

## The Occurrence of a Tracheal Tissue enveloping the Embryo in certain Capparidaceae.

BY

MATTHEW YOUNG ORR,

Assistant in Laboratory, Royal Botanic Garden, Edinburgh.

---

With four figures in the text.

---

THE ovules and seeds of the Capparidaceae have certain peculiarities of structure which, so far as is known, are not possessed by those families to which it approximates in systematic position, and one of the most striking is the presence in the seed, in some of the genera at least, of a highly specialised cellular tissue surrounding the embryo.

In ripe seeds this tissue is to be found adpressed to the inner wall of the testa, to the internal configuration of which it closely conforms, but from which it can be easily detached by careful dissection. On its inner side it is in close contact with the embryo, which it completely envelops.

In longitudinal sections of the seed this envelope or sheath has the appearance of an additional internal seed-coat,\* and in some cases its intimate relationship to the included embryo is further emphasised by an infolding of the tissue between the radicle and the cotyledons.

When perfectly dry the whole envelope has an opaque, silvery appearance and can be easily distinguished from the dark-coloured testa, but when moistened it visibly expands and becomes transparent. Microscopic examination of this pellicle shows that it is composed of one or more layers of cells, which are differentiated in a remarkable way. The extent of this modification and the particular form it has taken vary in different genera, but its main features are more or less constant for each genus. The various types of envelopes will be described individually, but the distinctive features of this tissue and its possible function may be briefly referred to at this point.

In the seeds of the species examined, the layer, or layers, referred to above are composed of cells without protoplasmic contents, the walls of which elements are strengthened in various

\* This third seed-coat is referred to by Baillon (Nat. Hist. of Plants, vol. iii, 1874, p. 152, note 1).

[Notes, R.B.G., Edin., No. LX, January 1921.]

ways, giving to the tissue a distinctive appearance when viewed under the microscope. This thickening is in the form of annular and spiral bands or reticulations, which in some cases are found on the surface walls of the cells, and in others are confined to the lateral walls.

Such elements as those referred to above possess the form and structure of tracheides, indicating that the specialised layer surrounding the embryo is tracheal in character.

Such tracheal tissues are not entirely unknown in the seeds of living plants, for Beauregard \* refers to a similar layer in his description of the seed of *Daphne*, and their presence in the seeds of certain other Thymelaeaceae was subsequently recorded by Guérin.† This latter author compared this pellicle with its tracheides to the tracheal sheath of the Cycadofilicales, but regarded it as representing in the Thymelaeaceae the vestige of a primitive structure.

In the Capparidaceae, such a tissue, with its different types of structure, suggesting separate lines of development within the family, would appear to be not merely vestigial, but actively functioning at some period in the growth of the seed.

Before the seed is liberated, the tracheal envelope is in close association with the vascular strand of the funicle, and may possibly function for a time at least as an accessory water-supply system for the embryo. On the other hand, its late development seems rather to imply that it plays a more important part in the economy of the seed at the time of germination. It is found that the apex of the tracheal sheath projects slightly into the micropylar pore, and, in the presence of moisture, its absorptive properties, already referred to, would ensure a supply of water being conveyed to all parts of the embryo, and especially to the radicle through the infolding of the envelope in that region.

It would appear, then, that in the seeds of the Capparidaceae the enveloping sheath acts as a sponge, absorbing moisture through the micropyle, and constituting a kind of "water-jacket" surrounding the embryo.

The investigation of the sheath characters of the different genera was carried out mainly on seeds taken from herbarium specimens, no other source of supply being available at the time, and there are of necessity numerous gaps in the sequence. A full list of the seeds examined will be found at the end of this paper, and when possible the actual specimen from which they were obtained has been indicated. The nomenclature followed is that contained in Bentham and Hooker's *Genera Plantarum*.

\* M. Beauregard in Bull. Soc. Bot. Fr., xxiv (1877), p. 385.

† P. Guérin in C. R. Ac. Sc. Paris, clvi (1913), p. 398, and in Ann. Jard. Bot. Buitenzorg, ser. 2, xiv (1915), p. 1.

# I. Cleomeae.

The three genera examined were *Cleome*, Linn., *Isomeris*, Nutt., and *Polanisia*, Rafin., and, as might be expected, their natural affinities are further emphasised by the similarity of structure found in the tracheal envelopes of their seeds. In the species examined, the tracheides are parenchymatous cells with delicate annular thickenings on their periclinal or surface walls, a feature which, so far as can be ascertained, is peculiar to the Cleomeae.

In many of the cells these fine bands of thickening are laid down in two, or even three, distinct concentric zones, and in

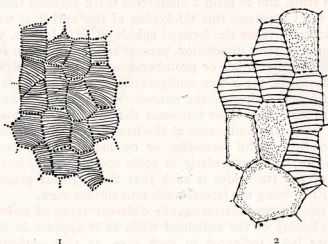


FIG. 1.—A portion of the tracheal envelope of (1) *Cleome spinosa*, Jacq., and (2) *Isomeris arborea*, Nutt., in surface view.  $\times 250$ .

surface view this conformation gives to the sheath a characteristic appearance.

Of the genera investigated, the tracheal envelopes of *Cleome* and *Polanisia* are identical in the configuration and size of the constituent elements, while *Isomeris* differs mainly in its larger tracheides. In some of the cells of the tracheal tissue of *Isomeris* protoplasmic contents were still visible, but this might possibly have been a transient condition due to the immaturity of some of the seeds examined.

The similarity of structure exhibited by the tracheal envelopes of these three genera is of special interest in view of their natural relationship and systematic position within the family. This raises the question of the possible value of this seed character, apart from its physiological significance, as an accessory factor in natural classification.

## 2. Cappareae.

Among the included genera of the Cappareae various types of tracheal envelopes are represented, differing in detail from one another, but all easily distinguishable from those of the genera already described in one definite feature. In *Cleome* and its allies the thickened bands are found on the periclinal or surface walls of the tracheides, and so are easily seen in surface view under the microscope; but in *Capparis* and its associates it is the anticlinal or lateral walls of the cells which are strengthened, while the surface walls remain unthickened. Notwithstanding the varieties of structure represented in the Cappareae, this anatomical feature would appear to indicate definitely the limits of each tribe, and to form a distinctive mark between them.

In the Cappareae this thickening of the anticlinal walls of the tracheides takes the form of spirals or reticulations, which, on account of their disposition, present an appearance in surface view of irregular lobes or protuberances on the lateral walls.\* In many of the types this configuration is often the most characteristic, for, owing to the extreme shallowness of the cells, the fact that these lobes represent the end views of thickened bands, which are continuous to the base of the cell, can only be observed by careful focussing, or by means of sections. In other cases, and particularly in some species of *Capparis*, the depth of the tracheides is such that the slightest pressure is sufficient to bring the lateral walls into surface view.

In the figures illustrating the different types of envelopes, the thickening of the anticlinal walls as it appears in surface view has been indicated in each case, as this configuration seems to be more or less typical of each genus examined, and is expressive of the extent of the thickening over the surface of the walls, which cannot always be seen from this point of view.

Under *Capparis decidua*, Pax, a diagrammatic representation of an individual tracheid has been figured to illustrate the deeper type of element with reticulate thickening on its lateral walls. This deeper type of tracheid is best seen in *Capparis*, and the lateral walls can be easily flattened out, thus enabling the observer to determine the nature of the thickening. For this reason the sheath characters of this genus will be described first.

### *Capparis*, Linn.

Among the different species of *Capparis* examined, both the deep and shallow types of tracheal elements are represented,

\* The type of thickening found on the lateral walls of these elements in the Cappareae bears a marked resemblance to that figured by Guérin to illustrate his descriptions of the structure of the seed-coat in certain species of the Gentianaceae (Journ. de bot., xviii, 1904, pp. 37-52).

and the extent of the thickening of the tracheid walls is by no means uniform. It is therefore possible to classify them artificially for purposes of description on the basis of these minute structural differences.

1. The tracheal envelopes of *Capparis decidua*, Pax (*aphylla*, Roth), and *Capparis spinosa*, Linn., are composed of isodiametric cells with relatively deep anticlinal walls. In the case of *Capparis decidua* the anticlinal walls are closely reticulated, while in *Capparis spinosa* the thickening is more of a spiral conformation. Owing to the depth of the tracheides these anticlinal walls are easily seen in surface view, and the two types are readily distinguishable.



FIG. 2.—(1) A portion of the tracheal envelope of *Capparis decidua*, Pax, in surface view. (2) Diagrammatic drawing of an isolated tracheid.  $\times$  about 350.

In the remainder of the species the tracheal elements are much shallower, and the nature of the thickening cannot be so readily observed, nor does it appear to be uniform in the cells of any one species. In the portions of the tracheal envelopes which have been figured, the thickened lateral walls are shown as if in section, which is the most characteristic appearance presented by these sheaths in surface view. The irregular configuration distinguishes them definitely from the two species just described, and in some cases it more closely approximates to the type of structure found in allied genera. This diversity of sheath character within the limits of the genus is suggestive of its composite character.

2. Of the species possessing shallow tracheides, *Capparis micracantha*, DC., most closely resembles *Capparis decidua*. The tracheides are approximately the same size in surface view, but are of the shallow type, while the thickening is not so definite. The spirals on the lateral walls are broad bands, but in some elements they assume the form of a network. A somewhat



similar type of cell is found in the tracheal envelope of *Capparis xanthophylla*, Coll. et Hemsl., but in this species the lignification of the anticlinal walls is much more pronounced, and it is difficult to determine its features in surface view on account of the shallowness of the tracheides.

In *Capparis flavicans*, Wall., the tracheides are larger than those of the preceding species, and the lateral walls are so strongly thickened that in surface view an impression is given of a succession of unequal protuberances, projecting into the cell cavity. This marked configuration has been indicated in the figure below, but in actuality it represents the arrangement of the thickening on the surface of the lateral walls.

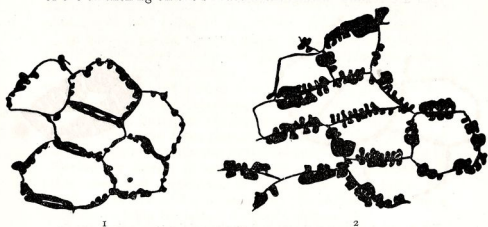


FIG. 3.—A portion of the tracheal envelope of (1) *Capparis micracantha*, DC., and (2) *Capparis flavicans*, Wall., in surface view.  $\times 350$ .

3. The structure of the envelope represented in *Capparis flexuosa*, Blume, is almost identical with that of *Apophyllum anomalum*, F. Muell. Both are composed of the same shallow type of tracheid with delicate spiral bands of the "spinosa" type on the lateral walls.

#### Apophyllum, F. Muell.

In this somewhat anomalous genus, represented by one species, the structure of the envelope surrounding the embryo closely resembles that found in *Capparis flexuosa*, referred to above. The lateral walls of the shallow tracheides are strengthened by fine spiral bands, and the whole sheath is mainly distinguishable from that of its *Capparis* prototype by the more rounded outline of the constituent elements. In general configuration it also approximates to the envelope of *Maerua*, from which it differs, however, in having only one layer of tracheides.

**Maerua, Forsk., and Niebuhria, DC.**

Between these two genera there is practically no distinction in the structure of the envelope. There are two superimposed layers of tracheides, deeper than those of the preceding species, and possessing bands of thickening somewhat similar to those found in *Capparis spinosa*, but not so clearly visible in surface view.

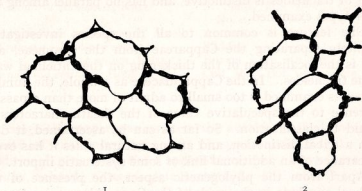


FIG. 4.—A portion of the tracheal envelope of (1) *Apophyllum anomalum*, F. Muell., and (2) *Maerua parvifolia*, Pax, in surface view.  $\times 350$ .

**Crataeva, Linn., and Euadenia, Oliv.**

These two genera are closely related, and in the characters of the tracheal tissue surrounding the embryo there is no distinction between them. In surface view the tracheal elements appear much larger in area than those described for other genera, but they are extremely shallow, and the irregular configuration of the lateral walls, which is such a distinctive feature in many types, is entirely absent. There is practically no indication of thickening on the walls when the sheath is examined in surface view, and it is only by means of pressure applied to the cover-glass, and careful focussing, that the fine annular bands are brought into view.

The presence of a well-defined layer of cells with thickened walls of a cellulose nature, underlying the tracheal tissue, is a characteristic feature of the enveloping sheath of these genera. This layer is evidently a store of reserve-cellulose destined for the use of the embryo.

It will be evident from the descriptions and figures of the tracheal envelopes found in the genera included under Cappareae that there is a considerable variation in the extent and arrangement of the thickening on the walls of the tracheides. This is

mainly a difference in degree, the varieties of configuration seen in the tissues in surface view being brought about by the varying depths of the tracheides, which accounts to a certain extent for the considerable lack of uniformity among the species of *Capparis*.

In minor details of structure the differences exhibited by the tracheal tissues are more often of the nature of generic distinctions. For example, in *Maerua* (sensu Pax) \* the double layer of tracheides is distinctive, and has no parallel among the other types examined.

One feature is common to all the species investigated, definitely separating the Cappareae from the Cleomeae, and that is the localisation of the thickening on the anticlinal walls of the tracheides. In the Capparidaceae as a whole, the number of species examined is too small to admit of more than a passing reference to the speculative value of the sheath characters as an aid to classification. So far as can be ascertained, it does form a tribal distinction, and among natural allies it has every appearance of an additional link of some systematic import.

Apart from the phylogenetic aspect, the presence of the tracheal envelope in the seeds of the Capparidaceae is of much greater interest from a physiological point of view. Its structural features and position in the seed imply a relationship between this tissue and the included embryo which is not historical, but definitely functional, and apparently connected with the supply of moisture during germination. It is not confined to xerophyllous species alone, although it reaches a high state of development in the seeds of such types.

It is possible that further researches may lead to a discovery of the existence of similar tracheal tissues in the seeds of other families besides the Thymelaeaceae and Capparidaceae.

In conclusion, I desire to express my indebtedness to Prof. W. G. Craib, for his valuable advice and criticism.

### LIST OF SPECIES EXAMINED.

<i>Cleome spinosa</i> , Jacq.	Cult. Roy. Bot. Gdn., Edin.
" <i>lutea</i> , Hook.	Idaho, Macbride, No. 226.
" <i>platycarpa</i> , Torr.	California, Heller, No. 8010.
" <i>Stocksiana</i> , Boiss.	Baluchistan (1889), Lace.
" <i>gigantea</i> , Linn.	University Botanic Garden, Copenhagen.
<i>Polanisia viscosa</i> , DC.	N.W. Himal., Lace, No. 1188.
" <i>cheledonii</i> , DC.	Siam, Khoon Winit, No. 458.
<i>Isomeris arborea</i> , Nutt.	Cult. Roy. Bot. Gdn., Edin.

---

\* Pax in Engler u. Prantl, *Pflzfam.*, iii, 2 (1891), p. 234.



<i>Capparis spinosa</i> , Linn.	Baluchistan (1888), Lace.
„ <i>decidua</i> , Pax ( <i>aphylla</i> , Roth).	Baluchistan (1887), Lace.
„ <i>flavicans</i> , Wall.	Burma, Lace, No. 4879.
„ <i>xanthophylla</i> , Coll. et Hemsl.	Burma (1909), Lace.
„ <i>micracantha</i> , DC.	S. Siam, Mrs D. J. Collins, No. 7.
„ <i>flexuosa</i> , Blume.	Cult. Roy. Bot. Gdn., Edin.
<i>Maerua parvifolia</i> , Pax.	S. Africa, Dinter, No. 272.
<i>Niebuhria siamensis</i> , Kurz.	S. Siam, Mrs D. J. Collins, No. 4.
<i>Apophyllum anomalum</i> , F. Muell.	Australia.
<i>Crataeva religiosa</i> , Forst.	Sikkim.
„ <i>lophospermum</i> , Kurz.	Burma, Lace, No. 5354.
<i>Euadenia eminens</i> , Hook. f.	Cult. Roy. Bot. Gdn., Edin.

Since this paper was written, the author has had an opportunity of examining ripe seeds of species belonging to three additional genera of the Capparidaceae, viz. *Dactylaena micrantha*, Schrad., *Gynandropsis pentaphylla*, DC., and *Steriphoma cleomoides*, Spreng., the seeds of which were obtained from the University Botanic Garden, Copenhagen.

The tracheal envelopes of the species of *Dactylaena* and *Gynandropsis* are well defined, and have the characteristic structural features possessed by *Cleome* and *Polanisia*. Since these four genera belong to the Cleomeae section of the family, this similarity of structure serves to confirm the conclusion arrived at in the paper, namely, that the configuration of the tracheal envelope is a distinctive feature separating the Cleomeae from the Cappareae.

In the seed of *Steriphoma cleomoides* the sheath is of the shallow type, with delicate annular markings on the anticlinal walls of the tracheides. It most closely resembles that of *Maerua*, but consists of only one layer of tracheal elements. This apparent affinity corresponds with the position assigned to the genus in Bentham and Hooker's Genera Plantarum.