ON THE MORPHOLOGY OF THE STOMATA OF *EUCALYPTUS TERETICORNIS, OURATEA SPECTABILIS AND CEDRELA FISSILIS*

HELENA VILLAÇA and MARIO G. FERRI

ON THE MORPHOLOGY OF THE STOMATA OF *EUCALYPTUS TERETICORNIS*, *OURATEA SPECTABILIS* AND *CEDRELA FISSILIS*. (1)

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INTRODUCTION

The literature concerning the morphology of stomata shows a peculiar fact: the several types of stomata are established not on the basis of the organization of the guard-cells but on the presence or absence of subsidiary cells, and on their disposition in relation to the guard-cells, their development, and so on. Thus Solereder (7) classifies the stomata of the Dicotyledones in four types: 1 — without subsidiary cells, but with three or more neighbouring cells (Cruciferae and Ranunculaceae); 2 — with subsidiary cells parallel to the stomatal aperture (Rubiaceae); 3 — with subsidiary cells normal to the stomatal aperture (Caryophyllaceae); 4 — stomata of the cruciferous type in adult leaves.

Though Metcalfe and Chalk (5) state in their book that the word stoma is taken "to mean the pair of guard-cells together with the aperture between them" (p. XIV), they have maintained the same classification introducing special names for the different types of stomata. In both treaties there appears a reference to the special type of stomata of the Gramineae which differ from those of the Dicotyledones by the organization of the guard-cells.

This classification does not appear satisfactory for two different reasons: 1 — it is based, not on the organization of the

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(2) The present investigation was undertaken by Miss H. Villaça under the direction of Prof. F. Rawitscher who suggested the problem. Soon after, however, Prof. Rawitscher became sick and was forced to a temporary retirement. The study that had just begun was then proceeded under the direction of Dr. Mario G. Ferri. The authors take this opportunity to acknowledge their indebtdness to Prof. Rawitscher.

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stoma proper, but on the subsidiary cells; 2 — it does not cover all the types of organization which are to be found among different plants.

The present paper will deal with the morphology of the stomata of *Eucalyptus tereticornis* (Myrtaceae), *Ouratea spectabilis* (Ochnaceae) and *Cedrela fissilis* (Meliaceae). Our interest in this problem arose during an investigation on the transpiration of *Eucalyptus*. On studying the literature concerning the subject, we found in Accorsi (1) a description of the stomata of *Eucalyptus citriodora* and *E. tereticornis* which, according to the author, had an organization comparable to that of *Pilea elegans* (see fig. in Haberlandt (4), p. 466). In the substomatic chambers of these stomata, there occured at times a special cell which Accorsi called "obturating cell" and which, due to the great thickness of its outer membrane, would decrease in length on absorbing water, thus leaving open the stomatal aperture. On the contrary, this cell's length increased on loosing water and clogged up the stomatic pore. The guard-cells themselves would not participate in the stomatal movements; due to the great thickness of their walls they would remain always open.

The present investigation partially confirms Accorsi's observations. It shows however that *Eucalyptus tereticornis* has an especial type of organization in the guard-cells which we did not find described in the literature available to us (3).

MATERIALS AND METHODS

For the present study differently aged leaves of *Eucalyptus tereticornis* were employed. Observations were also made with adult leaves of *Ouratea spectabilis* and *Cedrela fissilis*. Microscopic preparations were generally made of recently harvested leaves. To study the surface-view of the stomata, a segment of the epidermis was removed from the leaf and mounted in water. Transverse sections of the leaves, parallel and normal to the principal vein were made by hand with a sharp razor blade and mounted in water. Such sections supplied views of both median and tip cross sections of the stomata and also the longitudinal section of the guard-cells. When a better vision

(3) This paper was ready for the press when Katherine Esau's "Plant Anatomy" (1953) came to our knowledge. We found there (p. 147) good drawings representing the stomata of *Prunus* which, however, are not described in detail in the text. It seems to us that on the whole the organization of such stomata is very much like the one described in this paper for *Eucalyptus tereticornis*.

of the walls was desired the preparations were treated with chloral-hydrate. It was later observed that excellent results could be obtained by using a hypochlorite solution such as those found in the market for laundry use. More lasting preparations were made by gradually fixing the material in alcohol and mounting it in a solution made of equal parts of 70% alcohol and 60% glycerine.

When thinner sections were desired, a freezing microtome was employed. Some preparations were treated with Sudan III to emphasize the cuticular layer.

Drawings were made by transferring to a squared paper the figure of the stoma as observed superimposed on the ocular grid. To evaluate the magnification the preparation was substitued by a micrometric scale, a few divisions of which were also drawn.

ANALYSIS OF MICROSCOPIC SLIDES

1. Stomata of *Eucalyptus tereticornis*

Surface views of the stomata of *Eucalyptus tereticornis* can be studied in preparations of either epidermis. The first plane that comes into focus is that of the cuticular layer where we

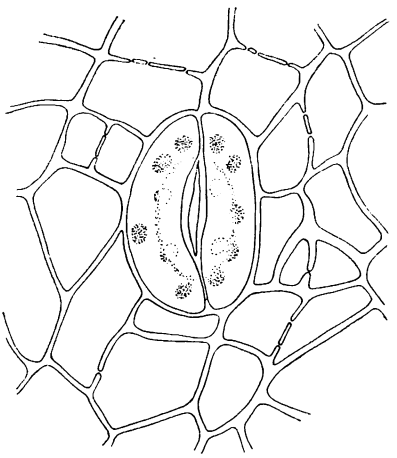

Fig. 1 — Superficial view of a stoma of *Eucalyptus tereticornis*.

can find pores just above the stomatal apertures. As we lower the focus, a clear view of the stomatic apparatus is obtained, and the cuticular pore appears then just as a circular shadow around the ostiole. This is presented in Fig. 1 where it can

be seen that this stoma, in a surface view, does not differ, essentially, from the type most frequently found among the Dicotyledones. The figure also shows that the guard-cells are surrounded by a number of small cells disposed at different angles in relation to the ostiole.

The analysis of cross-sections of the leaf-blade gives the opportunity of seeing transverse as well as longitudinal sections of the stomata. This last view is presented in Fig. 2 where

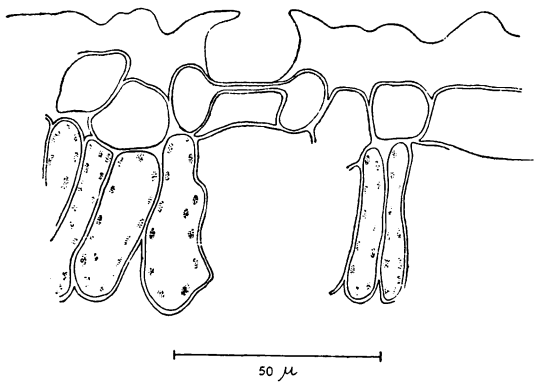

Fig. 2 — Longitudinal section of one guard-cell of the stoma of *Eucalyptus tereticornis*.

it can be seen that the guard-cell has an organization comparable to that of the Gramineae: the cell-wall is thin in both tips and very thick in the middle. Most of the cell-contents is found in the cell-tips which are linked together by a thin layer

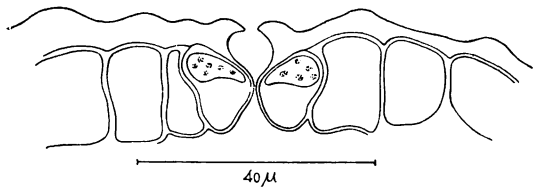

Fig. 3 — Cross-section passing by one tip of the guard-cells of the stoma of *Eucalyptus tereticornis*.

of protoplasm lying just below the external thin wall. The thickness of the internal wall in this region is very considerable. Fig. 3 presents a transverse section of the stoma passing by one of

the tips of the guard-cells, and Fig. 4 gives a view of a cross-section median to the stomatic pore.

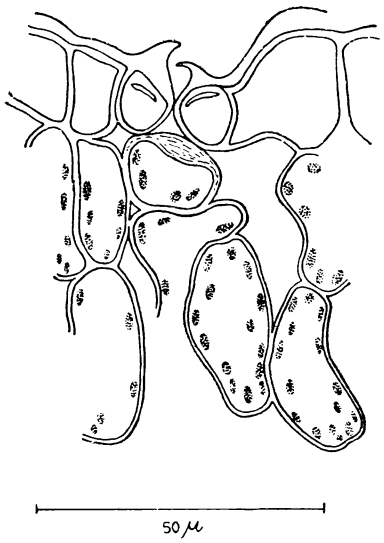

Fig. 4 — Cross-section passing by the median part of the guard-cells of the stoma of *Eucalyptus tereticornis* with one obturating cell in the air-chamber.

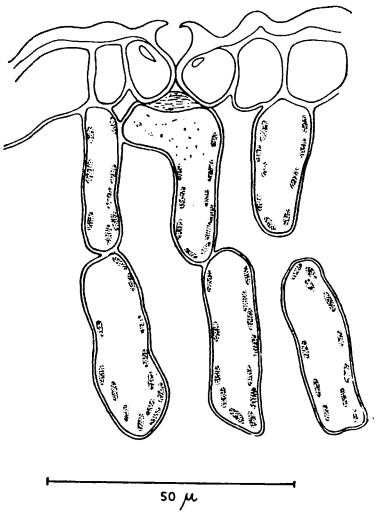

Fig. 5 — Cross-section passing by the median part of the guard-cells of the stoma of *Eucalyptus tereticornis*, with one obturating cell in the air-chamber.

Obturating cells. This figure shows already the obturating cell mentioned by Accorsi (1). The shape and size of this cell can vary greatly, as it can be seen in Figs. 4, 5 and 6. Its most constant feature is the considerable thickness of the outer wall. In all the cases figured this cell is in close contact with the guard-cells so as to keep closed the aperture between them. In other cases we have however seen the stomatic pore open (Fig. 8).

During the course of the present study we were able to find that instead of one obturating cell in the sub-stomatic chamber, there could be present several such cells, with localized wall thickenings. This fact is clearly seen in Figs. 7 and 8. These cells may be found in different planes giving the impression of closing all the air-chamber. In Fig. 7 the guard-cells, which are in contact, show thin membranes and large lumina. These facts indicate that the cross section is passing by one of the tips of the guard-cells. Fig. 8 then presents a view of a cross-

section passing by the middle of the guard-cells which show very thick wall and small lumen; the stomatic aperture is open.

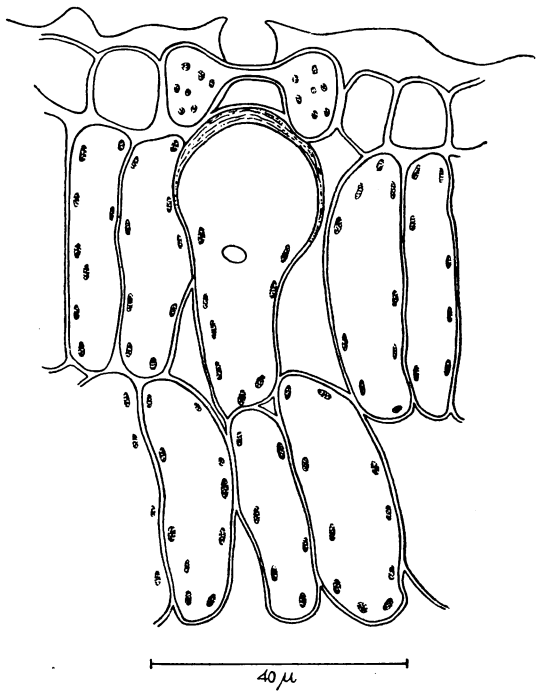

Fig. 6 — Longitudinal section of the guard-cell of the stoma of *Eucalyptus tereticornis*, with one obturating cell in the air-chamber.

Reconstruction of the guard-cells morphology. To get a better understanding of the peculiar organization of this stoma let us consider the three-dimensional scheme of Fig. 9: in *A* we see the surface of the stoma which does not differ from surface-views of the stomata of most Dicotyledones. We can see through the upper membrane that the living contents of the guard-cells fill up all the space outlined by the lateral walls. If we remove, in an imaginary tangential section, a thin layer of this stoma, we get the view presented in *B*, which just shows the living contents of the guard-cells, not by transparency any more but directly. In *C* we have the view when such an ideal tangential section passes by the lower half of the guard-cells. It is to be noted that the living contents are now

limited to the tips of the guard-cells with a very thick membrane in between. In this plane there is no connection between the

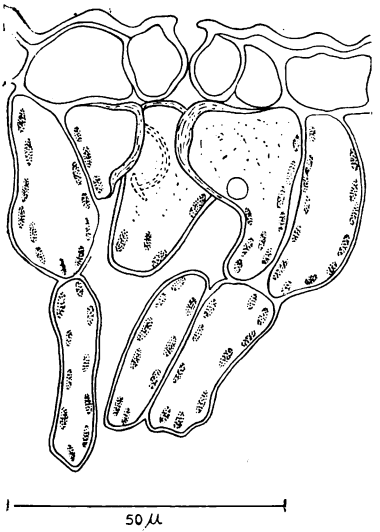

Fig. 7 — Cross-section passing by one tip of the guard-cells of the stoma of *Eucalyptus tereticornis*, with several obturating cells in the air-chamber.

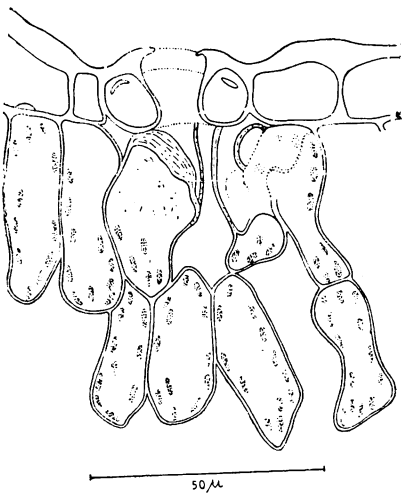

Fig. 8 — Cross-section passing by the median part of the guard-cells of a stoma of *Eucalyptus tereticornis*, with several obturating cells in the air-chamber.

contents that lie in the tips. This connection is brought about only in an upper plane by the thin layer of protoplasm which

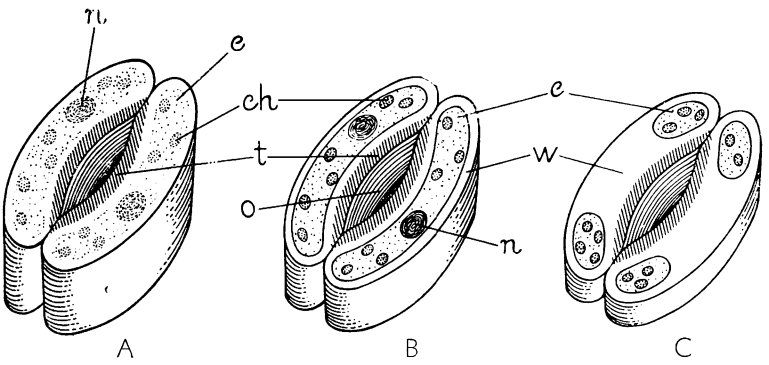

Fig. 9 — Ideal three-dimensinal reconstruction of the stoma of *Eucalyptus tereticornis*. In *A* superficial view, in *B* tangential section close to the sufarce, in *C* deeper tangential section. *n* = nucleus, *c* = cytoflasm, *ch* = chloroplast, *t* = wall thickening around the stomatic aperture *o*, *w* = wall.

lies just below the upper wall and to which reference has been already made.

2. Stomata of *Ouratea spectabilis.*

The surface view of the stomata of *Ouratea* is presented in Fig. 10 which indicates that the cell-contents are accumulated

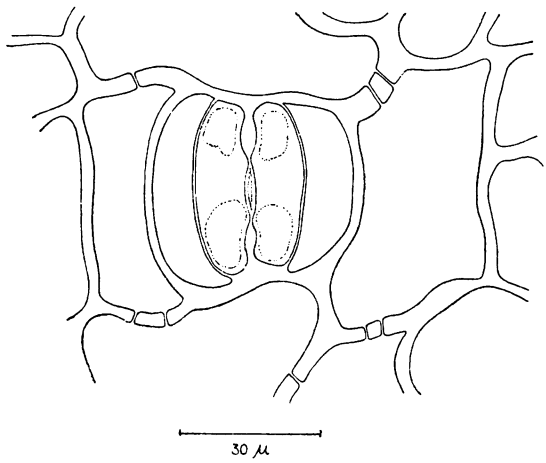

Fig. 10 — Superficial view of a stoma of *Ouratea spectabilis.*

in the tips of the guard-cells. The figure also shows that there are two subsidiary cells parallel to the stomatal aperture.

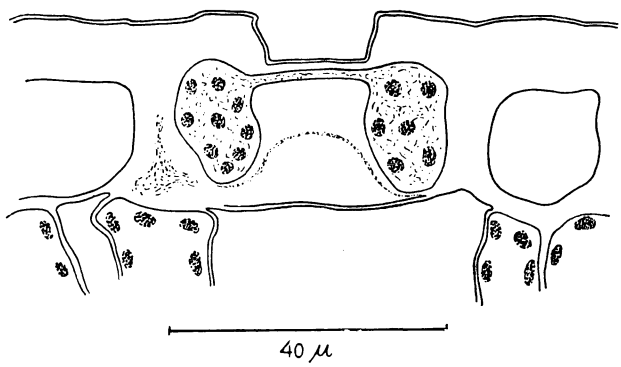

Fig. 11 — Longitudinal section of a guard-cell of the stoma of *Ouratea spectabilis.*

Figure 11 presents the longitudinal section of one guard-cell. We can see that its organization is very similar to that of the Gramineae. It is to be seen also that above the epidermis

lies a thick cuticular layer in which pores are present in correspondence with the stomatic apertures.

Cross sections passing by the middle and the tips of the guard-cells are drawn in Figs. 12 and 13, respectively. The

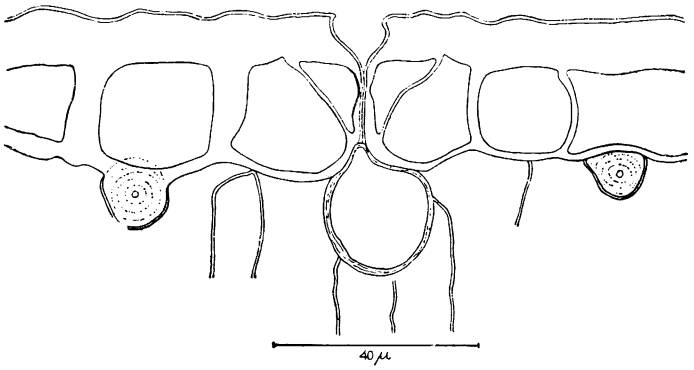

Fig. 12 — Cross-section passing by one tip of the guard-cells of *Ouratea spectabilis,* with one obturating cell in the air chamber.

first is recognized by the large lumen of the guard-cells which are in close contact; in the second, the lumen appears much

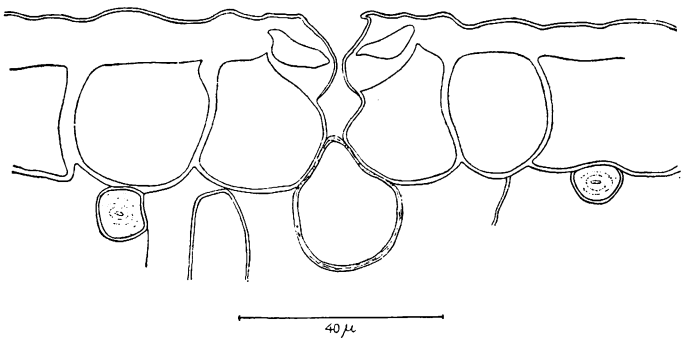

Fig. 13 — Cross-section passing by the median part of the guard-cells of a stoma of *Ouratea spectabilis,* with one obturating cell in the air-chamber.

smaller, the membrane thick and the guard-cells show an aperture between them.

Obturating cells. In both cases figured above, a very distinctive cell lying in the substomatic chamber and obturating the

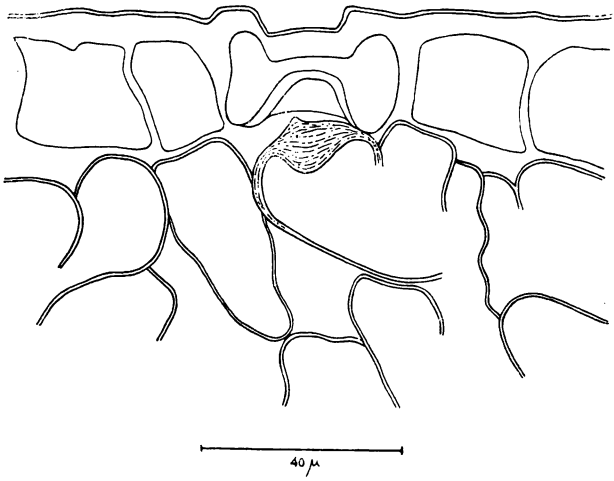

Fig. 14 — Longitudinal section of a guard-cell of the stoma of *Ouratea spectabilis*, with one obturating cell in the air-chamber.

ostiole can be seen. Such a cell can also be found in preparations where the guard-cell is cut longitudinally as is the case

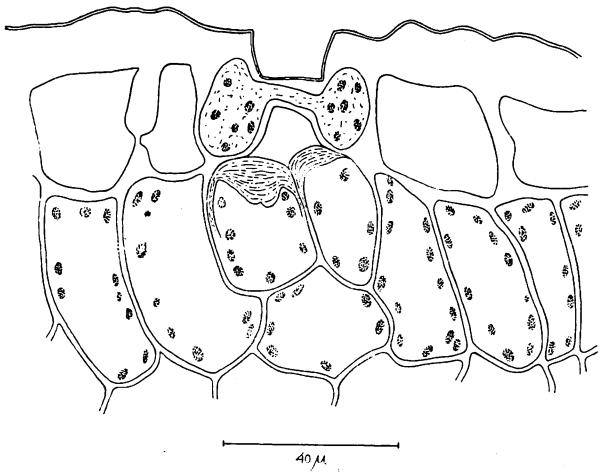

Fig. 15 — Longitudinal section of a guard-cell of a stoma of *Ouratea spectabilis*, with two obturating cells in the air-chamber.

in Fig. 14. Figures 15 and 16 give examples for more than one obturating cell lying in the air-chamber.

3. Stomata of *Cedrela fissilis.*

That the stomata of *Cedrela* are also of the type found in the Gramineae can be easily seen in Fig. 17 which presents the surface view of such stoma. This view is obtained in preparations of the lower epidermis, and shows that the living contents

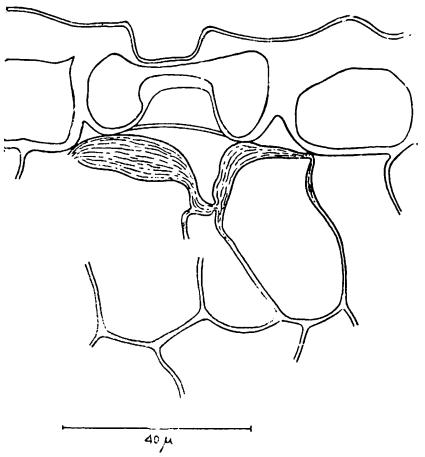

Fig. 16 — Longitudinal section of a guard-cell of a stoma of *Ouratea spectabilis,* with three obturating cells in the air-chamber.

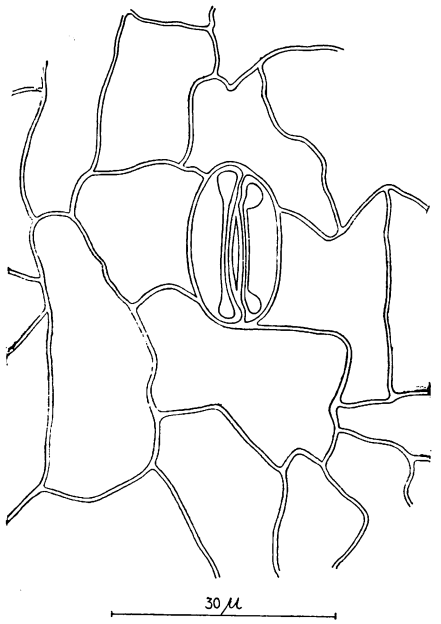

Fig. 17 — Superficial view of a stoma of *Cedrela fissilis.*

of the guard-cells are distributed mainly to the cell-tips. Since in this case the cuticular layer is not as thick as it is in both *Eucalyptus* and *Ouratea,* the surface view allows a much clearer insight of the organization of the guard-cells. Even the small canal that links together the living contents of both tips can be seen. There are two subsidiary cells parallel to the stomatal aperture.

In Fig. 18 the longitudinal section of the guard-cell is presented.

Figures 19 and 20 are cross-sections passing by the tip and the middle of the stoma, respectively. The thin membrane of the guard-cells in Fig. 19 and the very thick one in Fig. 20

can leave no doubt about the Gramineae type of the organization of the stoma of this plant.

Obturating cells. Obturating cells can be seen in Fig. 18, 20 and 21. The frequency in which such cells are found in

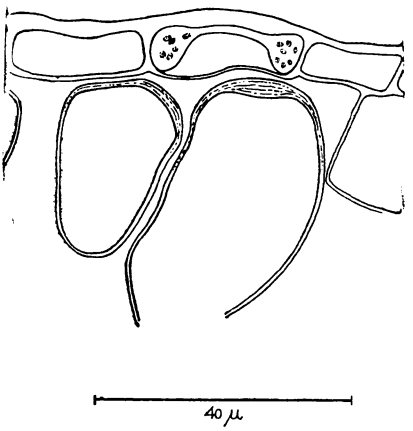

Fig. 18 — Longitudinal section of a guard-cell of the stoma of *Cedrela fissilis*, with two obturating cells in the air-chamber.

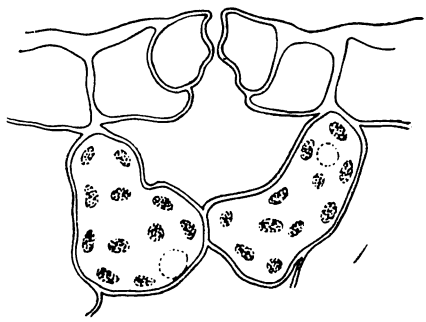

Fig. 19 — Cross-section passing by one tip of the guard-cells of a stoma of *Cedrela fissilis*.

Cedrela is much lower than in both cases previously studied. More frequently one cell only is found in the substomatic chamber of this plant. In a few cases two such cells were found. Attention should be called to the fact that this plant has heterobaric stomata.

DISCUSSION AND CONCLUSIONS

The little information we found in the literature concerning the morphology of the stomata of *Eucalyptus* is unsatisfactory. Nothing especial was noted in Solereder's (7) and Metcalfe & Chalk's (5) books. Accorsi (1) described the stoma of *Eucalyptus tereticornis* (p. 39) which he reported to have the same organization as *E. citriodora* (p. 85). The author presented a figure (1. c. Fig. 57) of a cross-section of the same. As a main difference from the type most frequently found among the Dicotyledones, he indicated the extremely thickened walls of

the guard-cells which have a very small lumen. It is believed by the author that these cells are kept constantly open and that the regulation of the stomatal aperture is exercised by an especial cell found in the substomatic chamber; this cell which has the outer tangential membrane very thick, on loosing or absorbing water would perform movements that would lead to the closing or opening of the stomatic pore. Such a cell to which the name "obturating cell" was given by Accorsi, was compared to the equally differenciated cells existing in the air-chambers of the stomata of *Pilea elegans* (see Haberlandt, 4, Fig. 181, p. 466). It should be mentioned that Haberlandt does not ascribe to these cells the function of regulating the stomatal opening. He states that "In *Pilea elegans* the air chambers on the adaxial side of the leaf become invaded by parenchymatous

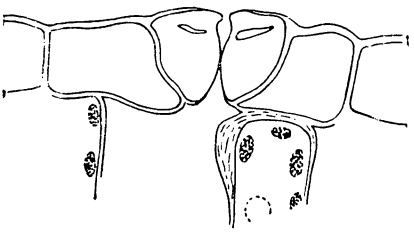

Fig. 20 — Cross-section passing by the median part of the guard-cells of a stoma of *Cedrela fissilis*, with one obturating cell in the air-chamber.

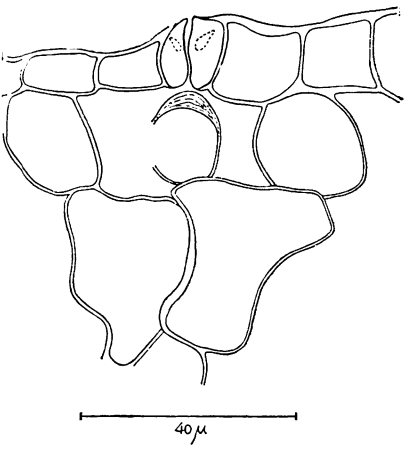

Fig. 21 — Cross-section passing by the median part of the guard-cells of a stoma of *Cedrela fissilis*, with one obturating cell in the air-chamber.

cells, containing abundant protoplasm but few chloroplasts. These cells show a decided tendency to thicken their outer tangential walls. As a rule, one intrusive cell in each chamber develops its cellulose pad immediately below the stoma, which thus becomes completely occluded" (pp. 465-466). This case is mentioned among others to exemplify the fact that some plants can

block the air-chambers, either during periods of lasting drought, or when the guard-cells die, or else loose, by any reason, the capacity of closing the aperture between them. Among such cases Haberlandt mentions that of *Dischidia bengalensis* which, according to his findings, during the dry periods fills the air-chambers with a resinous substance that seems to be secreted by the subsidiary cells which develop vesicular processes into the air-chambers. It is also mentioned that when *Tradescantia viridis* is cultivated in dry atmosphere, some elements adjacent to the stoma also produce similar vesicular processes that are intimately adjusted to the guard-cells thus occluding the stomatic pore (4). It seems to us that such information indicates that Haberlandt did not attribute to the especial cells found in the air-chambers of *Pilea elegans* the function of regulating the stomatal aperture; it rather seems that Haberlandt believed that they were a means employed by the plant to exclude, either temporarily or permanently, the gas exchange through such stomata. Thus the role of regulating the stomatal aperture was ascribed to these cells by Accorsi who however did not give data to support this view.

The present authors describe in detail the organization of the stoma of *Eucalyptus tereticornis*. It is believed that the organization of the guard-cells in this case though remembering that of the Gramineae is not identical with it. This fact is already brought about by comparing the surface views of both stomata. In the Gramineae, in this view, the cell contents appear in the tips of the guard-cells, being linked together by a thin thread of living substance. In *Eucalyptus tereticornis* the living cell contents appear, in the surface view, distributed evenly throughout the guard-cell, as it is the case in the commonest type of stomata of the Dicotyledones. In longitudinal sections of the guard-cells it is clearly seen that the *Eucalyptus* stomata differ from those of the Gramineae: in this case the canal that links together the tips of the guard-cell is almost median and shows the wall, both above and below it, equally thick; in the

(4) That changes in the humidity contents of the atmosphere can induce modifications even in the situation of the guard-cells, was recently shown by Aykin (2). This author showed that in the primary leaves of *Phaseolus multiflorus* the stomata rise above the level of the epidermis when such young leaves are kept in an atmosphere saturated with water-vapor. On the other hand when such leaves are kept in drier conditions, the stomata are maintained at the epidermis level.

Eucalyptus guard-cell the tips are linked by a thin layer of protoplasm close to the surface, so that the wall below it is much thicker than above (Compare Figs. 2 and 22).

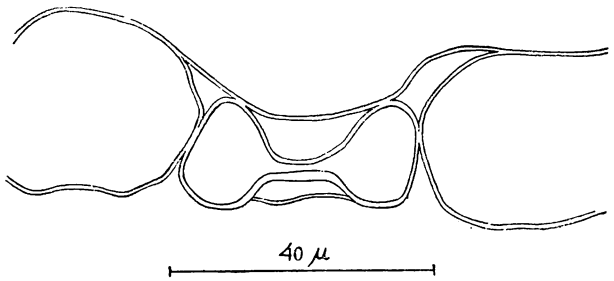

Fig. 22 — Longitudinal section of one guard-cell of the stoma of corn.

For a better understanding of this type of organization, Fig. 9, which is an ideal reconstruction, is presented (see p. 39): in *A* the guard-cells are seen from the surface; in *B* they are pre-

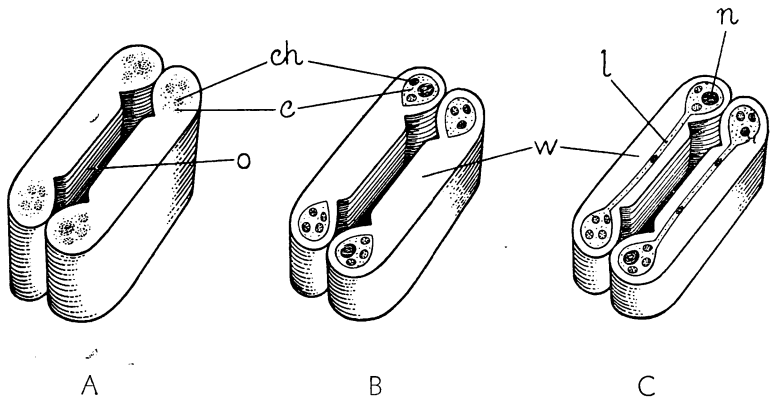

Fig. 23 — Ideal three-dimensional reconstruction of a stoma of the Gramineae. In *A* superficial view, in *B* tangential superficial section, in *C* deeper tangential section. *ch* = chloroplast, c = cytoplasm, *o* = stomatic pore, *w* = wall, *l* = cell-lumen, in the median part of the guard-cell, *n* = nucleus.

sented after a superficial tangential section was ideally made; in *C* such ideal section cut the guard-cells in their lower third. Figures 23 and 24, also ideal reconstructions, represent, respecti-

vely, the stomata of the Gramineae and of the most frequent type among the Dicotyledones; they are presented here so that a comparison of the different types can be made.

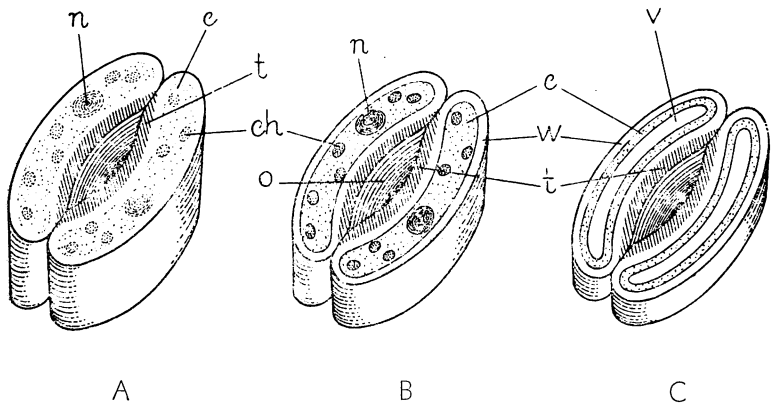

Fig. 24 — Ideal three-dimensional reconstruction of a stoma of the commonest type in the Dicotyledones. In *A* superficial view, in *B* superficial tangential section, in *C* deeper tangential section. *n* = nucleus, *c* = cytoplasm, *t* — wall-thickening around the stomatic aperture *o*, *w* = wall, *v* = vacuole.

With reference to the "obturating cell" as called by Accorsi (1), the present paper adds to his observation the fact that more than one cell with especial wall thickenings can be often found in the air-chambers (Figs. 7 and 8). That such cell (or cells) takes part in the regulation of the gas-exchange through the stomata, the present authors are not convinced. It is their belief that the explanation given by Haberlandt (4) in comparable instances, namely, that such cells put out of function those stomata below which they are formed, is preferable. This seems to be the case especially when several such cells are found in the air-chamber; a very well coordinated movement of all of them would be required to effectively regulate the stomatal opening. When only one cell is present in the air-chamber, it would be easier to visualize how such a regulation could be made. However, to decide whether the guard-cells are really functionless, and whether the obturating cells do or do not regulate the stomatal aperture, "in vivo" experiments are required.

Ouratea spectabilis shows stomata of the Gramineae type as reported previously by Ferri (3). This author presented such

stomata in cross-sections passing by both the middle and the tips of the guard-cells and also the longitudinal section. The figures presented in this paper, add a superficial view of the stoma and give as well several instances in which one or more cells with especial wall thickenings are found in the air-chambers. Figures 15 and 16, especially, suggest that the hypothesis that these cells block permanently the stomata, is the more probable.

The stomata of *Cedrela fissilis* are equally of the Gramineae type as shown by Rawitscher and Ferri (6). The present figures, in addition to confirming this fact, show the existence of the so-called "obturating cell" in the air-chambers of the stomata of this plant.

It is the present authors' desire to end this paper by emphasizing once more the necessity of making a revision in the classification system used until now in reference with the stomata. As mentioned before, this system is not satisfactory because it is based not on the organization of the essential part of the stoma, the guard-cells, but on the subsidiary cells which can even be lacking. It is our belief that a better system would first establish groups based on the organization of the guard-cells and sub-groups could be established later on the basis of other characteristics, among them those related to the subsidiary cells.

RESUMO

O presente trabalho estuda a morfologia dos estômatos de *Eucalyptus tereticornis, Ouratea spectabilis* e *Cedrela fissilis*.

Diversos desenhos representam êstes estômatos quando vistos pela superfície, e em cortes transversais e longitudinais. Foi verificado que *Eucalyptus tereticornis* apresenta um novo tipo de organização, entre o das Gramíneas e o tipo mais frequente das Dicotiledôneas. Visto pela superfície parece um estômato normal, enquanto que no corte longitudinal apresenta o conteúdo distribuido principalmente pelas extremidades das células-guardas.

A fig. 9 é uma reconstrução imaginária, tri-dimensional, dêste estômato.

Na câmara sub-estomática uma ou mais células com reforço especial da membrana tangencial externa podem ser encontradas. Se estas células, ao absorverem ou perderem água, executam movimentos que levam a uma regulação das trocas gazosas através dos estômatos, ou se elas bloqueiam permanentemente os mesmos, não se pode ainda decidir por falta de dados experimentais "in vivo".

Ouratea spectabilis e *Cedrela fissilis* têm estômatos do tipo das Gramíneas. Em ambos os casos uma ou mais células com reforços especiais da membrana podem ser encontradas nas câmaras sub-estomáticas.

Os autores chamam a atenção para o fato de que a classificação de estômatos até hoje aceita não é satisfatória, pois que não se baseia em característicos da parte essencial dos estômatos, que são as células-guardas, mas sim em atributos das células subsidiárias, que até podem faltar. Parece-lhes que um sistema mais satisfatório criaria grupos baseados na morfologia das células-guardas e estabeleceria sub-grupos em função de outros característicos, inclusive os referentes às células subsidiárias.

ZUSAMMENFASSUNG

Die vorliegend Arbeit befasst sich mit der Morphologie der Spaltöffnungen von *Eucalyptus tereticornis, Ouratea spectabilis* und *Cedrela fissilis.*

Einige Zeichnungen stellen diese Organe im Oberflächenbild wie auch in Quer-und Längsschnitten dar. Es wurde an *Eucalyptus tereticornis* ein neuer Bautyp festgestellt, der zwischen dem Gramineen-Typ und dem häufigsten Dikotyledonen-Typ vermittelt. Bei Oberflächenansicht scheint es sich um eine normale Spaltöffnung zu handeln, während beim Längsschnitt der Inhalt der Schliesszellen hauptsächlich auf ihre beiden Enden verteilt erscheint.

Figur 9 ist eine drei-dimensionale Rekonstruktion dieser Spaltöffnung.

In der Atemhöhle können eine oder mehrere Zellen mit besonderer Verstärkung der Aussenmembran angetroffen werden. Ob diese Zellen bei Wasseraufnahme oder-verlust Bewegungen ausführen, die den Gas-Austausch durch die Spalte regulieren, oder ob sie diese Spalten ständig blockieren, kann vorläufig noch nicht gesagt werden, da experimentelle Daten an lebendem Material noch ausstehen.

Die Spaltöffnungen von *Ouratea spectabilis* und *Cedrela fissilis* sind vom Typus der Gramineen. In beiden Fällen können eine oder mehrere Zellen mit besonderer Wandverdickung in den Atemhöhlen angetroffen werden.

Die Verfasser machen darauf aufmerksam, dass die bis heute anerkannte Klassifizierung der Spaltöffnungen nicht befriedigt, weil sie nicht auf Merkmalen des wesestlichsten Teils der Stomata,

d. h. der Schliesszellen beruht, sondern auf Eigenschaften der gelegentlich garnicht vorhandenen Nebenzellen. Es scheint ihnen richtiger, Gruppen zu schaffen, die auf der Morphologie der Schliesszellen selber beruhen, und diese Gruppen in Untergruppen auf Grund anderer Merkmale einschliesslich der Nebenzellen einzuteilen.

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