, indicates that this is not the case. The narrowly rectangular depression beneath which the guard cells are situated is not itself cellular in organization, although it gives the illusion of being so in plastic peel impressions. This illusion is produced in part by the sunken position of the guard cells and in part by the flangelike thickening of the guard cell wall flanking the stomatal aperture. These flangelike or hingelike projections can best be seen in sectional view, where they appear as horns or ledges (fig. 2). *Orontium* exhibits only an upper ledge on each of the guard cells, whereas the guard cells of some plants exhibit both an upper and a lower ledge (ESAU 1953). The long axis of the stomatal depression as seen in surface view is oriented in the same direction as the long axis of the guard cells and their conspicuous thickened wall ledges. The stomatal depressions thus appear as slitlike cavities or

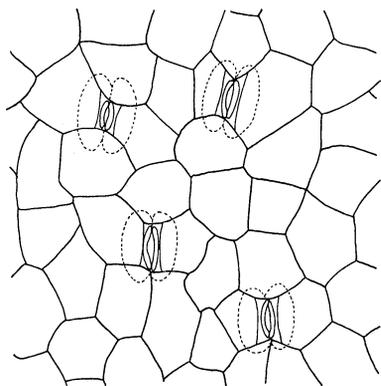


FIG. 1.—Pattern of upper leaf epidermis of *Orontium aquaticum* as obtained by means of plastic peel. The dotted lines represent the obscured portion of the guard cells, which are sunken below the level of the epidermis in surface view ($\times 340$).

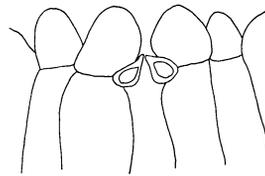


FIG. 2.—Transverse section of stomatal apparatus of *Orontium aquaticum* showing the upper ledge-like thickening of guard cells adjacent to stoma, a portion of papillose upper epidermis, and the palisade parenchyma ($\times 340$).

crypts, in which the liplike wall thickenings of the guard cells are centered and so conspicuous as to resemble entire cells. In reality, however, the sunken guard cells are largely obscured in surface view by the overlapping ordinary epidermal cells, which jut out over them (fig. 2). So erroneous was the initial impression of stomatal structure and organization in *Orontium* obtained by means of plastic peels alone that it seems appropriate to emphasize the importance of judicious use of the technique and its limitations.

The ordinary cells of the upper epidermis are scarcely longer than they are wide, their dimensions essentially equaling the width of the cells of the lower epidermis. The stomata are interspersed among these cells at frequent intervals, usually no more than two to four ordinary epidermal cell-widths apart. The ordinary epidermal cells are conspicuously papillose, each with its convex walls forming a conspicuous mammose contour (fig. 2). In plastic peels, these papillae appear in surface view as circular optical expressions under magnification, the diameter of which varies with the depth of focus. The height of these outer surface convexities essentially equals, or is somewhat less than, the depth of the anticlinal walls. Air, entrapped between the papillae and/or in the stomatal depressions of the upper epidermis, may be the cause of an iridescent sheen observed when the leaves are submerged. The under surface of the leaf epidermis, composed of nonpapillose cells, does not exhibit this sheen on submergence.

It is clear that the stomatal apparatus of *Orontium* lacks subsidiaries. Thus, all three of STEBBINS and KHUSH's classes of stomatal organization are represented by the Araceae. Insofar as is known, this is the first report of a member of the Araceae having no subsidiary cells associated with the stomata. The significance of this finding is not at all clear, although the condition is not unknown in the Arales. Absence of subsidiaries is also the case in *Lemna* (Lemnaceae), as previously indicated. Whether or not the absence of subsidiaries is to be

expected in highly derived plants, such as *Lemna* and *Orontium*, is at this point a matter of speculation. It is clear, however, that no correlation exists between the aquatic habit and the absence of subsidiaries, for many terrestrial monocots are known to lack them.

In this connection, a cursory examination was made of the epidermis of herbarium samples of the allied genera *Lysichitum* and *Symplocarpus*. The following descriptive information was obtained. Stomata are present on both upper and lower surfaces of the leaves of both genera. Subsidiaries do not appear to be associated with the stomatal apparatus, the cells adjacent to the guard cells being of the same size and form as the ordinary epidermal cells. The structure and sunken position of the stomatal apparatus appear to be essentially the same in both genera and to be essentially similar to those of *Orontium*. The pattern of the ordinary epidermal cells of the lower leaf surface of *Orontium*, consisting of long rectangular cells, is dissimilar to that found in *Lysichitum* and *Symplocarpus*, where the cells are more isodiametric in surface view. With the exception of the unique papillose upper leaf surface in *Orontium*, the three genera are otherwise quite comparable in their

epidermal structure, sharing a similar large cell size.

STEBBINS and KHUSH pointed out that the families Araceae, Lemnaceae, Palmae, Pandanaceae, and Cyclanthaceae, which comprise the order Spadiciflorae of ENGLER and GILG (1924), agree, with the exception of the Lemnaceae, in having stomatal complexes with many subsidiaries. They also state that these families agree in having epidermal cells of a small size, except for certain probably highly evolved genera within the Araceae, such as *Lysichitum* and *Arisaema*. In view of the exceptions mentioned, together with the absence of subsidiaries in *Orontium*, *Symplocarpus*, and *Lysichitum*, and the large size of the epidermal cells in these genera also, it may prove instructive to extend the survey of araceous members, among which the Calloideae appear critical. It seems likely that a comprehensive survey may derive greater taxonomic significance from comparative epidermal studies than had previously been supposed.

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