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THE JURASSIC FLORA FROM GROJEC NEAR KRAKÓW IN POLAND
PART II
CAYTONIALES AND ANATOMY OF *CAYTONIA*

Flora jurajska z Grojca koło Krakowa
Część II
Caytoniales i budowa anatomiczna kajtonii

ABSTRACT

From the Jurassic of Grojec and its vicinity, in Poland are described *Caytonia harrisii* n. sp., *C. sewardi*, *Sagenopteris colpodes*, and a microsporangium of *Caytonanthus* sp. with unripe pollen. On the basis of compressions of *C. harisii* macerated in different ways and sectioned with a microtome the structure of the fruit is described and its restoration, showing the distribution of tissues, is given. The hypothesis of Harris that seeds communicated with canals of the mouth is confirmed by the sections. The lateral extension of the mouth, the inner epidermis of the fruit, and the vascular system of the fruit and seeds are described for the first time. The structure and the functioning of the fruit are discussed.

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* Praca została wykonana w ramach problemu resortowego PAN nr 26.3.1.

INTRODUCTION

The *Caytoniales* consist of a single Mesozoic plant genus known so far as separate organs which have separate generic names. The leaves are widespread in the Northern Hemisphere and have long been known as *Sagenopteris*. The much less conspicuous reproductive organs discovered much later are known from a few localities; the male is *Caytonanthus* (Harris 1937, 1941) and the female *Caytonia* (Thomas 1925, Harris 1933, 1940, 1958, 1964).

Species of *Sagenopteris* were described from Poland by Raciborski (1891, 1894) but without microscopic details, and pollen grains *(Caytonisporites)* by Rogalska (1956, 1962). This paper describes leaves (with microscopic details) and associated fragments (fruits) of *Caytonia* and *Caytonanthus*. Some of the *Caytonia* material is well-preserved and by a vigorous programme of maceration and sectioning it has been possible to learn new facts about their structure.

A whole specimen of *Caytonia* is a pinnately branched organ a few cm long bearing little sacs containing seeds. Since the main organ branches like a leaf it is called a megasporophyll and since the little sacs look like berries they are called fruits, though this word is used colloquially for they seem very different in nature from angiosperm fruits which are composed of one or several carpels (megasporophylls).

This fruit has a short stalk and a thickly cutinised epidermis enclosing it completely except for a thick fold (lip) next to the stalk; between the lip and the stalk is a narrow, slit-like mouth. This at an earlier stage admitted pollen to the ovules but later closed.

MATERIAL AND METHODS

The material of *Caytoniales* consists of compressions found in the Grojec clays together with fragments of other plants. They were separated from the clay by washing on sieves and preparations of cuticles were obtained in the usual way, by maceration with nitric acid followed by ammonia.

Certain fruits when cleaned with hydrofluoric acid and then washed with a weak solution of ammonia released fragments of the flesh into the macerating fluid (see Table I). These fragments were fixed with ammonia acetate and calcium chloride and then embedded under a cover glass in glycerine jelly. The fragments showed cell walls, branched sclereids, and tracheids with fragments of pitting.

In addition, fruits of *Caytonia* were macerated in order to obtain their structure, then embedded in celloidine and sectioned with a microtome along one of three planes: transverse to the mouth, longitudinal parallel

Table 1
Tabela 1

Tissues of *Caytonia* shown by different methods of maceration
Tkanki kajtonii uwidocznione przez różne metody maceracji

Structures \ Methods		entire fruits or seeds		sections		
		nitric acid + ammonia *	hydrofluoric acid + ammonia	bleach **	sodium chlorite **	sodium hydroxide + alcohol **
Fruit	outer epidermis, mouth	thick yellow cuticle	no observations	often complete cells	as after bleach	as after bleach
	cells of flesh	—	complete cells, walls present	complete cells with thin walls	as after bleach	cell walls inconspicuous, broken
	vascular strands	—	dark brown strands forming a net, often tracheids visible	elongated cells with granular contents	as after bleach, but more distinct	dark brown strands forming a net
	pitting of tracheids	—	occasionally circular to elongated bordered pits, sectioned walls pitted	occasionally sectioned walls pitted	occasionally bordered pits visible	circular to elongated bordered pits
	filiform sclereids	—	distinct branched sclereids	probably as yellow granular substance in intercellular spaces	as after bleach	distinct branched sclereids
	inner epidermis	delicate cuticle ?	thin cuticle with narrow elongated cells	single layer of cells with small lumen	as after bleach	as after bleach
Seeds	outer epidermis	undulate cuticle	no observations	flat cells	as after bleach	as after bleach
	stone layer of the testa	stone cells, „spicules"	,,	very distinct stone cells	as after bleach	tendency to dissolve
	spotted layer	rarely visible	,,	elongated cells with outwards pointing papillae	as after bleach	as after bleach
	tracheids	rarely visible	,,	—	—	very distinct
	inner epidermis of testa	rarely visible	,,	—	—	—
	nucellus	distinct	distinct	distinct	distinct	distinct
	aleurone cells	rarely visible	no observations	granular substance	as after bleach	as after bleach

* Harris 1958
** Reymanówna 1970

to the mouth, and longitudinal vertical to the mouth. (cfr. Text-fig. 12, A—C). The macerating fluids used for the sectioned fruits were either commercial bleach („Bielinka"), sodium chlorite with hydrochloric acid, or sodium hydroxide and alcohol. It was found that only four out of the 23 sectioned fruits had their internal structure preserved and that different macerating fluids revealed different tissues (see Table 1). The methods of maceration are described and discussed in a separate paper (Reymanówna, 1970). The quality of these sections is poorer than that of petrological sections of coal-ball material. They are usually thick and dark so that it is often difficult to distinguish the cell walls and the pitting of the tracheids. They are also difficult to photograph, because some of the tissues are very dark and others very light. Nevertheless, the best specimens, when sectioned, show the position of the inner cutinised parts of the fruit, the sclereids, and the vascular strands. Sometimes even details of more delicate tissues are visible.

SYSTEMATIC DESCRIPTIONS

Class *Caytoniales*

Genus ***Caytonia*** Thomas

(Synonyms in Harris 1964)

Type species: *Caytonia sewardi* Thomas.

Proposed additions to diagnosis of the genus as published by Harris (1964). In fruits canals leading separately from under the lip to the micropyle of each seed. Main vascular strand in pedicel side of fruit, giving off a network of smaller strands running in the flesh. Tracheids scalariform or with alternate bordered pits. In seeds vascular strand consisting of scalariform tracheids entering through hilum and giving off two branches running in integument along margins of seed.

Discussion. These additions to the diagnosis of the genus *Caytonia* are based on characters observed in *C. harrisii*, but I believe that they are likely to occur also in other species of this genus. I already observed some of them in the type species, either in the material from Yorkshire kindly provided by Professor T. M. Harris or in that from the Grojec area. In *C. sewardi* from Grojec two vascular strands of the same distribution, as in *C. harrisii*, were seen during the maceration of seeds. In macerated fruits of *C. sewardi* from Yorkshire and from the Grojec area appears a network of strands similar to that in the flesh of *C. harrisii*. In it can be distinguished fragments of tracheids.

Caytonia harrisii sp. n.

Pl. I; Pl. II figs. 1, 3; Pl. IV figs 5, 6, Pl. V; Text-figs 1, 4—12.

Holotype S-315.

Locus typicus. Grojec, near Kraków, Poland.

Stratum typicum. Grojec clays („glinki projeckie" in Polish), Upper Liassic-Aalenian (cf. Jurkiewiczowa, in press).

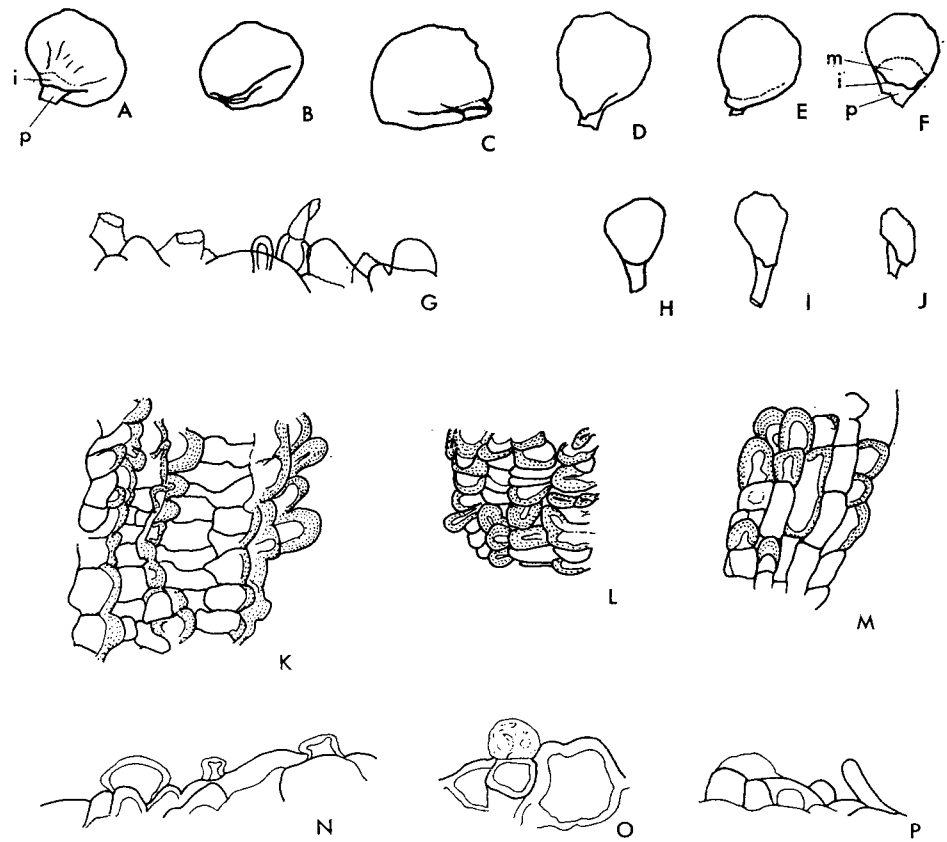
The material was collected from the waste tip Grojec 4. Plant fragments associated with *Caytonia harrisii* belong to species found also in an exposure and in a borehole core containing the Grojec clays from Zabierzów, another locality in this area (Jurkiewiczowa, in press). Specimens and slides are deposited in the Palaeobotanical Department, Institute of Botany of the Polish Academy of Sciences in Kraków, nos S 301 — 317, S 325, S 337, S 340, S 348, S 376—379, S 414, S 418—422.

Diagnosis. Fruits rounded, up to 3 mm wide, small fruit elongated; pedicel narrow, up to 0.5 mm wide. Lip of fruit curved around pedicel and concealing the mouth, on lip present up to eight cutinised bars. Rim of lip not specially thickened, its margin covered with strong cutinised papillae. Mouth of fruit typically 1.1 mm wide (measured along the curve). Up to eight seeds present in one fruit, seeds arranged close together, seed packet surrounded by inner epidermis of fruit consisting of single layer of cells. Space between inner and outer epidermis of fruit filled with flesh consisting of large rounded cells and filiform branched sclereids. Between cells of flesh dense net of vascular strands, their metaxylem consisting of tracheids with densely spaced alternating bordered pits.

Cuticle of fruit very thick, epidermal cells typically square, their end walls thin and straight, their longitudinal walls strongly cutinised and forming bulges or ridges extending along a number of cells. Thickly cutinised papillae and short glandular hairs frequent on fruit and pedicel. Hairs consisting of two cells, the basal one thickly cutinised, the upper thickly cutinised and filled with dark contents (secretion and upper part of glandular hairs easily destroyed in maceration). Ridges and hairs often obliterating cell outlines. Cells of pedicel elongated on upper side, square on lower side, bearing numerous papillae and hairs.

Seeds flat, ovate with pointed apex, $1{\cdot}2 \times 0{\cdot}8$ mm and up to 0·2 mm thick when broken across. Surface of seeds showing delicate longitudinal striae and wrinkles. Testa containing a palisade layer on the flat sides and several layers of fibrous stone cells, their contents resistant to maceration. „Spotted layer" present deep in the integument in the form of elongated cells with their peripheral walls bulging into broad papillae.

Vascular strand entering through hilum and dividing into two branches running in the integument along each margin of seed up to the



Text-fig. 1. *Caytonia harrisii* sp. n. A — E: series of normal fruits; F, H — J: series of small, abortive fruits; A — E, H, J — S 348, F — S 310, I — S 337, all × 5; G: hair bases on fruit, S 314, × 200; K: epidermis of upper part of fruit, S 306, × 200; L: epidermis of lower side of pedicel, S 310, × 200; M: epidermis of upper side of pedicel, S 310, × 200; N, O: glandular hairs on fruit; N — S 306, O — S 313, × 200; P: papillae and hair on pedicel, S 314, × 200
i — lip, m — mouth, p — pedicel

Ryc. 1. *Caytonia harrisii* sp. n. A — E: seria normalnych owoców; F, H — J: seria małych, niedorozwiniętych owoców; A — E, H, J — S 348, F — S 310, I — S 337, wszystkie × 5; G: nasady włosów na owocu, S 314, × 200; K: skórka górnej części owocu, S 306, × 200; L: skórka dolnej strony trzonka, S 310, × 200; M: skórka górnej strony trzonka, S 310, × 200; N, O: gruczołowate włosy na owocu; N — S 306, O — S 313, × 200; P: brodawki i włos na trzonku, S 314, × 200
i — fałd, m — szczelina, p — trzonek

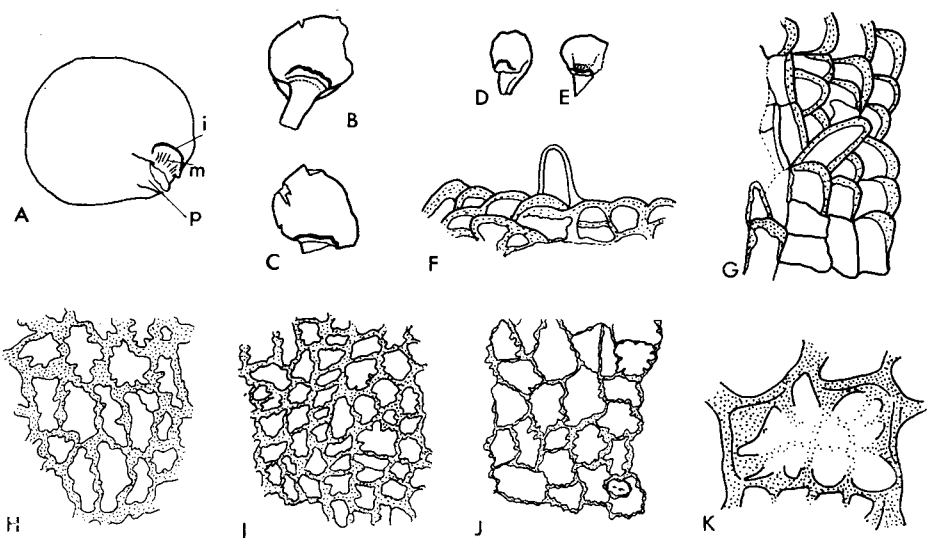
apex, each branch consisting of two to three scalariform tracheids and of narrow elongated elements.

Micropylar canal consisting of elongated cells. Pollen grains of *Caytonanthus* type found in micropylar canal.

The species is named after Professor T. M. Harris.

Discussion and comparison. *Caytonia harrisii* is different from all other species described so far in having fruits covered by a great number of glandular hairs. The only other species showing glandular hairs is *C. thomasi* but there the hairs are longer and occur on the pedicel of the fruit. *C. harrisii* also differs from other species of the genus in having much thickened and cutinised cell walls in the epidermis of the fruit. Only *C. kendalli* Harris (1964) shows thickened and jagged cell walls but never to that extent. *C. kendalli,* however, is different from *C. harrisii* in having larger fruits which contain a larger number of seeds. The mouth of *C. harrisii* is a little wider than in *C. sewardi* but narrower than in *C. nathorsti, C. thomasi,* and *C. kendalli.*

The seeds of *C. harrisii* possess a layer of „palisade" stone cells, like the seeds of *C. sewardi* and *C. thomasi;* they differ, however, from those of *C. sewardi* in not showing a pitted, honeycomb-like surface. The surface of the seeds of *C. harrisii* shows longitudinal wrinkles, thus differing from the seeds of *C. thomasi* and *C. nathorsti* which are smooth.



Text-fig. 2. *Caytonia sewardi* Thomas. A: normal fruit; B — E: small abortive fruits; A — S 416, B — S 341, C — S 423, D — E — S 417, all × 5; F: hair on pedicel, S 341, × 200; G: epidermis of upper side of pedicel, S 401, × 200; H, I: epidermis of fruit, S 342, × 200; J: epidermis of lower side of pedicel, S 341, × 200; K: cell of epidermis of small fruit, S 341, × 800
i — lip, m — mouth, p — pedicel

Ryc. 2. *Caytonia sewardi* Thomas. A. normalny owoc; B — E: małe niedorozwinięte owoce; A — S 416, B — S 341, C — S 423, D — E — S 417, wszystkie × 5; F: włos na trzonku owocu, S 341, × 200; G: skórka górnej strony trzonka, S 401, × 200; H, I: skórki owocu, S 342, × 200; J: skórka dolnej strony trzonka, S 341, × 200, K: komórka skórki małego owocu, S 341, × 800
i — fałd, m — szczelina, p — trzonek

In the material of *C. harrisii* fruits in three stages of development seem to be represented. Firstly, there are fruits much smaller than the rest and flat, because their seeds have not developed. These appear to be abortive fruits arrested at early stages of development. The larger ones fall into two types, representing probably different stages of ripening. Some are flattened and wrinkled and when sectioned do not show cell structure. Others are spherical and only occasionally show small bulging areas, or a network of protruding wrinkles. They are the best material for sections because their internal structure is preserved.

Caytonia sewardi Thomas

Pl. III figs 1—5; Text-fig 2.

1925 *Caytonia sewardi* Thomas, p. 315, pl 12, figs 14—24; pl. 13, figs 25—32; pl. 15, fig. 48; Text-figs 5—9.
1940 *Caytonia sewardi* Thomas: Harris, p. 714, pl. 7, figs 1, 2, 4, 6, 9—11.
1958 *Caytonia sewardi* Thomas: Harris, p. 93, pl. 1; pl. 2, figs 7, 8, 10; Text-figs 1, 4, 8.
1964 *Caytonia sewardi* Thomas: Harris, p. 20, pl. 1, figs 2, 3, 8, 9; Text-fig. 9.

Lectotype. V. 18589 British Museum (Natural History), London.

Locus typicus. Cayton Bay, Yorkshire, England.

Stratum typicum. Gristhorpe Bed, Middle Deltaic (Bajocian), Middle Jurassic.

Described material. Grojec 4: a few typical fruits (as several forms of *Caytonia* occur in this sample, loose seeds were not taken into consideration); borehole Zabierzów, depth about 240 m (cf. Jurkiewiczowa, in press): several macerated typical fruits; borehole Zabierzów, depth about 253 m: a few fruits and several well-preserved seeds (in the same sample *Sagenopteris colpodes* leaves).

Specimens and slides are deposited in the Palaeobotanical Department, Institute of Botany of the Polish Academy of Sciences in Kraków, nos S 318—324, S 341, S 342, S 415—417, S 423.

Description. Fruits rounded, up to 3·5 mm wide, small fruits rounded, pedicel narrow (up to 0·7 wide). Mouth of fruit 1 mm wide, curved; lip a thin semicircular flange standing out from the fruit and showing about eight thickened bars. About eight seeds present in fruit; flesh with large sclereids. Cuticle of fruit thick, cell walls sinuous or showing jagged thickenings. Seed ovate, with truncate apex, 1·3×0·8 mm and up to 0·2 mm thick when broken across. Surface of seeds showing nearly isodiametric cells on the flat side and narrow cells at edges; periclinal cell walls sunken and forming a honeycomb pattern. Testa consisting of an outer layer of „palisade" stone cells and elongated, fibre-like stone cells; interior of stone cells resistant to maceration. If pre-

served, „spotted layer" of the integument visible as a membrane with blocks of dark resistant substance. Micropylar canal with isodiametric cells, bulging cells at its mouth present, but no specialized cells extending along edges of seed.

Discussion and comparison. The fruits and seeds of *C. sewardi* from the Grojec area are similar to *C. sewardi* from Yorkshire in essential characters but they differ in a number of characters of minor importance. The two fruits agree in having cuticles with sinuous cell walls with jagged thickenings, in the small size and the shape of the lip and the mouth, in the number of bars in the mouth, and in the number of seeds. The seeds from my material resemble those of *C. sewardi* from Yorkshire in having on their surface a network of ridges forming a honeycomb pattern, which does not occur in any other species, and in having a layer of „palisade" cells and fibrous stone cells in the testa.

Table 2
Tabela 2

Comparison of the *Caytonia* species from Grojec
Porównanie gatunków kajtonii z Grojca

Characters	*C. harrisii*	*C. sewardi*
shape	round	round
mouth	1·1 mm	about 1 mm
epidermal cell walls	thickened ridges	strongly jagged
epidermal papillae	present	none
glandular hairs	present	none
micropylar cells	long	isodiametric
integument	strongly fibrous	strongly fibrous
cells on seed surface	long and narrow	isodiametric (narrow at margin) Remark: In *C. sewardi* from Yorkshire all cells isodiametric

There are slight differences in size between the Yorkshire and the Grojec material. The pedicel in my material is slightly wider and so is the lip, which is also less curved. There are, too, differences in the seeds. These are 1·5×1·0 mm in the Yorkshire material but only 1·3×0·8 mm in the Grojec one. In seeds from the Grojec area most of the surface shows isodiametric cells but there are narrow cells at the edges of the seeds, in which the latter differ from *C. sewardi* from Yorkshire. The apex of the Grojec seeds is truncate and shows an edge about 0·5 mm wide covered with bulging cells, while those from Yorkshire have a more or less pointed apex. In a small proportion of the Grojec seeds only half of the micropyle consists of isodiametric cells.

When all the characters of the fruits and seeds from the two areas are considered, it is evident that they are very close to each other and represent the same type, which is different from all the remaining species of *Caytonia*. It appears to me that the differences between the two materials are small, such as exist between geographical variations of one species of a recent plant. Therefore I include the material from the Grojec area into *Caytonia sewardi* Thomas.

Genus ***Sagenopteris*** Presl 1838

Sagenopteris colpodes Harris

Pl. III, fig. 7; Text-fig. 3.

1940a *Sagenopteris colpodes* Harris, p. 250, Text-figs 1, 2, 6F—H.
1964 *Sagenopteris colpodes* Harris, p. 4, Text-figs 1, 2, 3.
Leaves of similar shape but with unknown cuticle:
1902 *Sagenopteris rhoifolia* Presl, Möller; p. 56, pl. VI, figs 11, 12. (Bornholm).

Holotype. V. 26441, figured by Harris (1940, Text-fig. 6 G).

Described material: borehole Zabierzów depth about 240 m (cf. Jurkiewiczowa, in press): fragments of macerated cuticle; borehole Zabierzów depth about 253 m: fragments of leaflets showing venation.

Specimens and slides deposited in the Palaeobotanical Department, Institute of Botany of the Polish Academy of Sciences in Kraków, nos S 333, S 344—346, S 401—412.

Description. Leaflets (only fragments known) either almost symmetrical or midrib considerably nearer one margin than the other, length unknown but estimated to reach 1·2 cm, width up to 0·5 cm. Apex of leaflet obtuse, margins entire, midrib dissolving into a network of veins considerably below the apex. Midrib depressed above, prominent below, lateral veins conspicuous and prominent below; vein meshes 0·6 mm wide. Hairs not obvious on lamina, sculpture of surface not specially pronounced.

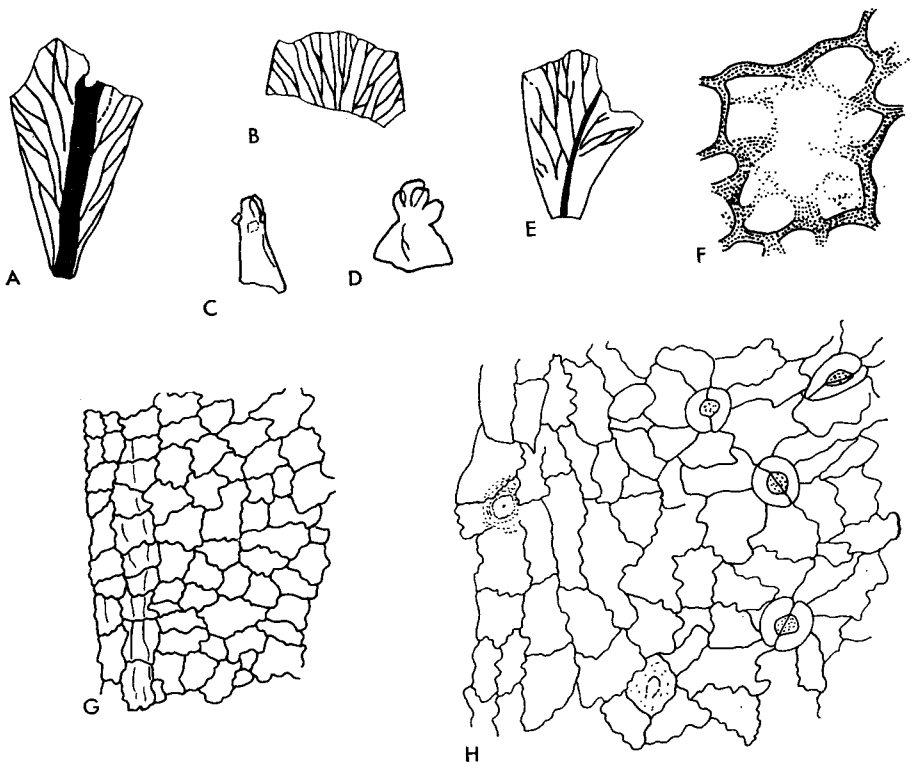
Upper cuticle fairly thick, outlines of epidermis cells very distinct, sinuous; cells above veins rectangular, elongated and arranged in rows, between veins cells approximately rectangular and arranged in more or less distinct rows. Cell surface with parallel striations along veins, obscurely mottled between, without trichomes or papillae.

Lower cuticle somewhat thinner, outlines of epidermis cells distinct; cells above veins rectangular, elongated, with sinuous walls; cells between veins irregular with coarsely sinuous to straight walls. Surface of cells smooth, above veins with longitudinal striations. Trichomes frequent

above veins, scarce between them, consisting of a small thickly cutinized cell with a bulge in the middle; bulging part often missing, leaving a ring-like scar.

Stomata oval, their outline distinct, their surface with radiating striations. Guard cell walls facing the stomatal aperture thickly cutinized. Subsidiary cells unspecialized, only rarely extending slightly under the guard cells.

Petioles. In the sample from 240 m several fragments of petioles showed cuticle of *S. colpodes* type and usually with longitudinal rows of stomata. Two fragments showed scars after shedding leaflets.



Text-fig. 3. *Sagenopteris colpodes* Harris. A, B, E: fragments of leaflets showing venation; A — S 345, B — S 346, E — S 344, all × 4; C, D: small leaves with petioles expanded into scales, S 333, × 4; F: cell of upper epidermis, S 404, × 800; G: upper epidermis of leaf, midrib to the left, S 402, × 200; H: lower epidermis of leaf, S 328, × 200

Ryc. 3. *Sagenopteris colpodes* Harris. A, B, E: fragmenty listków z widoczną nerwacją; A — S 345, B — S 346, E — S 344, wszystkie × 4; C, D: małe liście z ogonkami rozszerzonymi w łuski, S 333, × 4; F: komórka górnej skórki, S 404, × 800; G: górna skórka liścia, nerw główny po lewej stronie, S 402, × 200; H: dolna skórka liścia, S 328, × 200

Small leaves. In the sample from 240 m a small leaf was found consisting of the petiole expanded into a scale and of four small leaflets. The epidermis of the petiole is thickly cutinised on its outer (morphologically lower) part and thin on its inner (morphologically upper part); it consists of square cells with sinuous walls arranged in rows, on lower side stomata of *S. colpodes* type present. Leaflets very thinly cutinised, showing cells with straight walls, upper part of leaflets missing. A second similar small leaf did not show stomata (Text-fig. 3 C, D).

Leaf mesophyll. The mesophyll of the leaf is resistant to maceration and had to be removed with a brush when the cuticles of the leaf were prepared. It consists of small rounded cells between which there runs a network consisting of elongated narrow elements. The network resembles that of vascular strands in the flesh of the fruit. In stained preparations of the leaf mesophyll, among the elements forming the network tracheids can occasionally be observed. Among the elements of the network are small branched sclereids which occur also apart from the network between cells of the mesophyll. These sclereids agree in shape and in showing a thread-like lumen with those found in the flesh of the fruit, but they are much smaller.

Discussion and comparison. The leaflets agree with *S. colpodes* from Yorkshire, except for minor features. The leaflets from Grojec are small, which may well be typical for this local form of *S. colpodes*. The leaves do not have a sculptured upper surface due to protruding mesophyll cells, which occur in *S. colpodes* from Yorkshire. Also the cuticles show small differences. They are thicker than in *S. colpodes* from Yorkshire, the cell outlines, even on the lower cuticle, are clearly visible, and the upper parts of trichomes are often preserved.

Raciborski described from Grojec *Sagenopteris goeppertiana* with leaves of a shape similar to *S. colpodes* but with unknown cuticle. I have investigated these specimens but did not obtain preparations of cuticle.

Genus *Caytonanthus* Harris 1937

Caytonanthus sp.

Pl. IV, figs. 1—4

Material. Only one synangium was found in the waste tip Grojec 4 in the same sample as the fruits of *C. harrisii* and *C. sewardi*.

Specimen and slides are deposited in the Palaeobotanical Department, Institute of Botany of the Polish Academy of Sciences in Kraków, nos S 331, S 338, S 339.

Description. Synangium 3 mm long, 0·9 mm wide, composed of

four loculi, each containing a pollen mass. Cuticle of synangium showing square cells often with longitudinal striations. Between cuticle and pollen mass a thin granulous membrane.

Pollen grains (immature) disaccate, corpus darker than sacci, circular in polar view. Sacci not wider than corpus in polar view, inclined towards distal side of corpus in equatorial view. Roots of sacci forming a ring with thick protruding margin on proximal surface of corpus, leaving its central part free; on distal surface roots of sacci running parallel, separated only by a narrow very light stretch of corpus. Sacci showing regular round pits about 1 μ in diameter.

Size range (10 grains measured, terminology after Townrow 1962):
Width of total grain: 15—20 μ, medium 19μ
Width of corpus: 8—15 μ, medium 10μ
Depth of corpus: 10—12 μ, medium 11μ
Depth of saccus: 9—12 μ, medium 10μ
Height of saccus: 3—6 μ, medium 4μ

Discussion and comparison. The synangium and the pollen grains are typical of *Caytonanthus*, though the pollen grains are clearly immature. They are folded and adhere closely together, forming pollen masses, and are easily destroyed in maceration. In the few separate grains obtained, the sacci are still folded and their height is 3—4 times smaller than in pollen of *Caytonanthus arberi* or *C. oncodes*. (cf. Harris 1941, 1964; Townrow 1962). Other dimensions of the pollen grains are smaller than in other *Caytonanthus* pollen but they do not differ much and sometimes they partially overlap.

These pollen grains are similar to *C. oncodes*, as described by Townrow (1962), in showing only a small distance between the roots of the sacci on the distal surface and in having the sacci distinctly pitted.

GENERAL REMARKS

The *Caytoniales* are represented in Grojec and its vicinity by two species of fruits and one species of leaves; this leaf and one species of fruit belong to the same species of plant. The only synangium also possibly belongs to this species of plant. In addition there were found several specimens of fruits different from any of the described species, which might belong to new species but were not described because the material was too scanty. It is interesting to note that among these single fruits there were also two fruits with a wide and short mouth like that in *Caytonia kendalli*.

In having a large number of *Caytoniales* the flora of Grojec and its vicinity is similar to the Rhaeto-Liassic flora of Greenland, though there are no species common to them. The only flora with which the Grojec

area has common *Caytoniales* is that of the Middle Jurassic of Yorkshire, the common species being *Caytonia sewardi* and *Sagenopteris colpodes*. The fact that also in the Grojec area these two species are associated in the same sample adds to the evidence from Yorkshire that they were produced by the same species of plant. The specimens from Grojec and Yorkshire differ slightly, this possibly being the result both of the distance between the localities and of the difference in time, since the Grojec flora is somewhat older.

ANATOMICAL STRUCTURE OF *CAYTONIA HARRISII* SP. N.

DESCRIPTION

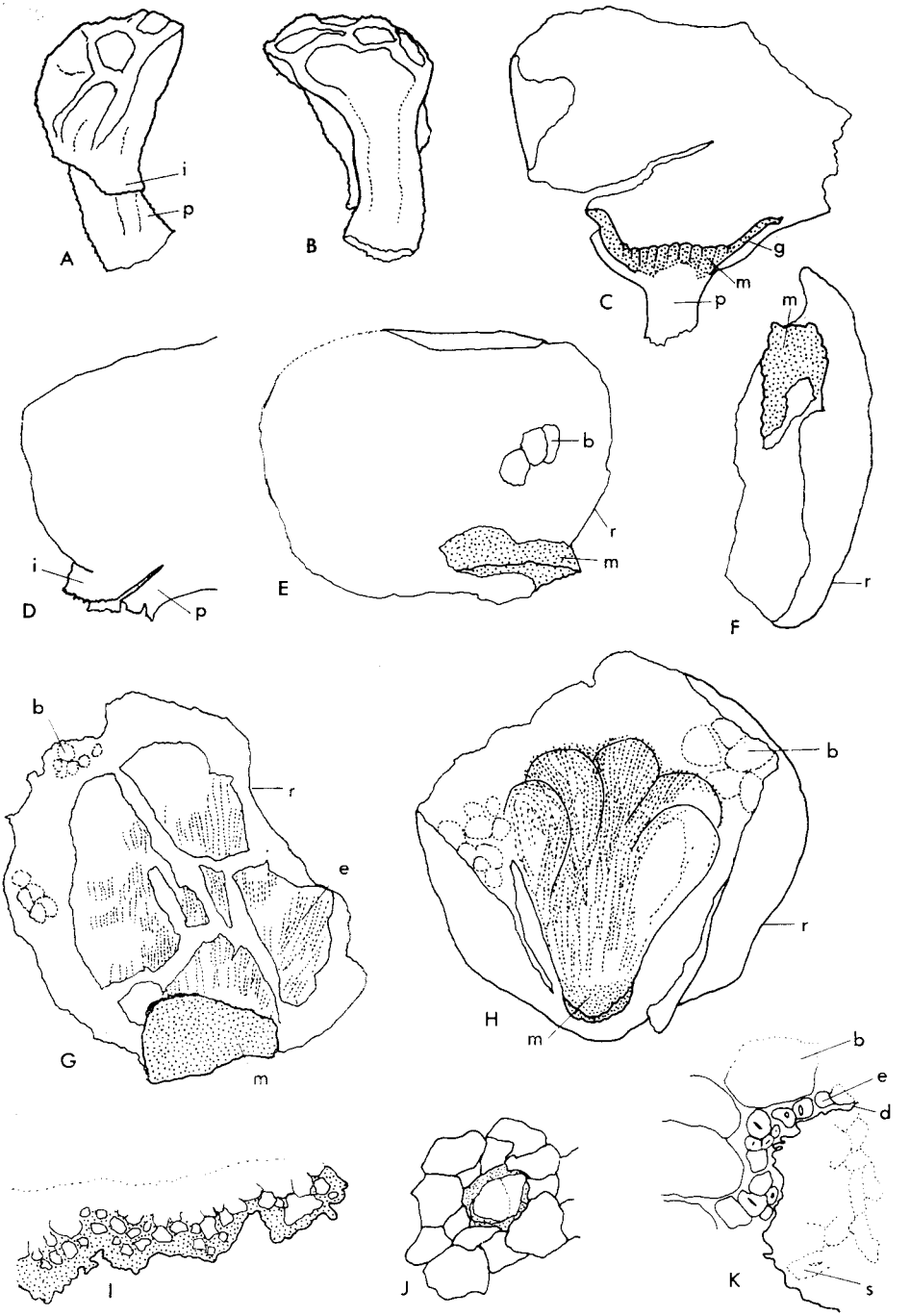
Epidermis and hypodermis

The description of the outer epidermis of the fruit given in the diagnosis of the species (p. 49) is supplemented here by a few details. In section the cells of the epidermis are filled with dark, finely granular

Text-fig. 4. *Caytonia harrisii* sp. n., outer and inner epidermis, mouth. A, B: small fruit showing a system of probably hypodermal ridges, S 418, × 20; C: fragment of fully macerated fruit showing zone 2 of mouth and its lateral extensions, S 419, × 20; D, E, F: half of a fully macerated fruit showing the mouth from inside (E), from outside (D), and from below (F), S 420, × 20; G: part of fruit wall showing fragment of mouth below and flesh lined with inner epidermis of fruit (cracked) above; direction of striations shown by stippling S 421, × 20; H: fragment of fruit lacking pedicel side of fruit wall; visible is the packet of seeds covered with inner epidermis of fruit and vascular tissue which completely obliterate the connection of the seeds and the mouth, S 377, × 20; I: projecting ridges on upper cuticle of zone 1 of the mouth, seen in transverse section, section I/e, × 200; J: thin place in outer epidermis of fruit, S 306, × 200; K: section through flesh and seed, maceration with bleach, section I/55, × 200

b — cell of flesh, d — cuticle of outer epidermis of seed, e — inner epidermis of fruit, g — lateral extension of mouth, i — lip, m — mouth, p — pedicel, r — outer epidermis of fruit, s — stone cell of seed testa

Ryc. 4. *Caytonia harrisii* sp. n. (wewnętrzna i zewnętrzna skórka, szczelina). A, B: mały „owoc" z widocznym systemem żeberek, prawdopodobnie hypodermalnych, S 418, × 20; C: fragment zupełnie wymacerowanego owocu z widoczną strefą 2 szczeliny oraz jej bocznymi przedłużeniami, S 419, × 20; D, E, F: połowa zupełnie wymacerowanego owocu okazująca szczelinę od wewnątrz owocu (E), od zewnątrz (D) i od dołu (F), S 420, × 20; G: fragment ściany owocu z widocznym u dołu fragmentem szczeliny i powyżej popękanym miękiszem, ograniczonym wewnętrzną epidermą owocu. Kierunek jej prążkowania jest zaznaczony liniami przerywanymi, S 421, × 20; H: fragment owocu, z którego usunięto jego zewnętrzną część (będącą przedłużeniem trzonka); widoczny jest pakiet nasion otoczony wewnętrzną skórką owocu i tkanką przewodzącą, które zakrywają połączenie nasion ze szczeliną, S 377, × 20; I: żeberka wystające na górnej kutikuli strefy 1 szczeliny widoczne w poprzecznym przekroju, przekrój I/e, × 200; J: cienkie miejsce w górnej epidermie owocu, S 306, × 200; K: przekrój przez miękisz i nasienie, maceracja „bielinką", przekrój I/55, × 200



b — komórka miękiszu owocu, d — kutikula zewnętrznej skórki nasienia, e — wewnętrzna skórka owocu, g — boczne przedłużenie szczeliny, i — fałd, m — szczelina, p — trzonek, r — zewnętrzna skórka owocu, s — komórka kamienna testy nasienia

contents. Their strongly cutinised periclinal walls are thick and the cutinisation extends downwards along the anticlinal walls. The thickness of the periclinal walls varies, being smaller on the pedicel side of the fruit and greater on the mouth side. Also the frequency of the papillae and the glandular hairs varies; on the whole they are most frequent near the mouth. The thick papillae are best developed on the edge of the lip, where they cover the whole surface of the epidermis and reach a length of 30 μ.

The epidermis of almost every fruit contains a few very thin places. These consist of a thin oval area of 45×30 μ in which outlines of cells suggesting guard cells can occasionally be observed. The thin places are surrounded by a ring of strongly cutinised epidermal cells (Text-fig. 4 J). Similar structures were observed in *C. nathorsti* by Harris (1940), who suggested that they were poorly preserved stomata.

The epidermal cells either border immediately on a layer of small cells of the flesh or else on small rounded cells also filled with granular contents.

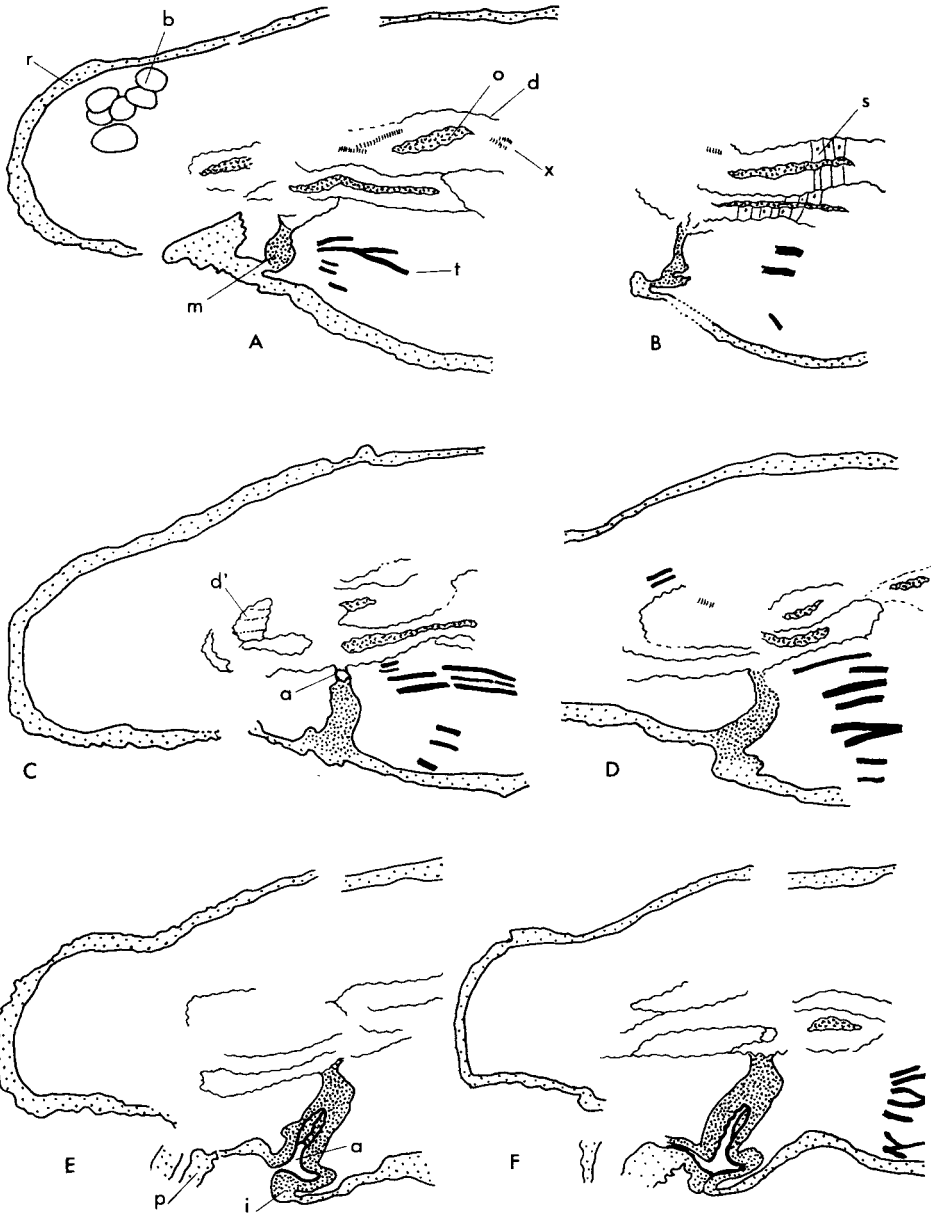
The fruit of *C. harrisii* shows a pattern of protruding ridges which is constant in most fruits of this species. This pattern begins with two ridges running up the pedicel side of the fruit which are connected by a transverse ridge below the apex of the fruit and from there they give off a network of ridges over the rest of the fruit (Text-fig. 4 A, B). The tissue forming these ridges was not identified, but it appears that they are hypodermal.

Mouth

Zones of the mouth. At the base of the fruit the epidermis of the lip turns inwards and forms, together with the epidermis of the pedicel, a flat funnel-like structure reaching inside the fruit (cf. Pl. IV, fig. 5, Pl. V, figs 1—2). This structure is visible in the sections published by Thomas, who regarded it as the stigma. In 1940 Harris named it the mouth and published its detailed description. Harris found that in *C. sewardi* and *C. nathorsti* the mouth consisted of three zones: zone 1, where the epidermis of the lip and pedicel were still apart, zone 2, which is very thick, and the thinly cutinised zone 3, which forms the

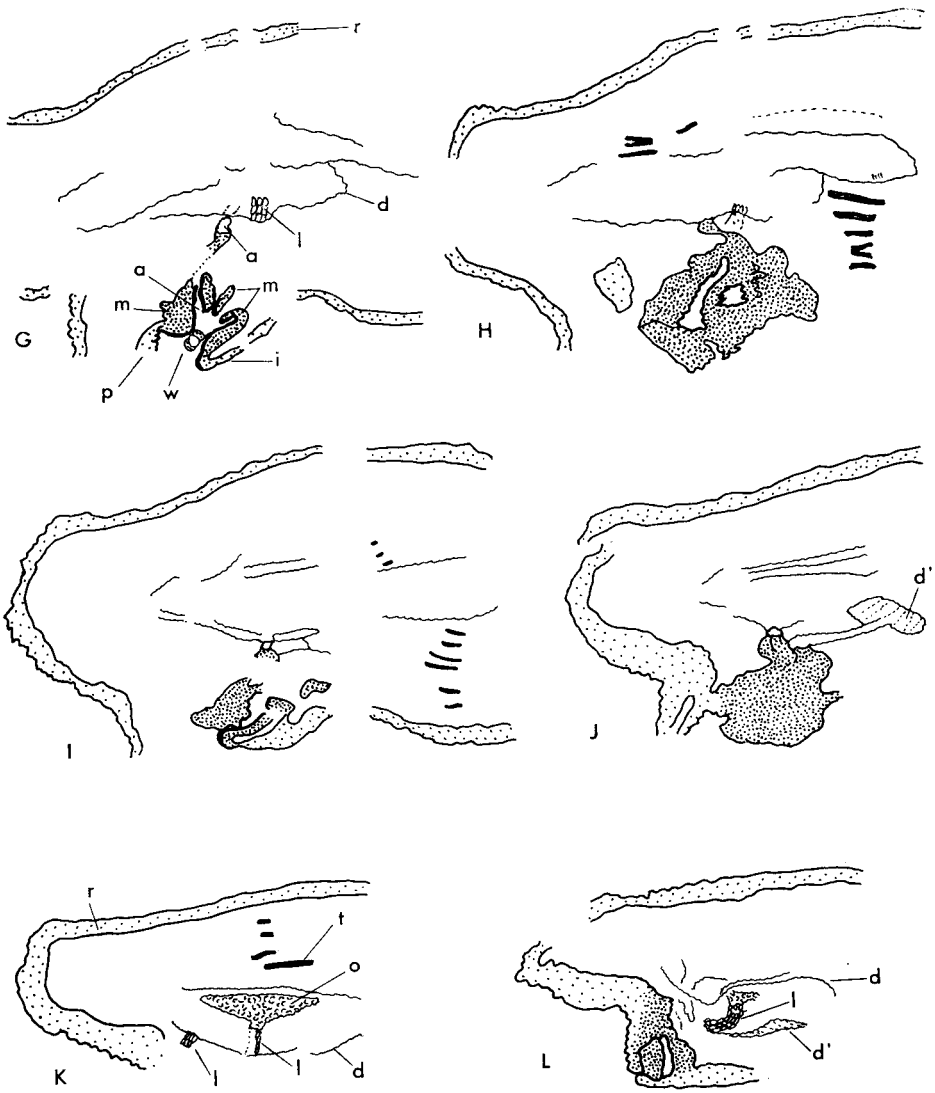
Ryc. 5. *Caytonia harrisii* sp. n. Seria podłużnych przekrojów przez owoc XI z widoczną zewnętrzną skórką, szczeliną, kutikulami nasion w jej sąsiedztwie i fragmentami tkanki przewodzącej. A ukazuje pozycję wiązek przewodzących w nasieniu, C ukazuje pusty kanał szczeliny w przekroju. Maceracja wodorotlenkiem sodu. A — przekrój XI/15, B — XI/16, C — XI/17, D — XI/19, E — XI/22, F — XI/23, wszystkie × 50

a — kanalik szczeliny, b — komórka miękiszu owocu, d — kutikula zewnętrznej skórki nasienia w przekroju, d' — to samo od góry, i — fałd, m — szczelina, o — nucellus, p — trzonek, r — zewnętrzna skórka owocu, s — komórka kamienna testy nasienia, t — wiązka przewodząca owocu, x — tracheida w nasieniu



Text-fig. 5. *Caytonia harrisii* sp. n. Series of longitudinal sections through fruit XI showing outer epidermis, mouth, cuticles of seeds in its vicinity, and fragments of vascular tissue. A shows the position of the vascular strands in a seed, C shows an empty canal of mouth in section. Maceration with sodium hydroxide. A — section XI/15, B — XI/16, C — XI/17, D — XI/19, E — XI/22, F — XI/23, all × 50

a — canal of the mouth, b — cell of flesh, d — cuticle of outer epidermis of seed in section, d' — the same from above, i — lip, m — mouth, o — nucellus, p — pedicel, r — outer epidermis of fruit, s — stone cell of seed testa, t — vascular strand of fruit, x — tracheid in seed



Text-fig. 6. Continuation of Text-fig. 5, showing longitudinal sections through mouth; seed apices often with micropyles visible in vicinity of inner edge of mouth. G — section XI/24, H — XI/25, I — XI/26, J — XI/27, K — XI/28, L — XI/29
1 — micropyle of seed, w — pollen grain; other abbreviations as in Text-fig. 5

Ryc. 6. Ciąg dalszy ryc. 5, z widocznymi podłużnymi ukośnymi przekrojami przez szczelinę; szczyty nasion często z mikropyle widocznym w sąsiedztwie wewnętrznego ujścia szczeliny. G — przekrój XI/24, H — XI/25, I — XI/26, J — XI/27, K — XI/28, L — XI/29
1 — mikropyle nasienia, w — ziarno pyłku; inne skróty jak na ryc. 5

inner margin of the mouth and is irregularly torn at its end. He also described thickly cutinised transverse bars running across these zones and supposed they were obliterated canals which admitted pollen to the

ovules. He thought, however, that there was no anatomical proof that such canals existed and that they were connected with the ovules.

The sections in three planes of *C. harrisii* show a mouth of the same structure as that described by Harris in *C. sewardi* and *C. nathorsti*, though differing slightly in size. It also shows three zones: in zone 1 the two epidermises are not much thickened and are apart, with a cavity between them. On the epidermis of the lip there are projecting ridges formed of 2—3 additional layers of cells with thickly cutinised walls (Text-fig. 4 I). The epidermis of the pedicel is covered with large round papillae (Text-fig. 8 B).

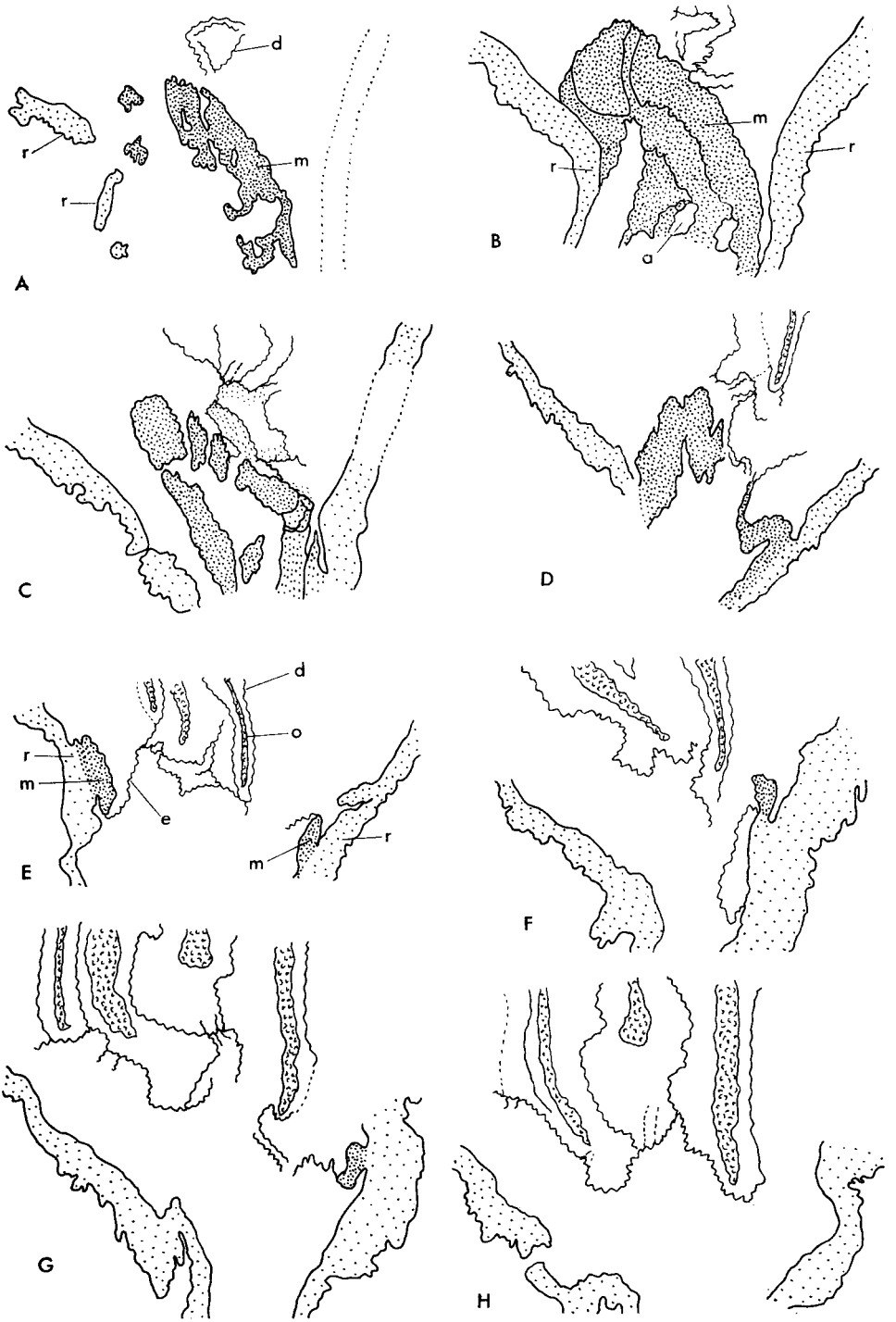
In zone 2, the two epidermises forming the mouth are very much thickened, because here they consist of elongated, thickly cutinised cells in a somewhat oblique position (cf. Harris 1940). In this zone the ridges of the upper epidermis reach the papillae of the lower one forming thus a system of canals running inwards. Inside the mouth, both in zone 1 and zone 2, pollen grains and spores of various plants were found.

Zone 3 consists of thinly cutinised cells. Seen from above, this zone looks like a band consisting of thick bars connected by a much thinner cuticle and it is irregularly torn at the inner margin of the mouth (Pl. I, fig. 9). In several strongly macerated sections it can be observed that the dark bars are in fact empty canals about 40 μ in diameter (Text-fig. 5 c). In little macerated sections the empty spaces inside the canals are not visible.

Relation of mouth to seed apices. A new detail shown by sections of *C. harrisii* are seed apices, sometimes with the micropyle visible, adhering to the inner margin of the mouth, though the sections do not show whether a micropyle is as a rule strictly opposite the opening of a canal in the mouth. However, a macerated fruit of *C. sewardi* from the Grojec area appears to show that this is so. In this fruit the inner edge of the mouth was torn a little further inside than in others. Here zone 3 of the mouth consisted, as usual, of two thin cuticles adhering together and showing parallel thicker bars corresponding to canals. But further inside the fruit these two cuticles separated in such a way that each canal widened into a funnel, where the cuticles were torn. It appears to me that each such funnel surrounded the apex of one seed and was, in fact, identical with the inner epidermis of the fruit.

Sections show that apparently the two cuticles lining the mouth separated at its inner edge to line the fruit cavity on the lip side and pedicel side of the fruit, as had been supposed by Harris (1940). This separation and then the course of the two cuticles was followed for some distance on sections, which would appear to be evidence that the cuticle of the mouth was continuous with the inner epidermis of the fruit.

Lateral extensions. Another feature of the mouth not yet described are its strongly cutinised lateral extensions through which it



Text-fig. 7. *Caytonia harrisii* sp. n. Sections through fruit XIII passing parallel to the plane of the mouth, B, C showing empty canals in the mouth and cuticles, probably of zone 3 of the mouth, at its inner edge. Maceration with sodium hydroxide,

is connected with the outer epidermis of the fruit (Pl. I, fig. 9; Text-fig. 4 c). The structure of the extensions can be understood best from a sequence of tranverse sections of fruit I beginning at the lip. As can be seen in text-fig. 8, at first the epidermises of the lip and pedicel are not connected at all, then they fuse at both sides, leaving in the middle the open cavity of the mouth. This cavity diminishes as the two epidermises gradually fuse along a longer distance, and these fused parts connected with the epidermis of the fruit I call the extensions of the mouth. They do not end at the level where zone 3 of the mouth ends but continue, tapering gradually, for about 1/4 of the length of the fruit. The fruit seen from outside shows a more or less marked furrow bordered by two ridges in the place where an extension of the mouth joins its outer epidermis (Text-fig. 12 D). The furrow can also be seen in transverse sections (Text-fig. 8 B, G, 9 K).

It can be seen on transverse sections of the fruit going through the upper part of the seeds that each lateral extension of the mouth grows thinner towards the centre of the fruit and then divides into two single layers of cells which reach the packet of seeds, one at its upper and one at its lower side (Text-fig. 9 K). Each layer consists of flat cells with a distinct cuticle on one side which is visible even where the cell outlines are obscure. It is possible that this layer is continuous with the layer of flatt cells surrounding the packet of seeds which will be described later as the inner epidermis of the seed. Both are single layers of cells and they look much alike in shape and size. There are differences, however, because the cells of the inner epidermis of the fruit have a small lumen and thick uncutinized walls, while in the layers proceeding from the extensions of the mouth the cells appear to have thin walls cutinized on one side.

Between the two layers connected with the extensions of the mouth there lies a group of cells which is triangular in transverse section and will be described in the next chapter. It could not be established whether there is a layer of flat cells between this triangular group of cells and the seed packet.

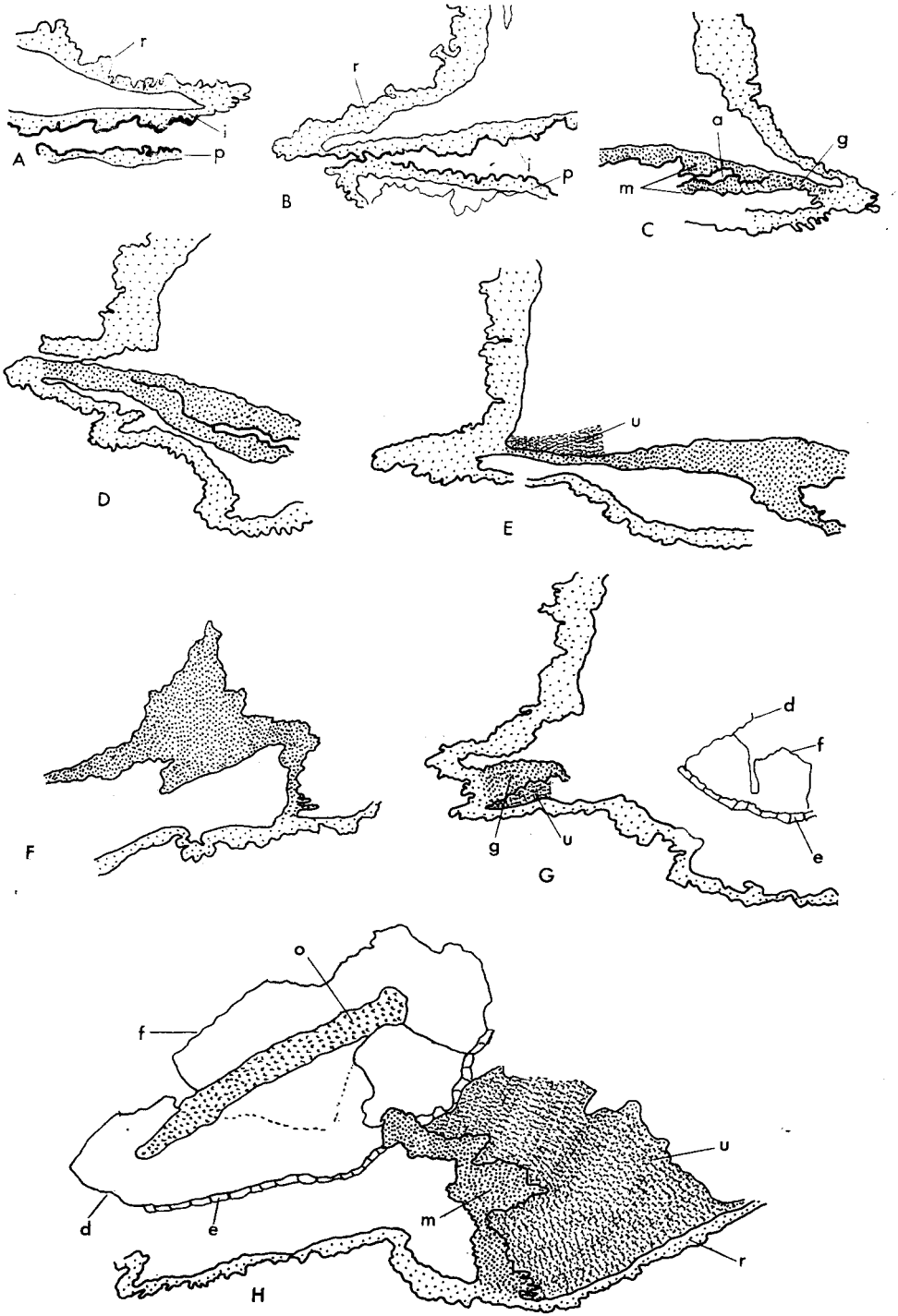
←

× 100. A — section XIII/13, B — XIII/14, C — XIII/15, D — XIII/17, E — XIII/21, F — XIII/25, G — XIII/27, H — XIII/28

a — canal of the mouth, d — cuticle of outer epidermis of seed, e — inner epidermis of fruit, m — mouth, o — nucellus, r — outer epidermis of fruit

Ryc. 7. *Caytonia harrisii* sp. n. Przekroje przez owoc XIII, przechodzące równolegle do płaszczyzny szczeliny, na B, C widoczne puste kanaliki oraz kutikule, należące prawdopodobnie do strefy 3 szczeliny. Maceracja wodorotlenkiem sodu, × 100. A — przekrój XIII/13, B — XIII/14, C — XIII/15, D — XIII/17, E — XIII/21, F — XIII/25, G — XIII/27, H — XIII/28

a — kanalik szczeliny, d — kutikula zewnętrznej skórki nasienia, e — wewnętrzna skórka owocu, m — szczelina, o — nucellus, r — zewnętrzna skórka owocu



Text-fig. 8. *Caytonia harrisii* sp. n. Series of transverse sections of fruit I showing the gradual fusion of the epidermises of the lip and pedicel into the mouth and its lateral extensions, H showing seed apex adhering to mouth. Maceration with

Mouth of *C. sewardi*. It is of interest to note that in a proportion of *Caytonia sewardi* fruits from Yorkshire and from Grojec, zone 1 of the mouth is open, so that the lip is a semicircular flange projecting from the fruit wall at a certain distance from the pedicel (Text-fig. 2 A—E). In such fruits the ridges in zone 1 of the mouth are not well developed and from the outside the openings of the canals can be seen. In other specimens, however, the lip is as in *C. harrisii*, where an open mouth was never found.

Undetermined tissues connected with the mouth

The tissues described under this heading were preserved in transverse sections of fruit I which were macerated with bleach or with sodium chlorite and hydrochloric acid. In other fruits which were macerated with sodium hydroxide and alcohol these tissues have dissolved. I do not think, however, that they were accidental structures.

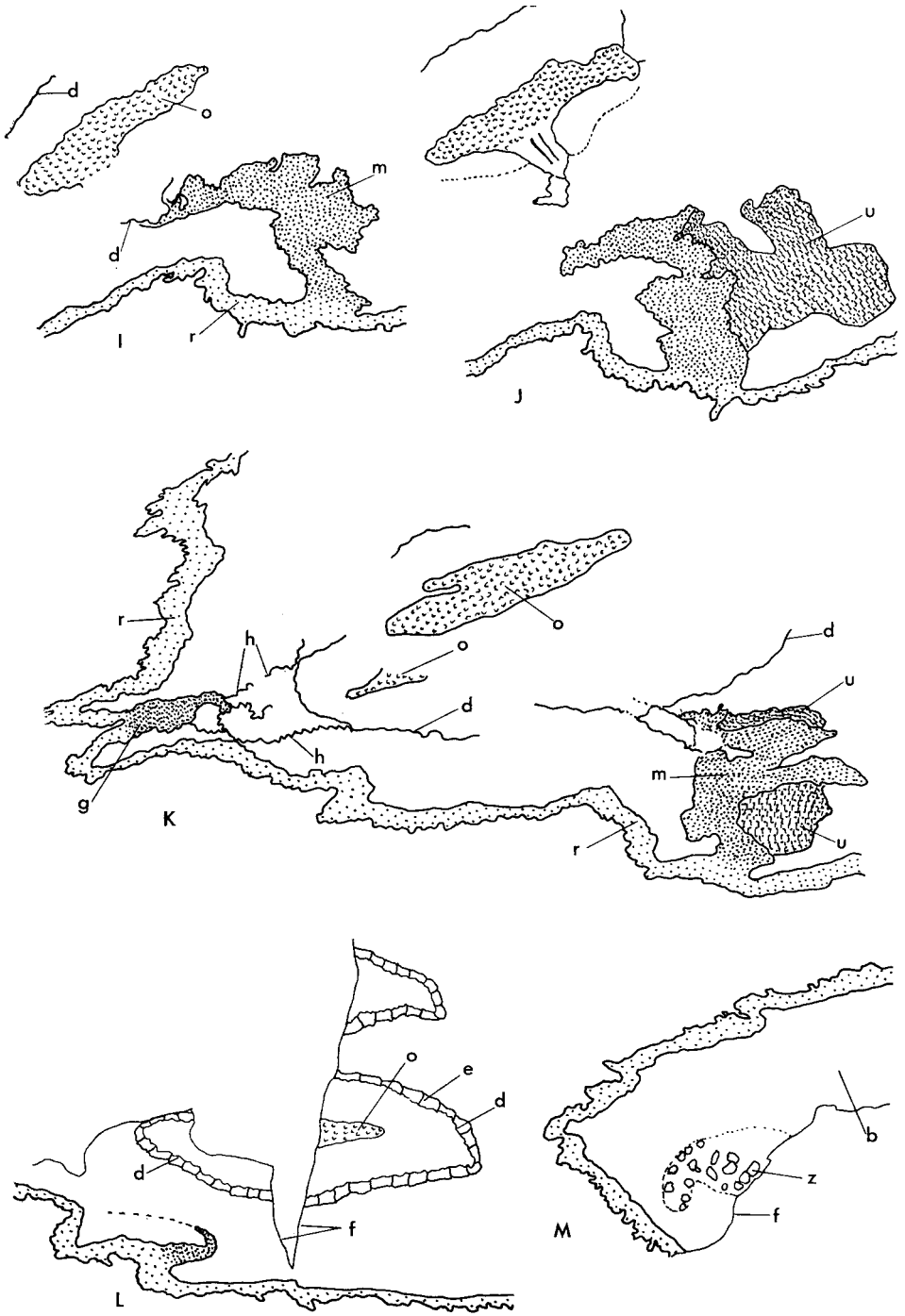
Tissue between extension of mouth and seeds. As was mentioned in the previous chapter, in transverse sections on each side of the seed packet there can be seen a triangular group of cells. It abuts on the seeds with its base and reaches the cutinized extension of the mouth with its apex (Text-fig. 9 K, between the seed and the cuticles marked h). It consists of rectangular cells which are aligned in radial rows. Whether they were all of one type, or whether their walls were smooth or pitted, could not be established but in arrangement they recall a vascular strand of a gymnosperm leaf in transverse section. This tissue was not identified in longitudinal section; it can only be assumed that it corresponds to certain strands of elongated elements occurring in a similar position. Again, they were not distinct enough to show their struc-

bleach, × 100. A — section I/e, B — I/e', C — I/c, D — I/3—7, E — I/11, F — I/16, G — I/21, H — I/23

a — canal of the mouth, d — cuticle of outer epidermis of seed, e — inner epidermis of fruit, f — broken edge of section, g — lateral extension of mouth, i — lip, m — mouth, o — nucellus, p — pedicel, r — outer epidermis of fruit, u — periderm-like tissue

Ryc. 8. *Caytonia harrisii* sp. n. Seria poprzecznych przekrojów przez owoc I ukazująca stopniowe zrastanie się skórki fałdu oraz trzonka owocu, dzięki czemu powstaje szczelina i jej boczne przedłużenie łączące się z zewnętrzną epidermą owocu. H ukazuje szczyt nasienia przylegający do szczeliny. Maceracja bielinką, × 100. A — przekrój I/e, B — I/e', C — I/c, D — I/3—7, E — I/11, F — I/16, G — I/21, H — I/23

a — kanalik szczeliny, d — kutikula zewnętrznej epidermy nasienia, e — wewnętrzna skórka owocu, f — ułamany brzeg preparatu, g — boczne przedłużenie szczeliny, i — fałd, m — szczelina, o — nucellus, p — trzonek, r — zewnętrzna skórka owocu, u — tkanka podobna do perydermy



Text-fig. 9. *Caytonia harrisii* sp. n. Continuation of Text-fig. 8: I, K showing cuticles of seed apex adhering to mouth; M, lateral extension of mouth already absent, visible group of cells resembling vascular strand (z). Other abbreviations as in Text-fig. 8. I — section I/27, J — I/28, K — I/33, L — I/46, M — I/72

ture. It was not established how far towards the top of the fruit this tissue reached but at any rate it is present in sections where the extensions of the mouth are already absent (cfr. Text-fig. 9 M).

Periderm-like tissue. This tissue consists of a few layers of flat rectangular cells, usually aligned in radial rows. Their walls are thin, and as far I could establish, without pitting. These cells lie on the inside of the epidermis lining the mouth and are connected with it either directly or through a layer of cells with thickened walls bearing simple pits. In some places inside this tissue can be seen groups of a few narrow tracheids with spiral thickenings.

The periderm-like tissue can be seen in transverse sections next to the side of the mouth facing the interior of the fruit (Text-fig. 8 H). It appears to be developed best along zone 2 of the mouth where it consists of up to six layers, and probably also along zone 3, because the thin-walled cells may be arranged around an empty small space. This structure may represent a transverse section through a thickened bar of zone 3 of the mouth with an empty canal inside. Small amounts of the periderm-like tissue were also present in zone 1 of the mouth.

In longitudinal sections macerated with sodium hydroxide there is an empty space at both sides of the mouth, where the network of vascular strands does not reach. This space was apparently filled with the periderm-like tissue.

In having cells aligned in radial rows this tissue is similar both to vascular tissue and to periderm. Because I did not observe any pits, it appears that it is rather of the nature of a periderm layer which originated from the epidermis of the mouth. Periderm connected with epidermis has been reported from leaves and bud-scales of various groups of gymnosperms (Napp-Zinn, 1966).

Inner epidermis of fruit

Harris (1933) obtained from *C. thomasi* strips of a delicate cuticle which he thought might belong to the interior of the fruit. In 1964 he described and figured two superimposed cuticles of *C. kendalli* showing parallel elongated cells differing in width and wall thickness. He interpreted them as the cuticles of the seed epidermis and of the inner epidermis of the fruit.

Ryc. 9. *Caytonia harrisii* sp. n. Ciąg dalszy przekrojów z ryc. 8: I, K ukazują kutikule szczytu nasienia przylegające do szczeliny; na M boczne przedłużenie szczeliny już niewidoczne, widoczna natomiast tkanka przypominająca wiązkę przewodzącą (z). Pozostałe skróty jak na ryc. 8. I — przekrój I/27, J — I/28, K — I/33, L — I/46, M — I/72

In *C. harrisii* it is difficult to decide whether a separate fragment of cuticle derived from the seed epidermis or from the inner epidermis of the fruit. But the inner epidermis of the fruit in connection with other tissues was observed both in broken unmacerated fruits and in sections. In fragments of unmacerated broken fruits which have shed their seeds the flesh is lined from inside by a thin layer which shows in surface view a fine striation parallel with the long axis of the fruit (Text-fig. 4 G). In a corresponding position in sections there occurs a single layer of flat cells. In surface view they appear to be elongated while in section they are about 17 μ high and show thick walls and a small lumen filled with a granular substance (Text-fig. 11 P). These thick cell walls dissolve in maceration, therefore they are not cutinized. Between them and the adjacent seeds there lies the distinct undulate cuticle of the outer epidermis of the seed, but rarely can there be observed a second, thinner cuticle belonging, it would seem, to the layer of thick-walled cells.

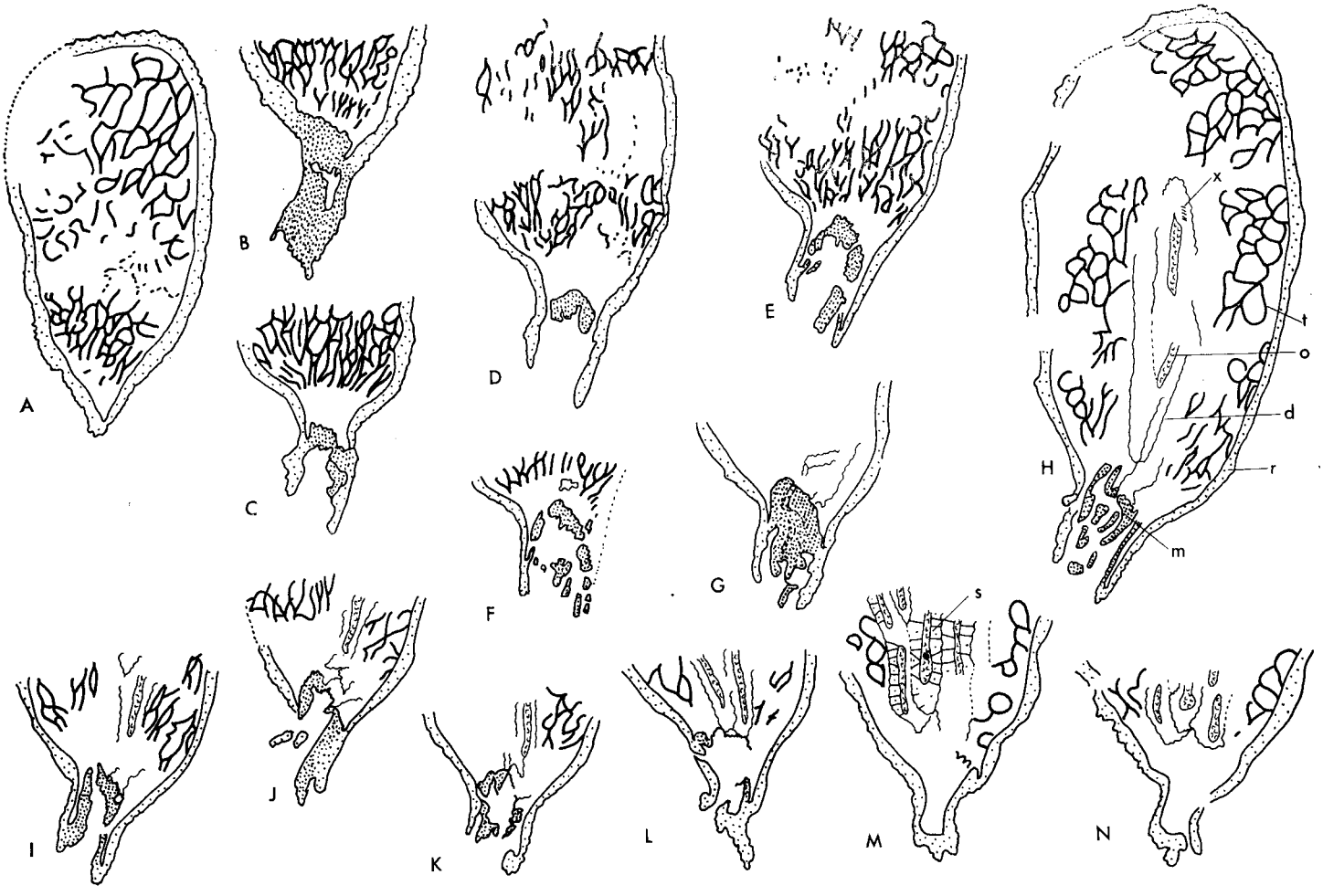
This layer of flat thickwalled cells is interpreted as the inner epidermis of the fruit because of its distribution. It surrounds the packet of seeds but was not observed between two seeds. It is present at the basal and apical part of seeds and it appears to line the apex of each seed, at least up to the place where it abuts on another seed. As was shown before, this layer appears to be continuous with the epidermises forming the mouth and with the lateral extensions of the mouth.

Flesh of fruit

The space between the inner and outer epidermis of the fruit is filled with large rounded bodies described by the previous authors as cells of the flesh. Thomas (1925) figured on pl. 13, fig. 28 a section of the flesh of *C. sewardi*. He supposed that it consisted of large rounded cells with thickened walls. Harris (1940) on pl. VII, fig. 10 figured the flesh of *C. sewardi* and in 1964 reported the existence of large sclereids in the flesh of several species.

In *C. harrisii* the cells of the flesh were observed in broken unmacerated fruits, during maceration of fruits, and in sections. They are rounded, about 120 μ long, and 50 μ wide in the middle of the flesh and only about 60 μ long next to the outer and inner epidermis of the fruit. Each cell is surrounded by a wall, which is seen in section as a thin line, and the cell contents are a reddish brown substance not showing granules. The cells either adhere to each other or are separated by intercellular spaces.

Between the cells of the flesh there runs a dark network consisting of vascular strands, which will be described in the next chapter, and of sclereids. The sclereids may also form dense clusters or they occur in small numbers between adhering cells. The sclereids are of the type



Text-fig. 10. *Caytonia harrisii* sp. n. Series of sections through fruit XIII passing parallel to the plane of the mouth. Visible mouth, cutinised membranes of the seeds, and network of vascular strands in the flesh. Maceration with sodium hydroxide, × 50. A — XIII/5, B — XIII/7, C — XIII/9, D — XIII/10, E — XIII/11, F — XIII/12, G — XIII/14, H — XIII/15, I — XIII/16, J — XIII/17, K — XIII/18, L — XIII/21, M — XIII/27, N — XIII/28

d — cuticle of outer epidermis of seed, m — mouth, o — nucellus, r — outer epidermis of fruit, s — stone cell of seed testa, t — vascular strand of fruit, x — tracheid in seed

Ryc. 10. *Caytonia harrisii* sp. n. Seria przekrojów przez owoc XIII przechodząca równolegle do płaszczyzny szczeliny. Widoczna szczelina, skutynizowane warstwy nasion oraz wiązki przewodzące w miękiszu. Maceracja wodorotlenkiem sodu, × 50. A — XIII/5, B — XIII/7, C — XIII/9, D — XIII/10, E — XIII/11, F — XIII/12, G — XIII/14, H — XIII/15, I — XIII/16, J — XIII/17, K — XIII/18, L — XIII/21, M — XIII/27, N — XIII/28

d — kutikula zewnętrznej skórki nasienia, m — szczelina, o — nucellus, r — zewnętrzna skórka owocu, s — komórka kamienna testy nasienia, t — wiązka przewodząca owocu, x — tracheida w nasieniu

occurring in the fruits and leaves of *Olea*. They appear to be of two kinds, either showing a thicker body giving off numerous branches similar to filiform sclereids in *Olea* leaves (E s a u 1961, p. 57, fig. 6.4. L, M) or showing only the filiform branches. They are about 70 μ long and the branches are of uniform diameter, different in different sclereids and reaching from 3 to 6 μ. The sclereids show a small thread-like lumen and in transverse section each sclereid looks like a small circle with a dot in the middle (Text-figs. 11 B, E—G).

V a s c u l a r s y s t e m o f f r u i t

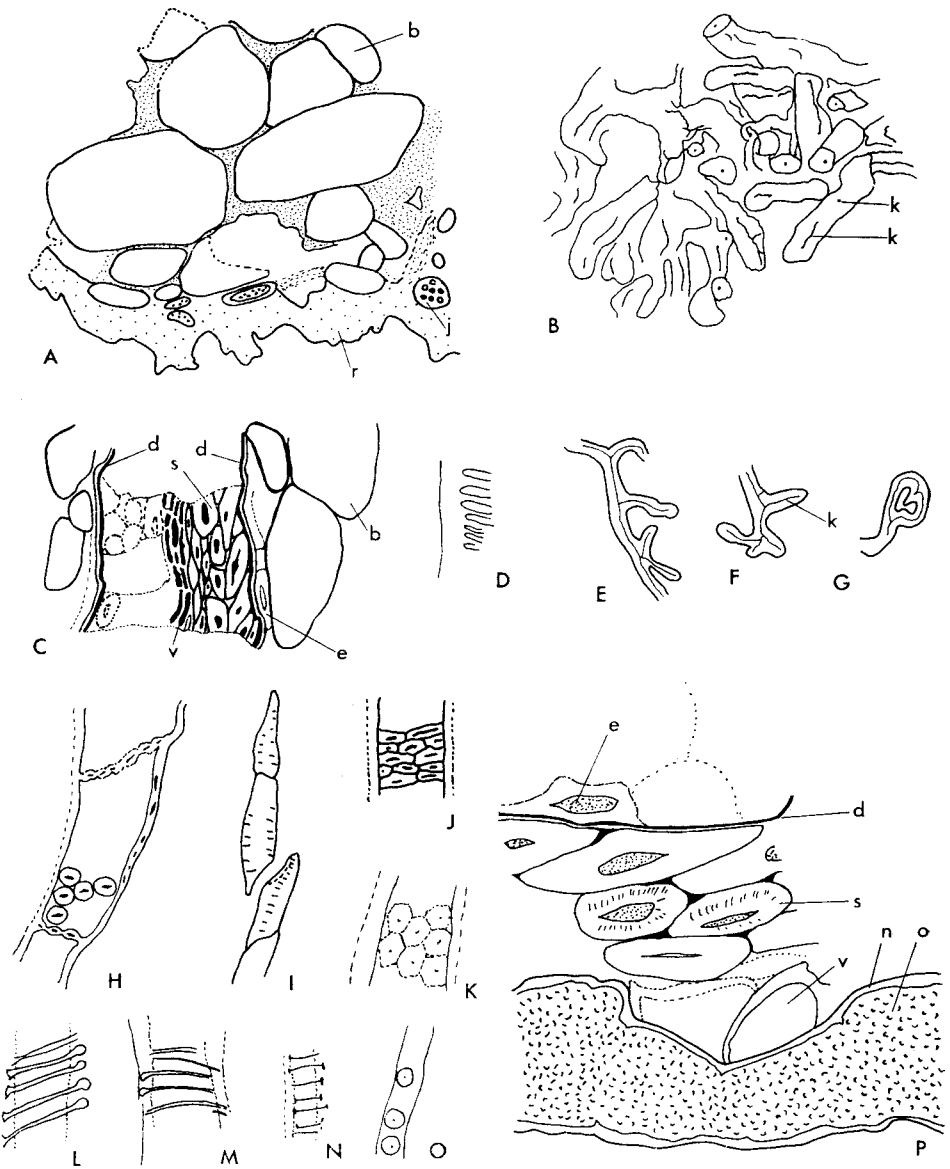
H a r r i s (1947) observed fragments of scalariform tracheids in *Caytonia* fruits and *Sagenopteris* leaves.

In *Caytonia harrisii* a fairly detailed picture of the vascular system can be made out when details seen in macerated sections and in unmacerated broken fruits are put together.

The space between the mouth and the pedicel side of the outer epidermis is occupied by a tissue, different from the flesh of the fruit, which is apparently the continuation of the tissue of the pedicel. Its structure is insufficiently known because only fragments of it are preserved in sections of fruit I. As seen in transverse section, this tissue consists of a few layers of isodiametric cells which appear to be of two kinds. Some are rounded and may be parenchymatous cells. Others are angular in outline and are apparently tracheids because in certain sections they show bordered pits on the sectioned walls. As far as could be observed, these tracheids do not appear to be arranged in radial rows.

This tissue is not known in longitudinal section but a damaged unmacerated fruit showed, in a corresponding position, a flat mass of narrow elongated elements running upwards from the pedicel. When seen under a microscope for reflected light, some of these elements show transverse thickenings or bordered pits which is evidence that they are tracheids and the tissue is a vascular tissue. As for the distribution of this vascular tissue in this particular fruit, it appears to form a thick flat band which covers the mouth from the pedicel side and also the seed apices, so that they are not visible. Farther up this band of vascular tissue gradually becomes thinner and eventually it forms a dense network of strands adhering to the seed packet.

As can be seen in sections, apart from this there is a network of vascular strands running between the cells of the flesh of the fruit, whose meshes correspond in size with these cells. The network is particularly dense near the seeds and in the region above the lip and here its meshes are elongated and very narrow (Pl. IV, fig. 6, Text-fig. 10). These vascular strands are visible only in sections macerated with sodium hydroxide and alcohol and, very occasionally, when fruits cleaned with hydrofluoric



Text-fig. 11. *Caytonia harrisii* sp. n., details of flesh and seed. A: cells of flesh of fruit, maceration with bleach, section I/59, × 200; B: cluster of small sclereids in flesh, maceration with sodium hydroxide, section XI/9, × 1000; C: section through flesh and seed, maceration with bleach, section I/65, × 200; D: fragment of tracheid in flesh with probable scalariform pits, section VII/28, × 1000; E, F, G: fragments of sclereids in flesh; E, F — section XIII/12, G — secton XIII/27, × 400; H, J, K, O: fragments of tracheids in flesh showing bordered pits. H, J, K — section XIII/10, O — section XIII/8, all × 1000; I: probably tracheids showing transverse walls, section XIII/12, × 400; L, M, M: fragments of tracheids in seeds. L, M — section XI/12, N — section XIII/21, all × 1000; E — O — maceration with sodium hydroxide;

acid are neutralized with ammonia and fragments of the flesh appear in the macerating fluid.

Of the elements belonging to the vascular strands, only rarely can narrow protoxylem tracheids with spiral thickenings or a few elongated cells without pitting be seen. Only larger tracheids, possibly of the metaxylem, are conspicuous but their relation to the protoxylem and phloem is not known. These tracheids of the metaxylem are straight or curved, depending on their position in the network, and appear to be arranged continuously one above the other. Tracheids about 30 μ long and about 11 μ wide were observed but this is probably not the complete range of variability, because the length of the tracheids is difficult to establish on sections. Their side walls are covered with closely spaced bordered pits in alternate arrangement (Text-fig. 11 H, J, K, O). The bordered pits show a horizontal slit and are either circular or elongated in the horizontal direction. Their vertical diameter is about 3 μ. The transverse walls observed in section show bordered pits (Text-fig. 11 H). There were also observed fragments of tracheids with closely spaced bars and suggesting close scalariform thickenings or perhaps scalariform bordered pits. It is not certain whether they occur on the side walls or transverse walls of the tracheids (Text-fig. 11 D).

In addition, as was mentioned on p. 67, in transverse sections of the lower part of the fruit two groups of radially arranged cells, occurring

←

P: fragment of section through seed and inner epidermis of fruit, maceration with bleach, section I/56, × 400

b — cell of flesh, d — cuticle of outer epidermis of seed, e — inner epidermis of fruit, j — hypodermal cell (?), k — lumen of sclereid, n — nucellar cuticle, o — nucellus, r — outer epidermis of fruit, s — stone cell of seed testa, v — spotted layer in seed

Ryc. 11. *Caytonia harrisii* sp. n., szczegóły budowy miękiszu i nasion. A: komórki miękiszu owocu, maceracja bielinką, przekrój I/59, × 200; B: grupa małych sklereid w miękiszu, maceracja wodorotlenkiem sodu, przekrój XI/9, × 1000; C: przekrój przez miękisz i nasienie, maceracja bielinką, przekrój I/65, × 200; D: fragment tracheidy z miękiszu owocu prawdopodobnie z jamkami drabinkowatymi, przekrój VII/28, × 1000; E, F, G: fragmenty sklereid z miękiszu owocu, E, F — przekrój XIII/12, G — przekrój XIII/27, × 400; H, J, K, O: fragmenty tracheid z miękiszu ukazujące jamki lejkowate. H, J, K — przekrój XIII/10, O — przekrój XIII/8 wszystkie × 1000; I: prawdopodobnie tracheidy z widocznymi poprzecznymi ścianami, przekrój XIII/12, × 400; L, M, N: fragmenty tracheid z nasion, L, M — przekrój XI/12, N — przekrój XIII/21, wszystkie × 1000; E — O: maceracja wodorotlenkiem sodu; P: fragment przekroju przez nasienie i wewnętrzną skórkę owocu, maceracja bielinką, przekrój I/56, × 400

b — komórka miękiszu owocu, d — kutikula zewnętrznej skórki nasienia, e — wewnętrzna skórka owocu, j — komórka hypodermy (?), k — światło sklereidy, n— kutikula nucellusa, o — nucellus, r — zewnętrzna skórka owocu, s — komórka kamienna testy nasienia, v — warstwa plamista w nasieniu

at both sides of the packet of seeds can be observed. They give the impression of vascular strands similar to those in sections of gymnosperm leaves, but the cells are not distinct enough to show for certain their nature.

Seeds

The seeds of *C. harrisii* show the same layers as those of *C. sewardi* and *C. nathorsti* (Harris 1958): the cuticle and the outer epidermis of the testa, the stone cells of the testa, the spotted membrane of the testa, the inner epidermis of the integument, the cuticle of the nucellus, and the aleurone layer of the endosperm (Text-fig. 11 P). Therefore I shall consider in this description only those features in which seeds of *C. harrisii* differ from other species, or features which are new.

Outer epidermis of testa. The cuticle of this layer is thicker than in other species and shows distinctly marked outlines of elongated cells. The macerated cuticle is uneven, showing small round bulges pointing outwards and wrinkles along the seed. In sections of the fruit this cuticle is seen as a distinct undulating line staining well with iodine green, which helps to determine the outlines of particular seeds (Text-fig. 4 K, 11 P).

Stone cells of testa. On the flat side of the seed the stone cells appear in section as one layer of square palisade cells. At the margin of the seed and at both its ends there are up to five layers of fibrous stone cells. Complete stone cells can be seen in sections but in maceration their inner casts appear, these being, like the „spicules" described by Thomas and Harris in *C. sewardi* and *C. thomasi.*

Spotted layer. Next to the stone cells of the testa occurs a layer of elongated cells with pointed ends which are orientated longitudinally (Text-fig. 11 C). They are about 22 μ long and 5 μ wide and contain a dark homogeneous substance. They are not stone cells because their walls are thin, though very distinct. In sections their outer walls show bulges in the shape of broad papillae, which resemble the „spots" in the spotted layer described by Harris in the seed of *Caytonia* (Text-fig. 11 P). I assume that this layer of cells is the same as the spotted layer, because it shows the bulges corresponding with the „spots" and because its position in the seed corresponds with that of the spotted layer.

Inner epidermis of integument. A layer of cells showing outlines similar to those described by Harris for this layer was seen during maceration of a few seeds.

Nucellus. The nucellar cuticle and the aleurone layer of the endosperm are similar to those in other species. (Pl. II, fig. 1). Below the aleurone layer there occurs a yellow granular substance without cell structure which possibly represents the endosperm. Near the micropylar

end of the seed this substance contains rounded masses of a lighter colour which may represent remains of archegonia.

Vascular strands. A feature of *Caytonia* seeds not described so far are the vascular strands, some details of which were seen during maceration and others in section (cf. Reymanówna 1970, Pl. CXVIII, figs. 5, 7, 8). When a *Caytonia* seed is macerated with nitric acid followed by ammonia, at first only peripheral layers of cells are visible, which then separate from the seed and dissolve, while a deeper layer appears for a short time. It was observed during such maceration that along the seed margin at first there appeared separate epidermal cells, then fibrous stone cells, and finally elongated narrow elements suggesting a vascular strand. In two or three seeds among these narrow elements there appeared fragments of tracheids with scalariform thickenings. In another seed similar tracheids were seen in the region of the hilum.

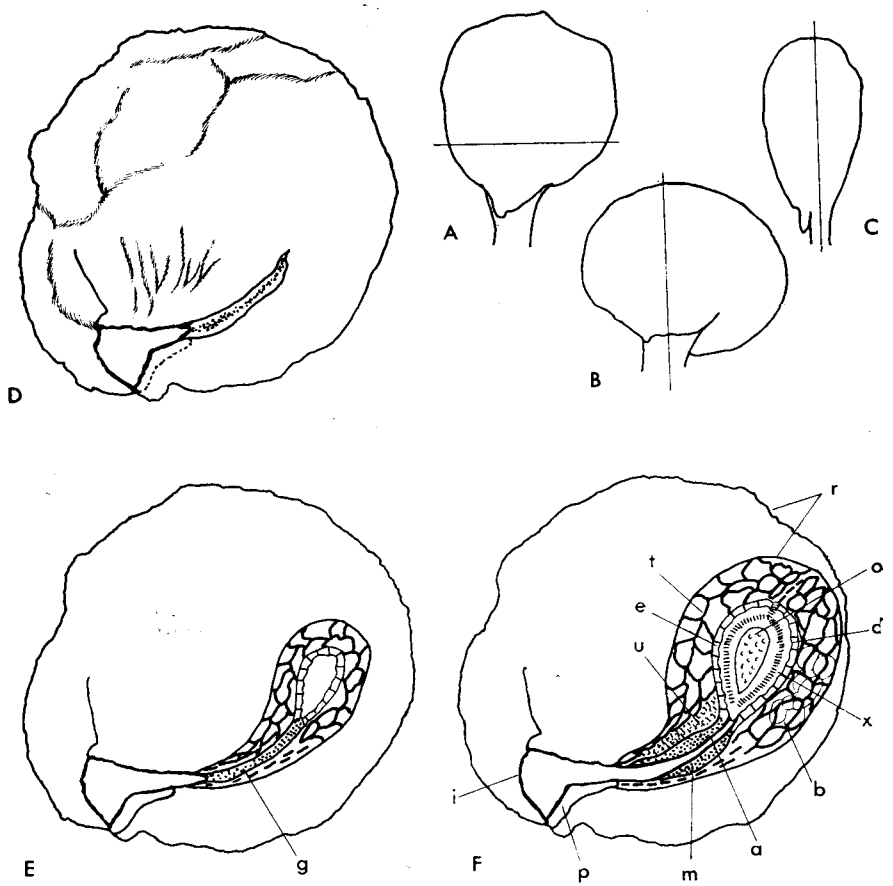
More details of the vascular strands of the seeds were seen in sections treated with sodium hydroxide and alcohol. Fragments of strands with tracheids 6—11 μ wide were seen, the longest tracheid fragment being 130 μ. The tracheids are scalariform to reticulate (Text-fig. 11 L, M, N); they are accompanied by much thinner elongated elements possibly belonging to the vascular strand. In a few sections near the tracheids there appear elongated dark elements looking like secretory ducts filled with a dark substance and divided by transverse walls. It was established that there is one vascular strand which enters through the hilum and divides into two, each running along one margin of the seed up to its apex (cf. Text-fig. 5 A).

DISCUSSION OF THE STRUCTURE OF *CAYTONIA*

Mouth

The sections of *C. harrisii* show a mouth of the same basic structure as that described by Harris in *C. sewardi* and *C. nathorsti*, the differences being mainly in size of the zones and in the degree of their cutinization. Moreover, details of cellular structure agree.

These sections also confirm certain hypotheses concerning the mouth which were formulated by Harris. In particular, I think that my sections prove that empty canals run through zone 3 of the mouth and that these communicated directly with the apices of the seeds (cf. Harris 1940 p. 729—730). Although in general these observations confirm the views of Harris, they do not agree in all details. Harris (personal communication) is of the opinion that, at least in *C. sewardi*, the canals connecting the mouth with the seed apices were much longer than those seen in my preparations.



Text-fig. 12. *Caytonia harrisii* sp. n. A — C: schematic drawings of fruits showing planes of sections, A — fruit I (Text-figs. 8, 9), B — fruit XI (Text-figs. 5, 6), C — fruit XIII (Text-figs. 7, 10); D: fruit from outside showing mouth and furrow on outer epidermis marking the extension of the mouth, S 422, × 20; E: drawing of fruit showing restoration of longitudinal section through lateral extension of mouth; F: drawing of fruit showing restoration of longitudinal section through canal of mouth

a — canal of the mouth, b — cell of flesh, d — cuticle of outer epidermis of seed, e — inner epidermis of fruit, g — lateral extension of mouth, i — lip, m — mouth, o — nucellus, p — pedicel, r — outer epidermis of fruit, t — vascular strand of fruit, u — periderm-like tissue, x — vascular strand of seed

Ryc. 12. *Caytonia harrisii* sp. n. A — C: schematyczne rysunki owoców z zaznaczonymi płaszczyznami przekrojów, A — owoc I (ryc. 8, 9), B — owoc XI (ryc. 5, 6), C — owoc XIII (ryc. 7, 10); D: owoc widziany od zewnątrz ukazujący szczelinę oraz bruzdę na zewnętrznej skórce, znaczącej jej przedłużenie, S 422, × 20; E: rysunek owocu z rekonstrukcją podłużnego przekroju przechodzącego przez przedłużenie szczeliny; F: rysunek owocu z rekonstrukcją podłużnego przekroju przechodzącego przez kanalik szczeliny

a — kanalik szczeliny, b — komórka miękiszu owocu, d — kutikula zewnętrznej

Not absolutely proved is a third hypothesis of Harris (1940 p. 724) that the epidermises of the mouth separated above its inner margin and lined the cavity of the fruit. The observation of this region is difficult because the sections are thick and two edges of the cuticle might simulate two cuticles. In this way the same seed cuticle may be taken for the cuticle of the seed epidermis and for the inner epidermis of the fruit. Eventually, however, I became convinced that at the fruit wall at the inner margin of the mouth there indeed occurred two cuticles, the outer one continuous with that of the mouth, and the inner one belonging to a seed. I believe that this observation is correct because it was made on more than one preparation. As the position of the cuticles lining the fruit cavity is that of the inner epidermis of the fruit, it appears that the inner epidermis of the fruit is continuous with the mouth.

A new feature of the mouth are its lateral extensions, which are connected with the outer epidermis of the fruit. From pictures shown by transverse sections (Text-fig. 8) they can be explained as a result of partial fusion of the upper (adaxial) epidermis of an incurved megasporophyll segment and this interpretation appears to be sound. The fusion apparently occurred along the margins of the segment, while the median part of the epidermis lined the mouth. It could be expected that further inside the fruit, where the place of the mouth is taken by the seeds, these lateral extensions would be continuous with the inner epidermis of the fruit. There are, in fact, connecting cuticles (cf. Text-fig. 9 K) so that this connection appears probable, though at the moment the details are not clear.

Inner epidermis of fruit

Thomas (1925, p. 321) described the cells and position of this layer in detail as the "blow-off layer", but attributed it to the seeds. Harris (1933, 1940, 1964) described fragments of cuticle belonging to the inner epidermis of the fruit; he also thought it might be continuous with the mouth. It seems to me that the interpretation of this layer as the inner epidermis of the fruit is sound, because it occurs only between seeds and fruit wall and this was already observed by Thomas. He observed also that it was cutinized on the walls facing the seed, which is again evidence that it belongs to the fruit wall and not to the seed. Its distribution around the packet of seeds has been followed on sections and the connection with the mouth is fairly certain.

skórki nasienia, e — wewnętrzna skórka owocu, g — boczne przedłużenie szczeliny, i — fałd, m — szczelina, o — nucellus, p — trzonek, r — zewnętrzna skórka owocu, t — wiązka przewodząca owocu, u — tkanka podobna do perydermy, x — wiązka przewodząca nasienia

Flesh of fruit

The flesh of the fruit had been described before, but never in such detail. It appears certain that the main elements of the flesh were large thin-walled cells and branched sclereids, apart from the vascular strands.

Not certain, however, is the nature of the contents of these cells. They appear after different treatment either as empty cells or as filled with a dark substance, or else, in certain preparations, they give the impression of being filled with dense clusters of branched sclereids. I am not sure, however, whether the last observation is correct, because this picture may also be caused by sclereids occurring between cells. Hence for the moment I accept the interpretation that the cells were parenchymatous and the sclereids were situated between them. We remain, therefore with the interpretation, accepted by the previous authors, of the fruit having the consistence of a soft berry.

Vascular system

The vascular system of the fruit and seed of *Caytonia* is described here for the first time. Most of it was revealed by maceration with sodium hydroxide and alcohol, based on a method used to show venation in recent leaves. Nevertheless, it is still not fully understood.

It appears certain that from the pedicel there entered a flat vascular strand, which ran towards the apex of the fruit between the mouth and the pedicel side of the fruit epidermis. It appears also that upwards from the mouth it flattened and spread, giving off numerous small strands which formed a network between the cells of the flesh, though this branching is not known in detail. Somewhere in the apical region of the fruit each seed is supplied with a vascular strand, but again the place of departure and the course of these strands are not known. Best known and certain is the network of vascular strands in the flesh. On the whole, the pattern of the vascular system of the fruit appears to be the same as in a *Sagenopteris* leaflet, since they both consist of one main strand and a network of smaller lateral strands.

It is possible that the two groups of radially arranged cells at the sides of the seed packet (cf. p. 67) are also vascular strands, but there is not sufficient evidence. The pattern of ridges visible on the surface of the fruit also shows a network spreading over most of the fruit, but it is different on the pedicel side of the fruit, where it consists of two ridges running upwards from the pedicel. Probably these ridges are formed by hypodermis.

From the elements of the vascular strands only the metaxylem and rarely also the protoxylem tracheids were observed, but their mutual

position is not known. The phloem and its position in the strand is also not known.

The tracheids appear as elongated cells with walls showing fragments of pitting, seen from above or in section. The tracheids are usually filled with a granulous substance, different from the substance filling the cells of the flesh. In the fruit the pitting is only occasionally distinct, as the walls appear to dissolve more easily than in other cells. Occasionally, thin translucent membranes with round pores can be observed in alternate arrangement, which may also be remnants of tracheid walls. In the seeds the tracheids are much better preserved and show the pitting along their whole length.

It seems firmly established that the predominant pitting in the tracheids of the fruit are bordered pits, either round ones which resemble the pitting found in the pteridosperms, or pits elongated in the horizontal direction. Also spiral thickenings were observed with certainty on small tracheids in the fruit and seed. Apart from this, tracheids were observed in the fruit with thickenings suggestive of long scalariform pits, and this interesting point needs further observations.

Arrangement of seeds

It is difficult to establish the arrangement of seeds in *C. harrisii*, because, unlike *C. sewardi* and *C. nathorsti*, the seeds are not visible through the epidermis. Sections of fruits show that the seeds face the mouth with their micropylar ends and the top of the fruit with their chalazal ends, but otherwise their arrangement appears to vary. Two fruits were damaged before fossilization and it was possible to uncover their seeds with a needle (Text-fig. 4 H). In this fruit the seeds are arranged in a way which appears intermediate between that seen in sections of fruits I and XI and in sections of fruit XIII. It appears to me that this was probably their original arrangement and that the pictures seen in sections are due to partial shifting of the seeds under the pressure of sediment of fruits buried in different positions. Another result of pressure of the sediment appears to be the fact that in sections of fruits the seed apices often appear curved, while in detached seeds they are straight.

There is, however, one fact concerning the arrangement of seeds which is confirmed both by sections and by fossil damaged fruits. The seeds of *C. harrisii* are not separated by flesh but are closely pressed together forming a packet in the centre of the fruit. This is different from restorations of *C. thomasi* (Harris 1933) and of *C. nathorsti* (Harris 1951a), which show each seed surrounded by a pocket of flesh.

STRUCTURE AND FUNCTION OF THE *CAYTONIA* FRUIT

Caytonia is the earliest known organ which encloses the seeds almost completely. As a result, new constructional solutions were needed in order that the enclosed ovules might be pollinated and the mature seeds dispersed so as not to germinate together. It seems that the pollination mechanism is now fairly well known, but only little can be said about the manner of seed dispersal.

Pollination mechanism

Thomas (1925) seeing the fruit with enclosed seeds, did not realize that there was a different pollination mechanism than in the angiosperms. He supposed that the pollen grains germinated on the lip and that only the pollen tubes entered the fruit. When Harris (1933) found pollen grains in micropyles and pollen chambers of seeds it became evident that the pollination mechanism was different. He assumed that the pollen was transported through the mouth and thought that the mouth ended into a group of canals, each of them reaching one ovule. He assumed also that a pollination drop was produced at the lip and, thanks to it, the pollen floated through the mouth and its canals to the seed micropyles. There was, however, no anatomical proof of such communication between the canals of the mouth and the ovules.

I believe that the sections of *C. harrisii* give convincing evidence that the seed apices were placed close to the openings of the canals and this confirms the hypothesis of Harris as to the pollination mechanism of *Caytonia*. In addition, inside the wider part of the mouth, in its zones 1 and 2, there were found sporomorphs of plants other than *Caytonia*. I consider this as evidence that *Caytonia* produced a pollination drop, since I cannot think of any other way in which sporomorphs of other plants could enter the mouth.

Some of these foreign sporomorphs are much larger than *Caytonanthus* pollen and their size obviously prevented them from entering the canals. On the other hand, *Caytonanthus* pollen grains, being only about 30 μ long, are among the smallest Jurassic pollen grains and could pass through the canals of zone 3 of the mouth, which are about 40 μ in diameter. Hence it appears that the mouth with its elaborate structure had a second function, apart from pollen conducting. This was to prevent the spores and pollen of other plants from reaching the ovules. It is a fact that sporomorphs other than *Caytonanthus* were never found in the pollen chambers of the large numbers of seeds macerated from Yorkshire, and only in a few seeds from Greenland (Harris 1951 a).

It appears likely that a structure of this type and a similar pollination mechanism occurred also in the fructification of *Microcheiris*

enigma from the Lower Lias of Greenland (H a r r i s 1935) which is now interpreted as one valve of *Leptostrobus longus* (H a r r i s 1951). The structure of the fructification is not clear, for what is preserved is a scale containing five embedded megaspore membranes. Opposite each megaspore membrane is situated a cone-shaped mass of pollen grains belonging to various types but with two types prevailing. H a r r i s was of the opinion that these pollen masses are not accidental, but that their presence is connected with some structure of the fructification which is not preserved. To me these pollen masses look as if they resulted from a structure like the mouth of *Caytonia.*

As for the pollination mechanism of *Caytonia,* it appears strange that, as far as it is understood now, the connection of the seed apex with the opening of its corresponding canal seems rather loose. Therefore the question arises whether it was not easy for the young ovule to shift during growth and in this way to miss the opening of its canal. It seems, however, that there were several structures preventing this shifting. The first one was the inner epidermis of the fruit, which apparently surrounded the packet of seeds and also the apex of each particular seed, continuing afterwards as the cuticle of zone 3 of the mouth. In this way the seed apices were encased like fingers in a glove. Additional support against shifting was in the flesh. At each side of the seeds ran a strand of narrow cells, perhaps a vascular strand, which would not allow shifting to the sides. Then each cell of the flesh was surrounded by branched sclereids, hence it can be assumed that even at an early stage the flesh was elastic and not a soft parenchymatous tissue which could be squeezed away by growing ovules. This elasticity and toughness of the flesh was enhanced by the network of vascular strands accompanied by sclereids.

S e e d d i s p e r s a l

Very little can yet be said about the seed dispersal. The previous authors expressed the view that the fruit had the consistence of a soft berry and was edible, so that the seeds were dispersed by animals. It appears from my sections that this berry contained a considerable amount of sclereids, which also occur recently in the flesh of wild fruits. The fleshy consistence of the fruit appears to be confirmed by the fact that both rounded and flattened, wrinkled fruits were found. The rounded ones were possibly not quite mature and had the fleshy cells still filled and firm. The wrinkled ones were possibly overmature fruits where the juicy contents had dried out.

On the other hand, it occurs to me that there was also the other possibility that the mature fruit may have opened and ejected the seeds. There are in the fruit both thick-walled tissues which could cause ten-

sions inside the fruit and thin-walled tissues likely to break as a result of such tensions. There are also the small very thin places in the epidermis where a tear could easily start. I would guess that the internal tensions and then the opening of the fruits may have occurred rather as a result of falling into water than of drying out. Probably observations of damaged fruits, of which a considerable amount occurs, would indicate whether there was indeed a mechanism opening the fruit and scattering the seeds. Unfortunately, I had dissected most of them in my material before I arrived at this question. At any rate, whatever was the mechanism of seed dispersal it appears to have been effective, because large amounts of detached seeds were found in the matrix in each of the localities where *Caytonia* occurs.

It appears to me that it was a different case with the pollination mechanism. The very special construction admitting the pollen-grains appears to have had two weak points. One was that the narrow canals admitting the pollen grains could be easily blocked if in the pollination drop a larger amount of foreign sporomorphs was caught, especially if they were large. The second weak point appears to be that only a small shifting of the position of the apices of the ovules would also block the passage of pollen grains. Perhaps this is why the *Caytoniales* did not survive, while the angiosperms, where there was a different constructional solution to the problem of pollination of enclosed ovules, developed so well.

SUMMARY

1. From the Jurassic of the Grojec area, Poland, are described compressions of *Caytonia harrisii* sp. n., *Caytonia sewardi*, *Sagenopteris colpodes*, and a microsporangium of *Caytonanthus* sp. with unripe pollen.

2. Sectioning and various methods of maceration reveal not only the cutinized layers but also the structure of most of the tissues of the fruit.

3. Sections prove the existence of canals through the mouth and show seed apices close to the openings of the canals, thus confirming the view of Harris (1940) as to the pollination mechanism of *Caytonia*.

4. The inner epidermis of the fruit which surrounds the packet of seeds is described.

5. The mouth is shown to be connected with the outer epidermis of the fruit by cutinized lateral extensions. The mouth also appears to be continuous with the inner epidermis of the fruit.

6. Tissues of uncertain function are described from the vicinity of the mouth.

7. The flesh of the fruit is described in detail.

8. The vascular system of the fruit and seed and the structure of tracheids are described for the first time.

9. In the seeds a layer apparently identical with the „spotted layer" is described.

10. The structure and position of the mouth, of the inner epidermis of the fruit, of the vascular system, and the arrangement of the seeds are discussed.

11. The probable functioning of the *Caytonia* fruit is discussed, in particular its pollination mechanism, the mechanism keeping the ovules opposite the openings of the canals of the mouth, and the seed dispersal mechanism.

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STRESZCZENIE

FLORA JURAJSKA Z GROJCA KOŁO KRAKOWA. CZĘŚĆ II. *CAYTONIALES* I BUDOWA ANATOMICZNA KAJTONII

Caytoniales są obficie reprezentowane we florach mezozoicznych północnej półkuli przez liście *Sagenopteris*, natomiast ich żeńskie organy rozmnażania, zwane *Caytonia*, i męskie, zwane *Caytonanthus*, są znajdowane rzadko. Raciborski (1894) opisał z Grojca dwa gatunki liści, a mianowicie *Sagenopteris phillipsi* Presl i *S. goeppertiana* Zigno, a w obecnej pracy opisano jeszcze *S. colpodes* Harris. Po raz pierwszy opisano również w tej pracy z Polski organy rozmnażania, a mianowicie *Caytonia harrisii* sp. n., *C. sewardi* Thomas i jedno mikrosporangium *Caytonanthus* sp. zawierające niedojrzałe ziarna pyłku.

Kajtonia jest pierzastym organem o długości kilku mm, zakończonym małymi woreczkami, które zawierają nasiona. Twór ten można nazwać owocolistkiem, a ponieważ woreczki przypominają jagody, nazywa się je „owocami" („fruits" angielskich autorów). Jest to jednak termin użyty popularnie i nieściśle, ponieważ woreczki te różnią się bardzo swą naturą od owoców *Angiospermae*, które powstają z jednej lub większej liczby zalążni (owocolistków).

Podobnie jak wszystkie dotąd znane okazy kajtonii, także owoce z Grojca są zachowane w stanie uwęglonym. Jednak Thomas (1925) i Harris (1933—1964) wykazali, że przy zastosowaniu odpowiednich sposobów maceracji i przekrojów mikrotomowych można było w owocach kajtonii z Yorkshire zaobserwować niektóre tkanki. Do owoców *C. harrisii* zastosowano kilka sposobów maceracji, które zostały szczegółowo opisane w osobnej publikacji (Reymanówna 1970), oraz wykonano ich przekroje mikrotomowe w trzech płaszczyznach, uzyskując z czterech (na 23 przekrojone owoce) preparaty z dość dobrze widoczną budową mikroskopową. Preparaty pozwoliły na szczegółowe opisanie budowy anatomicznej kajtonii, przy czym kilka tkanek opisano po raz pierwszy.

Najbardziej interesujące obserwacje dotyczą szczeliny („mouth") w owocu, mieszczącej się u jego podstawy. Okazało się, zgodnie z hipotezą Harrisa, że kanaliki, w które ta szczelina przechodzi, kończą się we wnętrzu owocu w bezpośrednim sąsiedztwie mikropyle nasion. Obserwacja ta zdaje się potwierdzać przypuszczenie Harrisa, że zapylanie zalążków odbywało się za pośrednictwem kropli płynu zwisającej u nasady przyszłego owocu, w którym to płynie pyłek dostawał się poprzez kanaliki szczeliny do mikropyle i komory pyłkowej zalążków. Wyjaśnia to ostatecznie mechanizm zapylenia kajtonii, który jest odrębny od mechanizmu zapylania u roślin okrytozalążkowych, ale też nie jest całkowicie typowy dla roślin nagozalążkowych.

Poza tym opisano po raz pierwszy w tej pracy skutynizowane połączenia szczeliny z zewnętrzną epidermą owocu, wewnętrzną epidermę owocu, tkanki o nieznanej funkcji występujące w sąsiedztwie szczeliny („mouth"), system wiązek przewodzących w owocu i nasieniu oraz budowę tracheid. Stwierdzono również nowe szczegóły dotyczące tkanek opisanych już przez innych autorów, głównie budowy miękiszu owocu i znajdujących się w nim sklereid, a także warstwy w nasieniu określonej przez Harrisa jako warstwa plamista („spotted layer").

W dyskusji dotyczącej opisowej części pracy stwierdzono, że występowanie w szczelinie kanalików kończących się w sąsiedztwie mikropyle nasion można uznać za nie budzące wątpliwości. Niemal pewne wydaje się, że wewnętrzna epiderma owocu oraz epidermy wyścielające szczelinę oraz jej połączenia z zewnętrzną epidermą owocu tworzą jedną całość.

Stwierdzono także, że warstwa opisana w obecnej pracy jako wewnętrzna epiderma owocu była już znana Thomasowi (1925), lecz autor ten uważał ją za zewnętrzną warstwę nasienia. W miękiszu owocu potwierdzono istnienie dużych komórek i zdecydowano się przyjąć ich dotychczasową interpretację jako komórek miękiszowych odpowiadających komórkom w miękiszu współczesnych jagód. Przy zastosowanych sposobach maceracji można stwierdzić w miękiszu występowanie wielkiej ilości rozgałęzionych sklereid.

Zaobserwowano również szczegóły, pozwalające na odtworzenie systemu wiązek przewodzących w owocu i nasionach. Składa się on w owocu z płaskiej, jak się wydaje, wiązki, wchodzącej przez trzonek owocu. Wiązka rozgałęzia się w zewnętrznej jego części w siatkę mniejszych wiązek, biegnących między komórkami miękiszu oraz wchodzących do nasion. Tak zachowujący się system wiązek w owocu jest podobny do systemu nerwów w każdym z czterech listków złożonego liścia *Sagenopteris*, posiadającym również jeden nerw główny i siatkę nerwów bocznych. Z elementów tworzących wiązki udało się zaobserwować jedynie tracheidy protoksylemu, opatrzone spiralnymi zgrubieniami, oraz tracheidy metaksylemu, posiadające na bocznych i poprzecznych ściankach okrągłe jamki lejkowate, ustawione naprzemianlegle. Występują także owalne jamki lejkowate, a niekiedy obserwuje się fragmenty tracheid sugerujące występowanie ustawionych drabinkowato jamek.

System wiązek w nasieniu składa się z wiązki wchodzącej przez hilum, która dzieli się na dwie gałęzie biegnące wzdłuż brzegów nasienia aż do jego szczytu. Tracheidy wiązek w nasionach są opatrzone zgrubieniami od drabinkowatych po siatkowate.

Poznanie budowy anatomicznej owocu kajtonii pozwala na wysnucie wniosków co do sposobu jego funkcjonowania. Trzeba podkreślić, że niemal kompletne zamknięcie zalążków wymagało nowych rozwiązań konstrukcyjnych, ażeby takie podstawowe procesy jak zapylanie zalążków i rozsiewanie nasion mogły się odbywać. Rozwiązaniem, które pozwalało na zapylenie zalążków u kajtonii, było powstanie szczeliny („mouth'), której kanaliki kończyły się w sąsiedztwie ujść mikropyle zalążków. To rozwiązanie konstrukcyjne, umożliwiające proces zapylania, jest zupełnie inne niż u *Angiospermae*, wydaje się jednak, że funkcjonowało ono mniej sprawnie i być może było to przyczyną wymarcia *Caytoniales*.

Gdy zastanawiamy się nad budową anatomiczną kajtonii, nasuwa się również przypuszczenie, że pewne tkanki owocu spełniały funkcję utrzymywania szczytu każdego zalążka w sąsiedztwie odpowiadającego mu kanalika szczeliny. Wydaje się, że funkcję tę spełniała przede wszystkim wewnętrzna epiderma owocu, która otaczała grupę nasion, oraz szczyt każdego z nich, a następnie, jak się wydaje, łączyła się z epidermami wyścielającymi szczelinę. Poza tym występowanie pomiędzy komórkami miękiszu owocu siatki wiązek i licznych sklereid sprawiało, że miękisz był tkanką mocną i sprężystą, co również utrudniało przemieszczanie się rozrastających się zalążków.

Poprzedni autorzy, omawiając rozsiewanie nasion zamkniętych w owocu, uważali, że ma on charakter jagody o jadalnym miękiszu, której nasiona były rozsiewane przez zwierzęta. Taka interpretacja jest również przyjęta w tej pracy. Niemniej obserwacja preparatów nasuwa myśl o innej jeszcze możliwości, a mianowicie, że dojrzały owoc pękał

wysypując nasiona. Na taką możliwość wskazuje obecność zarówno tkanek grubościennych mogących wywołać napięcie wewnątrz owocu, jak i obecność tkanek cienkościennych podatnych na rozerwanie. Przypuszczenie to wymaga jeszcze dalszych obserwacji uszkodzonych owoców. Wyniki badań przeprowadzonych nad anatomiczną budową „owocu" kajtonii raz jeszcze potwierdzają pogląd, że jest to twór specjalny, nie mający odpowiednika w żadnej grupie roślin.

Instytut Botaniki Polskiej Akademii Nauk w Krakowie
Zakład Paleobotaniki

Plate I

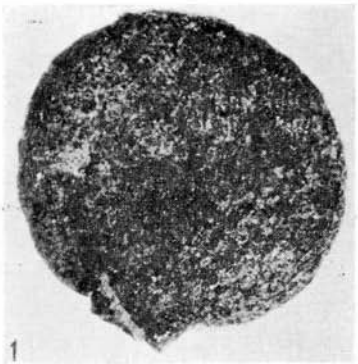
Caytonia harrisii sp. nov.

1. Holotype, S 315, ×15.
2. Small fruit, S 337, ×13
3. Fruit, S 316, ×15
4. Seed, S 317, ×20
5. Packet of seeds, S 376, × 20
6. Upper side of fruit showing network of protruding ridges, S 377, × 15
7. Small fruit, side view, S 378, ×20
8. Macerated small fruit showing mouth, S 310, × 10
9. Mouth separated from macerated fruit, showing fragments of zone 1, dark thickened zone 2, and thin zone 3 with dark bars representing canals. To the right — lateral extension connected with outer epidermis of fruit, S 379, ×50
10. Surface of seed showing longitudinal striation, S 317, × 150

Tablica I

Caytonia harrisii sp. nov.

1. Holotyp, S 315, × 15
2. Mały owoc, S 337, × 13
3. Owoc, S 316, × 15
4. Nasienie, S 317, × 20
5. Grupa nasion, S 376, × 20
6. Górna strona owocu z wystającą siatką, S 377, × 15
7. Mały owoc widziany z boku, S 378, × 20
8. Wymacerowany owoc, wewnątrz widoczna szczelina („mouth"), S 310, × 10
9. Szczelina wypreparowana z macerowanego owocu, widoczne fragmenty strefy 1, ciemna zgrubiała strefa 2 i cienka strefa 3 z ciemnymi pasami, przedstawiającymi kanaliki. Na prawo widoczne połączenia z zewnętrzną epidermą owocu, S 379, ×50
10. Powierzchnia nasienia z widocznym podłużnym prążkowaniem, S 317, ×150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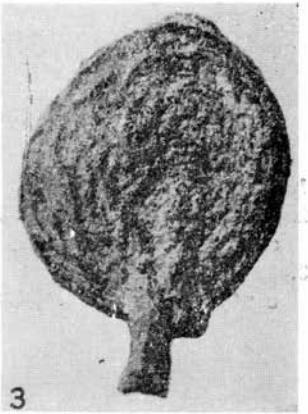
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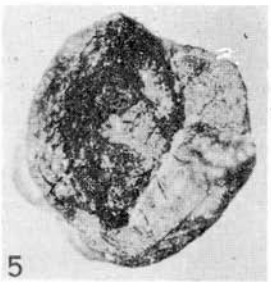
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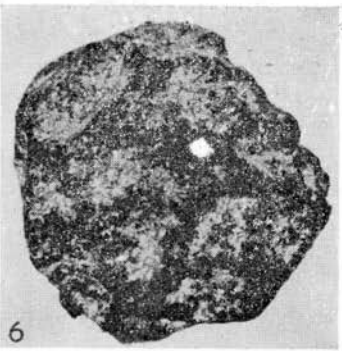
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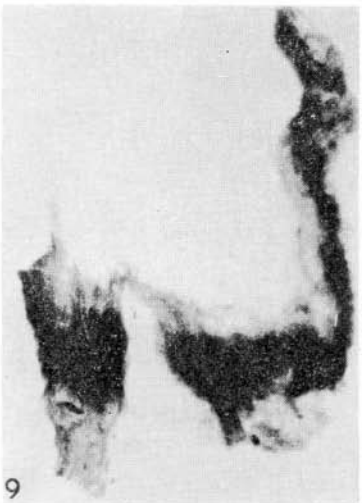
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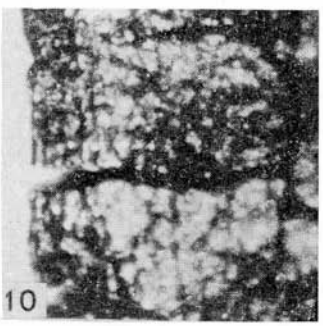
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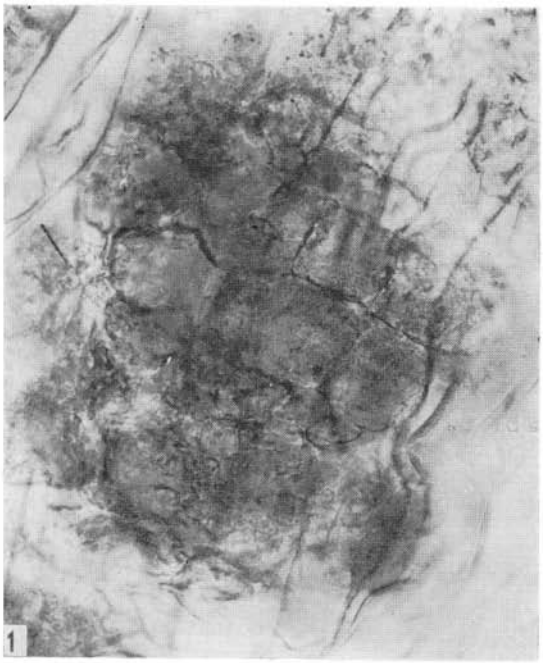
Plate II

1. *Caytonia harrisii* sp. n., cuticle of nucellus and aleurone cells, S 414, × 300
2. *Caytonia* cfr. *sewardi* Thomas, fragment of megasporophyll with one partly preserved fruit, S 332, × 10
3. *Caytonia harrisii* sp. n., apex of macerated seed showing elongated cells of micropylar canal, S 325, ×200

Tablica II

1. *Caytonia harrisii* sp. n., kutikula nucellusa i komórki z aleuronem, S 414, × 300
2. *Caytonia* cfr. *sewardi* Thomas, fragment owocolistka z częściowo zachowanym owocem, S 322, ×10
3. *Caytonia harrisii* sp. n., szczyt wymacerowanego nasienia z widocznymi wydłużonymi komórkami kanału mikropylarnego, S 325, × 200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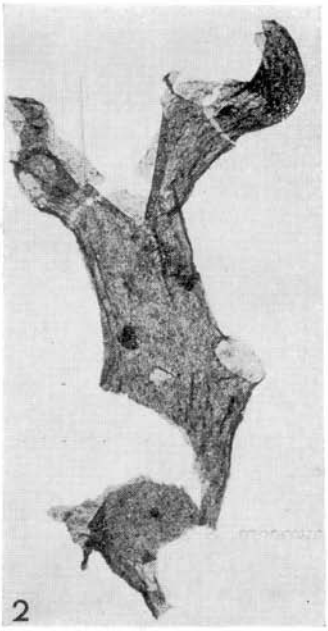
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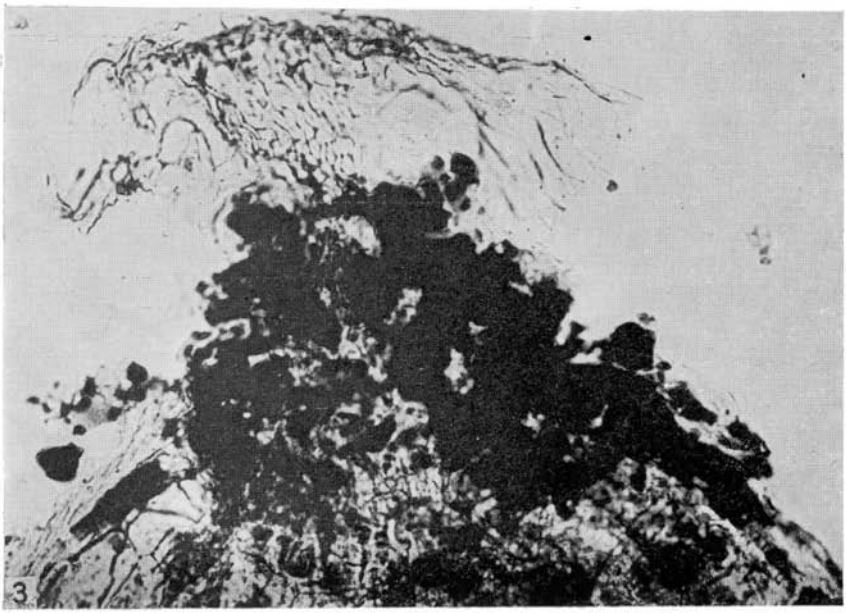
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Plate III

Caytonia sewardi Thomas

1. Damaged small fruit, macerated, S 415, × 50
2, 3. Seeds, truncate apex above, hilum below, S 319, × 20
4. Small fruit from below showing cutinised bars of lip and the pedicel, S 318, × 20
5. Fragment of fruit seen on fig. 1 showing lip projecting from the fruit wall and beneath the mouth with thickened bars (canals), S 415, × 120

Sagenopteris

6. *Sagenopteris* sp., petiole showing leaflet scars, S 330, × 10
7. *Sagenopteris colpodes* Harris, lower cuticle showing stomata, S 328, × 400

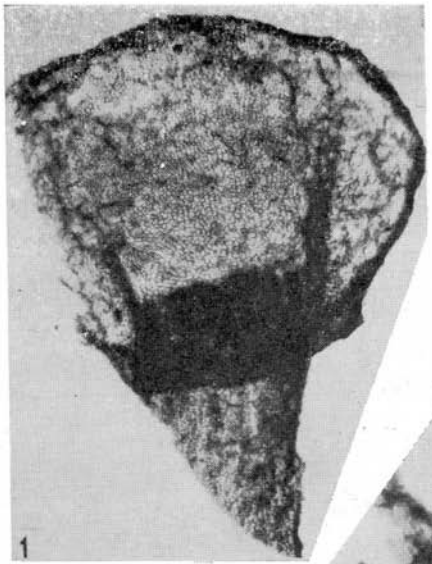
Tablica III

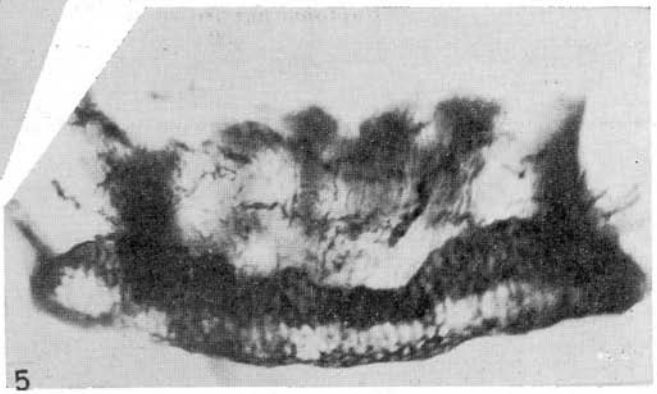
Caytonia sewardi Thomas

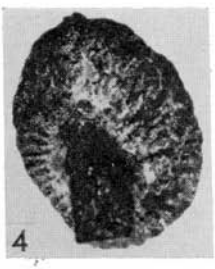
1. Uszkodzony mały owoc, macerowany, S 415, × 50
2, 3. Nasiona, tępo ucięty szczyt u góry, hilum u dołu, S 319, × 20
4. Mały owoc widziany od dołu, widoczne skutynizowane pasy fałdu i trzonek, S 318, × 20
5. Fragment owocu przedstawionego na fig. 1, widoczny fałd sterczący ponad ścianę owocu, poniżej jej widoczna szczelina z ciemnymi pasami (kanalikami), S 415, × 120

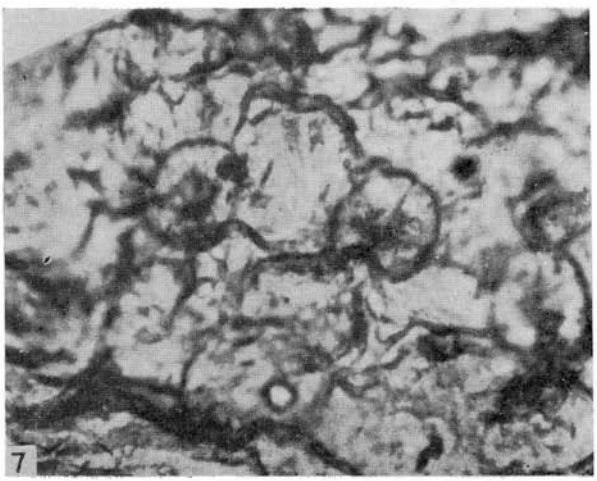
Sagenopteris

6. *Sagenopteris* sp., ogonek z widocznymi bliznami po odpadłych listkach, S 330, × 10
7. *Sagenopteris colpodes* Harris, dolna kutikula z aparatami szparkowymi, S 328, × 400









M. Reymanówna
Acta Palaeobotanica XIV/2

Plate IV

Caytonanthus sp.

1. Synangium, S 339, × 16
2. Pollen mass macerated from the broken end of the synangium, S 338, × 600
3, 4. Pollen grains macerated from the synangium, S 331, ×2000

Caytonia harrisii sp. n.

5. Longitudinal section through macerated small fruit showing epidermis, pedicel, mouth, and lip, XII/6, × 50
6. Section through epidermis and flesh showing network of vascular strands and a few sclereids; maceration with sodium hydroxide, XIII/12, × 300

Tablica IV

Caytonanthus sp.

1. Synangium, S 339, × 16
2. Masa pyłkowa wymacerowana z ułamanego końca tego synangium, S 338, × 600
3, 4. Ziarna pyłku wymacerowanego z tego synangium, S 331, × 2000

Caytonia harrisii sp. n.

5. Podłużny przekrój *Caytonia harrisii* sp. n. przez zmacerowany mały owoc, widoczna epiderma, trzonek, szczelina i fałd, XIII/6, × 50
6. Przekrój przez epidermę i miękisz, widoczna sieć wiązek przewodzących i kilka sklereid, maceracja wodorotlenkiem sodu, XIII/12, × 300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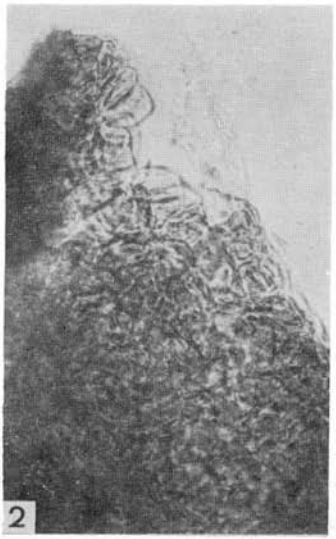
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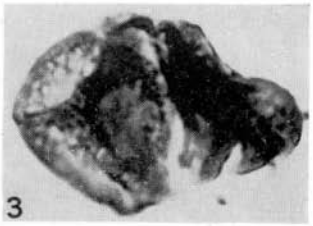
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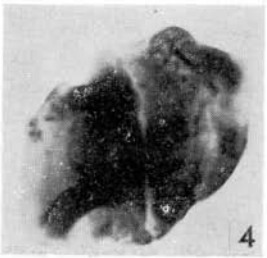
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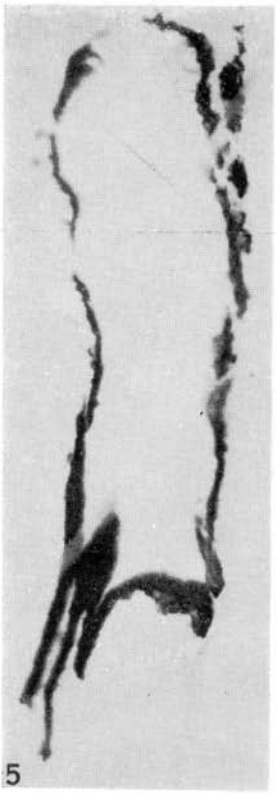
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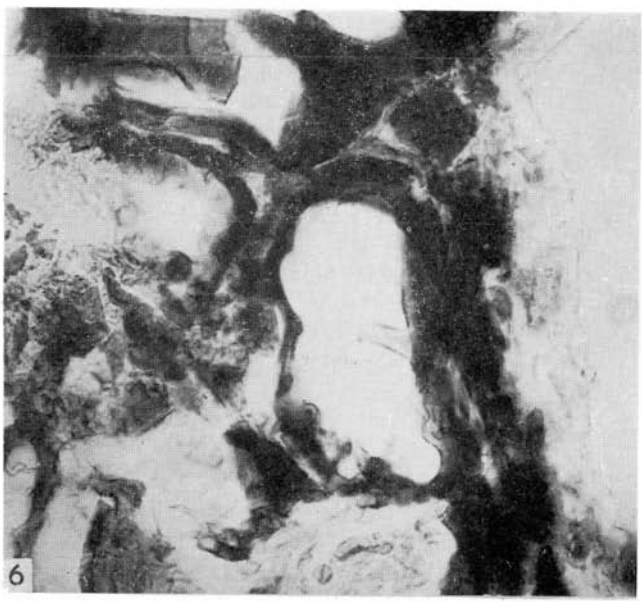
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Plate V

Caytonia harrisii sp. n.
sections macerated with sodium hydroxide

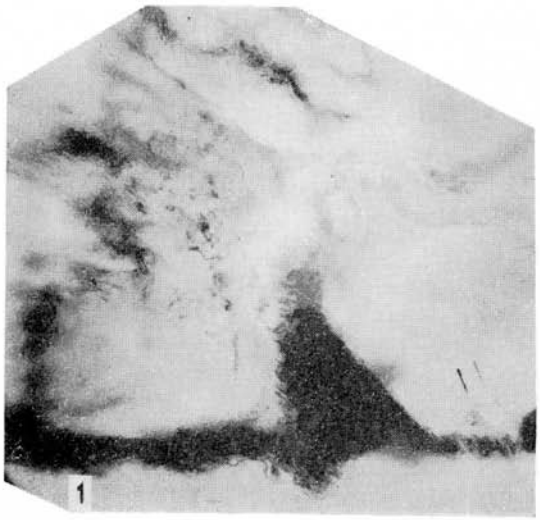
1. Longitudinal section of mouth near the fruit wall, XI/17, × 100
2. Longitudinal section through median part of mouth showing three zones, XI/22, × 100
3. Longitudinal section parallel to mouth going through its median part, XIII/14, × 100
4. Longitudinal section parallel to mouth going through its peripheral part, XIII/10, × 100

Tablica V

Caytonia harrisii sp. n.
przekroje macerowane wodorotlenkiem sodu

1. Podłużny przekrój szczeliny w pobliżu ściany owocu, XI/17, × 100
2. Podłużny przekrój przez środkową część szczeliny, widoczne trzy strefy, XI/22, × 100
3. Podłużny przekrój równoległy do płaszczyzny szczeliny przechodzący przez jej środek, XIII/14, × 100
4. Podłużny przekrój równoległy do płaszczyzny szczeliny przechodzący przez jej peryferie, XIII/10, × 100

Plate V
Tablica V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