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STUDIES ON PSARONIACEAE. II. TUVICHAPTERIS SOLMSI NOV. GEN. ET SP. FROM THE PERMIAN OF PARAGUAY AND URUGUAY.

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RESUMEN. Se describe un nuevo género y especie de una Psaroniaceae del Pérmico Superior de Paraguay y Uruguay.
Tuvichapteris nov. gen. tiene afinidades y diferencias con Tietea y Psaronius que se discuten en detalle, particularmente las tendencias de ciclicidad (o su ausencia) en las meristelas del estípite y la estructura mono- o polimeristélica de las trazas foliares y pecíolos.

INTRODUCTION

In the first contribution of this series (Herbst, 1986) I had redefined and diagnosticated the scope of the Family Psaroniaceae, based on anatomically preserved materials only. In that paper, the genus *Tietea* Solms-Laubach was restudied and included in this Family. All known specimens of *Tietea* come from the Permian of different localities in Brazil.

In this paper I will describe a new and rather big type of stem which can also be included in this Family. This time the specimens are mainly from Paraguay and a few come from Uruguay.

Some specimens show minute and delicate histological details which permit a fairly good description and, as will be shown, they are somewhat different from those of other known genera; this fact obliged to erect a new genus.

These new materials not only improve our knowledge of the Family but probably will also allow some speculations on the origin and evolution of the Gondwanic Marattiales; this subject, however, will not be treated in this paper as such an analysis should also include fronds and fructifications.

The only former mention of plants of this kind in our region belongs to Herbst (1975) who described a few, rather fragmentary, specimens under the names "Filice psaroniaceae 1" and "Filice psaroniaceae 2". Due to the scarcity of materials and its fragmentary condition it is impossible to ascertain wether they belong to the new genus *Tuvichapteris*, but this is quite possible.

MATERIALS AND METHODS

All the specimens studied are permineralized (silicified) with most of their anatomical structures well preserved. Due to the big size of the specimens (diameters of more than 35 cm) most of them were studied on polished surfaces, under stereoscopes. The peel method was tried but in general did not provide good results. Some smaller specimens were even studied under the optical microscope (with the platina removed) on polished surfaces. A few thin sections were also prepared. Photographs on these polished surfaces, with strong incident light, resulted the best.

Observation and photos were enhanced by differential natural colouring of some of the tissues, both cell-walls and their contents. Some tissues, when occasionally replaced only by silica, retain these dominant colours and facilitate interpretation even when cells are not easily distinguished.

GEOLOGY

Stratigraphically the specimens from Paraguay belong to the "sandy section" which Herbst & Leguizamón (1984) considered the base of the Upper Section of the Independencia Formation. This Section begins a few meters above the sediments that contain a typical "*Pinzonella neotropica* fauna" (*sensu* Runnegar & Newell, 1971) of Upper Permian age. Based on a somewhat different stratigraphic scheme Jalfin (1986) thinks that this Section should be considered a separate unit -Tapytá Formation- using this name as already applied in the Geological Map of Paraguay ellaborated by the Anschutz Co. (not publised yet). Environmentally, Jalfin & Herbst (1984) think that this sandy Section or Formation represents the fluviatile facies which follows the filling of the paleo-lake represented by the Lower Section (Tacuary Formation in the Anschutz nomenclature); these sandstones include channel deposits which contain the fossil logs (not only ferns but also gimnospermous wood not studied yet) as well as flood plain deposits. The complete sequence can thus be defined as a lacustrine-fluviatile cycle of continental (fresh-water) origin (Jalfin & Herbst, op. cit.).

The Independencia Formation as a whole has been correlated, based on its *Pinzonella* fauna and its plants (Herbst, 1981a, 1981b; Herbst & Leguizamón, 1984) with the Terezina Formation of the Estrada Nova Group (which some authors consider merely as Terezina Member of the Estrada Nova Formation) from Brazil. Its age in that

country has been established as Upper Permian (Kazanian to Lower Tatarian).

The specimens from Uruguay have been collected in the Yaguarí Formation. This unit has also been divided in two (sometimes in three) Sections, which in the latest papers (Herbst & Ferrando, 1985 for example) have been compared with the Caveira (Lower) and Armada (Upper) Members of the Estrada Nova Formation from southern Brazil. The fossil ferns were collected in the upper part of the Lower Section (equivalent to the Caveira Member), which bears a typical *Pinzonella neotropica* fauna which is being studied at present (Herbst, Morton & Ferrando, 1986, in preparation). The Yaguarí Formation overlies the Melo Formation, which has recently yielded a *Glossopteris* florule which has been dated as Kungurian-Kazanian (Herbst, Ferrando & Jalfin, 1986). This leaves the Kazanian-Tatarian interval for the Yaguarí Formation which is totally concordant with the stratigraphical position and age as correlated with the Paraguayan sediments.

SISTEMATIC DESCRIPTION

Class	:	Filicophyta (or Filicophytina)
Order	:	Marattiales
Family	:	Psaroniaceae (Unger) Herbst, 1986
Genus	:	*Tuvichapteris* nov. gen.

Diagnosis: arborescent stems of big size, general transversal outline oval-auriculate, with 6 auricles corresponding to interpetiole areas. Known specimens up to 35 x 30 cm in diameter. The stem is limited by a continuous sclerenchymatic ring, only interrupted at leaf-trace emission areas. Externally it is surrounded by a thick and dense root-mantle

Internally the stem consists of a great number of amfiphloi meristeles, of variable shape in transversal section, from almost circular and oval to complex C-shapes. No cyclic or other sort of organization is apparent. Meristeles are immersed in an homogeneous ground parenchyma.

Each meristele is composed of a mass of metaxylem, surrounded by phloem and pericycle (?), followed by a few rows of parenchyma which in turn are enclosed in a thick sclerenchymatic sheath. Protoxylem groups are endarch and numerous; each group is composed by a few small cells.

The root-mantle is undifferentiated Roots are polyarch (4-7

actinostelic), immersed in a "filamentous" -with radially aligned cells- root parenchyma.

There are six leaf-traces per transversal section, separated by the "auricle" bulges, which contain only stem meristeles. Each leaf-trace is composed by a variable number of small, rounded meristeles, which more outwards, at the petiole stage, is accompanied by a thick mass of "petiole parenchyma" with cells with more or less thickened walls.

Leaf-trace emission occurs by a gradual splitting of the sclerenchyma stem ring, which allows the exit of the meristeles; this is followed by an almost inmediate closing of the gap by sclerenchyma strips coming either from more inwardlly formed ones or laterally ones formed in the "auricles".The sequence of the leaf-trace emission could not be clearly established yet.

Type-species: *Tuvichapteris solmsi* nov.sp. (this paper)

Derivatio nominis: from the words *tuvichá*, meaning *big*, in one of its acceptions, in guaraní[1], and *pteris*, meaning fern in greek.

Discussion: a general discussion will be made following the species description.

Tuvichapteris solmsi nov. sp.

Figs. 1-18

Diagnosis: the same as the generic one. Specific details and histological description are given below.

Holotype: CTES-PB N°6668

Locality: Zona Cantera Cachimbo, Depto. Caaguazú, Paraguay.

Horizon: Independencia Formation; Age: Upper Permian

Derivatio nominis: dedicated to the memory of Hermann Count zu Solms-Laubach, an eminent german botanist and paleobotanist (1842-1915).

Additional material: CTES-PB N°6669 to 6672 from the same locality, horizon and age as the holotype;

CTES-PB N°6673 from A° Tacuara, Depto. Guairá, Paraguay; horizon and age, same as holotype;

CTES-PB N°6674 from ruta N°21, 16 km NW of Vichadero, Depto. Cerro Largo, Uruguay; horizon: Yaguarí Formation; age: Upper Permian

(1) Guaraní is an aboriginal language of South America, at present spoken by more than four million people in Paraguay, Brazil, Bolivia and Northeastern Argentina; it is also the second official language in Paraguay.

CTES-PB N°6675 from the road between Melo and Frayle Muerto, Depto. Cerro Largo, Uruguay; horizon and age, same as N°6674.

General Description

A) Stem: the stem is oval-auriculate in transversal outline as shown in Figs. 1-2 and pl. I Figs. 8-9; small specimens measure 18 x 10 cm long/short axes, while the biggest known (the holotype) is up to 35 x 30 cm. The holotype consists of 5 pieces with 2,10 m of total lenght (pl. I Fig. 7). The here called "auricles" as seen in transversal section, correspond to longitudinal bulges which contain complex-shaped meristeles. They stand out in contrast to the leaf-trace emission areas, but they also probably served as additional strenghtening "columns" for these big upright trees.

The external boundary of the stem is a more or less continuous sclerenchyma ring or band, in parts rather thick (up to 5 mm which means about 100 rows of cells) and only temporarily absent when and where the leaf-traces are emitted (see below, and Figs. 1-3). Internally the stem consists of an homogeneous mass of parenchyma in which the meristeles are immersed. Scattered in this ground-parenchyma gum-ducts (?) or nests of some kind, are frequently found (pl. I Fig. 10).

Individual meristeles are of variable size and shape. Although there is no apparent organization in cycles or other, as occurs in almost all species of *Psaronius* and still feebly in *Tietea*, two sorts of meristeles can be distinguished towards the outer (more external) portion of the stem: a) stem meristeles (or caulinar meristeles) located mainly in the "auricles", which are generally bigger and more complex C-shaped, or at least more or less tabular, and b) leaf-trace meristeles which are smaller and generally rounded to oval in their transversal outline. No histological distinction exists between these two types, and as there is no apparent organization in the inner part of the stem, there is no way to decide which of the inner is to be destined to one or other type of meristele. It is further assumed, although this has not been clearly seen, that the stem meristeles give rise to the roots. Each meristele is constructed as described in the diagnosis. A sketch is shown in Fig. 4.

B) Root-mantle: as in other genera of the Psaroniaceae the root-mantle consists of a thick layer of individual roots, immersed in a typical filamentous -with radially aligned

cells- root-parenchyma. No differentiation of inner and/or outer root-mantle could be detected in *Tuvichapteris*.

Individual roots are generally oval in transversal outline, but sometimes they appear tangentially compressed (although the cells do not show signs of post-mortem compression) as shown in Pl. I fig. 11. Roots are typically psaroniaceaous, that is, with a central metaxylematic actinostele (with a 4 to 7 pointed star), with protoxylematic groups at their tips, surrounded by a small amount of root-parenchyma (the root cortex) and the whole enclosed in a thick sclerenchyma sheath (Pl. II fig. 15). As shown in Pl. I fig. 11 (arrow) the sclerenchyma sheath presents apertures or interruptions through which the ground root-mantle parenchyma and the intra-root ones are connected (the latter giving rise to the former?).

C) Leaf-traces and petioles: they are polymeristelic, composed of a variable number of rounded to oval, sometimes elongated, meristeles which are produced by the division of more complex ones, these being tabular to C-shaped and located a little more inwardly in the stem. The leaf-trace meristeles "travel" outwards (on their way up) through a gap in the sclerenchyma ring, as shown in fig. 3, where also the closing of this gap, through strips of sclerenchyma originated in the stem (centrally to the gap or laterally from the "auricles") is shown. When already out of the stem, these meristeles constitute the petiole strands, and are here accompanied by a big mass, irregularly shaped, of "petiole-parenchyma", which probably serves to strenghten the future rachis. Although this tissue has thickened cell-walls, at this stage it is not yet a typical sclerenchymatic tissue; thus, the denomination of "petiole-parenchyma" is used here.

D) Histology

-Xylem: metaxylem cells of the meristeles are more or less isodiametric to slightly elongated in transversal section, from 85 x 115 mμ to 170 x 215 mμ in diameter (Pl. I fig. 12; Pl. II fig. 16-17). Seen in longitudinal section, they are not too long, about 500-600 mμ and have typical scalariform thickenings. In those parts where a meristele is about to be divided or separated, cells become more or less compressed and adopt triangular to poliedric outlines (Pl. I fig. 13; Pl. II fig. 14).

Protoxylem cells are much smaller, with much thinner walls, and average between 28 and 42 mμ in diameter.

-Phloem: this tissue is constituted by 1 to 3 layers of rounded to tangentially elongated, thin-walled cells, surrounding the xylem (fig. 4; Pl. I fig. 12; Pl. II Figs. 16-17). Average size of these cells is 28-35 mμ.

-Pericycle: one (or two ?) rows of tangentially elongated cells, are interpreted as being a possible pericycle, but it cannot be definitively ascertained. In transversal section they measure about 25-30 x 85-90 mμ (fig. 9; Pl. II figs. 16-17).

-Parenchyma: both ground stem and meristele parenchymas are alike. Cells are more or less isodiametric in all directions, variable in size: meristele cells are slightly bigger (115 to 170 mμ in diameter) while ground parenchyma cells are about 85 to 120 mμ in diameter. Inner root parenchyma (root-cortex) are close in size to those of the stem. Root-mantle parenchymatic cells are shortly tabular, radially elongated, giving a "filamentous" aspect (fig. 5 lower; Pl. II fig. 18); in transversal section cells are about 55-70 mu x 200-240 mμ.

-Sclerenchyma: sclerenchyma fibers are elongated longitudinally, up to 400 mμ long, isodiametric in transversal section, from 35 to 85 mμ in diameter. They have strongly thickened walls (fig. 4-5;Pl. II fig. 15, fig. 17 lower right) and are closely and densely packed, thus many times attaining a poliedric outline. The sclerenchymatic tissue has the same characteristics in all parts of the plant, that is in the meristele and root sheaths as well as the external stem ring or band.

DISCUSSION

The general structure of *Tuvichapteris* which can sinthetically be characterized as a "...stem composed of a great number of disorderly arranged meristeles, limited by a sclerenchymatic ring and surrounded by a thick root-mantle" brings it close to the Psaroniaceae and allies it with genera like *Psaronius* and *Tietea*. Notwithstanding, there are several differences which justify a generic distinction.

It is characteristic of *Psaronius* to have a regular, cyclic organization of (mainly) tabular meristeles. Where known, this genus has monomeristelic leaf-traces and petioles. Both characters are rather different in *Tuvichapteris*. *Tietea* is close to the latter in the general appearance of the meristeles but retains a certain degree of cyclicyty in its outer cycles. The general morpholo

gy of the leaf-traces and petioles of *Tietea* is more or less similar to that of *Tuvichapteris* but the latter is characterized by its "petiole-parenchyma" which is absent in *Tietea*. Additionally, the number of ortostichies of the only known species of *Tietea* is 4, while it is 6 in the only known species of *Tuvichapteris*. Finally, there are also important differences in the leaf-trace emission sequence in the three genera.

The summ and magnitude of these differences cannot be considered of specific value alone and therefore the new species should not be included either in *Tietea* or *Psaronius*. There are, on the other hand, additional and more subtile differences, which of course have only specific value. These correspond to the histological characters and the structure of the tissues.

The general structure and organization of the different parts of these plants is remarkably similar. The meristeles, for example, of the three genera are constructed in almost the same way, as is the outer sclerenchyma band or ring. It is also worthwhile to mention here the great resemblance among the roots and root-mantles of the genera of the Psaroniaceae, which are even very close to the extant Marattiales. They are all build in the same way, i.e., polyarch, sclerenchyma ensheathet roots, rather variable in details in the same specimen. Several authors have since long carefully described these roots and if true that in some cases specificic distinctions can be made, their structure is so similar that, when only roots are available for study, it becomes extremely difficult to define species. More so to distinguish genera having -at least now in South America- three of them to choose among. Specific and/or generic assignments based on roots only should therefore be discouraged.

A few words can still be said when the three South American genera are compared. There are two important characters (fig. 6) which show definite trends but at the present state of knowledge it is impossible to decide which is their direction, as both could be considered as evolving in either way and still be valid as evolutionary facts. One of them is the cyclicyty of the meristeles, which is well established in *Psaronius*, not only in *P. brasiliensis-P. arrojadoi* from S. America, but also for most (if not all) species from elsewhere; there is an intermediate stage in *Tietea* where only the outer cycles are still feebly visible, and a *Tuvichapteris*-stage where no organization at all seems to be the structure. Only the fact that there exist Upper Carboniferous and Lower

Permian species of *Psaronius* would tend to indicate that this could be a more primitive stage. Otherwise one could find enough solid arguments to support the contrary trend, that is, from non organized meristeles to a well established cyclic arrangement.

The other character is the monomeristelic (*Psaronius*) to the polymeristelic (*Tietea* and *Tuvichapteris*) leaf-trace organization. Here again the only argument for one position could be the greater antiquity of *Psaronius*, because good and solid arguments can be found (and they exist) to support the contrary view.

These two important evolutionary trends will have to be taken in account when future speculations are made, together with frond organization and fructification structure, in regard to the marattialean evolution.

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EXPLANATION OF FIGURES AND PLATES

FIGURES

1) and 2): Sketches of transversal sections of the stem showing general outline, the leaf-trace (t), inter leaf-trace or "auricles" (a) and the petiole parenchyma (pp) (heavily stippled). 1) section of holotype N°6668; 2) specimen N°6669.

3): Stages of leaf-trace emission: A: sclerenchyma ring is still closed; B to D: the opening and outward going of meristeles is shown; E: the closing of the gap is taking place; F: the gap is closed again (stage A). Heavy stippling is petiole parenchyma.

4): Sketch of the tissular structure of a meristele. x = metaxylem; ph = phloem; pc = pericycle; pq = parenchyma; scl = sclerenchyma.

5): Sketch showing the differences of ground and root parenchymas, at the area in contact with the sclerenchyma ring of the stem.

6): Sketches of the three genera showing the cyclicyty of the meristeles and the structure of the petioles (while close to stem).

PLATES

Plate I

Fig. 7): Aspect of the holotype, measuring 2,10 m. The arrow marks the slice of the surface shown in text-fig. 1; the piece marked A was cut into several slices of unequal thickness. The rod measures 1 m.

Fig. 8): Transversal section of specimen N°6669 (see text-fig.2); aprox. x 0,4.

Fig. 9): Transversal section of another slice of the holotype; aprox. x 0,18.

Fig. 10): Gum-duct or nest in ground parenchyma; note the alignment of bordering cells; aprox. x 110.

Fig. 11): Part of a root-sclerenchyma sheath; arrow denotes radial direction. Note that parenchyma cells are not tangentially compressed.

Fig. 12): Metaxylem (left) surrounded by phloem and pericycle(?) followed by meristele parenchyma (see text-fig. 4); aprox. x 90.

Fig. 13): Compressed xylem cells close to a dividing (or about to divide) place of a meristele; aprox. x 100.

Plate II

Fig. 14): Same legend as fig. 13; aprox. x 120.

Fig. 15): Portion of the sclerenchyma from the external (stem) ring; aprox. x 150.

Fig. 16) and 17): Same legend as fig. 12; fig. 16 aprox. x 70; fig. 17 aprox. x 180.

Fig. 18): Root parenchyma showing radially aligned cells (see also text-fig. 5); aprox. x 75.

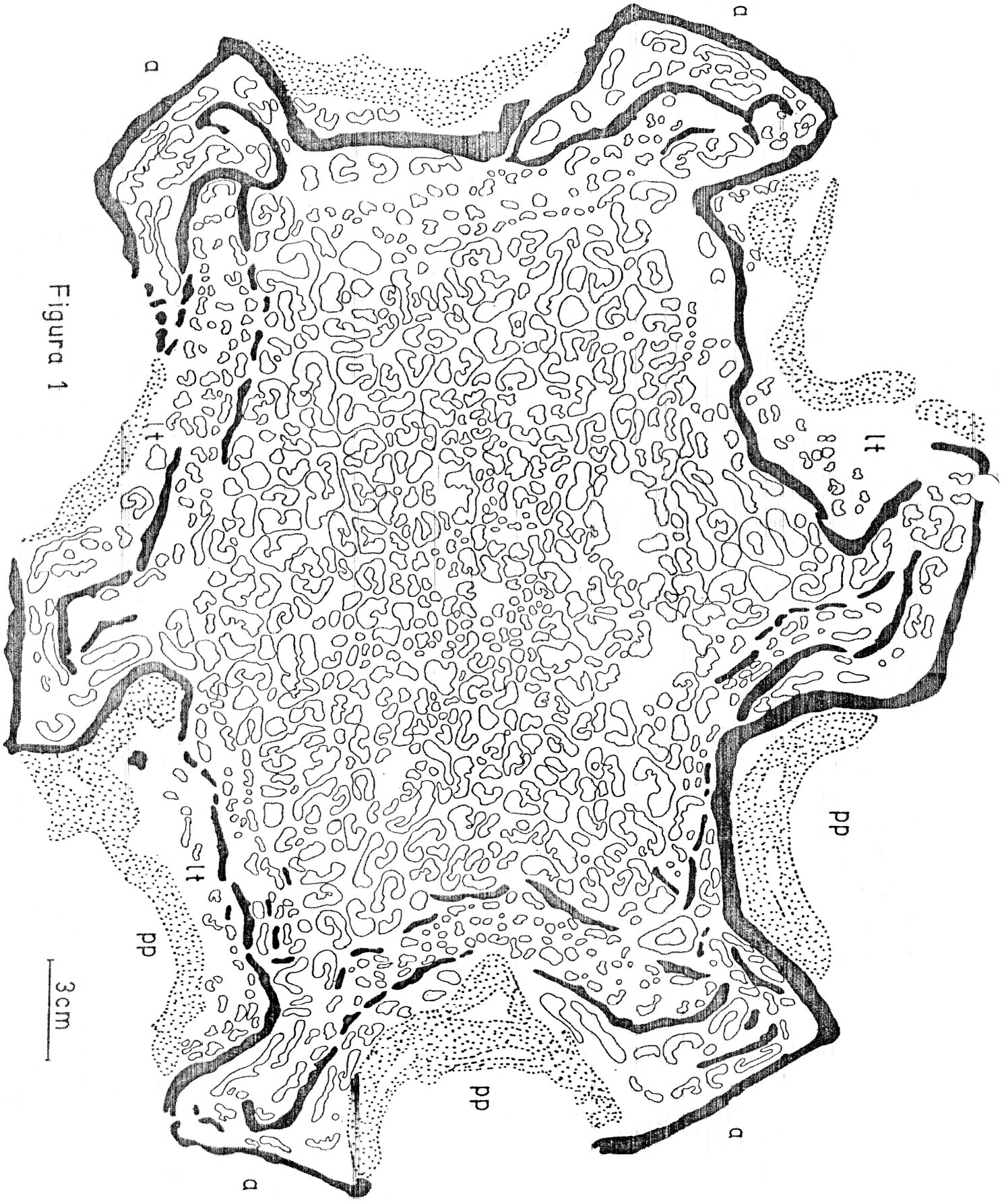
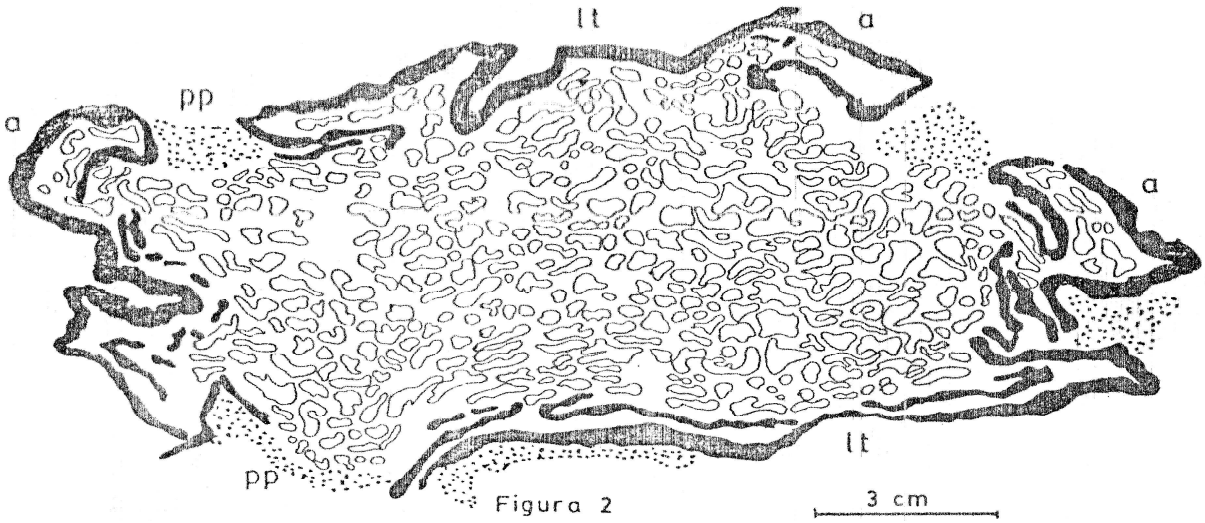


Figura 1



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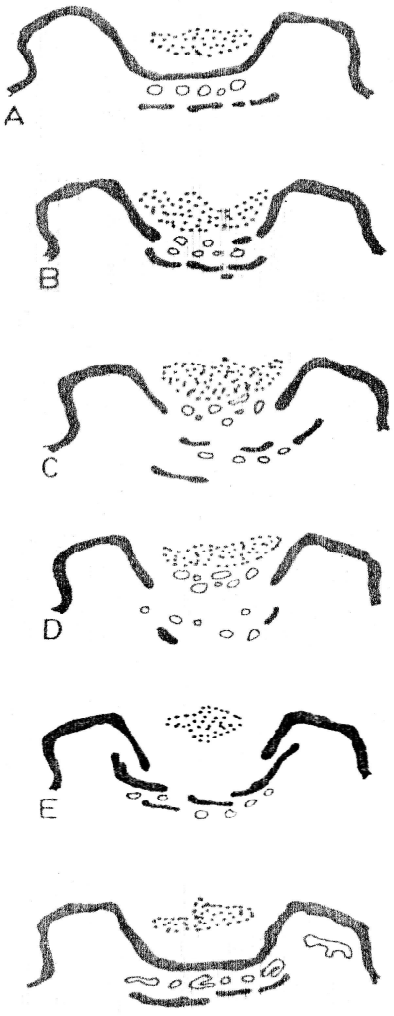

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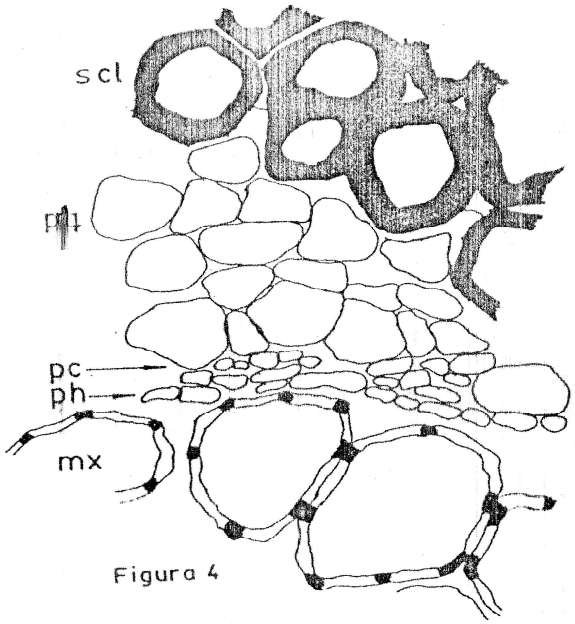

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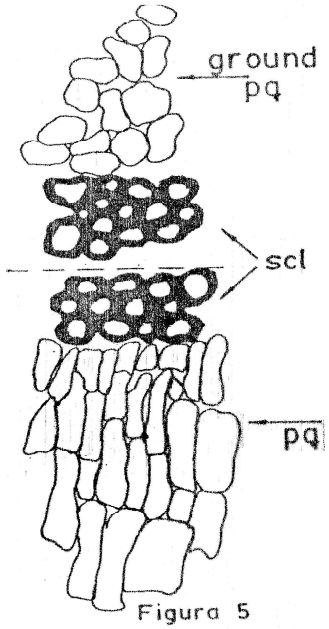

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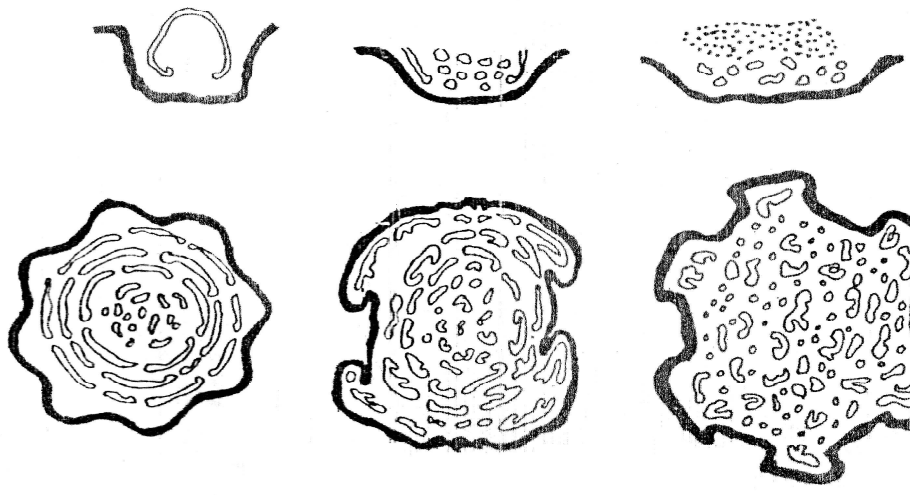

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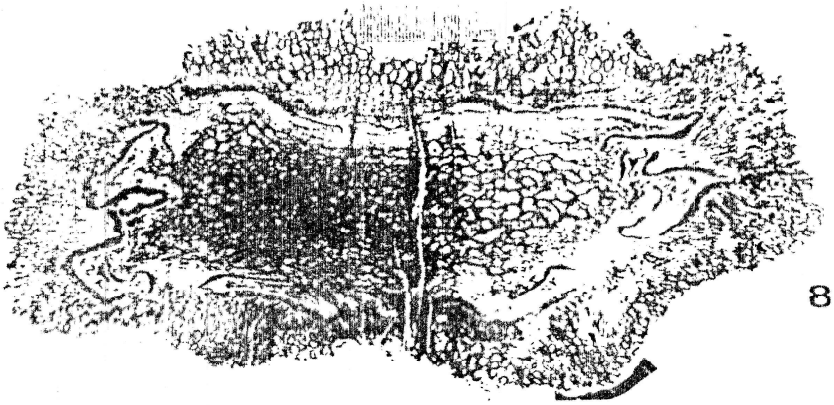

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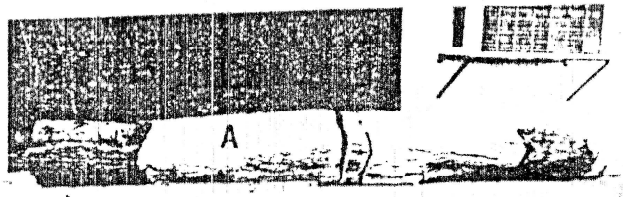

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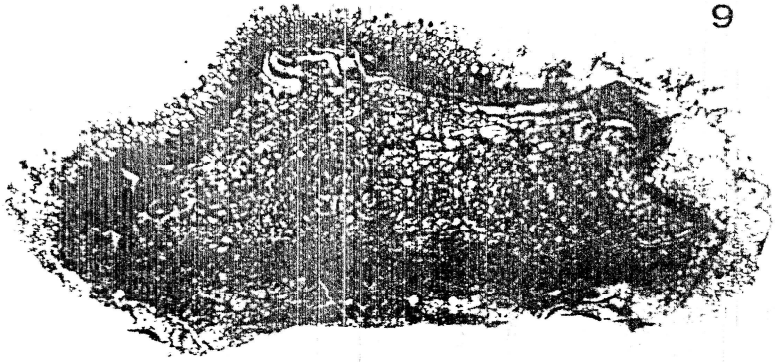

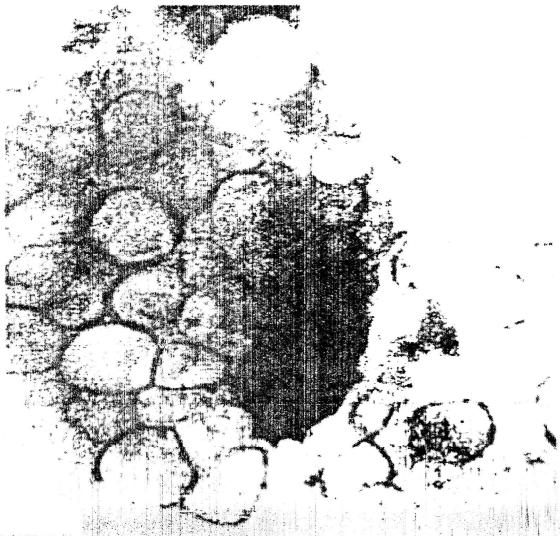

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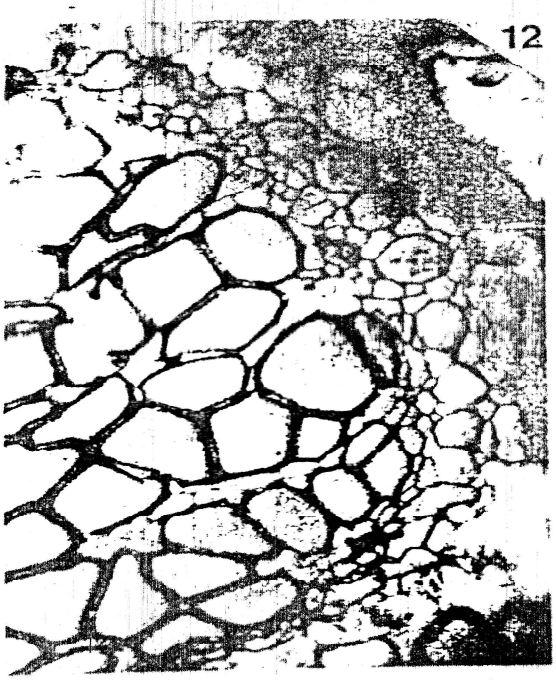

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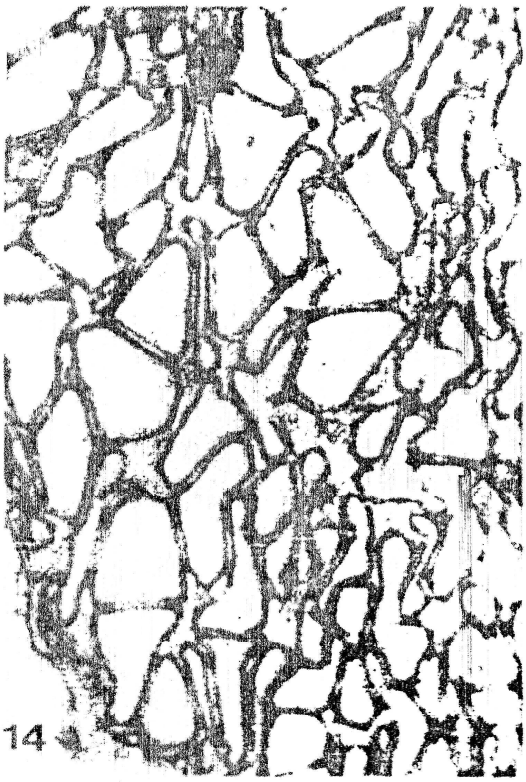

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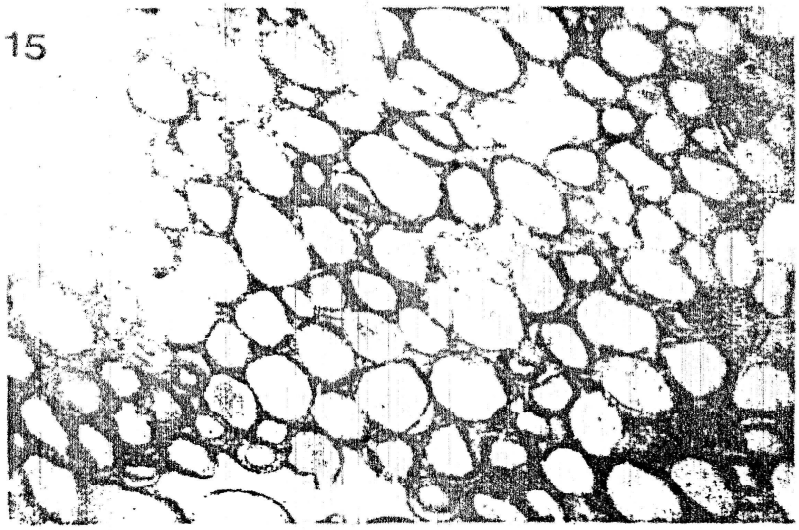

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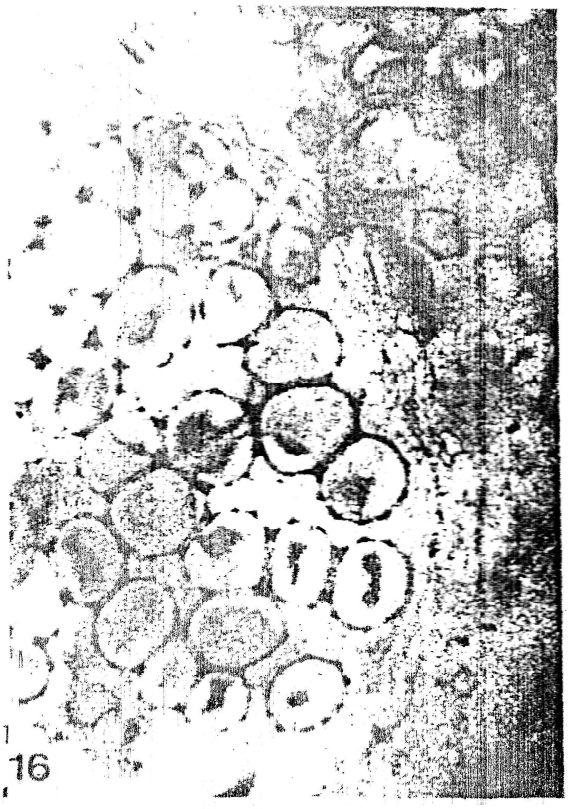

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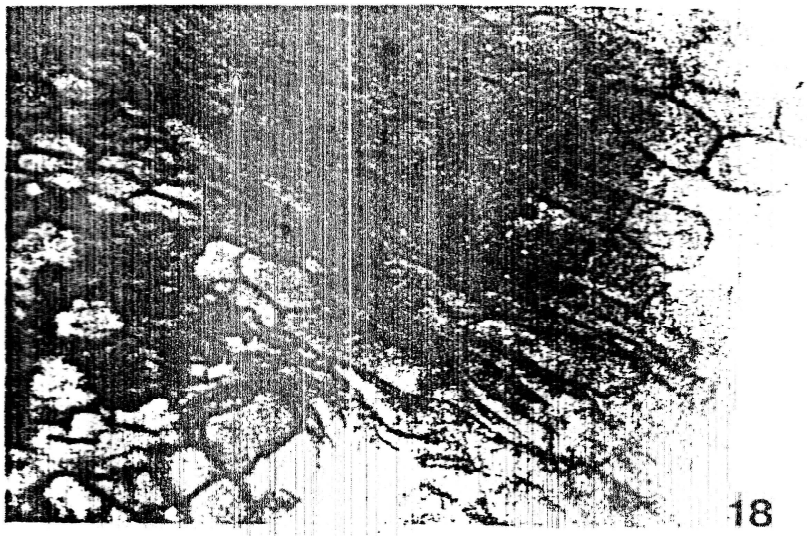

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