THE FLESHY CORTEX OF ARTICULATED CHENOPODIACEAE

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(Received for publication on March 2, 1963)

Many Chenopodiaceae growing in salt marshes and desert areas show reduction of leaf size and the young branches are built of succulent green internodes which give the young shoots an articulated appearance (Text-Figs. 1, 2; Plate I, Figs. 1–3).

Bentham (1858), de Bary (1877), Hooker (1884), Ganong (1903), Cross (1909) and Schischkin (1936) simply describe these plants as being aphyllous, or almost so, and as having stems with a green fleshy cortex. However, the peculiar structure of the articulated stems of these plants, whose leaves are variously reduced, caused many plant morphologists to interpret the cortex as being a tissue which has been derived from the leaves. So, for instance, according to Dangeard (1887–1888), Monteil (1906), Leysle (1949), Backer (1949) and Keller (1951), the fleshy cortex developed by fusion of the opposite leaves (or only their sheaths) and their adnation to the stem.

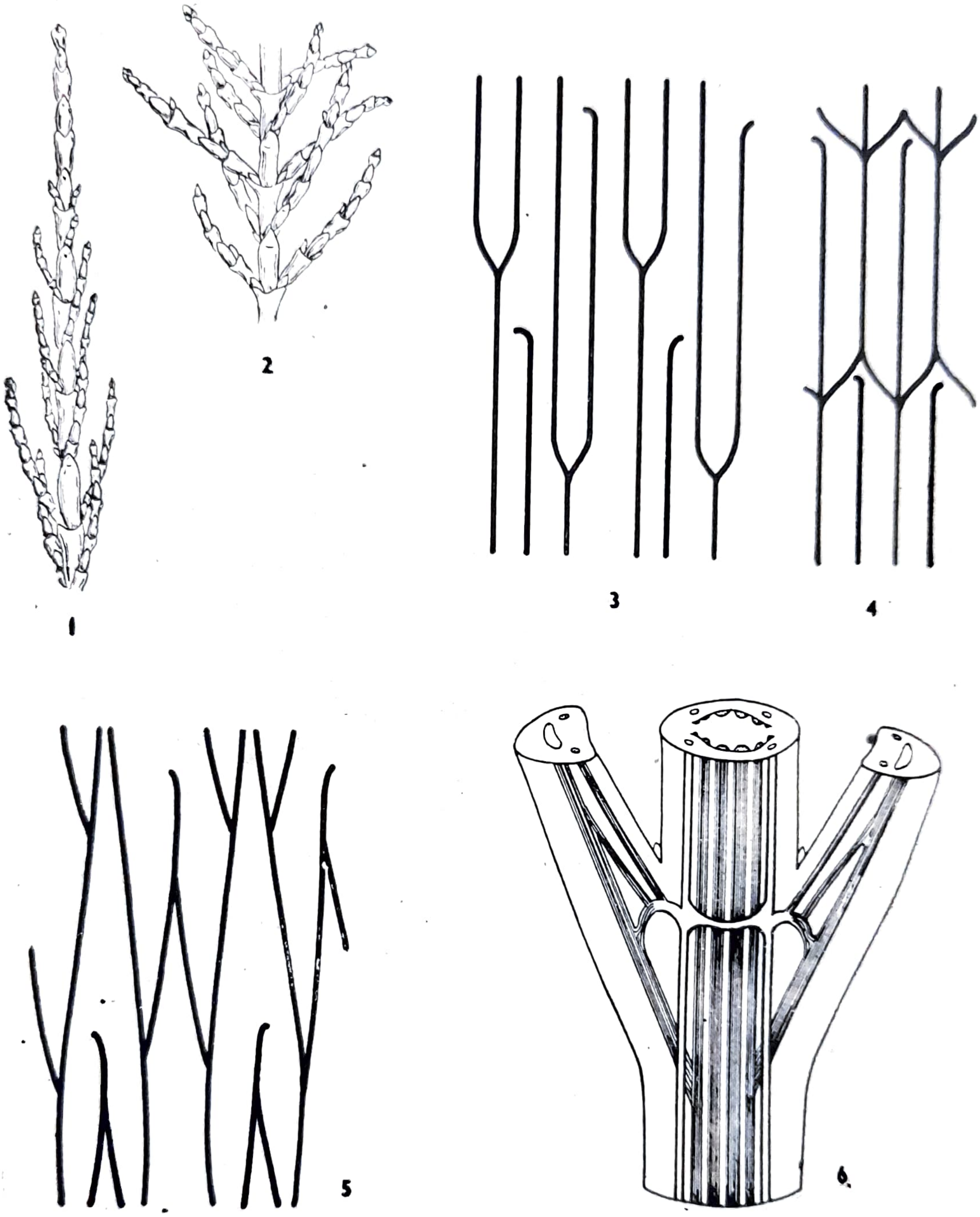
Other attempts to interpret the origin of the cortex as being foliar were made by Duval-Jouve (1868), Cooke (1911), de Fraine (1912) and Halket (1928). According to these authors the cortex originates through the decurrent growth of the leaf-bases.

The above two views of foliar origin of the cortex are completely different and one cannot be used as support for the other.

THE VIEW OF LEAF FUSION AND ADHESION TO THE STEM

Leysle (1949), who worked on *Anabasis aphylla*, supports his view of adnation of the opposite leaves to the internodes with the following: In the seedling the lowest nodes adjacent to the cotyledons have quite prominent leaves, while in the later developing nodes the leaves become gradually reduced. From the scaly leaves to the base of the internodal cortex similar palisade and water storage tissue can be seen. Leysle also regards the different leaf lengths in various species of *Anabasis* (*i.e.*, *A. micradena*, *A. brevifolia* and *A. salsa*) as a proof for his theory.

Keller (1951) reached the same conclusion by studying some anomalies in *Salicornia* plants. He found seedlings with three cotyledons and unifoliate nodes and asymmetric arrangement of the internodal fleshy cortex.



TEXT-FIGS. 1–6: Fig. 1. Branch of *Arthrocnemum glaucum* (Del.) Ung.-Sternb. Fig. 2. Branch of *Anabasis articulata* (Forsk.) Moq. Figs. 3–5. Diagrammatic reconstruction of the longitudinal course of vascular strands of the stele. Fig. 3. *Arthrocnemum glaucum*. Fig. 4. *Anabasis articulata*. Fig. 5. *Salsola longifolia* Forsk. Fig. 6. Diagrammatic representation of the primary vascularization of a young branch of *Calycanthus* in which the stelar and foliar strands are hatched and the cortical bundles merely outlined.

THE VIEW OF DECURRENT GROWTH OF THE LEAF-BASES

Duval-Jouve (1868) states that the young fleshy cortex originated through downward growth of the bases of two opposite leaves which fused along the adjacent edges. Duval-Jouve supports his view by anatomical observations, additional to the similarity of the tissue in the cortex and reduced leaves. He found that there are two networks of vascular bundles in the fleshy cortical tissue, each of which derived from the two descending lateral branches of each opposite leaf-trace, which enters the leaf of the node above. These two networks (Plate I, Figs. 5, 6) anastomose (Fahn and Arzee, 1959). The median branch of each leaf-trace ascends into the reduced leaf. Duval-Jouve considers his view confirmed by the following behaviour of the fleshy cortex during the maturation of each internode. These cortex segments become yellow and then wither and so behaving, according to him, as deciduous leaves.

Cooke (1911) and de Fraine (1912) who investigated the various tissues and venation of the reduced leaves and fleshy cortical segments, as well as the structure of the flowering shoots of various species of *Salicornia*, came to the same conclusion as Duval-Jouve. De Fraine also brings evidence from the morphology of seedlings. Halket (1928) uses the form and structure of some abnormal nodes of *Salicornia herbacea* to support the above theory. He noticed plants in which two deep lateral indentations appeared along the internodes.

RECENT DEBATE ON THE NATURE OF THE FLESHY CORTEX

Van Royen (1956), from his anatomical studies on *Tecticornia*, states that the theory of leaf-fusion and adnation to the stem cannot be accepted. He bases his view on the departure of the leaf-traces and branch traces, from the stele at the top of the articulated internode and not at its base, as we should expect if cortex represents fused leaves.

In order to clarify the problem whether fusion of leaves occurred along the internodes, Fahn and Arzee (1959) studied the vascularization pattern of the stele of some articulated genera of the Chenopodiaceae. They found two types of steles: *Salicornia-Arthrocnemum* type (Text-Fig. 3) including *Halocnemum* and *Anabasis* type (Text-Fig. 4) including *Haloxylon*. Comparison of the stele of the above plants with the stele of other opposite-leaved Chenopodiaceae genera, which have a similar stelar pattern but which are not articulated and do not exhibit a fleshy cortex (Text-Fig. 5) shows no sign of addition of foliar strands to the stele. If such a process would have taken place, a greater number of strands would be expected to occur in the stele and the leaf-traces in the stelar region would be expected to be longer than in species in which leaf-fusion and adnation to the stem is not suggested. From this investigation the contrary situation can be seen. The number of vascular strands in *Anabasis* for instance is smaller or the same as in the different *Salsola* species which also have opposite leaves and which lack a fleshy cortex. Therefore, the view of foliar fusing and adnation to the stem seems to me as an unsatisfactory one.

The theory of decurrent growth sounds more logical, but as will be shown later is not convincing, in my opinion.

The vascular network of the cortical segments which is derived from the lateral branches of the leaf-trace at the top of the internode could suggest a hypothesis of a downward prolongation of the leaf-bases. This, however, does not seem to me to be the only possible explanation of the existence of a vascular network in the cortex. Cortical vascular strands are known to appear not only in the articulated Chenopodiaceae but also in many families (Metcalfe and Chalk, 1950), which do not exhibit a fleshy cortex as, for instance, in the Calycanthaceae (Fahn and Bailey, 1957). The cortical strands here run throughout the stem but are not interrupted at each node, as the stem here is not constricted and no intercalary growth takes place. However, vascular connections between the cortical bundles and the leaf-traces at the nodal level exist also in the Calycanthaceae (Text-Fig. 6). The position of the phloem of the cortical bundles of the Calycanthaceae is interior to the xylem as is also in the cortical bundles of the articulated Chenopodiaceae. A fleshy cortex, such as that of the articulated Chenopodiaceae, in which the processes of photosynthesis take place, requires a more well-developed vascular system than the Calycanthaceae. The view of purely functional development of the vascular network of the cortex can be strengthened by the fact that in some articulated Chenopodiaceae, such as *Anabasis* species, the large part of this network is derived from branches given off from stelar strands at various levels along the internode (Plate I, Fig. 4). Additional support for the functional interpretation of the appearance of vascular bundles in the cortex can be found in the following statement from Eames and MacDaniels (1947, p. 314): "In plants with fleshy cortex, such as many of the Cactaceae, where the leaves are reduced and photosynthesis is carried on largely by the cortex, branches from the base of the leaf-traces penetrate the cortical tissues."

The shedding of the cortex, which occurs in each internode separately, has been interpreted by some authors as a proof of their foliar nature.

James and Kyhos (1961) doubt the view of Fahn and Arzee (1959), that the phellogen separates the vascular cylinder from the cortex and that the cortex is constricted at the base of the node, which is the cause of the characteristic way in which the cortex is shed. James and Kyhos write further that "If this were true, the cortex would have to be discontinuous, since in the constricted area the phellogen develops directly underneath the outer layer of cells. That is, we would have the rather anomalous situation of the stele being surrounded only by an epidermis".

If these authors had examined better a longitudinal section of two adjacent internodes, they would have seen in the constricted area of the internodes, several layers of compressed parenchyma cells not only between the phellogen and the epidermis, but also between the cells outside the periderm, which become suberized before phellogen activity starts. Exterior to the vascular strands, phloem or pericycle fibres can also be seen (Plate I, Figs. 7, 8). The constriction may be either the outcome of the suppression of the activity of the intercalary meristem or of the pressure of the rudimentary leaves or of both.

The fact that the cortex of *Allenrolfea occidentalis* is thinner on the side of the internode opposite to that below the reduced leaf (James and Kyhos, 1961), or the fact that in some abnormal plants of *Salicornia* two deep lateral longitudinal indentations appeared in the cortex (Halket, 1928) does not necessarily prove the cortex to be of foliar origin. In a great many of dicotyledons there can be observed cortical thickenings running decurrently from the leaf-base down along the substanding internode. This is the cause of the oval outline as seen in cross-sections of, at least, the upper part of the internodes of most of the species with opposite leaves and the asymmetry of young stems with alternate leaves.

It is important, here, to bear in mind the difficulty in drawing an exact borderline between stem and leaf. Both organs develop from a common meristem, *i.e.*, from the apical meristem. The connection and the mutual interdependence of leaf and stem exist during the whole period of the plant growth (Wardlaw, 1960). Moreover, according to Arber (1950), the leaf represents basically a stem organ which became secondarily flattened. It has been shown in some ferns that it is possible to change by surgical methods, the developmental trend of primordia from future leaves to buds (Cutter, 1959).

The main reason which caused the earlier authors to regard the cortex of the articulated Chenopodiaceae to be of foliar origin was that photosynthesis is carried out in its tissues. However, numerous plants are known in which the leaves are reduced and in which stems then become concerned with photosynthesis, sometimes even resulting in the formation of phylloclades. This proves that the interchange of function between leaf and stem is possible.

Therefore, it seems to me that no convincing evidence exists as to the foliar origin of the fleshy cortex of the articulated Chenopodiaceae and so the simple view according to which the fleshy cortex is of axial origin and has acquired photosynthetic function as a result of the reduction of the leaves, has to be retained.

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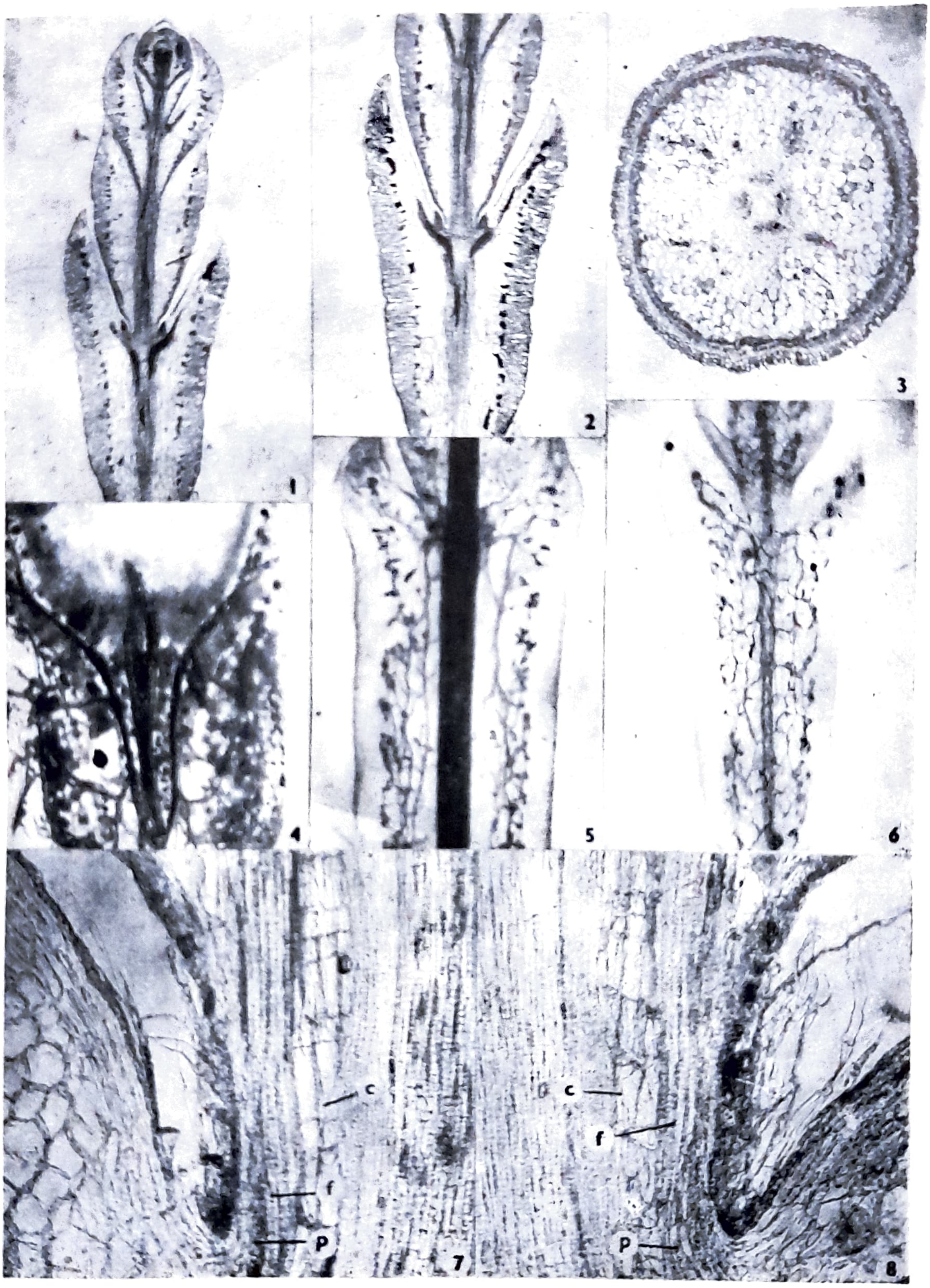
EXPLANATION OF PLATE I

FIGS. 1–8

FIGS. 1–2. Longitudinal sections of a terminal portion of a shoot of *Salicornia fruticosa* L. Fig. 1, × 10; Fig. 2, × 12.

FIG. 3. Cross-section of a young internode of *Anabasis articulata*, × 15.



FIGS. 1–8

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FIG. 4. A portion of a cleared shoot of *Anabasis articulata* in which branches given off along the internode from the vascular strands of the central cylinder can be seen entering directly into the cortical tissue. The strands of the central cylinder are seen to be somewhat spread as a result of pressure, × 13.

FIG. 5. A portion of a cleared shoot of *Arthrocnemum glaucum* showing the network of the cortex which is connected with the lateral branches of the leaf strands, × 11.

FIG. 6. As in Fig. 5 but showing the anastomosing of the network in cortex and reduced leaves. This photograph was made with the focus nearer the upper surface of the shoot, × 13.

FIGS. 7–8. Longitudinal hand-cut sections of a portion of a shoot of *Anabasis articulata* in which several cell layers consisting of fibres and compressed parenchyma cells, can be seen between the multiseriate epidermis and the cork in the constricted zone of the cortex, 68.

(*c*, cork; *p*, parenchyma cells; *f*, phloem or pericycle fibres.)