A Developmental Analysis of the Photosynthesizing Organs in *Prosopis Kuntzei*

By TYGE W. BÖCHER

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Synopsis

The striking morphology of a stem-assimilating South American tree, Prosopis kuntzei, invited renewed investigations in which most importance was attached to the development of its structure from the stage of seedling to adult, though not full-grown individuals. After a leafy juvenile period the plants continue in an apophyllous condition in which the photosynthesizing activity is mainly taken over by multinodal assimilating thorns (cylindrical cladodes and branches). During the first part of the development adventitious buds are responsible for the formation of some of the thorns. In leaf axils very peculiar club-shaped mucilaginous emergences are formed.

Of particular interest is the development of stomatal complexes in the multiple epidermis. The formative region consists of epidermal and hypodermoid cells and in most cases the mature guard cells are formed outside (at the level of) the periclinal wall which separates an outer epidermal and an interior hypodermoid layer. Meristemoids occur in both layers, and if meristemoids are cut lengthwise by the first anticlinal wall, there is further development of cell quadrants and small guard cells.

In stomatal depressions the true epidermal cells are generally dissolved, while the hypodermoid cells form the sunken guard cells. In a later stage the true epidermal cells develop densely spaced teichodes which probably take part in an exudation of cuticular wax.

In connection with the increase in girth, epidermal splits are formed and a kind of epidermal proliferation is ascertained. Moreover, pericyclic growth takes place largely by cells or cell plates issuing from the endodermal cells which encircle the primary fibre bundles.

In a late stage many wide intercellular spaces are formed between palisades inside the guard cells, while other parts of the green tissues are transformed into thick-walled, mainly chloroplast-less cells, thus creating a division of labour within the photosynthesizing tissues in the thorns.

Key words: Organization and development, multiple epidermis, hypodermoid cells, pericyclic activity, epidermal proliferation, teichodes.

TYGE W. BÖCHER
Professor
Institute of Plant Anatomy and Cytology
University of Copenhagen

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Contents

1. Introduction

The recording of plant development constitutes a branch of botany related to morphogenesis which deals with the process of development itself. A developmental analysis of single organs in a particular species may be looked upon as a modest contribution to the study of organization, a field which unfortunately is inclined to be lost in the multitude of taxonomical or purely descriptive morpho-anatomical investigations. In order to understand the organization of plant bodies it is necessary first to produce some reliable facts about the development of a number of single species representing certain characteristic life forms. Prosopis kuntzei Harms belongs to the apophyllous broom-like life form. It starts life as a small, leafy, branched shrub and ends as a 10 m high tree with a thick trunk and a crown of branched, multinodal, green thorns.

Material and methods

In a previous paper (Böcher 1975) the morphology and anatomy of the multinodal, assimilating thorns in Prosopis kuntzei were described in detail. The anatomical work was based on observations of SEM pictures of epistomatal cavities and slides produced from alcohol-preserved material of plants collected in Bolivia in 1971 by Hawkes, Hjerting & Cribb (No. 4371). The lack of access to living material made any kind of developmental research impossible. Consequently attempts were made to get seeds of the species. An approach to Dr. T. Myndel Pedersen in Argentina resulted in a seed sample from Provincia Corrientes in Argentina (Cult. No. 13103 from Dept. Sauce, near Estancia La Ovejita, 29°45′S, 58°40′W). Another sample was later brought to Denmark by J. P. Hjerting. It originated from Bolivia, Provincia Valle Grande near Comarapa, Dept. Santa Cruz. It corresponds to the collection No. 6490 by Hawkes & Hjerting, Feb. 28, 1980: "Thorn shrub-columnar cactus vegetation. The species grows into 10 m high tree with thick trunk. Stem assimilant. No leaves. 17°55′S, 64°31′W". The collection number (6490) was also used as cultivation number.

The very hard seeds were able to germinate after a rough mechanical treatment. The seedlings were grown in pots in an experimental greenhouse in the Copenhagen Botanical Garden. The plants were watered moderately and had access to artificial light in the winter. The cultivation of No. 13103 started in June 1979 (Fig. 1), that of No. 6490 in August 1980, but new germinations of seeds continued until May 1981. The two batches of seedlings behaved similarly.

The development of the seedlings and young plants was followed carefully. Fixations for anatomical studies were made in FAA. Embedding and sectioning were undertaken following partly the conventional procedure using paraffin and microtome sectioning at 10–15 μm, partly glycol methacrylate embedding and sectioning at 3–4 μm (cf. Feder & O'Brien (1968)). Most objects were stained with Safranin-Fast Green, Toluidine Blue or Sudan IV. In certain cases either Periodic Acid-Schiff (PAS) together with Aniline Blue Black (ABB) or Ruthenium Red were used.

The chromosome number in Prosopis kuntzei was determined to $2n = 28$ in plants of Cult. No. 13103, the number corresponds to that ascertained previously by Cherubini (1954).

In Prosopis kuntzei the young thorns are cylin-

drical cladodes or cladophylls. Their function as photosynthesizing organs appears intimately correlated with the early shedding of the foliage leaves. In some cases the green thorns can also be shed, but they have the character of a much more permanent structure. They develop a multiple (multiseriate) epidermis with stomatal complexes which are rather exceptional.

Acknowledgements

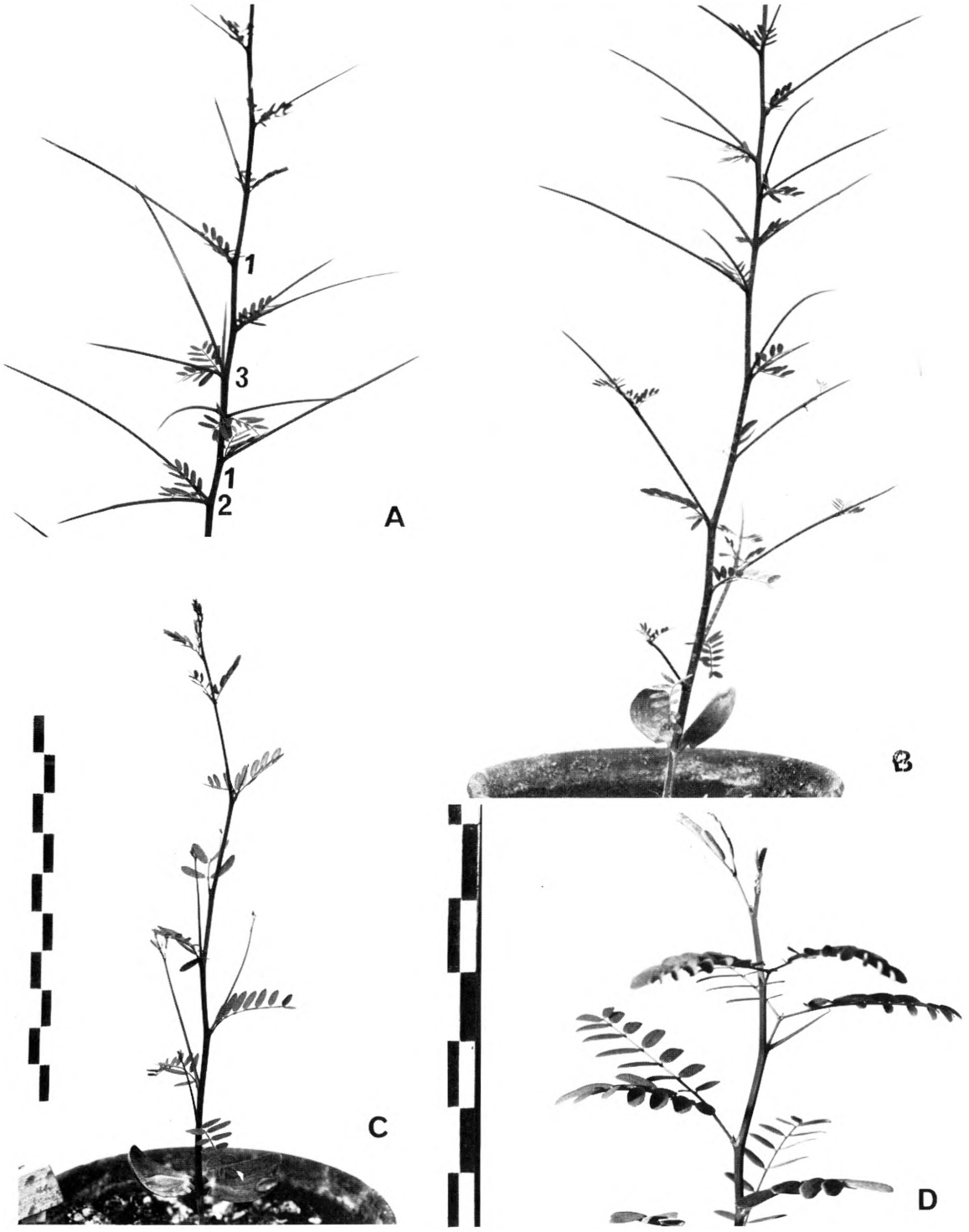
This study was supported by a grant from the Carlsberg Foundation which made possible the excellent microtechnical assistance of Mrs. Gunnel Holden. The writer is furthermore indebted to Mrs. Kirsten Pedersen and Mr. H. Elsted Jensen for very valuable assistance and to Dr. J. P. Hjerting and T. Myndel Petersen for the seed samples from South America.

2. Heteroblastic leaf development

Five stages in leaf formation were distinguished:
(1) The cotyledons are large, almost oval and entire, petioled, green on the adaxial side, whitish abaxially. They may persist for more than one month, in some cases one cotyledon is shed more than a week before the other. Their anatomy will be mentioned below.
(2) The first foliar leaves are paripinnate. The number of juvenile paripinnate leaves varies from two to five. In many specimens the uppermost (youngest) of these leaves has fewer pinnae. The number of pinnae varies from four to six, in the uppermost leaves from ten to sixteen. The juvenile paripinnate leaves persisted in culture for about three months, see Fig. 1.
(3) The adult foliar leaves, starting with leaf No. 3, 4 or 5, are bipinnate with two jugae. The two sections issue from a short rhachilla and each has 10–16 pinnae. The time of persistence in culture of the bipinnate leaves varies. All leaves produced on axillary shoots are bipinnate, but shedding of such leaves takes place very early, in particular on axillary shoots. Shedding of bipinnate leaves on the main stem (axis I) begins in the third month after germination and continues for some time. Finally a leafless (apophyllous) stage is reached. Under natural conditions, e.g. in Bolivia or Argentina, the leafless stage appears stabilized in dry periods, but may be interrupted in wet periods or during spring tides.

(4) The apophyllous stage is characterized by lack of foliar leaves and by the fact that green multinodal thorns and stems (axis I and axillary shoots, axis II) have taken over all photosynthesizing activity. The youngest parts of the axillary shoots may, however, still produce some few bipinnate leaves (Fig. 2B).
(5) In the cultivated specimens new bipinnate leaves were formed on third order axes (axis III). Such axes appear to be weak, but in nature they are coarse and strong and give rise to further branching or sometimes flowering (see Böcher 1975 Fig. 1–2).

The morphology of the seedlings in Prosopis kuntzei resembles that described in Acacia by Robbertse & Van der Schijff (1971). Here the first (juvenile) foliar leaves are also pinnate, while the later-formed leaves are bipinnate and often two-jugate.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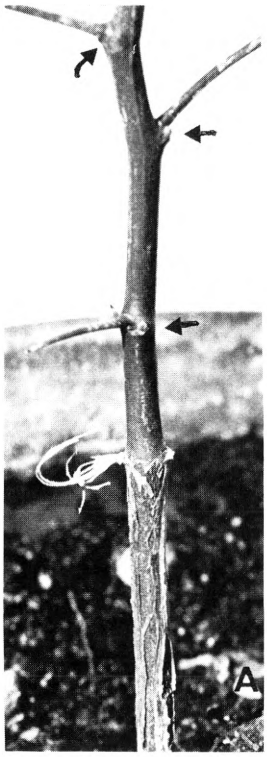
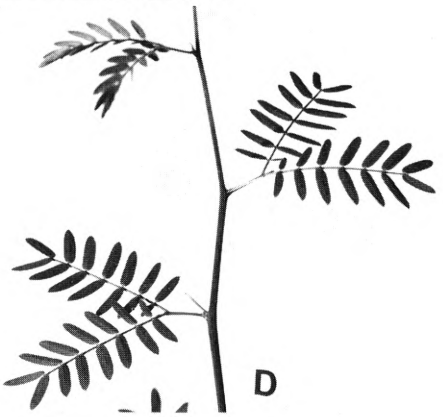




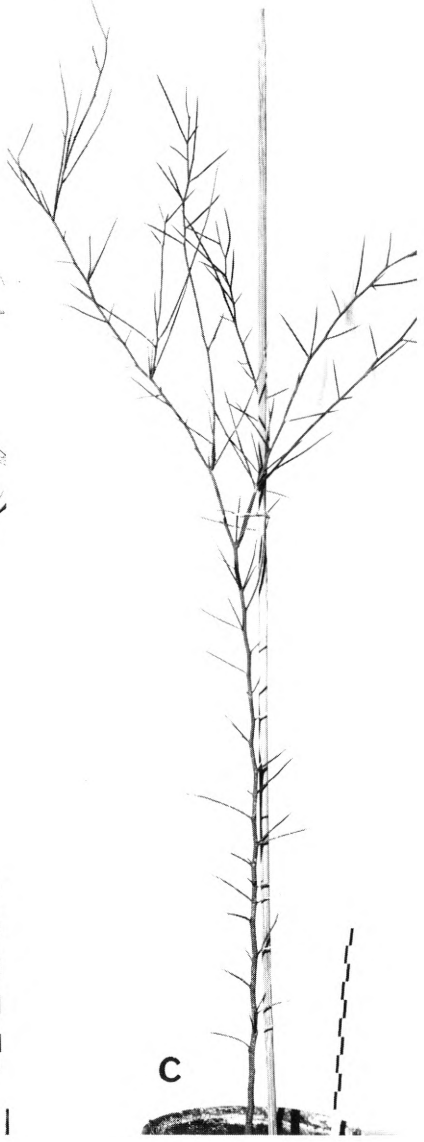


Fig. 1. Cultivated specimens of Prosopis kuntzei No. 13103 (A–C) and 6490 (D) in the experimental greenhouse in the Copenhagen Botanical Garden. In B–C transition from pinnate juvenile leaves to bipinnate leaves, cotydelons still present. In A bipinnate leaves only showing different numbers of thorns issuing from the same axil (1, 2, 3), in D a solitary thorn, the tip bending upwards. Scales divided in cm. Photo June-July 1979.

Fig. 2. Culture of Prosopis kuntzei. A–C No. 13103 (second year), D No. 6490. A. Base of stem showing remains of one cotyledon and hypocotyl with cork lists, adventitious buds at bases of thorns (arrows). – B. Specimen in which leaves are shed below, while young leaves occur in new shoots on the left part of the top. – C. Specimen showing branching in the upper part, no leaves left. – D. Small part of specimen with solitary thorns at the bases of two leaves.

3. Nature and sequence of green thorns and lateral branches

The axillary meristems in Prosopis kuntzei give rise to two kinds of buds, those developing into multinodal, green thorns and those which become axillary shoots, e.g. lateral branches. Adventitious buds are also produced. They are usually located in close connection with buds developing into green thorns and are considered to be accessory buds (cf. Sandt 1925, Priestley 1929). The twin thorns mentioned in the following text result from a nearly simultaneous development of an axillary and an accessory thorn. In the previous paper (1975 Fig. 2 and p. 8) the twin thorns are referred to as pairs of unequal, strong branches. The interpretation of the twin thorns deviates considerably from that proposed for the double thorns described in Prosopis dulcis by Velenowsky (1907 Fig. 407 and p. 650). His diagram of the axil in this species shows one axillary bud and two equally strong thorns on both sides of the bud and supported by two scales which Velenowsky interprets as stipules. However, according to Troll (1937: 557–558) the two thorns may more likely be supported by two suppressed prophylls at the base of the lateral axis. Thus they belong to the axillary bud. The above interpretation of the twin thorns in Prosopis kuntzei is made probable by two facts: that the thorns are usually of unequal size and direction and that they are multinodal, the nodes being marked by small scale leaves or sometimes even by weak foliage leaves.

When describing the sequence and position in Prosopis kuntzei of lateral axillary shoots (thorns and branches) we may distinguish between the following types:

a. Solitary thorns which issue from the lower axils e.g. particularly from axils of pinnate juvenile leaves. But solitary thorns are furthermore formed from axils of bipinnate leaves near the shoot endings. The first-formed solitary thorns often bear some few foliage leaves (Fig. 1B).

b. Twin thorns. Two thorns issuing from the same axil, often of unequal length and strength, occurring mainly at axils of bipinnate leaves. In relation to the direction of the rhachis of the supporting leaf, the first-formed thorn tends to deviate towards the left, while the later-formed thorn, which is usually smaller, deviates towards the right. The angle between the two thorns varies.

c. Triplet thorns. (Fig. 1A (3)). Three thorns at the same axil. One of them, and often the central one in the triplet, is frequently the most vigorous and may represent the "legitimate" axillary shoot, while the two other thorns may be accessory thorns. Transitions from central thorns in triplets to persisting lateral shoots are found occasionally.

d. Double twin- or triplet thorns occur in rare cases when two axils close up tightly.

e. Lateral branches. Axillary shoots developing into normal branches bearing foliage leaves and thorns in the same way as the main shoot (the primary axis).

Oddly enough there seem to be correlations between solitary thorns and juvenile pinnate leaves, and twin (or triplet) thorns and bipinnate adult leaves.

From the survey of the shoot generations in the specimen illustrated in the previous paper (p. 7–8) it appears that solitary (single) thorns are placed at the base of a shoot generation, thus in agreement with the behaviour of the cultivated

plants. Another correlation concerns the lateral persisting shoots. They issue usually from the axils of bipinnate leaves and in many specimens they increase in length with the distance from the basal juvenile part.

The scattered occurrence of solitary thorns in a sequence with predominance of twin thorns in the upper part of a specimen is not easy to understand. However, such solitary thorns often issue from axils following next to or shortly after axils from which lateral shoots branch off. Some kind of restraining effect due to the branch just produced is suggested.

The faint acropetal promotion (Germ.: akrotone Förderung) of lateral shoots is interesting. At an early stage of development it appears to be determined that the plant ultimately becomes a tree. Already some of the one-year-old specimens show acropetal promotion of the lateral branches and get a "crown" and a trunk part, the latter resulting from a continuation of an unbranched condition in the proximal part. In many of the cultivated specimens, the most vigorous lateral shoots grow obliquely upwards approaching the direction of the first-formed main axis. The "crown" results from the repeated acropetal development of secondary and tertiary branches and a steady although incipiently small deviation of the direction of the lateral axes from that of the mother axis. The result as it appears from the habit of an old tree (Böcher 1975 Fig. 1b) is similar to that found in globular shrubs described by Rauh (1942) in e.g. Centaurea spinosa and Genista horrida.

The branching system was explored in some specimens by counting internodia and recording the position of thorns and lateral axes.

Cult. 13103 No. 3

(1) Lower (proximal) zone bearing exclusively solitary thorns: 0–9.5cm (including hypocotyl). 5 internodia, length of thorns 3–7 cm, each thorn with 3–4 internodia. No lateral shoots.

(2) Upper branching zone from 9.5 cm to the top which at the time of measuring was 54 cm from the ground. Twin thorns predominating, usually unequal in length, the longer 3–5 cm, the shorter 1–4 cm. Uppermost part of main stem has mostly solitary thorns and resembles thereby the longer lateral shoots, see below: d, e and f. The position of the lateral shoots, a–g, indicated by the distance in cm of its base from the ground:

a. 14 cm from ground: 9.5 cm long with two twin thorns.
b. 15 cm from ground: Triplet, 2 cm long central thorn between two which are 5 and 4 cm.
c. 17.5 cm: Lateral shoot, 22 cm long, obliquely upright with twin thorn 9 cm from the base.
d. 24 cm: Lateral shoot, 23 cm long, with 11 solitary thorns and 1 twin thorn.
e. 25 cm: Lateral shoot, 20 cm, first with three solitary thorns, then a twin thorn and finally three solitary thorns.
f. 28 cm: Lateral shoot, 23 cm, sequence of thorns 1 (solitary), 2 + 2 (twins), 1, 1, 1, 2, 1.
g. 29 cm: Resembling (b) a short thorn-like shoot between two thorns in a twin-pair and an additional closely spaced twin thorn. The thorn-like shoot is 12 cm long and carries four solitary thorns.

Cult. 13103 No. 7

(1) Lower zone with solitary thorns, including hypocotyl: 0–5.7 cm with 2 internodia.

(2) Upper branching zone mostly with twin thorns of unequal length. Laterals, a–f, at distances from the ground in cm:

a. 10 cm. Length 8 cm with 4 internodia.
b. 11.7 cm. Length 19 cm with 0, 1 or 2 thorns or new (secondary) lateral shoots (s): 2, 1, 2, 2, 1, s, 0, 2, s, 0, s, s, s, 0, 0, s.
c. 19.7 cm. Length 20 cm. Thorns: 2, 2, 2 + 1, 2, 2 + 1, 2 + 2, 2, 2, 1, 0.
d. 24.5 cm. Length 6 cm. Thorns: 1, 0, 0, 0, 0, 0.
e. 26 cm. Length 2 cm. No thorns.
f. 30.3 cm. Length 6 cm. No thorns.

Total length of main stem at the time of measuring: 35.3 cm.

In both plants (3 and 7) the latest initiated laterals are short and with few or no thorns at the nodes. In No. 7b secondary laterals (shoots of third order) were produced 11.7 cm from the base. In sister plants (Nos. 5 and 6), however, secondary branching occurred near the top. From the node 23 cm and upwards new bipinnate leaves on secondary laterals were produced in the early spring of 1981 (Fig. 2B).

Cult. 6490

19 seedlings were followed. In June 1981 it was evident that only 2 specimens had the longest branches in the basal part, while 7 specimens had acropetal promotion of the lateral shoots. Five specimens were classified as intermediate with the longest or most vigorous laterals issuing from the middle part of the stem. From the latter, one (No. 19) was selected for a more detailed study.

No. 19.

May 5, 1981. Germination.

June 2. Cotyledons still present. First three leaves pinnate, at the axil of leaf No. 2 short lateral bearing one pinnate leaf with three pairs of leaflets. Thorns formed on the left of the leaf bases at leaves No. 1–8. At Nos. 9–10 no thorns at this time.

June 10. Cotyledons withering. Lateral branch at leaf No. 6.

June 25. Cotyledons shed. Short branches at leaf Nos. 2, 6, 7, 9 and 10, thorns at leaf Nos. 3, 4, 5, 8, 11 and 12.

October 26. Single main stem. (Axis I) length 84 cm, carrying 22 branches. About 10 cm above the ground the branches become 11–16 cm long, later 22–23 cm long, distally having new bipinnate leaves, then follow six nodi with thorns only, two with short laterals, and finally five nodi with thorns only and bipinnate leaves.

December 5. Height of plant 85 cm. Hypocotyl 6 cm, brownish. Stem above hypocotyl green. Branching and formation of thorns indicated as distance in cm of nodi from the scars of the cotyledons:

0.5 No thorns or laterals
1.3 Solitary thorn and short lateral (1.8 cm)
2.2 Solitary thorn and short lateral (0.3 cm)
2.8 Solitary thorn and short lateral (1.1 cm)
4.0 Twin thorn
5.5 Twin thorn and lateral (7 cm with 1 scale leaf)
7.0 Thorn rudimentary and lateral (8.5 cm)
8.3 Solitary thorn (0.5 cm)
10.0 Lateral 11 cm
11.0 Lateral 9 cm
12.5 Lateral 4.5 cm
14.0 Lateral 16 cm (distally carrying bipinnate leaves)
15.0 Solitary thorn
17.5 Weak twin thorn
19.0 Lateral 6 cm
21.0 Lateral 12 cm with 5 internodia
23.0 Lateral 24 cm with 5 bipinnate leaves and in all 14 internodia
24.5 Twin thorn and lateral (6 cm)
27.5 Lateral 22 cm with 4 leaves and 15 internodia
28.0 Lateral 7.5 cm with 2 internodia
30.0 Twin thorn
31.0 Rudimentary twin thorn
33.0 Solitary thorn (2 cm)
35.0 Lateral 21 cm with 12 internodia and 7 distal bipinnate leaves
37.0 Twin thorn and lateral 3.5 cm
39.5 Small solitary thorn
40.5 Twin thorn
42.0 Solitary thorn
44.5 Twin thorn
46.5 Twin thorn
51.0 Solitary thorn
53.0 Solitary thorn
55.0 Lateral with five internodia and four leaves

Top of shoot (30 cm) with 17 internodia carrying three short laterals and a number of bipinnate leaves.

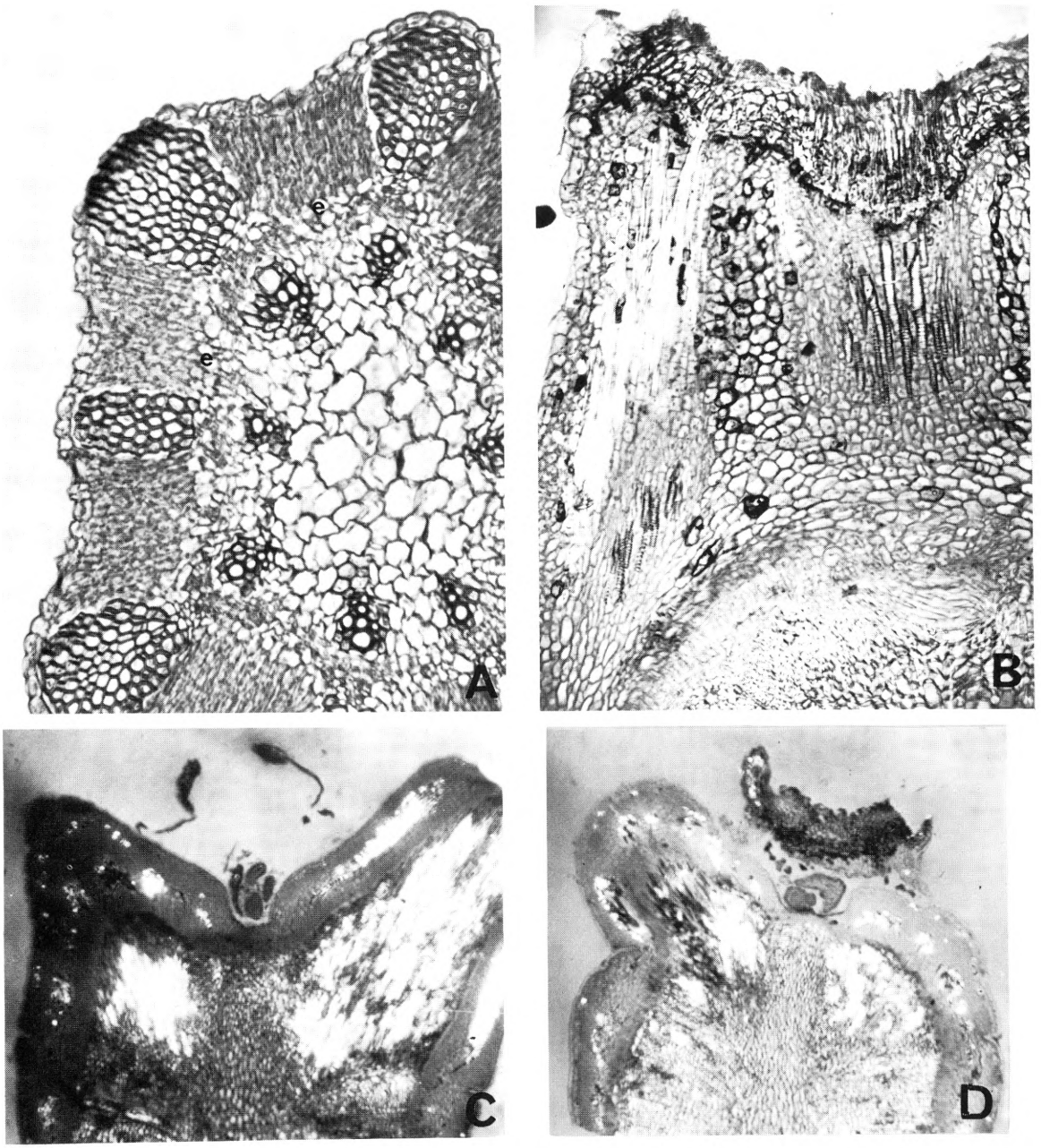


Fig. 3. A. Cross section of young thorn. Palisade tissue between primary fibre bundles, endodermis (e), vascular bundles and pith. – B. Scar after thorn which has been shed, vascular bundles and fibre bundles in cortex (birefringent), × 100. – C. Adventitious bud with two prophylls in angle between two thorns, xylem showing up in polarized light. – D. As the preceding, but bud emerging below remains of thorn base. C–D, × 25. Quadruple staining (C) or Toluidine Blue (D).

4. Anatomy of photosynthesizing organs

As it appears from the morphological analysis, the most important or effective part of the production of matter is connected with the green stems, including green thorns and lateral branches. The anatomy of the green thorns was already dealt with in the previous paper (Böcher 1975), but is repeated and amended below in the present paper.

The cotyledons in Prosopis kuntzei have an almost oval outline (Fig. 1C). They are dorsiventral, dark green above and pale below. Nevertheless they are amphistomatous, but some of the stomata are situated in small depressions in the abaxial epidermis (Fig. 4D). The dark green colour of the adaxial sides results from pellucidity and is due to the subepidermal palisades with their densely spaced chloroplasts (Fig. 4C and E). There is no typical spongy parenchyma, but very wide parenchymatous cells without chloroplasts which cause the pale colour of the abaxial side.

Surface views of the epidermis reveal an almost anomocytic arrangement of guard cells and neighbouring (agene) cells. There are no typical subsidiary cells (Fig. 4C, E). The guard cells appear to be surrounded by growth of an agene cell and may in several cases look as if suspended from the walls of the surrounding cell almost as in the desmo-mesogenous type described in ferns, e.g. species of Aneimia (cp. Maroti (1966), Fryns-Claessens & Van Cotthem (1973)). The cells in the abaxial epidermis are provided with many wall lists which extend from the outer to the interior cell walls (Fig. 4D).

The leaflets exhibit a dorsiventral structure. Two layers of palisades are developed along the adaxial sides, while a kind of spongy parenchyma occurs along the abaxial epidermis. The green cells in the spongy parenchyma are not very branched and with small intercellular spaces. The leaflets are amphistomatous, but there are comparatively few stomata in the adaxial epidermis. The cuticle is thin. The surface of the adaxial epidermal cells is vaulted. Near the midrib this vaulting becomes more pronounced. It may be responsible for the matt, non-light-reflecting appearance. In structure the leaflets resemble mesomorphic shade leaves (ombromorphic). The guard cells are small, unprotected and not sunken although often placed between larger arching epidermal cells. The arrangement of the stomata is paracytic as in other members of the Mimosaceae. The leaves of a xeromorphic species of the same genus, Prosopis glandulosa, have thick cuticular layers, three tiers of palisades and short spongy cells (Shields 1951 Fig. 30).

The position of stomata in relation to the subsidiary cells in assimilating thorns is illustrated in Fig. 5. The cell pattern in paradermal views shows a paracytic arrangement usually with two subsidiaries on each side of the guard cell and additional subsidiary cells wedging in between the first-formed (arrows). In transversely arranged cell files, the subsidiary cells become short and wide (Fig. 5C). In old thorns the arrangement tends to be staurocytic (cp. Fig. 5E).

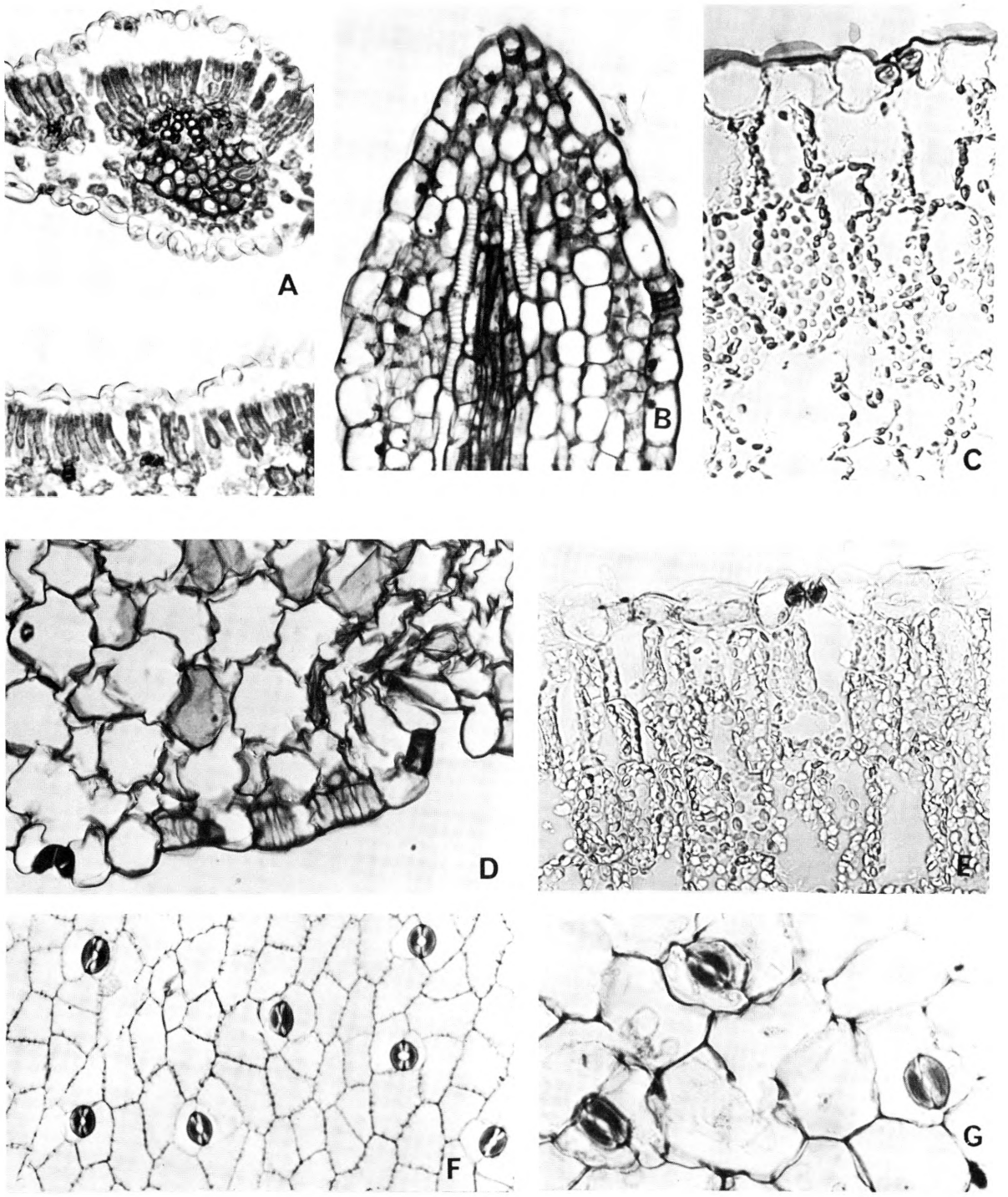
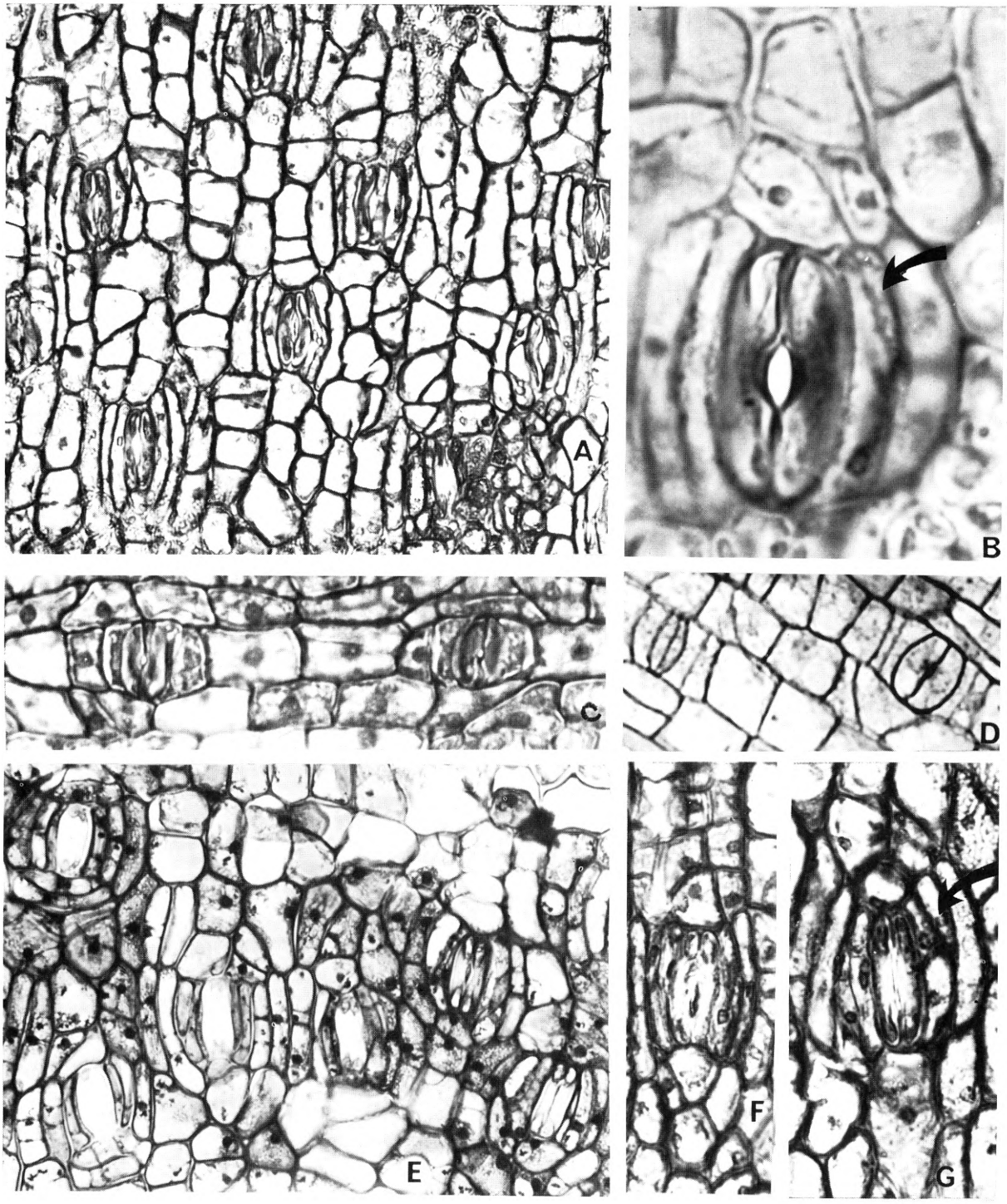


Fig. 4. A–B. Anatomy of pinnate leaf. A. Cross section with midrib and palisades. Stomata, × 160 F.S. – B. Top of rachilla with central tracheids and stoma, × 250 F.S. (Fast Green-Safranin) – C–G. Anatomy of cotyledon. C and E adaxial surface with stoma and palisades filled with starch. D. Abaxial surface with depression, epidermis with several wall lists. – F–G. Paradermal views of abaxial epidermis with stomata and (in F) cross sections of wall lists. C–E, × 250. C. Ruthenium Red. D. Toluidine Blue, E. Sudan IV, F. × 160, Toluidine Blue, G. × 320, Toluidine Blue.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5. Differentiation into defensive and nutritional green thorns

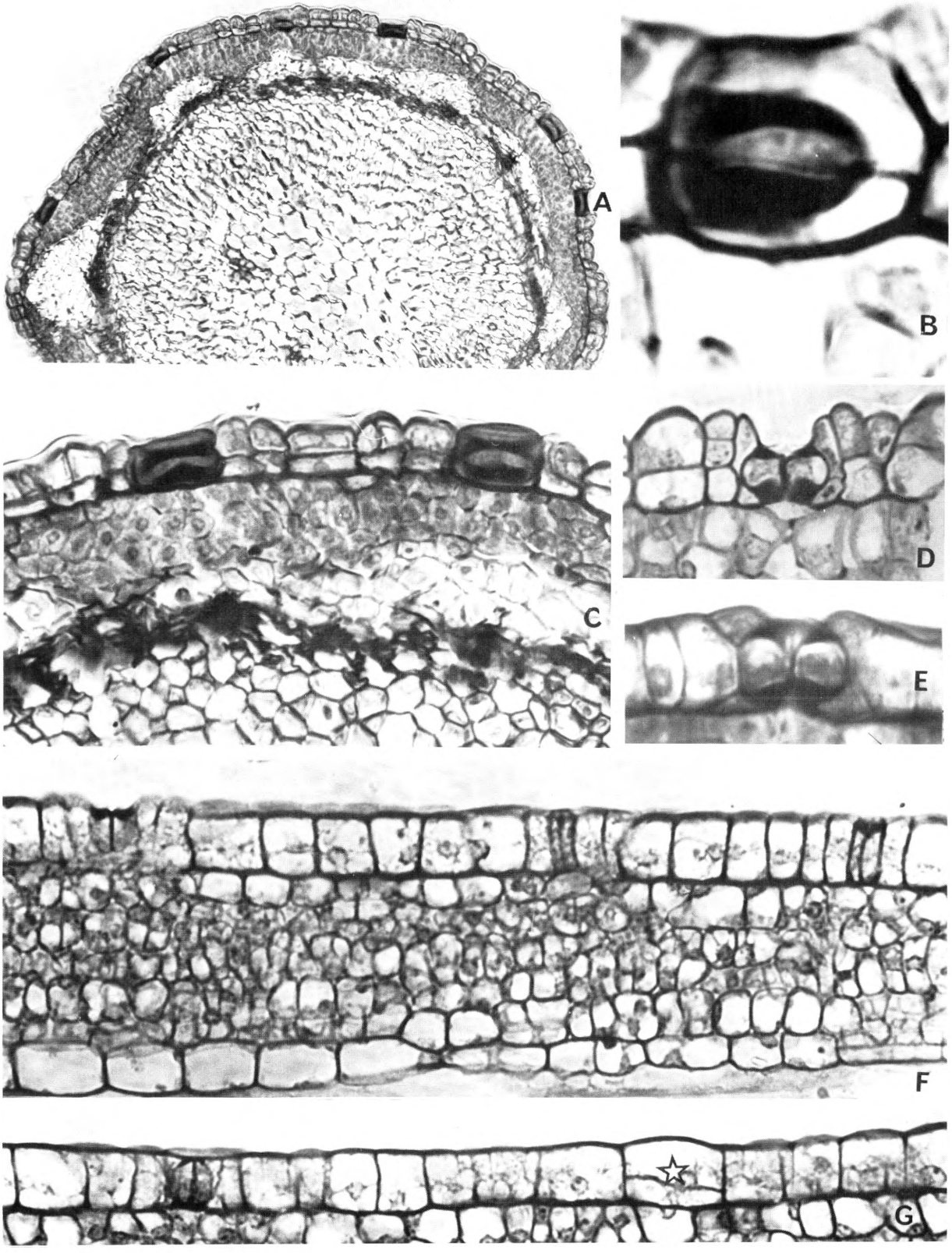
A differentiation into two types of green thorns takes place early. It has not been elucidated when the determination of the fate of a developing thorn becomes fixed, but an attempt to elucidate this point might be made by changing the cultivation conditions. From the observations which are available it is already evident that there are many transitional stages between the two thorn types. It also appears that the strongest thorns, which are usually persistent, belong to the nutritional type, while some of the smaller thorns, which are often finally shed, although transitory, are likely to be mainly defensive organs.

The differentiation manifests itself as a number of anatomical differences which can be outlined as follows:

Nutritional thorns. These are cylindrical cladodes or cladophylls. They have an almost normal, stem-like structure (Fig. 3A). Anatomically they consist of a multiple epidermis, a cortex, a vascular cylinder and a pith. The cortex contains several layers of photosynthetic cells, usually arranged as palisades. The strength of the thorns at the sharp points depends on the density of fibre bundles which occur in connection with the vascular bundles and continue to the points; other details in Böcher 1975: 10 and below.

Defensive thorns. Their photosynthesizing activity is restricted (Fig. 6A-C). The normal stem anatomy with its distinct layers becomes blurred. The most striking difference from the nutritional type concerns the formation of an almost closed cortical fiber layer and a simultaneous decrease in cells with a content of chloroplasts. Another important feature is the disappearance of vascular bundles or vascular tissues and the transformation of the pith and other parenchymatous tissue areas into thick-walled, almost sclerenchymatous cells. Defensive thorns may start as nutritional ones and during their maturation become more and more typically defensive.

Fig. 5. Paradermal views of epidermis in assimilating thorns showing position of stoma and subsidiary cells (paracytic arrangement), A–F. × 640 F.S., B. × 1260, G. × 640, PAS + ABB. Arrows in B and G point to additional subsidiary wedging in between the two subsidiaries first formed. D. Young stage. E. Older stage with almost staurocytic stomata.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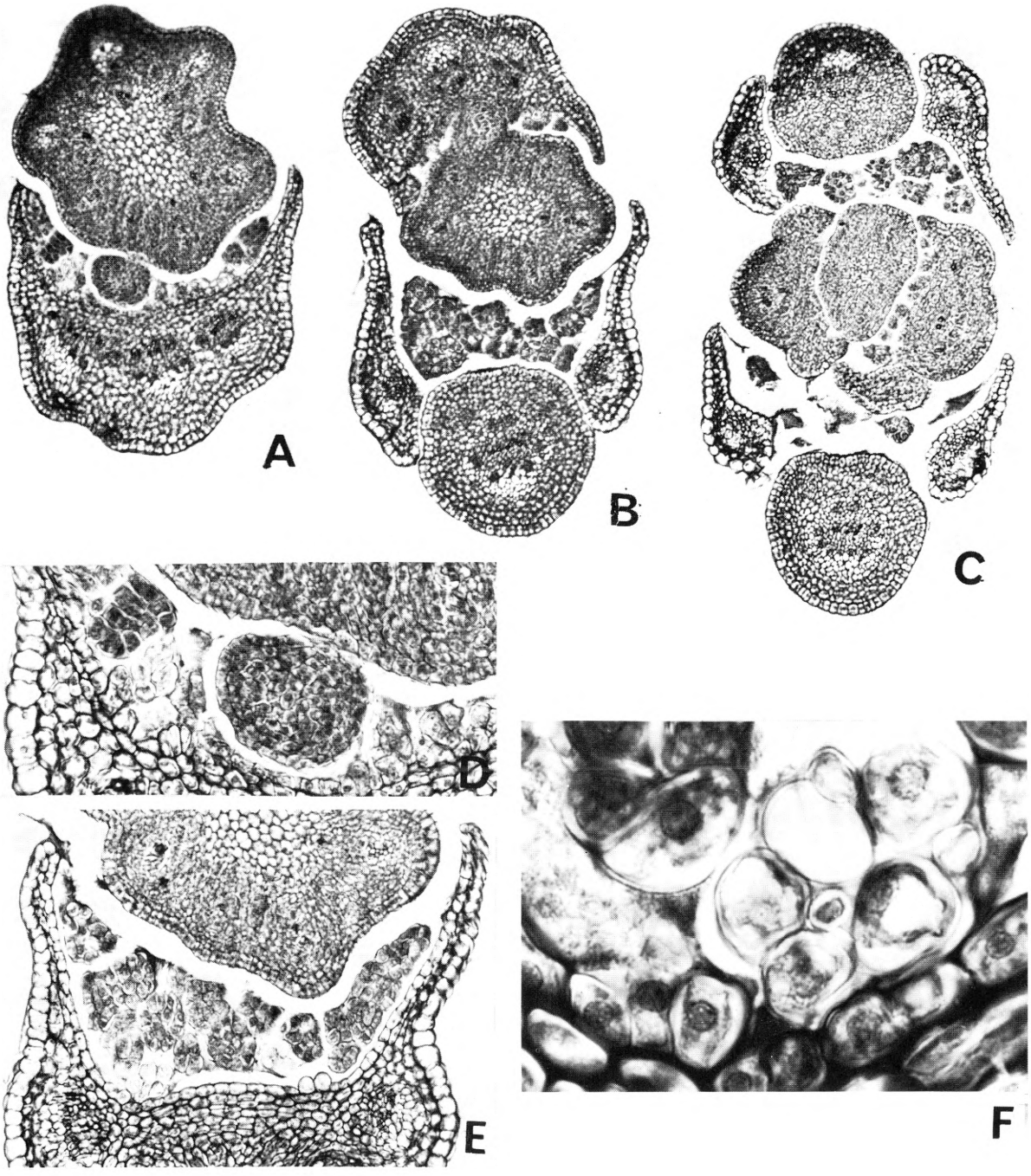
6. Axillary formative activities

The leaf axils in Prosopis kuntzei and their immediate continuations at the flanks of the leaf scars and stipule-remains constitute a formative region, easy to demonstrate, though difficult to circumscribe accurately, because of the inconstant appearance of adventitious buds which often develop into thorns. We may distinguish three types of axillary events.

(1) The axil encircles and protects the succeeding internode, thus the continuation of the primary axis. In cross section the stem has about six broad lobes, each containing a vascular bundle. At this stage the stipules are not separated from the leaf base, but appear as two "ears" at an acute angle (Fig. 7A). The lobed body contains the main stem and the base of the next leaf which soon becomes separated. Concomitantly the two stipules are disengaged, while new ear-like projections (stipules) are formed at the next leaf. Between the two leaves the main stem now appears as a transversely, faintly stretched, lobed body (Fig. 7B) giving rise to further leaves (Fig. 7C).

(2) An axillary meristem appears to be active, the cells being arranged in rows beneath the adaxial epidermis. However, the epidermal cells take part in the growth, undergoing anticlinal divisions and producing a number of swollen cells which are mucilaginous or become decomposed and turn into mucilage. Some of the cell clusters develop into club-shaped or branched emergences (Fig. 8–9). These, which arise at the bases of leaves, may have parallels in the shaggy hairs, described by Fahn(1974 Fig. 77, 4), issuing from the bases of the petioles in Portulaca oleracea. They are elongate bodies composed of several cells, but in Prosopis kuntzei the bodies are club-shaped, often stalked and branched below. Their basal cells often stain reddish with Safranin-Fast Green, while their distal part retains the green tint. The cells in the distal parts border swollen giant cells which also become reddish and seem to be transformed into a kind of plasmodia or cellular mucilage. The physiological importance of the mucilage production in the axils is not ob-

Fig. 6. A–C. Defensive thorns in Prosopis kuntzei. A. Survey in polarized light showing merging of phloem fibre bundles with an extracambial double-refractive, almost closed ring, also the central core of xylem and pit is showing up. – C. As A, but with higher magnification, also showing polygonal green cells replacing palisades and superimposed guard cells in the two-layered epidermis. – B. Two merging, superimposed guard cells. A–C. Toluidine Blue, × 160 (A), × 640 (C) and × 2000 (B). – D–E. Development of proximal subsidiary cells. E. Youngest stage with hour-glass-shaped subsidiaries in protoderm, × 630 F.S. – D. Late stage showing periclinal wall in the subsidiary cell on the right, × 630 F.S. – F. Protoderm, young palisades and endoderm, × 640 F.S. – G. Protoderm, initiation of proximal subsidiaries and in one cell (☆) the first periclinal wall, × 640.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vious. In the axils, however, being formative regions where shoots of various kinds emerge, some kind of lubrication may be advantageous.
(3) Some of the cells which appear in the axils form independent bodies, however, which in section have circular outlines and are interpreted as cross sections of young thorns. They are located slightly to the left of the median plane, cutting the middle part of the leaf and the main axis (Fig. 7A and D). This location indicates that buds which become thorns are generally adventitious, and not genuine lateral shoots which ought to be formed in the median plane.

Other thorns are initiated later and penetrate the epidermal and meristematic areas adjacent to the stipules. They appear to be supported by very small basal prophylls and are consequently interpreted as adventitious lateral thorny short shoots (cp. Fig. 3C, D).

The thorns of first order are sometimes able to produce some few bipinnate leaves, or at an early time change their destiny from green thorns to lateral branches bearing foliage leaves.

Twin thorns usually have one longer thorn which is initiated first and obtains at least one node (indicated by a scale leaf or a single bipinnate leaf). The young points of such thorns are mostly bent upwards (Fig. 1D) minutely hairy and carry a scale leaf. The second thorn in a twin pair is initiated later, being a branch on the larger and older one. If the primary thorn occurs e.g. in the middle of February, the second one may be delayed until the first part of April. The angle between the two thorns in a twin pair is general almost a right-angle, and the directions of the two correspond fairly well to that of the rhachillae in the two segments of the supporting bipinnate leaf (Fig. 1A).

Fig. 7. Development of axil in Prosopis kuntzei. A–C. Successive stages. A. Leaf base still with two acute ears, the leaf is supporting the stem which is seen as a lobed body (cross section). Between the stem and leaf base is a cross section probably of a thorn, cp. D. – B. The ears now becoming separate stipules. The base of the next leaf is seen above. – C. Stipules are disengaged in the two successive leaves. The main stem appears as a centrally placed body which has given rise to two further leaves, the leaf on the right carries a number of young pinnae on its adaxial side. A–C, × 40 F.S. D–E. Base of first leaf, in D with thorn, × 100 F.S., in E, stipular ears and production of swollen cells above meristematic surface of leaf base, × 64 F.S. – F. Surface of leaf base. Mucilage and swollen cells produced by epidermis of leaf base surface, × 2000 F.S.

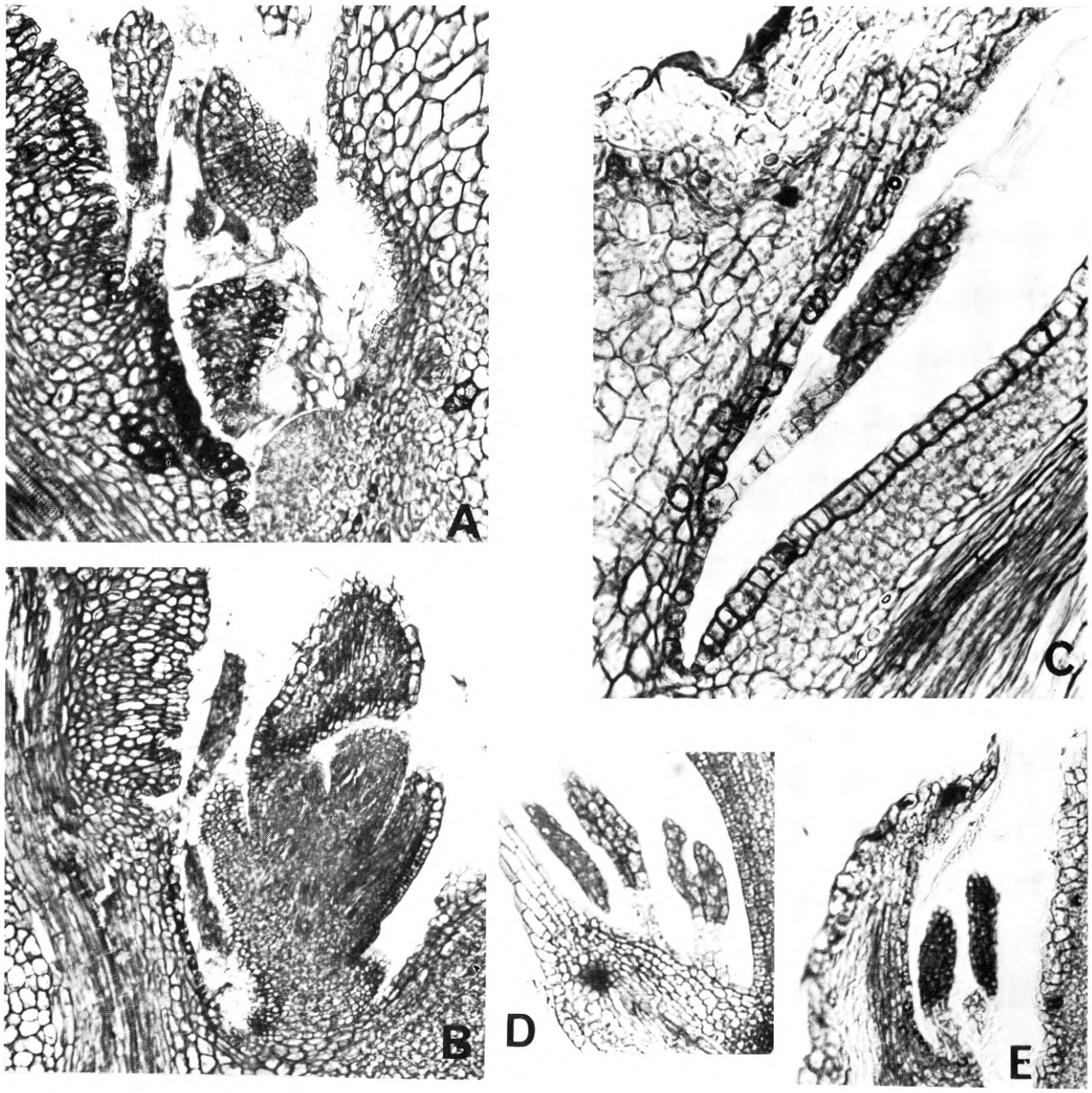


Fig. 8. A–E. Mucilage producing emergences issuing from leaf bases near axil, in B accessory bud, in C base of thorn, × 250 F.S.

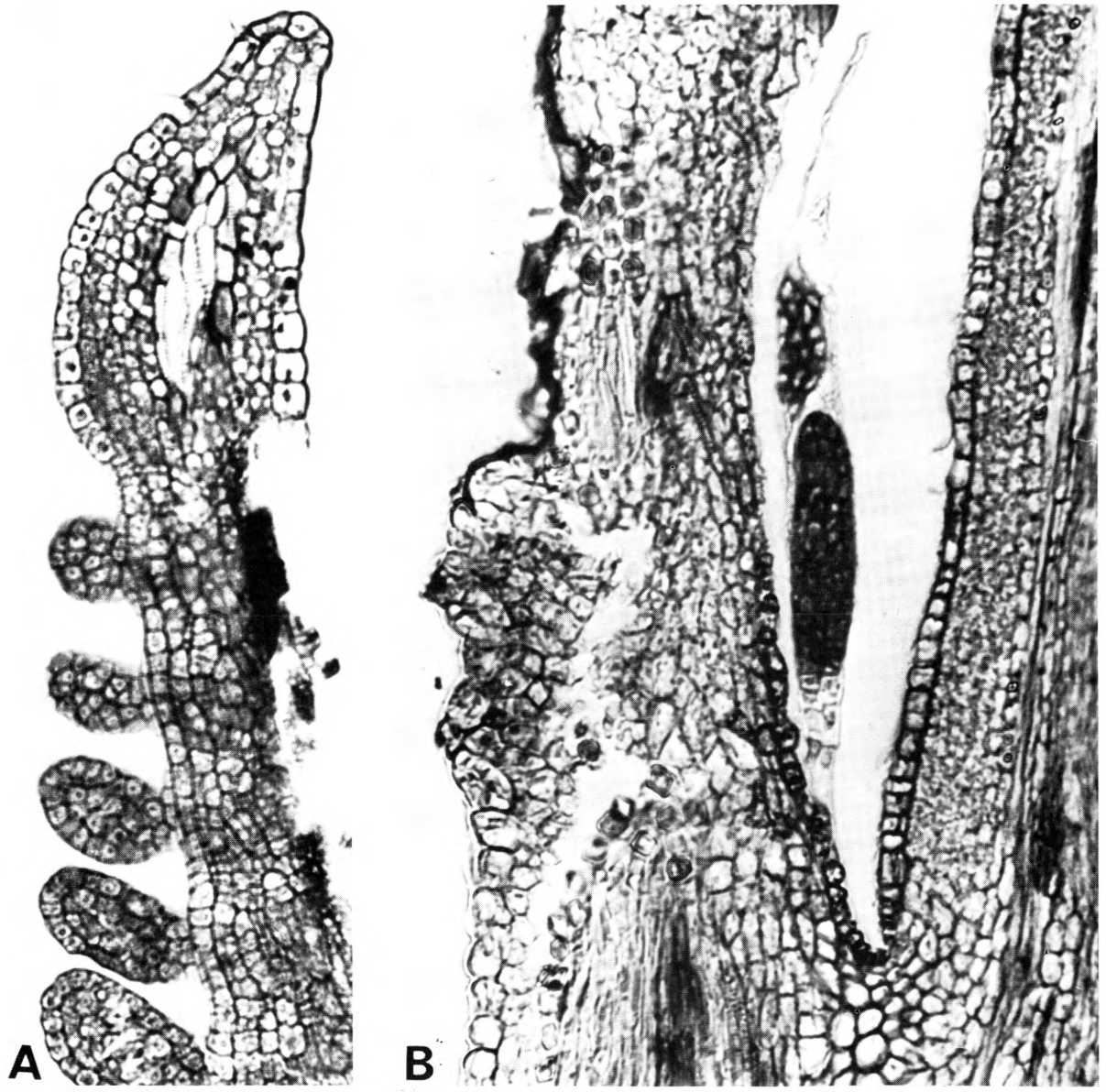


Fig. 9. A. Terminal part of primordium of bipinnate leaf, the rachilla ending has a median tissue of tracheids and may develop into a hydathode. Five pinnae, × 200 F.S. – B. Similar to Fig. 8C, but indicating successive production of three mucilaginous emergences, the youngest below, × 250 F.S.

7. Epidermal development in interstomatal parts

The one-layered phase is just a provisional maturation of the protoderm. Several new cells are inserted by radial divisions so that the epidermis keeps pace with the increasing girth. The one-layered phase appears to be very short. At a very early stage a periclinal wall separates an outer true epidermal and an interior hypodermoid cell. The divisions first occur randomly (Fig. 6G), but soon the majority of cells undergo periclinal divisions and the epidermis becomes multiple, though two-layered. For a very long period the outer walls in the true epidermal layer are distinguished from the interior cells by producing a cuticular layer which is thin at young stages. When young the outer walls are without any thread-shaped radial structures ("ectodesmata" or teichodes), but usually the walls soon become fairly thick and stain with Toluidine Blue (Fig. 17).

Teichodes are formed in the outer epidermal layer at a rather late stage and are confined to the outer layer. They were never observed in the epidermis of leaves, nor in epidermal layers of young, green thorns. They appear, however, in older, thicker thorns, but their first appearance differs. They occur as short stainable threads issuing from the plasmalemma in normal looking cells which do not yet taper adaxially, thus in the same way as observed in young stems of Bulnesia (Böcher & Lyshede (1968, Plate X)). The initial stage in the formation of teichodes in Prosopis appears from Fig. 21A. Teichodes in final stages become abundant in older thorns where a stretching and narrowing of the adaxial part of the outer epidermal cells have taken place. During this type of growth the teichodes close up and become much longer and form brushes on top of long tapering cells (Fig. 21B).

The tapering external epidermal cells in Prosopis were previously discussed in regard to their possible relation to cuticular wax exudation. The tapering narrow parts continue in teichodes which were called delicate micro-channels. They seemed to terminate or become invisible in LM exactly where the cuticular layer outside an interior isotropic band shows up in polarized light due to a content of wax (Böcher 1975: 11–15, Plates I–II).

Teichodes ("ectodesmata") have obsessed cytologists for several years, but e.g. Esau (1977), when referring to EM observations by Merkens, de Zoeten & Gaard (1972), now defines them as linear spaces or channels in the outer epidermal wall, filled with a coarse reticulum of cellulose fibrils extending from the plasmalemma to the cuticle and serving as pathways for absorption and excretion.

Esau does not explicitly mention excretion of waxes near the surfaces of cell walls. However, after heating and melting, cuticular wax in Prosopis is pushed out from the cell walls in mounted slides to form delicate – after recrystallization – birefringent strands of the same dimensions as the micro-channels (cf. teichodes) from which they are pushed out (Böcher l.c. Plate II). The teichodes forming the brushes in Prosopis become almost undetectable in their uppermost, distal parts. The best results referred to in the previous paper were obtained by using interference contrast equipment or Johansen's quadruple staining. In the new material, PAS together with ABB appeared to be the most satisfactory

staining procedure. PAS reacts intensely with the reticulum of cellulose fibrils in the teichodes. Their proximal parts become dark reddish and look like rhizomatous bases from which the upper branched brush parts issue (Fig. 21). The amount of wax embedded in the cuticular layer as well as the epicuticular wax deposits varies considerably. In Argentinian material an epicuticular wax cover including wax plugging of stomatal openings was conspicuous, while such a cover was very sparse in material originating from Bolivia (Böcher 1975, Plates IV–VIII). In the new material slight differences in cuticular wax content could be ascertained between Cult. No. 13103 from Corrientes and No. 6490 from Bolivia. In both cases the occurrence of cuticular and epicuticular wax was modest in the youngest material.

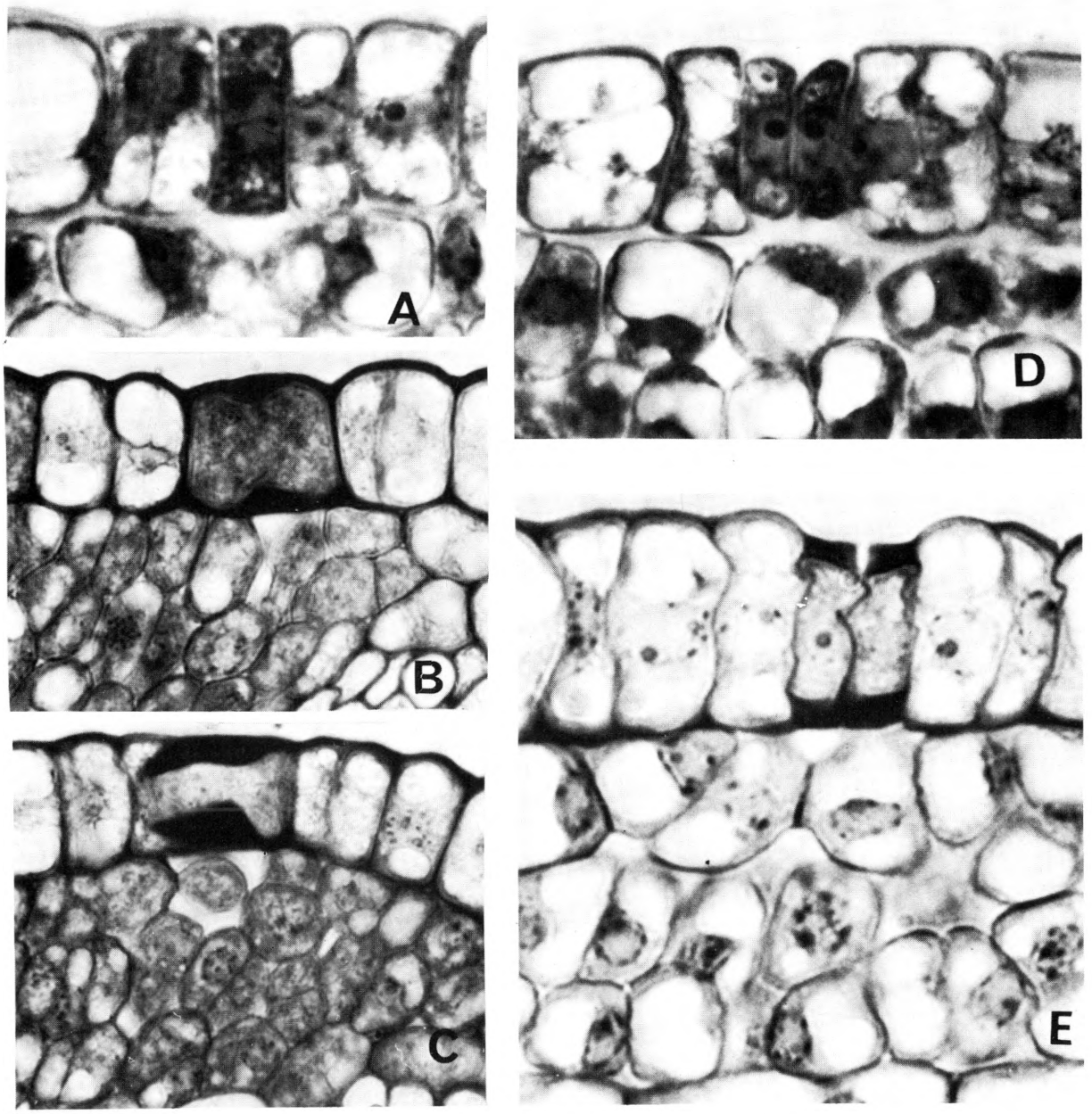


Fig. 10. Protoderm in green thorns in Prosopis kuntzei. Guard cell mother cell in longitudinal sections (A, D, E) and cross sections of thorns (B, C). In B–C, first anticlinal division has taken place, in D perhaps there are small extra nuclei on both sides of large central nuclei. Thickenings of outer and interior walls conspicuous in B, C and E due to staining with Toluidine Blue. In A and D, F.S. All, × 2000.

8. The development of stomatal complexes in a multiple epidermis

The previous anatomical investigations had revealed that the majority of guard cells in not too young thorns belonged to a cell stratum which was a hypodermoid layer. Hence, the guard cells were generally placed in a very deviating manner. This fact invited a detailed treatment using the new material with its possibility of following the fate of the guard cells from the very beginning, i.e. the mother cells (or stomatal meristemoids).

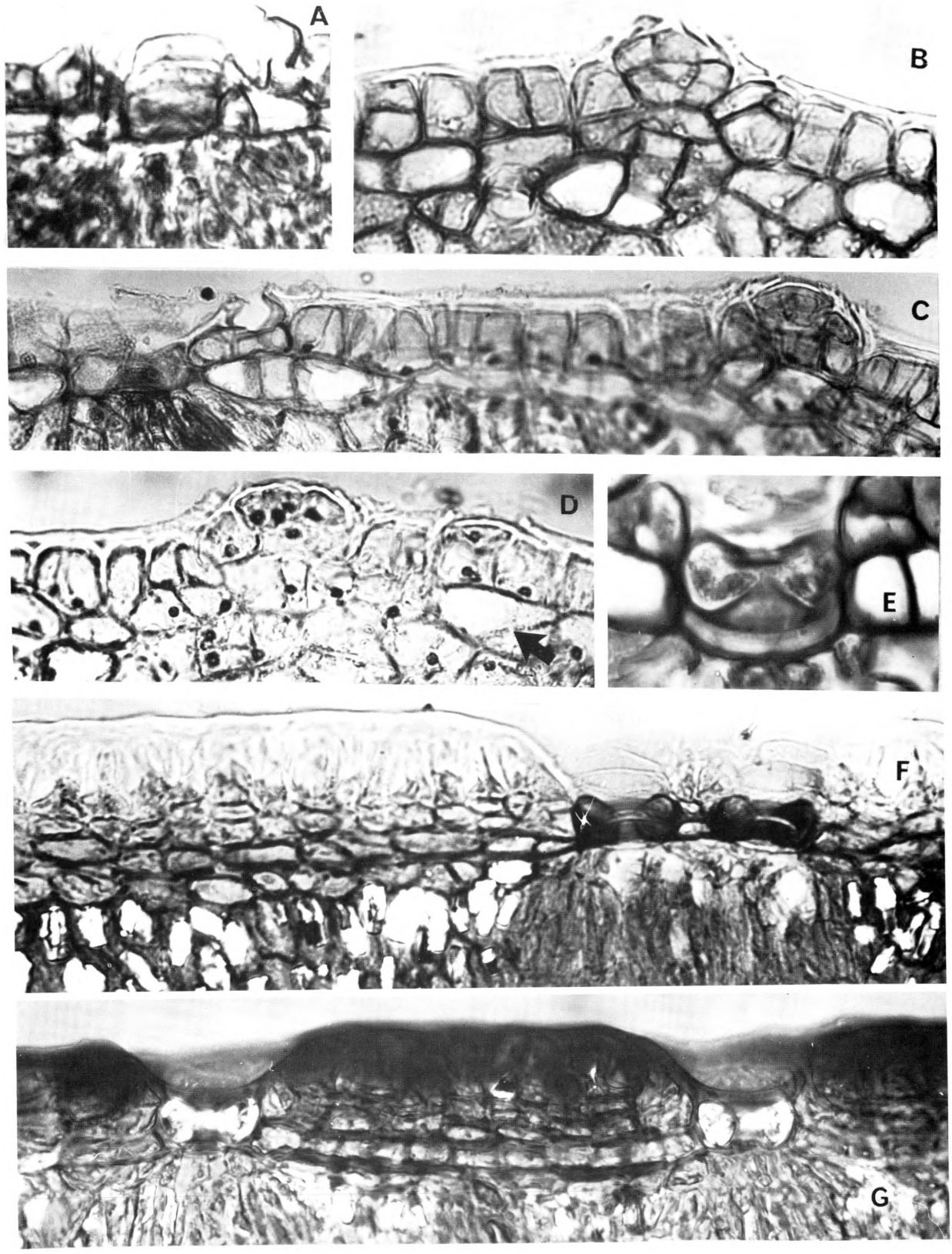
The protoderm was studied in recently formed photosynthetic thorns which were cut lengthwise and transversely. The orientation of the stomatal apertures is transverse, i.e. at right angles to the longitudinal axis of the thorns. Cross sections of thorns therefore result in longitudinal views of guard cells.

As already mentioned, the initial one-layered phase of the protoderm is short. In longitudinal sections of the thorns, the guard cell mother cells appear as short, low cells with large nuclei and dense cytoplasm (Fig. 10A). In cross sections of the thorns they are difficult to detect except in such cells where a thickening of the outer and interior walls has begun. The thickenings are intensively stained with Toluidine Blue (Fig. 10C, E). The guard cell mother cells soon divide to form two narrow guard cell precursors. Precursory cells occur outside young photosynthesizing tissues. They are very rare outside collenchyma or fibres in corners of the thorns.

Some observations indicate that the nuclei of the newly formed guard cells have cut off small nuclei (Fig. 10D), but the latter have hardly been able to form separate cells. Such small cells were suggested in the previous paper (l.c. Fig. 5b–d), but their existence is very doubtful. The differentiation of outer and inner stomatal ledges appears from Fig. 14A–D. The inner ledges may be comparable to those mentioned by Carr & Carr (1978) in Eucalyptus, where they are described as thin wisps or tenuous remains of the mother cell envelope.

The outer ledges in Prosopis kuntzei resemble the opposing bars described by Carr & Carr (l.c. Fig. 16–17) in Eucalyptus orbifolia. In mature stomata the outer ledges in Prosopis become strong outgrowths. They are cutinized and covered by the cuticle which during the early period of the stomatal maturation maintains adaxial closure of the split between the guard cells (Fig. 15G). During the maturation the lower thickenings in the guard cells are greatly augmented and the lumen of the guard cell protoplasts becomes reduced and invested with a thin separate layer (Fig. 14C), which resembles the apparent wall capsules described by Carr & Carr in Eucalyptus incrassata.

In Prosopis kuntzei subsidiary cells are initiated at the same time as the guard cell mother cells, one or two in each side (Fig. 10A, D, E and Fig. 14D). The two proximal ones will frequently be narrowed in their middle parts concurrent with an expansion of the two outer ones and an increase in breadth of the guard cells. In Fig. 6E the middle parts of the proximal subsidiary cells are reduced to thin connections between the adaxial and abaxial parts. The substomatal chamber is usually initiated at a very early stage, in fact at the same time as the differentiation of the guard cell mother cells takes place (Fig. 10). As a rule, subsidiary cells are placed in a paracytic way, parallel with the long axis of the guard cells, but subsidi-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ary cells or neighbouring (agene) cells can also be identified at right angles to the long axis of the guard cells (Fig. 5C). In late stages of the epidermal development, the stomata may be surrounded by subsidiary cells and their derivatives in a manner resembling the arrangements recorded in monocotyledons (Fig. 5 and cp. Tomlinson 1974). It is a characteristic feature of the late development of the system of subsidiary cells that additional subsidiary cells become wedged in between two parallel subsidiaries to form three or four subsidiaries on each side of the stoma (Fig. 5, arrows).

The further development towards a multiple epidermis begins with an increase in periclinal divisions, which implies that the epidermis becomes composed of groups of cells arranged on top of each other and, at the beginning, of many solitary cells. A long-lasting phase has two (three) cell strata of which the exterior undergoes many anticlinal divisions. In many cases each cell in the interior layer is covered by two exterior cells (Fig. 13B). At the early stage, the green cortex inside consists of densely spaced cells in 2–6 layers arranged between the two-layered epidermis and the endodermis.

In the one-layered epidermis, meristemoids occur at certain intervals as guard cell mother cells and adjacent subsidiary cell initials. In a two-layered epidermis, the meristematic activity is maintained in the exterior cell layer, the genuine epidermis, but some activity is transmitted to the interior hypodermoid layer and to the borderline area between the two cell layers, the majority of guard cells maturing on level with the periclinal wall which divides the two cell layers, cp. Fig. 14A–D.

Meristemoids are frequently divided further by periclinal walls to form groups of two or three superimposed cells. If the meristemoid is predestined to develop guard cells, a peculiar cell group is formed. It consists of two cells looking like oppositely directed, almost congruent semicircles surrounding a third narrow cell which may remain undivided or is cut lengthwise by the periclinal wall (Fig. 6B, C).

As it appears from Fig. 14F–G, the periclinal wall traverses the outer part of the plant body, forming a level surface which is interrupted only by the stomatal depressions. Morphogenetically this wall is particularly important and may be designated the periclinal main wall. The outer, true epidermal cell layer may locally be further divided (* in Fig. 19B, C). The hypodermoid layer, on the other hand, may sometimes after division give rise to cells which are genuine hypodermal cells (Fig. 19). However, other hypodermal cells are formed by reorganization of adaxial cortical cells which lose chloroplasts. The traversing periclinal main wall appearing from Fig. 19 marks the

Fig. 11. A–D. Epidermal splits and subsequent proliferation in epidermal and hypodermoid layer. A. Hypodermoid cell reaching stomatal subsidiaries. – B. Cluster of epidermal cells at split and cluster of underlying hypodermoid cells. – C. Two cuticular splits, proliferation in the one on the right, below the left one, an empty epidermal cell, but a growth in the hypodermal layer indicated by the short torpedo-shaped cell row. – D. Two splits, the right one with single protruding cell and oblique division in hypodermoid layer (arrow). – E. Narrow cell in hypodermoid layer below guard cell. – F. Accumulation of crystals in palisades in interstomatal parts. Air-filled intercellular spaces and top of fan-shaped palisades below the two stomata. – G. Crystals formed also in guard cells, walls in interstomatal, multiple epidermis stained with Sudan IV. A, × 640, F.S., B–D, × 500, F.S., E, × 1000, F.S., F, × 500, PAS + ABB, G, × 500, Sudan IV.

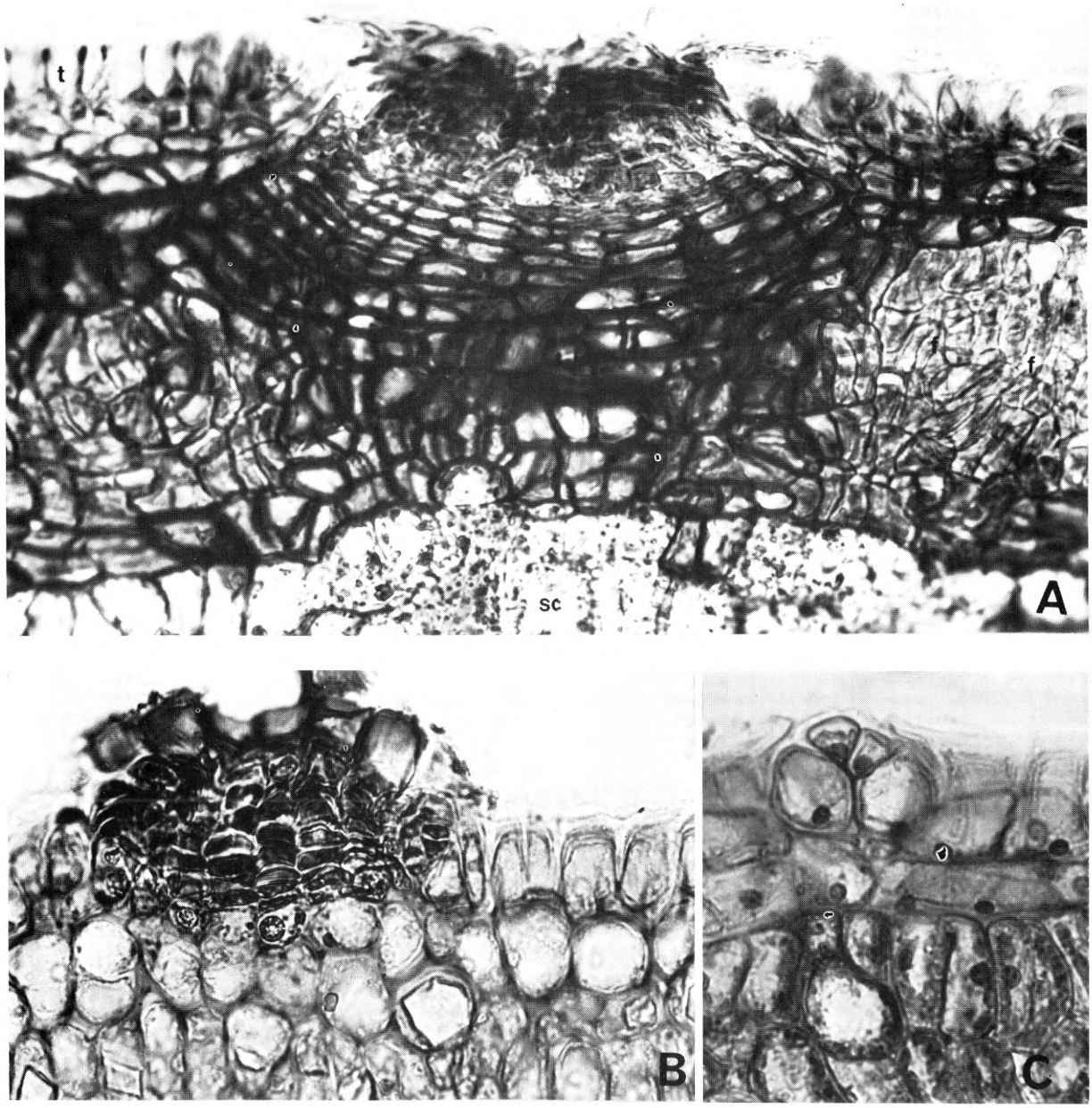
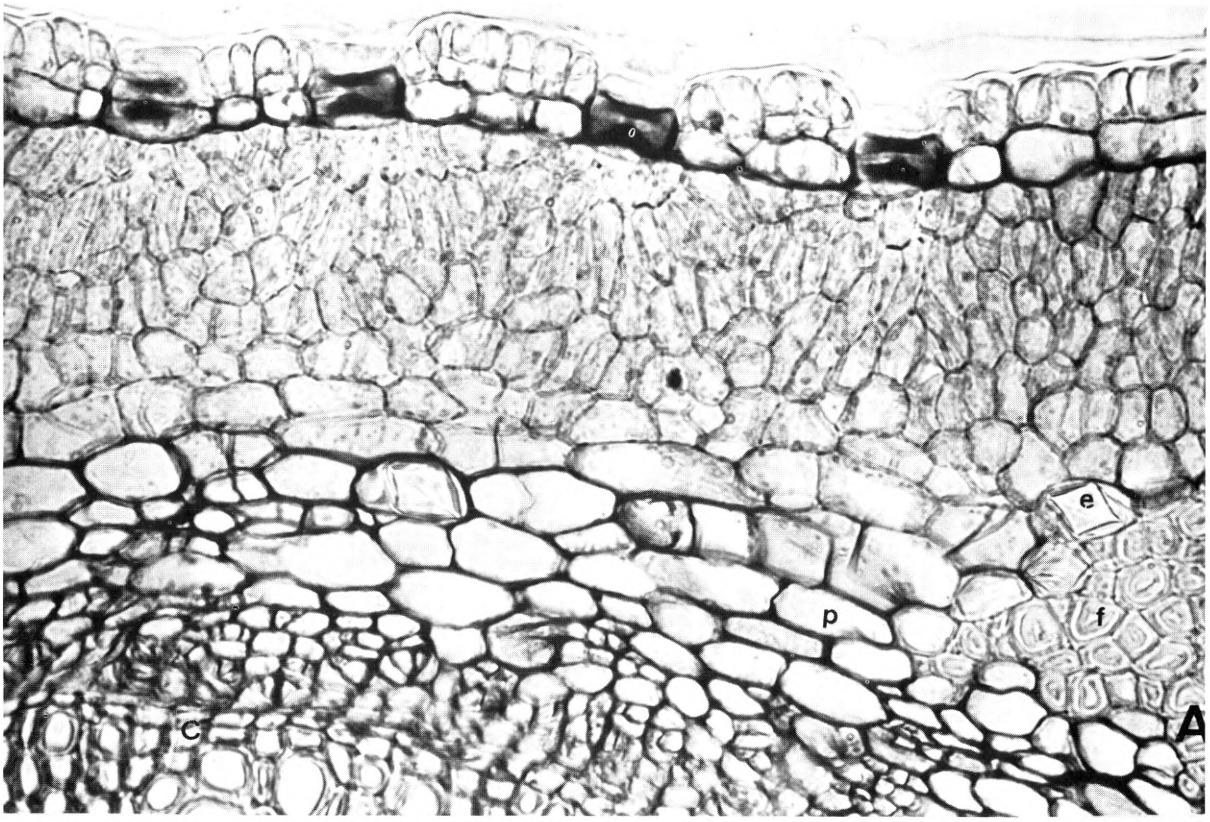


Fig. 12. A–B. Lenticel formation in multiple epidermis. B. Phellogen arising on the border between the epidermal and hypodermoid layer, in A, hypodermal cells appear involved and the lenticel produces few phelloderm cells. – C. Epidermal proliferation after cuticular split, t, teichodes, f, substomatal fan-shaped palisades with intercellular space, sc, sclerenchyma. A. × 500, PAS + ABB staining, B–C, × 480 F.S. (Fast Green-Safranin) and Toluidine Blue.

Fig. 13. Two-layered stage of epidermal development. In A and C superimposition of guard cells and remains of adaxial cells ("ghost cells"), in B hypodermoid position of guard cell and two cases of meristemoids with narrow underlying hypodermoid cells (arrows). f, fibre bundle, e, endodermis, p, pericyclic cells, c. vascular cambium. A, × 500, Toluidine Blue, B, × 640 F.S., C, D, E, × 640, Sudan IV.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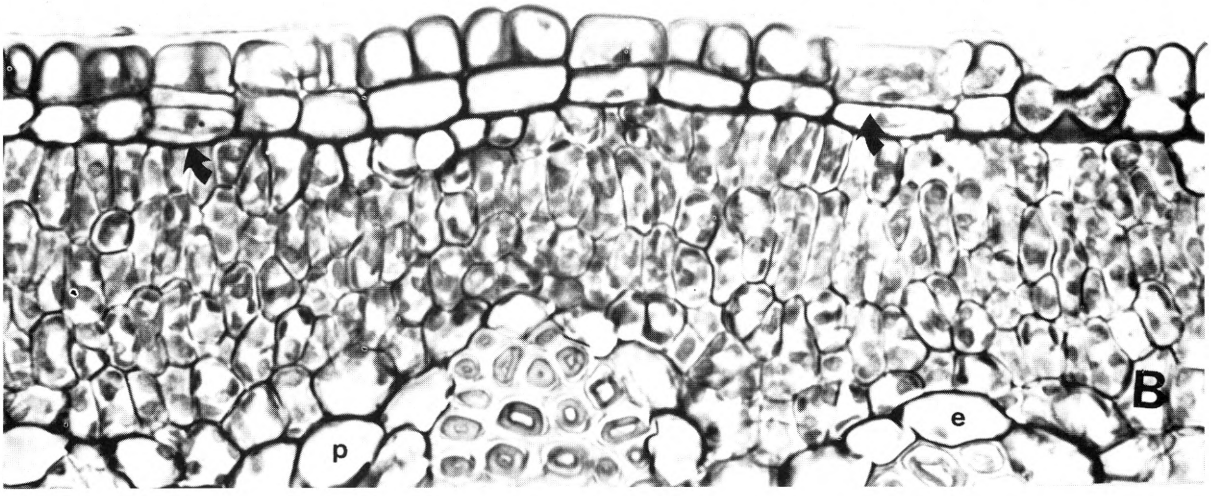
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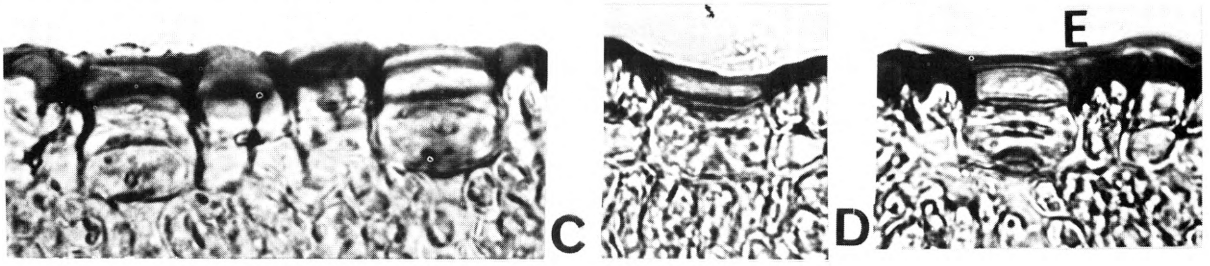
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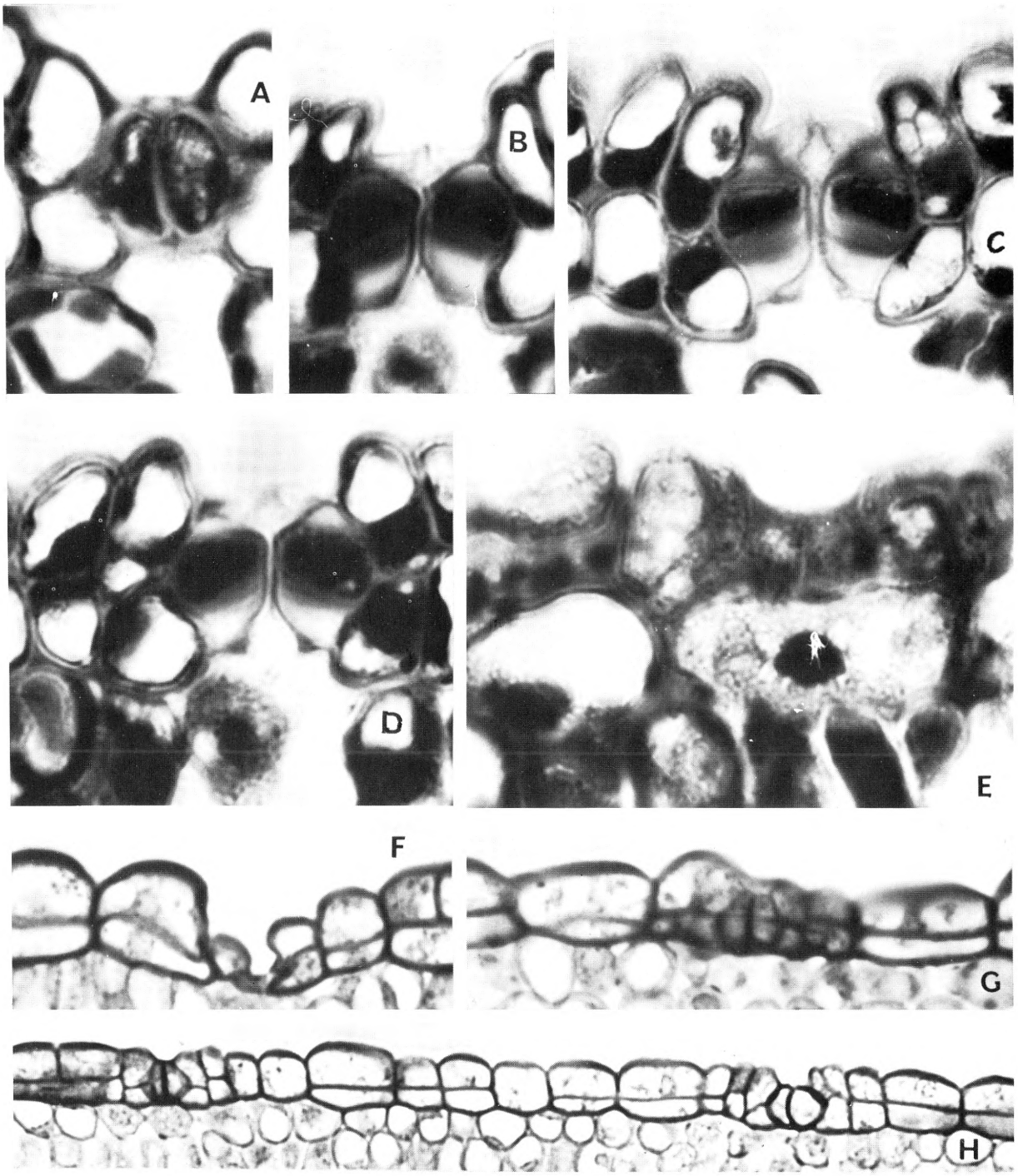
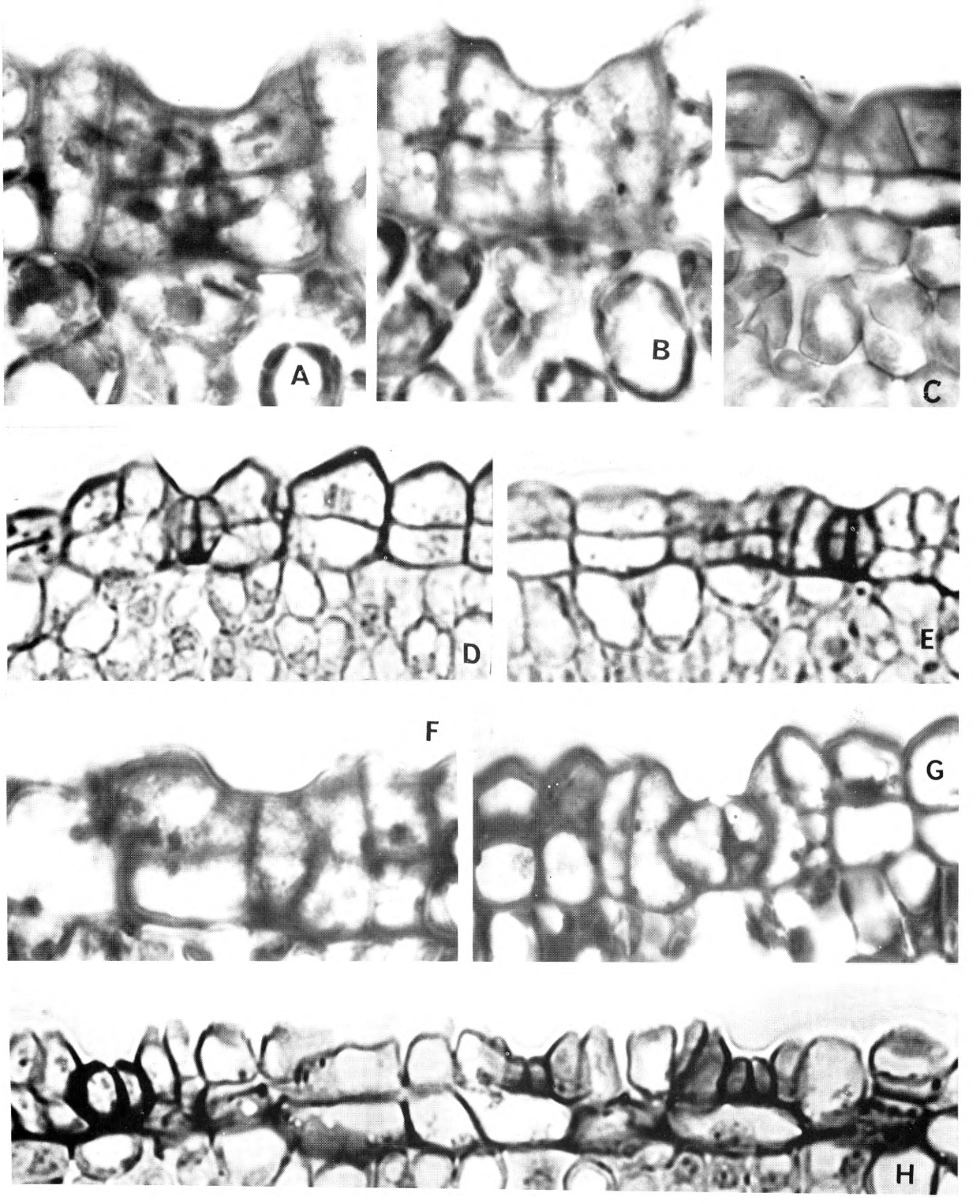


Fig. 14. F.S. A–B. Stomata, normal position of guard cells at the level of the periclinal wall, proximal subsidiaries divided. A. Younger stage, outer ledges not full-grown as in B–D. – E. The periclinal wall is formed. The hypodermoid cell with central nucleus. The epidermal cell forms a group of two small guard cells and subsidiaries, still immature. A–E, × 2000 F.S. – F. The periclinal wall cuts through abnormal stoma, × 984 F.S. – G. Periclinal wall cuts through the entire stomatal complex, × 640, Toluidine Blue. – H. Periclinal wall does not reach the guard cell (on the right) or only one of the guard cells (on the left), × 640, Toluidine Blue.

Fig. 15. Behaviour of periclinal wall in relation to stomatal complexes. A–D. The wall cuts the whole complex. A–B, × 2000 F.S., C, × 1000 F.S., D, × 984, Toluidine Blue. – E. Irregular periclinal divisions of guard cells, × 984, Toluidine Blue. – F. Periclinal division of complex almost finished, × 2000 F.S. – G. Young stage, outer stomatal ledges not mature, × 1000 F.S. – H. One normal complex on the left and two examples of small stomatal complexes and underlying undivided hypodermoid cells, × 984, Toluidine Blue.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guard cells as hypodermoid, while the epidermal cells above degenerate (see further p. 36). But in many other cases the guard cells develop on the same level as the periclinal main wall (Fig. 20C).

An important and striking feature at the stage with two cell layers is the formation of groups of four cells which all seem be predestined to be able to develop into guard cells or to become members of a stomatal complex. The four cells are surrounded by precursors of subsidiary cells. The periclinal main wall separating the epidermal and hypodermoid layers is sometimes also able to continue through cells which are already predetermined to become guard cells. The wall carries straight on and through in Fig. 14F–G, but in the case illustrated in Fig. 14H, the wall does not cut the guard cells, or its direction or position is changed when it penetrates subsidiary cells. In Fig. 14F it cuts abnormal guard cells and in Fig. 14G it goes through closely spaced small guard cells and subsidiaries. Obviously the wall formation is sometimes unable to defeat the morphogenetic forces which result in a normal and perfect guard cell development. If this happens, guard cell quadrants or bisected guard cells are formed. Generally the position of a pair of guard cells or the uppermost pairs in the quadrants is indicated by a depression in the superficial cell layer. The hollow includes the guard cells and the proximal subsidiary cells. The exterior subsidiaries may form a slightly protruding margin of the hollow. The hollow is distinct in very early stages (Fig. 10E), but it soon becomes deeper when the proximal subsidiaries grow upwards.

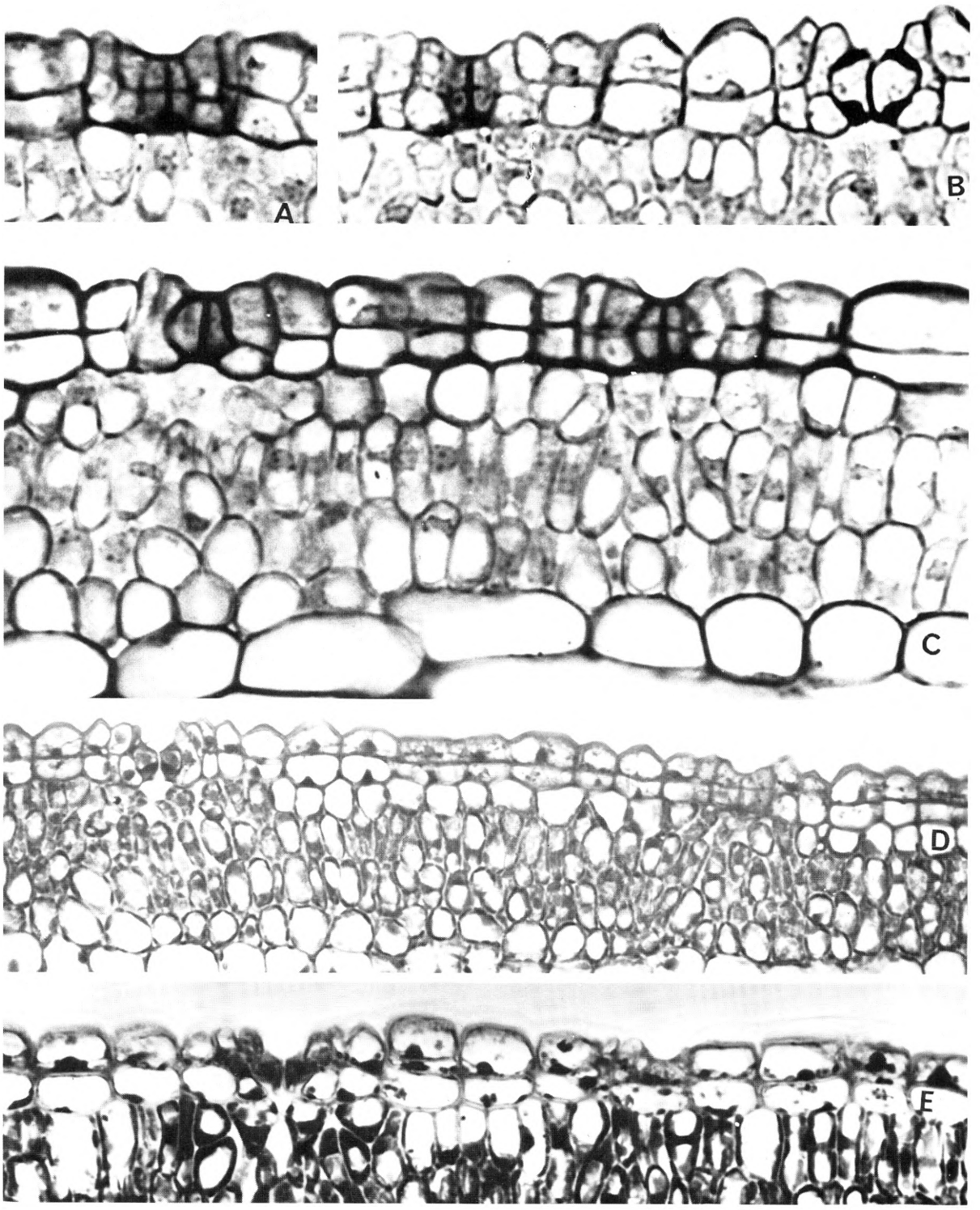
The quadrants arise in meristemoids which are cut lengthwise by the periclinal wall and across by other walls, among which the wall issuing from the bottom of the hollow is the most important and corresponds to the fissure between two normal guard cells. The two crossing walls beneath the hollow are obvious in Fig. 15A–D, G and Fig. 16 A–D. It is of particular interest that the dividing walls between the quadrant cells and the proximal subsidiary cells are initiated later than the anticlinal wall beneath the hollow, further that the guard cells in rare cases are not divided in two parts of equal size, but in smaller and larger parts (Fig. 15E).

In several cases the periclinal wall separates an upper (adaxial) cell group composed of a small pair of guard cells and a number of shorter subsidiaries and a lower hypodermoid cell which remains undivided (Fig. 15H, Fig. 14E, Fig. 16E). In a single case the pair of small guard cells appears to be a quarter of the normal size because an additional hypodermoid cell has developed below (Fig. 17D).

The other possibility – that the periclinal wall may separate an upper (adaxial) undivided cell from a lower cell group consisting of small guard cells and small (short) subsidiary cells – is also realized. Three examples are shown in Fig. 17A, B, C. In this case the guard cells become covered by normal epidermal cells and fail to form outer wall thickenings. It is assumed that the covering cell will be decomposed later.

The third possibility would be that two guard cells were found to be superimposed. This might

Fig. 16. Behaviour of periclinal wall in relation to stomatal complexes. In A, B and C distinct quadrant formation. In B and C two stomatal complexes stay undivided. A–C, × 984, Toluidine Blue. – D. Comparison of one completely normal mature complex on the left and one in which the quadrants are distinct (on the right). Fan-shaped arrangement of palisades beneath both complexes, × 500, Quadruple staining. – E. One normal complex (on the left) and one with two small guard cells covering undivided hypodermoid cell, × 640, PAS + ABB.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involve few functional problems if both guard cells were to form superimposed apertures. Superimposition and fusion of guard cells seem to have taken place in three-four cases in Fig. 13A. By staining with Toluidine Blue, the thick walls of the two cells are delimited, but the cells appear deformed and may even seem reciprocally turned (Fig. 6). It is very difficult to imagine any connection between the apertures, and hence the superimposition means that stomatal apertures become functionally disturbed. In the case of small guard cells being covered by normal epidermal cells, stomatal function will depend on possible enzymatic decomposition of the upper cell.

In Fig. 13B a normal guard cell occurs in a hypodermoid position and there is no epidermal cell above. The same figure shows close to this guard cell (*) a large epidermal meristemoid cell covering a narrow hypodermoid cell, and by the arrow on the left there are two superimposed meristemoids both with narrow cells below. Such narrow cells are occasionally found under normal guard cells which are then displaced upwards to the level of the periclinal main wall (Fig. 11D).

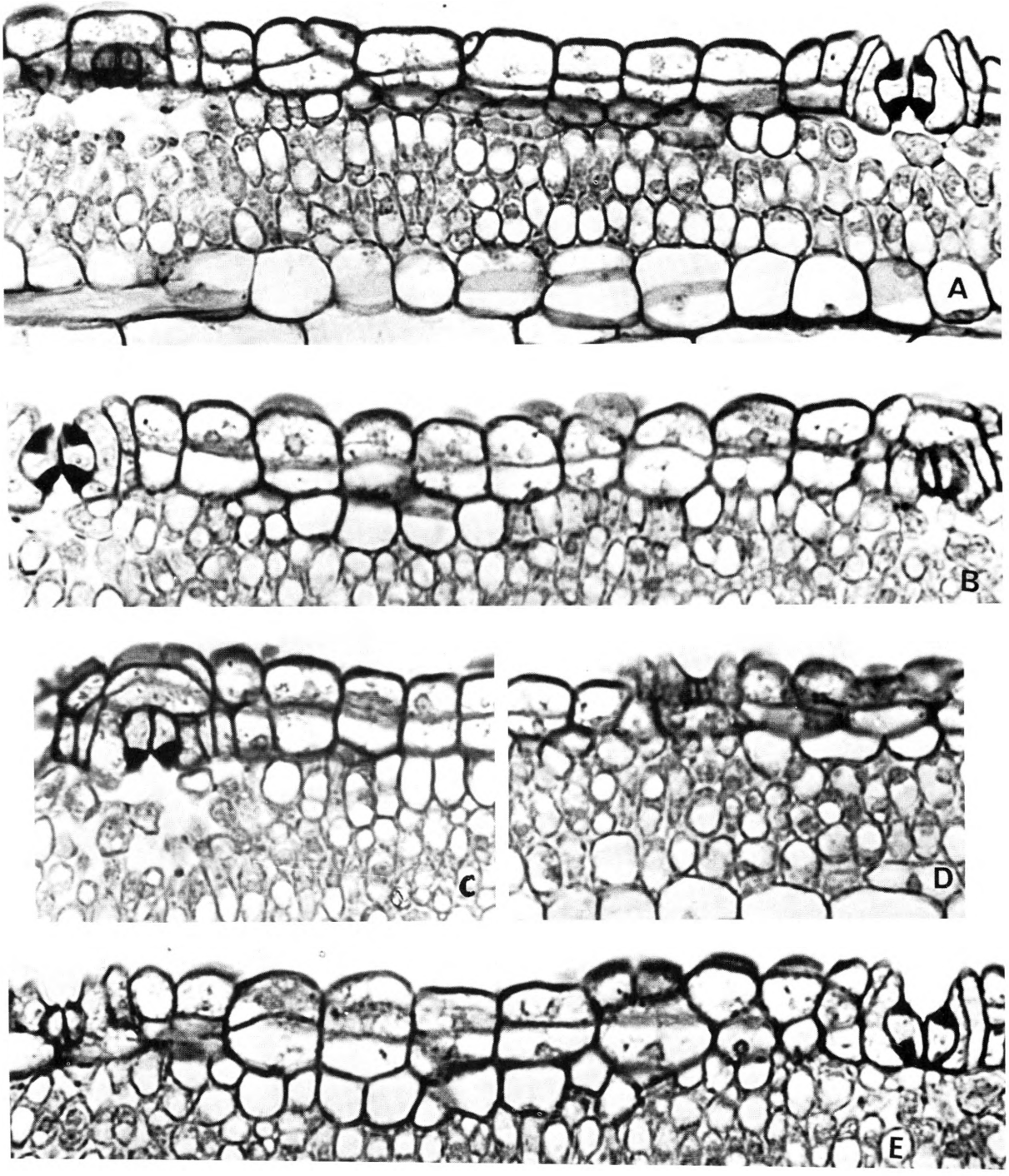
As the majority of guard cells belong to the hypodermoid layer, it seemed pertinent to focus on the fate of true epidermal cells, which at an earlier stage might have existed above the guard cells. It was possible to ascertain that such epidermal cells are occasionally formed, but in most cases their establishment is restrained or they are dissolved very early. Their existence was clear in longitudinal views of guard cells where sometimes their adaxial walls were maintained, while the protoplasts were solubilized (Fig. 13A). In cross sections of guard cells they were difficult to detect. Their existence was convincing in some cases which made it tempting to designate them "ghost-like" cells. They were translucent with very thin walls, but were revealed by some wall lamellae which were stained with Toluidine Blue (Fig. 18A). In other cases remains of their nuclei were seen just outside the hollow above the guard cells (Fig. 18E). Remains of the cell wall of ghost-like cells were stained with Sudan IV (Fig. 18C) or made visible by using interference contrast (Böcher 1975 Plate IVf).

In the previous paper the outer stomatal ledges were designated pseudo-ledges because they were considered to be remains of the wall between the ghost-like cell and the guard cell. This hypothesis appears still relevant.

The proximal subsidiary cells gradually stretch considerably and early divide periclinally, seeming to overarch the guard cells soon. In some cases it is difficult to distinguish overarching, proximal subsidiary cells which bend inwards from "ghost cells", but the latter are usually subject to disintegration and their walls are rarely entire. The median part of the proximal subsidiary cell is often turned in behind the guard cell (Fig. 6D), while the interior (basal) part is separated by a wall and becomes an independent hypodermoid cell which enlarges and expands beneath the interior part of the guard cell. In longitudinal views of the thorns, cross sections of stomatal complexes may have hit the upper and lower part of the proximal subsidiary cell tier as well as a strip of the guard cell (cf. Fig. 14B–D).

The proximal subsidiary cells constitute an integral part of the stomatal apparatus. In Equisetum very similar stomatal complexes have been described (Dayanandan & Kaufman 1972: Fig. 30). According to Pant & Kidway (1968) the guard

Fig. 17. Deviating small guard cells compared with normal ones. – In A, B, C the small guard cells are covered by undivided epidermal cells. D shows a case of a diminutive guard cell pair on top of a hypodermoid cell, in E the small guard cells on the left can be compared with the normal pair on the extreme right, × 640, Toluidine Blue.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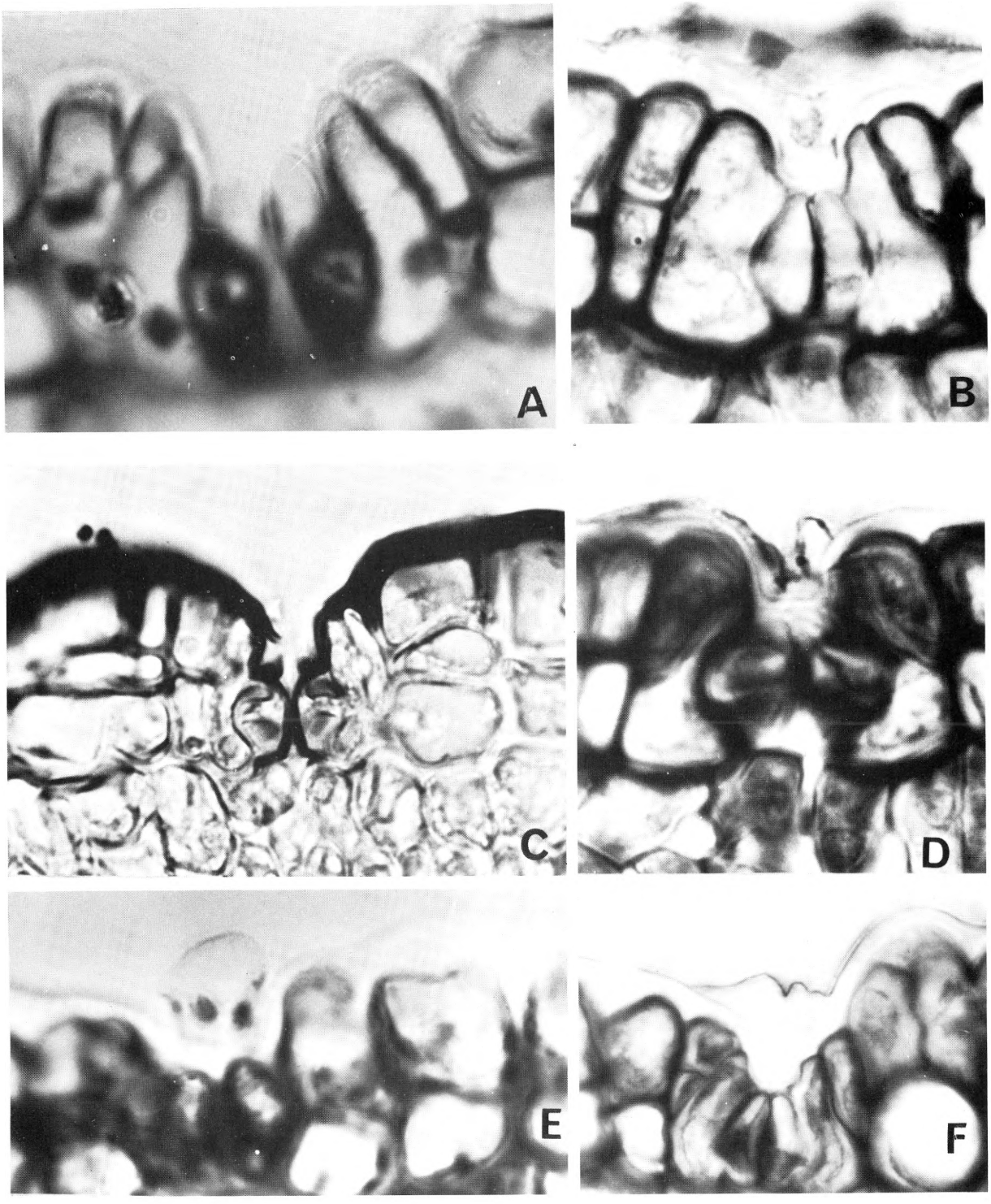
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cells in Equisetum during ontogenesis become partly overlapped by subsidiaries and partly by agene cells (l.c. Fig. 3D).

During growth the subsidiary cells are able to overarch the guard cells from both sides and merge (previous paper, Plate III). The process may almost lead to an occlusion of the pore and represents a new type of stomatal occlusion. Occlusions due to outbulging of interior parts of subsidiary cells or to cuticular plugs were mentioned in Gymnophyton (Böcher 1972), while in Prosopis kuntzei such occlusions result from the formation of alveolar wax plugs (Böcher 1975 Plates VI–VII).

Johnson & Riding (1981) described another case of cells covering the guard cells in Pinus strobus and P. banksiana. The covering cells in Pinus are designated polar subsidiary cells. However, their position and behaviour are quite distinct from what is ascertained in Prosopis kuntzei.

Fig. 18. A–C. Remains of epidermal cells ("ghost cells") on top of guard cells. A. Proximal walls by the pore stained with Toluidine Blue, × 2000. – C. Cell wall remains partly encircling "ghost" stained with Sudan IV, × 984. – E. Remains of wall and nuclei in the two "ghost-like" cells, Toluidine Blue, × 984. – B, D, F. Stomatal depressions showing cuticle and dissolved cell remains in depression. Johansen's Quadruple staining and F.S. × 2000.

9. Developmental changes in the extracambial tissue pattern

Figure 19 gives an outline of the tissues in a young green thorn. The photosynthesizing cortex is developed between strong primary fibre bundles. Bright cells in a single layer frame the bundles forming a sheath. This is an endodermis and it continues in wider bright cells inside the green cortex. Thus the endodermis can be followed around the stem with its vascular bundles. The epidermis consists at first of one layer only, but periclinal divisions are initiated and in the stomatal depressions (at *) the ghost-like cells are in a stage of dissolution. Inside the endodermis follow a few parenchymatous cells which do not belong to the primary phloem. They are pericyclic cells. They differ in size, but they are usually rather wide and undergo divisions.

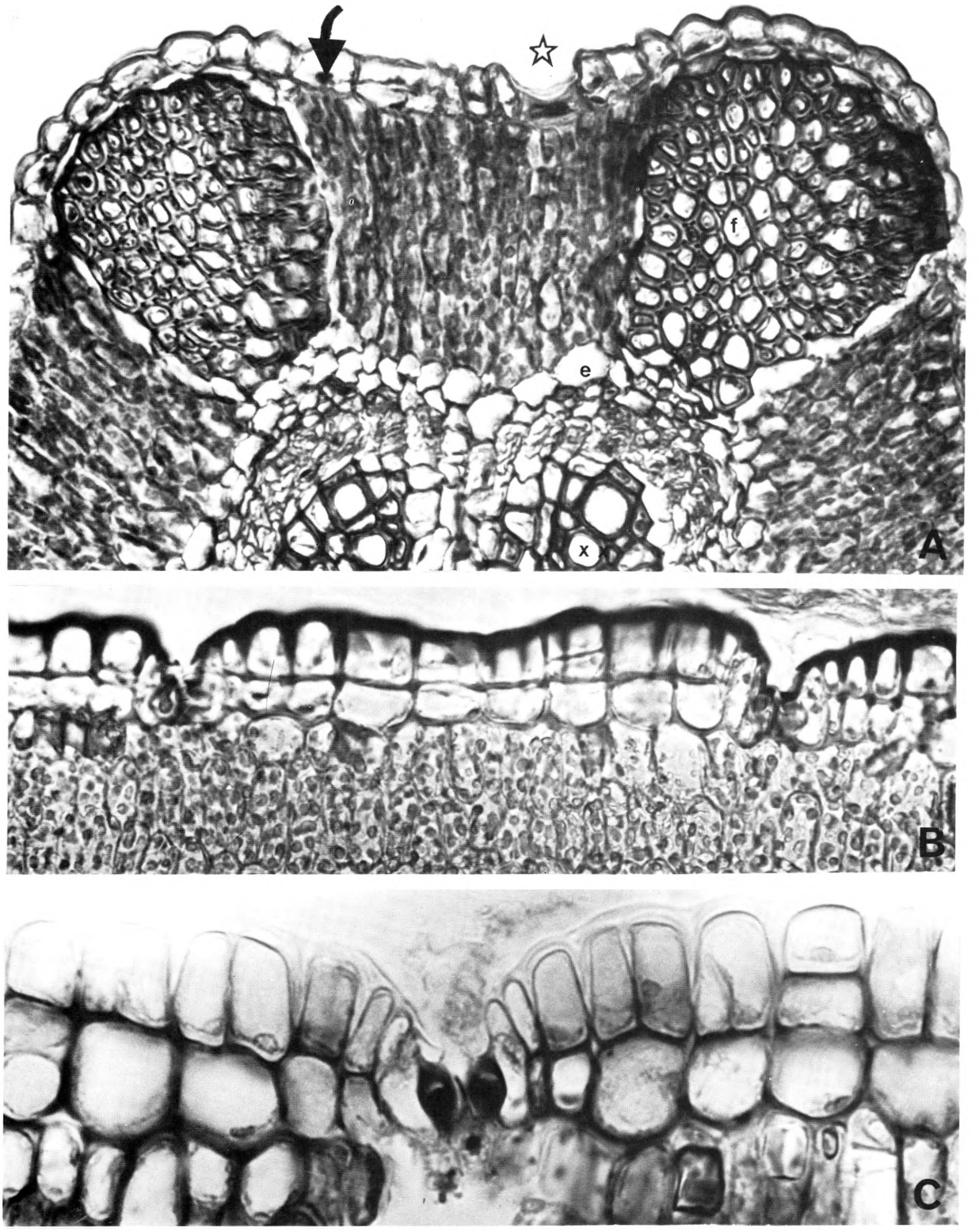
The previous paper (l.c.: 27–28) refers to the occurrence in Prosopis of a pericycle. It is a layer inside a not very well marked endodermoid layer of crystalliferous cells adjoining the perivascular fibre bundles. The crystalliferous cells are scattered and do not form a clear separate layer between the bundles which, on the other hand, are regularly connected with a tissue of parenchymatous, mostly thick-walled cells with conspicuous, simple pits and dark content. The primary fibre bundles border this pericyclic thick-walled tissue in their adaxial part, while smaller secondary fibre bundles occur totally embedded in this tissue (l.c. Fig. 11a).

The new material also showed an endodermoid layer of scattered crystalliferous cells and pericyclic cells which inside divide and expand, filling the inter-bundle parts as an interior non-photosynthesizing cortical parenchyma (Fig. 13A, 21A).

The increase in girth taking place in older thorns involves many alterations including ruptures or splits of the epidermal cuticular layer and a concomitant protruding growth of small, newly formed epidermal cells (Fig. 11A–D, 12C). This proliferation is not restricted to the outermost layer, but the process is transmitted inwards. Hypodermoid cells undergo divisions and triangular cortex cells are differentiated, giving rise to cells which are able to fill out wedge-shaped tissue areas in the cortex. Such areas appear mainly to be formed at the margins of primary fibre bundles. This type of increase in girth was already described in the previous paper (l.c. Fig. 10b), but the inwards proceeding wedge-forming growth starting with cuticular splits and epidermal proliferation only became evident after observations of cross sections of two-year-old thorns (Fig. 20).

The increase in the circumference of the thorns or stems is accompanied by a tangential stretching of pericyclic cells, which at the same time undergo

Fig. 19. A. Cross section of young thorn. Epidermis still mainly of one layer, but periclinal wall at arrow and cell remains above young guard cell at asterisk. e, endodermis, f, fibre bundles, x, xylem. × 500. – B. Periclinal wall also stained with Sudan IV. It stops exactly at the stomatal complexes. The "ghost cells" have dissolved. – C. Periclinal wall stops at stomatal complex, ghost cell dissolved but remains may be seen as a dark "cloud", Toluidine Blue. × 500.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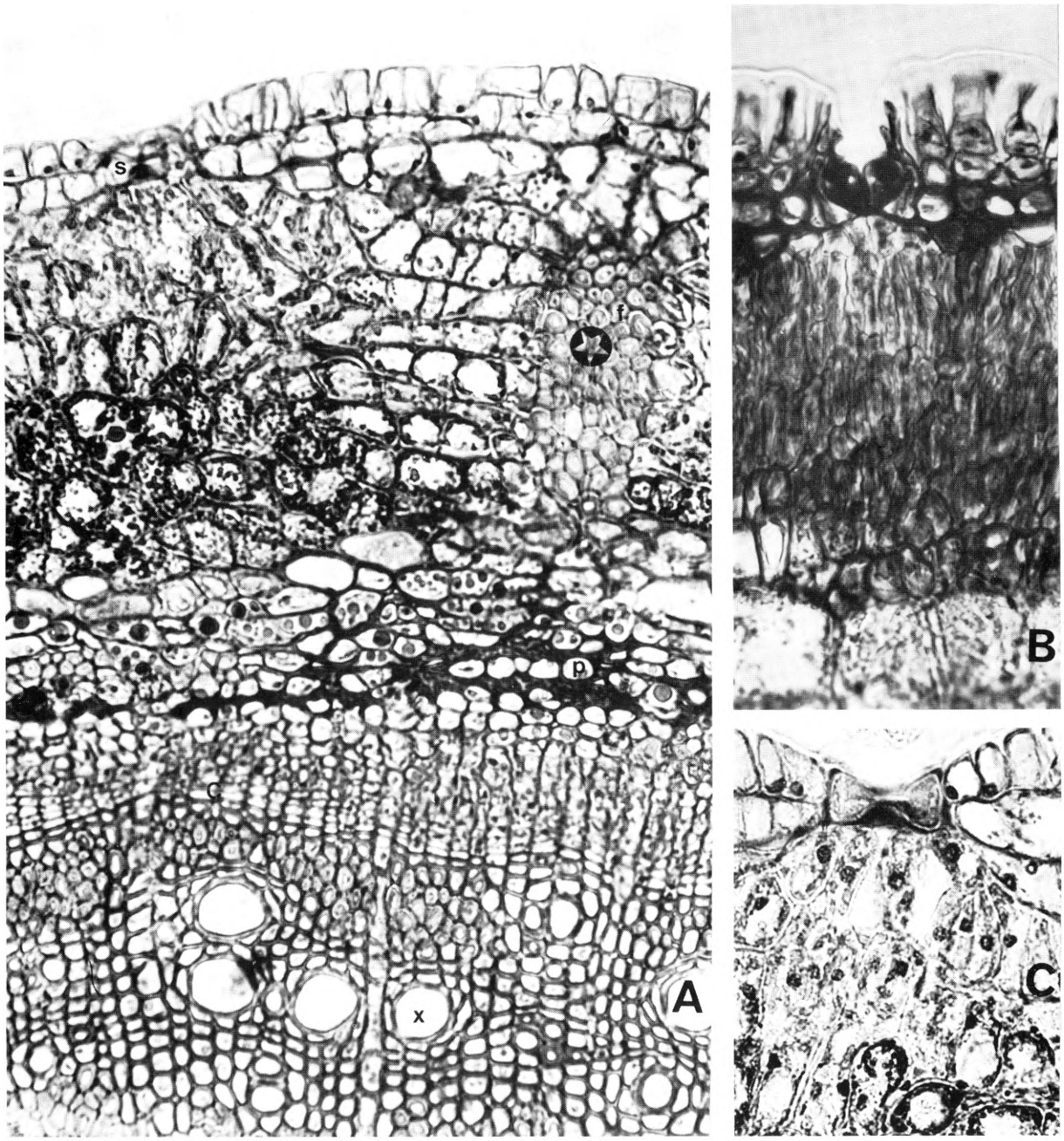

Fig. 20. A. Survey of older stem (thorn). Cross section. Triangular cortex area formed at margin of primary fibre bundle (f). A cell plate with tapering ends is inserted in the hypodermoid layer near stoma (s). Primary phloem (b), vascular cambium (c), xylem (x), × 320, Quadruple staining. – B. Longitudinal section of older thorn. Teichodes formed on top of tapering epidermal cells, one teichode brush-shaped, × 500, PAS + ABB. – C. Cross section. Guard cell bordering epidermal and hypodermoid layer (the latter with tapering proximal cells). Below first intercellular spaces found in fan-shaped palisade parenchyma, × 500, Quadruple staining.

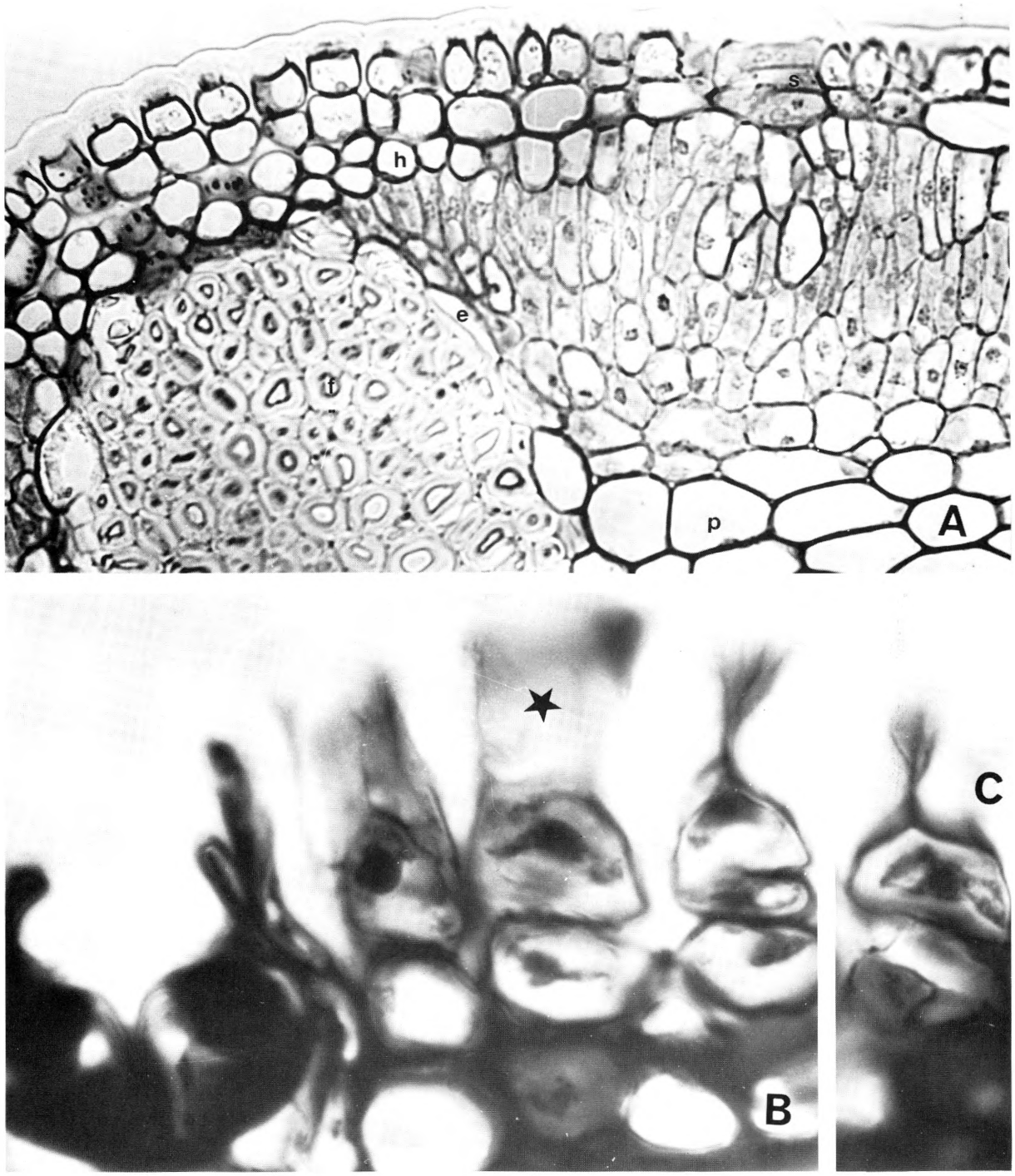

Fig. 21. A. Initiatory stage of teichode formation in outer epidermal layer, stomatal complex (s), hypodermal cells (h), endodermis (e), pericyclic cells (p), primary fibre bundle (f), × 500, Quadruple staining. – B. Final stage of teichode formation, showing terminal brushes of teichodes. Teichodes merging to a dark cloud at ★. No teichodes from subsidiary cells on the left, × 2000, PAS + ABB.

anticlinal divisions and form short plates of cells of which the outer ones are usually tapering, while the middle ones become almost quadratic. Similar short cortical cell plates originating from the same mother cells were described in Eucalyptus gigantea by Chattaway (1953: 405).

As mentioned, tangential growth areas are formed in the parenchyma adjacent to primary fibre bundles. These parenchymatous areas contain some cells which are endodermoid or are placed in close connection with endodermal cells that encircle the fibre bundle. In the present paper, areas of this kind are illustrated in Fig. 22B, 24A. The cortical tissues radiating from the growth areas at the bundles are cell plates which wedge in between older cells, the plates being irregularly stretched tangentially. The cells in the extreme ends of the plates are tapering or rounded.

Many of the cells which start as members of a radiating plate undergo a sclerification, so that finally large tangentially arranged sclerenchymatous areas are formed. The sclerenchyma mainly occupies two cortical strata, viz. an outer larger one between the primary fibre bundles (and adjacent parenchyma) Fig. 22–23, and an interior one close to or/and replacing primary phloem (Fig. 24) and often including secondary fibre strands. Together with the fibre bundles the sclerenchymatous strata constitute a strong protection of the vascular cambium inside.

The increase in girth brought about by anticlinal divisions in cortical cell plates is initiated in the hypodermoid layer where tangentially stretched cell plates (in transverse sections torpedo-shaped cell tiers) are frequently ascertained. Their tapering ends are often near stomatal openings in the epidermis. Their tangential growth seems to be interrupted at the guard cells where hypodermal files may be pushed upwards and reach the apparently superimposed subsidiary cells. This type of growth may bring about splits in the epidermis above (Fig. 11A).

In rare cases the epidermis is cracked in connection with the formation of phellem spots. A small and a larger spot of this kind are seen in Fig. 12. Similar spots were first described by Boke (1940 Plate 1 Fig. 2) as a "curious epidermal structure" formed at the bases of trichomes on phyllodes in Acacia phyllodes. On mature phyllodes they appear as small pellucid dots. Cork warts further occur on thorns of Hawaiian Lobeliaceae (Carlquist 1962 Fig. 21–22). In Prosopis they are initiated on the border between the hypodermoid layer and the epidermis which has peeled off (Fig. 12B). The cork spot in Fig. 12A has reached a more advanced stage and fills up a large part of the green cortex.

Two important changes take place in a late stage of development of the green cortex. One is the formation of rather wide intercellular spaces just inside the stomatal openings. The spaces are narrow at first, but widen; they occupy the uppermost parts of fan-shaped areas in the green cortex which are formed regularly, one fan-shaped part behind each guard cell (Fig. 11 F–G). They represent a modification of the substomatal chambers, but consist of several narrow or wider spaces in the upper part of the fan-shaped area (Fig. 20C).

The other change concerns the interstomatal areas. Here, as already mentioned, wide hypodermal cells develop below the hypodermoid ones, but a continuation of radially elongated cells takes place. These cells become gradually rather wide and their unlignified walls thicken and attain a dark brownish colour after staining with PAS + Aniline Blue Black. They appear to replace chloroplast-containing cells. Their function is obscure. When their photosynthesizing function is slowed down, they may gradually become a kind of water cells. In any case their position in the stems (thorns) constitutes an approach to a compartmentation of the photosynthesizing tissue, which becomes regularly divided in photosynthetic active areas in close connection with the stomata, and less active areas where the cells have few or no chloroplasts, and moreover have less access to light because of the shading effect of the

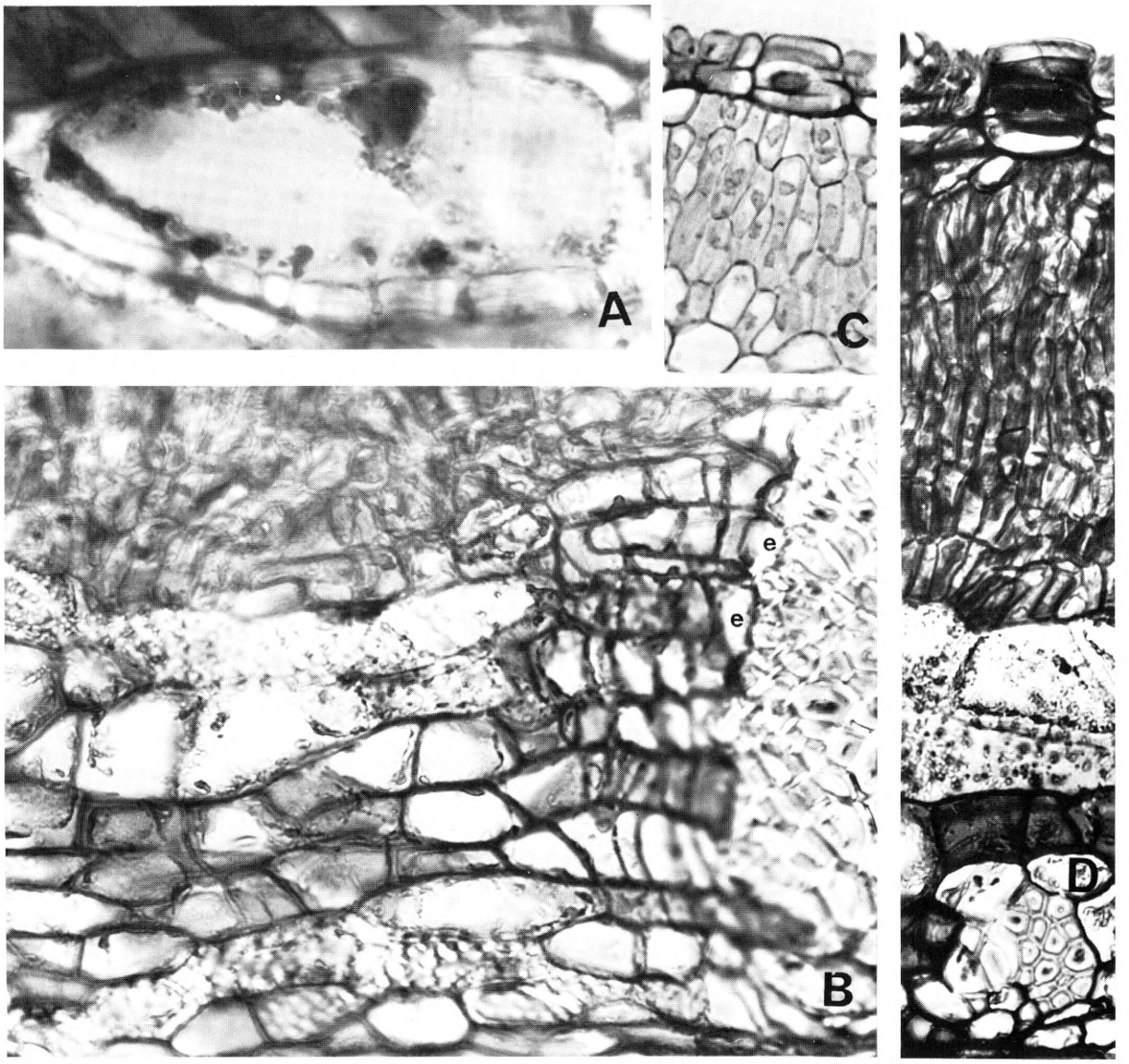

Fig. 22. A. Sclerenchymatous pericycle cell. Several primary pits traverse the thick, stratified wall connecting cytoplasm along the wall, × 1000, semipolarized light. – B. Cell plates issuing from endodermis framing primary fibre bundle undergoing sclerification, swelling and division at some distance from the fibres, endodermis (e), × 500, PAS + ABB. – C–D. Superimposition of guard cells formed in the epidermal and hypodermoid layer. C. Young stage. D. Late stage. Pericyclic cells forming plates or surrounding secondary fibre bundle, × 500, Quadruple staining (C), and PAS + ABB (D).

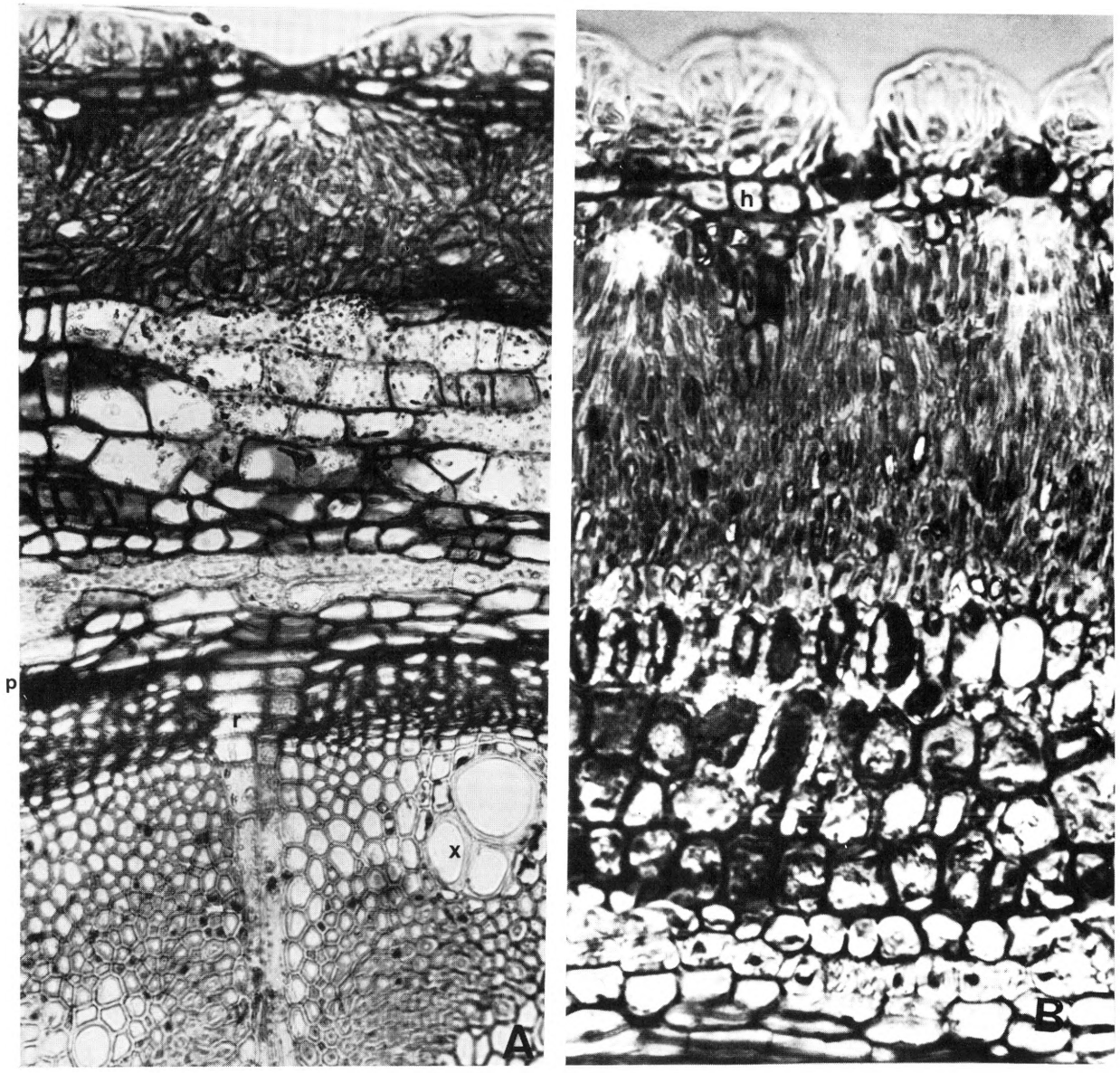

Fig. 23. A. Cross section. B. Longitudinal section of mature thorn. In A, fan-shaped palisades with air spaces inside stoma, two strata with sclerenchyma in pericycle. Primary phloem (p), ray (r), xylem (x). In A and B the fan-shaped palisades are divided by dark, thick-walled cells radiating from hypodermis (h), × 500, semipolarized light, PAS + ABB.

many adaxial cell tiers above (Fig. 23B, 24B). The active areas are characterized by the fan-shaped palisade tissue which nearest to the guard cells may resemble spongy parenchyma.

In the final stage of development the concentration of crystalliferous cells becomes particularly great in interstomatal areas. The crystals (probably of calcium oxalate) are formed in the

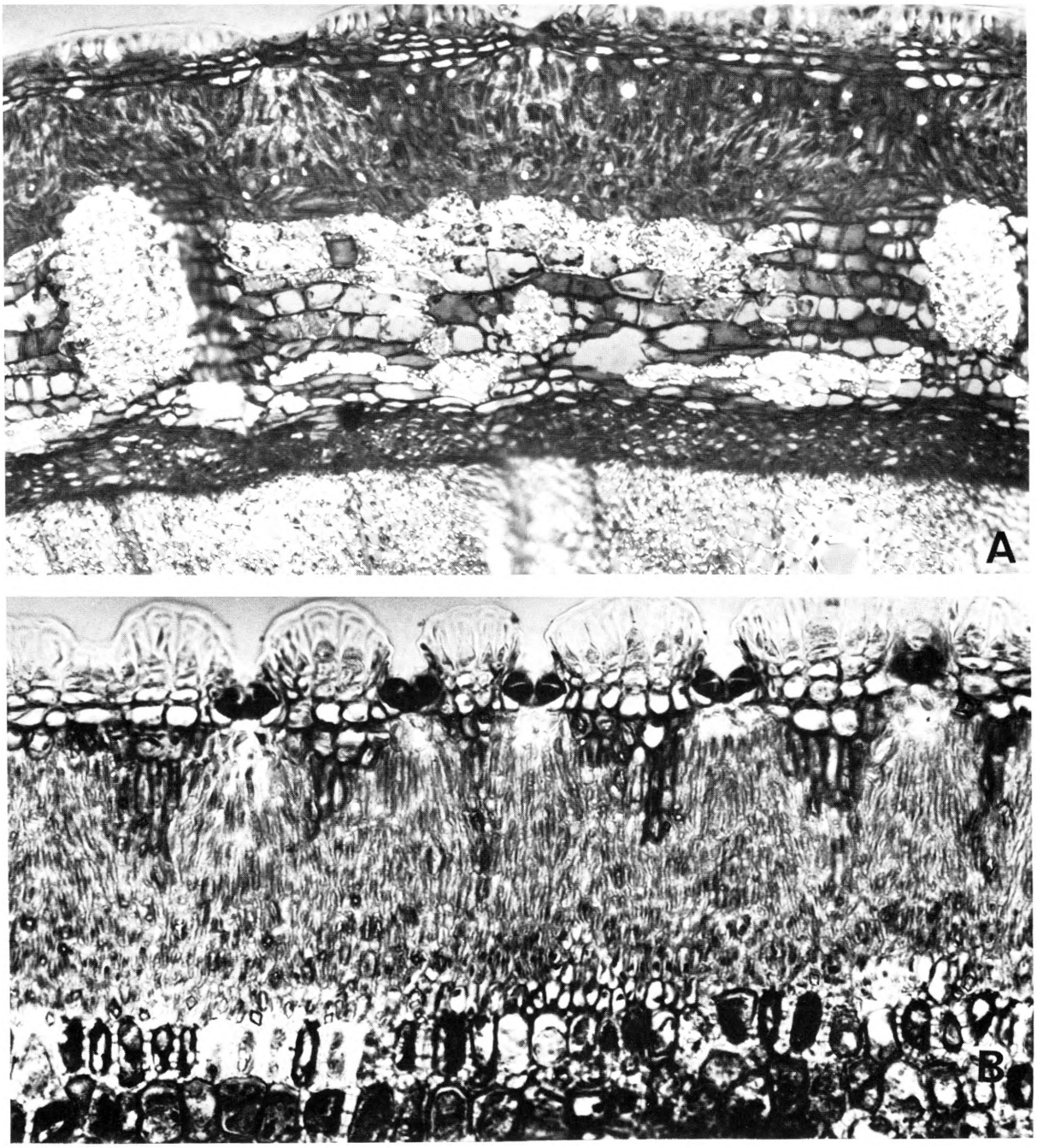

Fig. 24. A. Cross section. B. Longitudinal section of mature thorn. In A, the two sclerenchymatous strata showing up between two primary fibre bundles. Teichodes in all epidermal cells except the stomata. In B, the division of the palisade tissue into light fan-shaped parts and dark parts with thick-walled cells radiating from hypoderm cells, × 200, semi-polarized light, PAS + ABB.

green cells and even sometimes in guard cells, while being sparse in the multiple epidermis between the stomatal depressions (Fig. 11F). In the previously described material crystals were also abundant in the green palisades, but furthermore sphaerites were formed in substomatal chambers (Böcher 1975 Plates III–V).

From my experience cylindrical photosynthesizing bodies (leaves or stems) may in some cases show a much more pronounced compartmentation. I may refer to Sporobolus rigens, Böcher & Olesen (1978) and Anarthophyllum rigidum, Böcher (1979 Fig. 15E and p. 38). In Sporobolus rigens the very specialized leaf structure is closely connected with the C_4-type of photosynthesis.

10. Discussion

When studying the stages in the development of a morphologically singular species we are inclined to compare the ontogenetic stages with evolutionary stages of a distant past. It is not improbable that the developmental and sematophyletic stages were similar, which implies that the ancestors of Prosopis kuntzei were primarily utilizing foliar leaves and not green cladodes in the photosynthesis. However, we need documentation, fossil records, and we must at least produce some kind of ecological evidence which might explain the evolutionary advantages connected with the transition from one stage to another. It is already hardly possible to see any selective advantage connected with the transition from juvenile plants with paripinnate leaves to bipinnate leaves in younger plants. It is insufficient just to say that the basis of such a stage in the development is incorporated in the gene pool and the genes involved are harmless and therefore maintained. In Acacia some species have pinnate, others bipinnate leaves as the first ones after the cotyledons. It is suggested that the most original type had three pinnate juvenile leaves. In Prosopis the number of such leaves varies from two to five, but no specimens had none. All specimens thus have to pass the first juvenile stage, but also the bipinnate second stage which again is a condition for the leafless adult stage. It is highly probable that foliage leaves of both kinds by their production of matter make the outgrowth of cladodes possible, but this provides no obvious explanation for the advantages connected with the apophyllous stage.

Both types of foliage leaves are shed, the juvenile ones at an early stage, the bipinnate much later, and they have moreover the quality of being developed in young, mostly lateral branches or thorns which are formed late. However, both are thin and have a meso-hygrophytic structure, being clearly adjusted to high humidity in the soil or/and in the surrounding air.

The glaring contrast in behaviour and structure of the long assimilating thorns has to be stressed. These green cladodes are perennial structures which are immediately protected by a thick cuticular layer and strengthened by fibre bundles and a core with much xylem. They have furthermore a multiple epidermis and sunken stomata and the photosynthesizing cells are arranged in several layers of palisades. Without experimental evidence it is impossible to estimate the rate of their photosynthetic activity, but this activity must in any case be almost independent of climatic fluctuations during the year, and the many layers of palisades indicate a higher production of matter than that of the small foliage leaflets. This makes it probable that the transition from foliage leaves to green thorns gives an advantage at least in a desert climate. However, an evolutionary step from a leafy shrub to an apophyllous tree with a thick trunk is still no more readily understandable than an adaptation to desert conditions. But in a shrub-steppe vegetation with scattered columnar cactus species and many grazing mammals, it must be advantageous to elevate the assimilating part, the crown of green thorny branches, on a thick trunk. To be able to produce a trunk, the photosynthetic activity must be high. In this connection it is perhaps of some relevance to draw attention to the fact that during the development of the green thorns, a final stage is reached in which a higher protection against water loss is achieved by production of cuticular wax, and that a differentiation of the green tissue and stomatal depressions takes place which may justify the designation of the green thorns as cladophylls.

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