

# DIRHOPALOSTACHYACEAE - A NEW FAMILY OF PROANGIOSPERMS AND ITS BEARING ON THE PROBLEM OF ANGIOSPERM ANCESTRY

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With 5 Plates and 2 Figures in the Text

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## Abstract

A new family, Dirhopalostachyaceae, of Late Jurassic — Early Cretaceous age is based on the organ-genus *Dirhopalostachys* PRYNADA (MS) gen. nov. which includes the racemose ovuliferous fructifications (gynoclads) bearing paired monospermic capsules provided with a beak, and dehiscent along the ventral suture. These fructifications are attributed to the same plant as *Nilssonia schmidtii* (HEER) SEW. leaves and probably evolved from the mid-Jurassic *Beania*. The Dirhopalostachyaceae together with Caytoniales and Czekanowskiales belong to a proangiosperm group comprising plants of various lineages which underwent angiospermization, i.e. developed seed-bearing capsules with pollen-catching devices.

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## Introduction

Major contributions of palaeobotany to the problem of angiosperm evolution have been the discoveries of extinct plants which may be viewed as the links between gymnosperms and angiosperms. The first of these discoveries was made 50 years ago when H. H. THOMAS (1925) published his account of the Caytoniales. These Jurassic plants were believed to be if not the immediate predecessors of flowering plants then at least the nearst allies of their ancestral stock. The second discovery was that of the Czekanowskiales (HARRIS, 1951; KRASSILOV, 1968, etc.) — another group of Mesozoic plants bearing nearly the same relation to the angiosperms as the Caytoniales but not closely allied to the latter. The list of alleged ancestors is augmented now by a third Mesozoic group — the Dirhopalostachyaceae linking the mid-Jurassic cycad-like plants with primitive angiosperms.

Thus we have at least three documented lines leading to the angiosperm grade. This process of parallel acquisition of angiospermous characters in different lineages during the latter half of the Mesozoic era I term the angiospermization by analogy with "arthropodization" of MANTON (1973) or "homini- zation" of HEBERER (1956). These terms suggest similarity of evolutionary processes by which the taxa as different as angiosperms, arthropods and *Homo* have originated. The angiospermization progressed through the proangiosperm grade to the genuine angiosperms.

## Material and Methods

*Dirhopalostachys*, the type-genus of the new family Dirhopalostachyaceae, was established by late Dr. V. D. PRYNADA in his unpublished work on the Mesozoic flora of Bureja basin. His material was collected mainly from the outcrops at the right bank of the Bureja River and on the slopes of Urgal valley. This collection is now in the Central Geological Museum, Leningrad. PRYNADA described ovuliferous trusses (gynoclads: see explanation of this term in MELVILLE, 1960; MEEUSE, 1963, etc.) of *Dirhopalostachys* as strobili consisting of an axis and spirally attached bracts. True nature of the gynoclad lateral branches was not recognized. VASSILEVSKAJA & PAVLOV (1963, Pl. 49, fig. 4) figured rather completely preserved specimen from the Lower Cretaceous of Lena basin under the name *Dirhopalostachys* sp. It certainly belongs to the same genus as the Bureja gynoclads.

My collection of *Dirhopalostachys* came from the Late Jurassic — Early Cretaceous deposits of the upper reaches of the Bureja River (tributary of the Amur, Far East). They are rather frequent fossils in the Talynjan, Dublican, and Soloni Formations of respectively Callovian — Oxfordian, Tithonian — Berriasian, and Valanginian age (see KRASSILOV, 1973a). In the deltaic beds of the Talynjan Formation cropping out on the right bank of the Bureja River near the mouth of its tributary, the Umalta River there are two horizons with gynoclads. The lower horizon (locality 514) consists of tuffites and tuffaceous siltstones resting immediately above the marine sandstones with the cephalopod *Arctocephalites* of Bathian age. This locality yielded the most favourably preserved gynoclad compressions. Other plant fossils are ferns (*Osmunda*, *Conio- pteris*) and gymnosperms *Nilssonia schmidtii* (HEER) SEW., *Heilungia amurensis* PRYN., *Pseudotorellia pulchella* (HEER) VASSIL., *Pityophyllum* sp., *Pityospermum* sp., *Podozamites* sp. This horizon is overlain by coal-bearing sandstones and shales with *Czekanowskia* and taxodiaceous conifer *Elatides*. They grade upwards into the second *Dirhopalostachys* horizon (locality 517) consisting chiefly of siltstones and fine-grained sandstones. Gynoclad compressions are common but their preservation is less favourable. Other plant fossils are *Osmunda*, *Coniopteris*, *Nilssonia schmidtii* (HEER) SEW., *Pterophyllum sensinovanum* HEER, *Sphenobaiera huangii* (SZE) KRASSIL., *Sphenobaiera umaltensis* KRASSIL., *Karkeniania asiatica* KRASSIL., *Stephanophyllum burejense* KRASSIL., *Ixostrobus schmidtianus* (HEER) KRASSIL., and *Leptostrobus mollis* PRYN. This horizon also yielded insect remains.

The gynoclads occur abundantly in yellow sandstones of Dublican Formation cropping out on the left bank of the Urgal River, tributary of the Bureja (locality 508). They are preserved as impressions and are associated with *Nilssonia schmidtii* (HEER) SEW., *Nilssoniopteris amurensis* (NOVOPOKR.) KRASSIL., and *Pityophyllum* sp. Hundreds of specimens have been collected from the contemporaneous locality 547 in the upper reaches of the Urgal River. Partially silicified gynoclads literally fill the matrix — a silicified shale. They outnumber other fossils which are *Nilssonia schmidtii* and *Pityophyllum*.

Numerous gynoclads of Valanginian age came from mines situated along the Urgal valley (localities 509, 510 and 512). They are accompanied by various ferns, together with *Nilssonia schmidtii*, *Heilungia amurensis*, *Ctenis*, *Nilssoniopteris*, *Pterophyllum*, *Baiera*, *Stenophyllum*, *Pityophyllum*, etc. Other less important localities are scattered in the Bureja basin.

Silicified material from locality 547 has been sectioned but with negligible results. Numerous compressions have been transferred from the rock by the WALTON method and individual capsules have been extracted by HF treatment. Fragments of capsule cuticle as well as outer and inner seed cuticles have been obtained by HNO<sub>3</sub> + KClO<sub>3</sub> oxidation followed by dilute KOH. Unfortunately all oxidizing agents broke the compressions into small pieces.

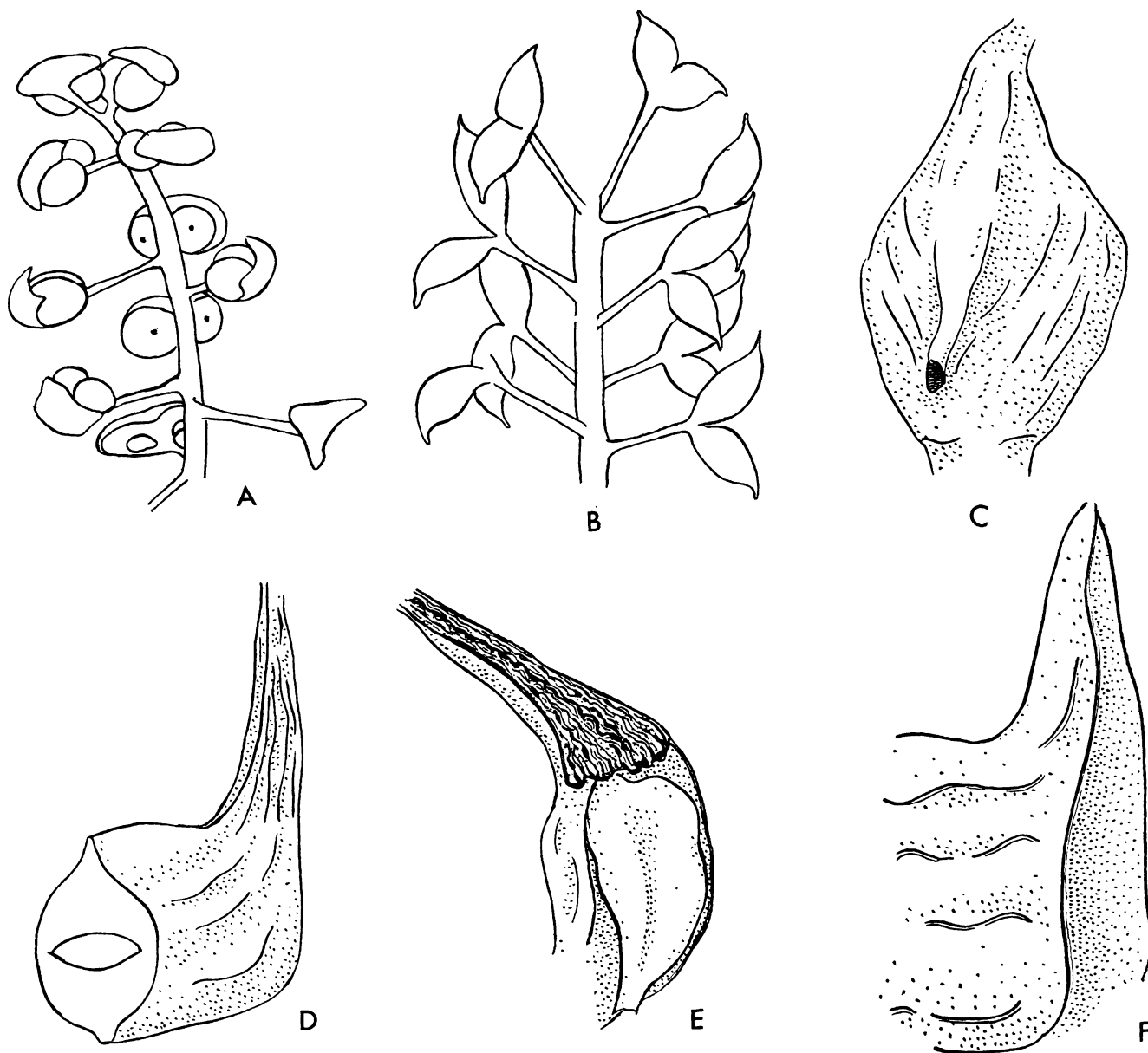
## Description

### Family Dirhopalostachyaceae fam. nov.

**Diagnosis:** Trees or shrubs. Leaves of *Nilssonia* type on long shoots and brachyblasts. Gynoclads racemose with spirally attached paired capsules. Capsules monospermic, dehiscent along the ventral suture, provided with long apical beak.

**Type genus:** *Dirhopalostachys* (PRYNADA) M. S. gen. nov.

**Remarks:** Mesozoic plants with the leaves of *Nilssonia* type have been classified as Cycadales, *Nilssonia-Ctenis* group, Nilssoniales, and Protocycadopsida (see SCOTT, 1924; HARRIS, 1932, 1964; MEEUSE, 1963). At least two species of Middle Jurassic *Nilssonia* have been attributed to the same plant as the *Beania* ovuliferous trusses. It appears that plants with *Nilssonia* foliage did not constitute a natural order but fell into



Text-fig. 1. A. Reconstruction of a *Beania* gynoclad (after HARRIS, 1964, fig. 65G). B. Reconstruction of a *Dirhopalostachys* gynoclad. C—F. *Dirhopalostachys* capsules, x 10. C. Ventral aspect showing suture. D. Diagrammatic transverse section. E. Ventral aspect with a wall partially removed to expose a seed, F. Deeply grooved beak of a ripe capsule.

different orders in respect to their female fructifications. Thus, it seems expedient to name higher taxa after fructification-genera rather than after leaf-genera. The Beaniaceae had racemose gynoclads with paired ovules borne nakedly on distally expanded lateral branches whereas in the Dirhopalostachyaceae rather similar ovules occurred in closed capsules. Another comparable family is the Corystospermaceae with paired ovuliferous capsules (or cupules) arranged in paniculate gynoclad (THOMAS, 1955). However in the Corystospermaceae the forked micropyle of the ovules projected from the proximal openings of the cupules. Among angiosperm families, the Hamamelidaceae resembles the Dirhopalostachyaceae in having paired carpels of comparable external form but differs from it in the mode of dehiscence and seed characters.

### Genus *Dirhopalostachys* PRYNADA (MS), gen. nov.

**Diagnosis:** Ovuliferous fructifications (gynoclads) racemose, cylindrical, axis bearing paired capsules in a loose spiral. Capsules free or partially adnate, elliptical or obovate, with reflexed apical beak, bearing single seed in expanded ventral part, dorsally compressed into a keel, externally ornamented with occasionally anastomosing ribs diverging from conspicuous ventral suture. Beak straight or slightly curved, adaxially ribbed, abaxially pitted or (in the ripe capsules) grooved. Ripe capsules dehiscent along the ventral suture. External cuticle of the capsule thin, showing elongated straight-walled cells and trichome bases. Capsule wall with resin bodies. Seed flattened, ovate, pointed towards capsule base. Outer cuticle of integument moderately thick, cells more or less isodiametric, trichomes present. Joint cuticles of integument interior and nucellus thin, showing large elongated cells.

**Type species:** *Dirhopalostachys rostrata* sp. nov.

**Remarks:** Comparable genera are discussed below, under the description of the type-species.

#### *Dirhopalostachys rostrata* sp. nov.

Pl. 1, figs. 1—17; Pl. 2, figs. 18—30; Pl. 3, figs. 31—43; Pl. 5, figs. 60—64

1963 *Dirhopalostachys* sp. — VASSILEVSKAJA and PAVLOV, Pl. 43, figs. 4—5.

**Description:** Gynoclads racemose, cylindrical, about 100—120 mm long, 18—27 mm wide. Axis 2—2.5 mm thick, straight, longitudinally striated. Lateral branches borne spirally at acute angle (about 48°). They look different depending on the plane of cleavage which reveals either the surface of the gynoclad with overlapping capsules of subsequent branches or a median section with two parastichies of lateral branches inserted at interval of about 7 mm. They become more crowded upwards and almost whorled at the apex. Lateral branches consist of a stalk and two capsules. Sometimes only one capsule is seen on the rock surface but the other can be readily excavated. The stalk is about 5—6 mm long, 1 mm thick, apical branches usually have longer stalks. In some specimens stalks are only 2 mm in length. Capsules diverge at 45—75°, free to base or partially adnate (Pl. 3, fig. 37). The capsules are elliptical or obovate, provided with a beak, transverse section rounded, average dimensions 8 x 4 mm but a few gynoclads have much longer capsules — up to 12 x 5 mm. The beak is reflexed, straight or slightly curved, about 3 mm long (Pl. 2, figs. 19—22, 26—30).

Casts of unripe capsules show a ventral suture as a conspicuous ridge folded at the junction with a stalk (Pl. 1, figs. 13—15). This ridge is extended along the beak. Casts of ripe capsules reveal an opened ventral suture (Pl. 1, fig. 17). In the majority of capsules cleared from rock matrix by HF the ventral suture is opened and the seed is shed. A locule with smooth interior occupies the ventral half of the capsule which is dorsally compressed and keeled. The capsule wall is ornamented with ribs which diverge at an acute angle from the ventral suture and occasionally anastomose on the side walls. The beak of the unripe capsule (Pl. 2, figs. 19—22) is pointed, adaxially ribbed, and abaxially covered with irregular pits. The extension of the ventral suture is evident as a narrow ridge. The beak of the ripe capsule (Pl. 2, figs. 26—28) is stouter, abaxially deeply grooved.

The seed is seen in unripe capsules transversely sectioned by cleavage (Pl. 1, fig. 12). Several capsule casts have been sectioned (Pl. 3, fig. 38) but their internal structure is scarcely preserved. A few capsules

extracted by HF show intact seed. The broken capsule in Pl. 2, fig. 20 reveals half of the seed, other half being covered by capsule wall. In Pl. 2, fig. 21 this part of the wall is removed and the seed is fully exposed. It is ovate, pointed towards the base of the capsule, flattened, 3 mm long, 2 mm wide, with median groove.

The cuticle of the capsule wall is very delicate showing elongated cells about  $62-93\mu$  long,  $30-45\mu$  wide, arranged in longitudinal files. The anticlinal walls are thin, straight, often indistinct, surface wall flat, without papillae (Pl. 5, figs. 61—62).

Stomata are absent. Trichome bases, which are scattered, consist of rounded cell encircled by several ordinary cells forming an irregular ring. Numerous resin bodies about 0,5 mm in diameter occur in the flesh of the capsule wall. They often emerge as rounded tubercles on the capsule compressions.

Seed compressions yielded two kinds of cuticles: outer cuticle of the integument and an inner double cuticle, i. e. the interior cuticle of the integument adhering to the nucellar cuticle. A megaspore membrane was not recognized with certainty. The outer cuticle is moderately thick (thicker and more resistent than both capsule cuticle and inner double cuticle of the seed). Cells are isodiametric or somewhat elongated, polygonal, rectangular, or irregular, with prominent, straight anticlinal walls, about  $37\mu$  long,  $31\mu$  wide, irregularly oriented or forming short files (Pl. 3, figs. 40—41). Occasional cells are spindle-shaped. There are bands of somewhat smaller slightly bulging cells (Pl. 3, fig. 41). Stomata are absent. Trichome bases are scattered, consisting of an oval cell surrounded by an irregular ring of five cells.

The joint cuticles of the integument interior and the nucellus are thin, with cell outlines clearly marked. The cells are variable, mostly elongated with wedge-shaped terminations, about  $75,5 \times 25\mu$  (Pl. 3, figs. 42—43).

Pollen grains have been found on the capsule cuticle. They occur solitarily or in groups of two-five grains stuck together. The pollen grains are elliptical or spindle-shaped, monosulcate, about  $30\mu$  long. (Pl. 5, figs. 63—64). The attribution of these pollen grains to the same plant as the gynoclads can not be asserted. No pollen grains have been observed on the capsule beak or on the seed micropyle which was in no case sufficiently preserved.

**Holotype:** Specimen 547—70 (Pl. 1, fig. 9); Institute of Biology and Pedology collection, Vladivostok.

**Remarks:** PRYNADA (MS) identified his specimens with *Stenorhachis dubius* ANTEVS and proposed the new combination *Dirhopalostachys dubia*. However *S. dubius* as well as *S. scanicus* NATHORST appears to be closely allied (if not congeneric) to *Beania* (NATHORST, 1909; HARRIS, 1964). Specifically Bureja gynoclads are no doubt distinct from the European. The external form of *Dirhopalostachys rostrata* resembles that of *Beania gracilis* CARRUTHERS which consists of an axis bearing lateral branches ("megasporophylls") in a loose spiral. The dimensions of gynoclads are much the same. However in *Beania gracilis* the axis is more stout (about 5 mm wide) and lateral branches are inserted at right angles (HARRIS, 1964). They are distally expanded into broadly rhomboidal heads bearing two inward pointing seeds. "Megasporophylls" of ripe gynoclads with stalks about 20 mm long and seeds up to 10—15 mm wide are much larger than lateral branches of *Dirhopalostachys*. However, juvenile specimens of *Beania gracilis* have stalks only 5 mm long and attached seeds 3 mm wide, i. e. comparable with the corresponding parts of *Dirhopalostachys*. They are also similar in such seed characters as strongly cutinized integument and thin double cuticle of integument interior and nucellus.

The capsules of *Dirhopalostachys* look like those of some angiosperms and especially like those of *Trochodendrocarpus arcticus* (HEER) KRYSH. (see KRASSILOV, 1973b). The latter is a widespread Late Cretaceous fossil attributed to the same plant as *Trochodendroides* leaves. The fruits of *Trochodendrocarpus* are borne in panicles. The lateral branches are racemes up to 100 mm long bearing paired fruits attached by a stalk and arranged in a loose spiral. The fruits are elliptical with a reflexed style. Thin ribs diverge obliquely from the ventral suture which is marked by a conspicuous groove. Racemes of *Trochodendrocarpus* may be equivalent to those of *Dirhopalostachys*. External features of the capsules are nearly identical in both genera. However in *Trochodendrocarpus* they are many-seeded and split along the ventral as well as dorsal suture.

**Localities:** 508 — the Urgal River near the mouth of its tributary the Chemduko River; 509, 510 and 512 — mines along the Urgal valley; 514 and 517 — the Bureja River near the mouth of its tributary the Umalta; 547 — upper reaches of the Urgal River.

**Age:** Late Jurassic—Early Cretaceous.

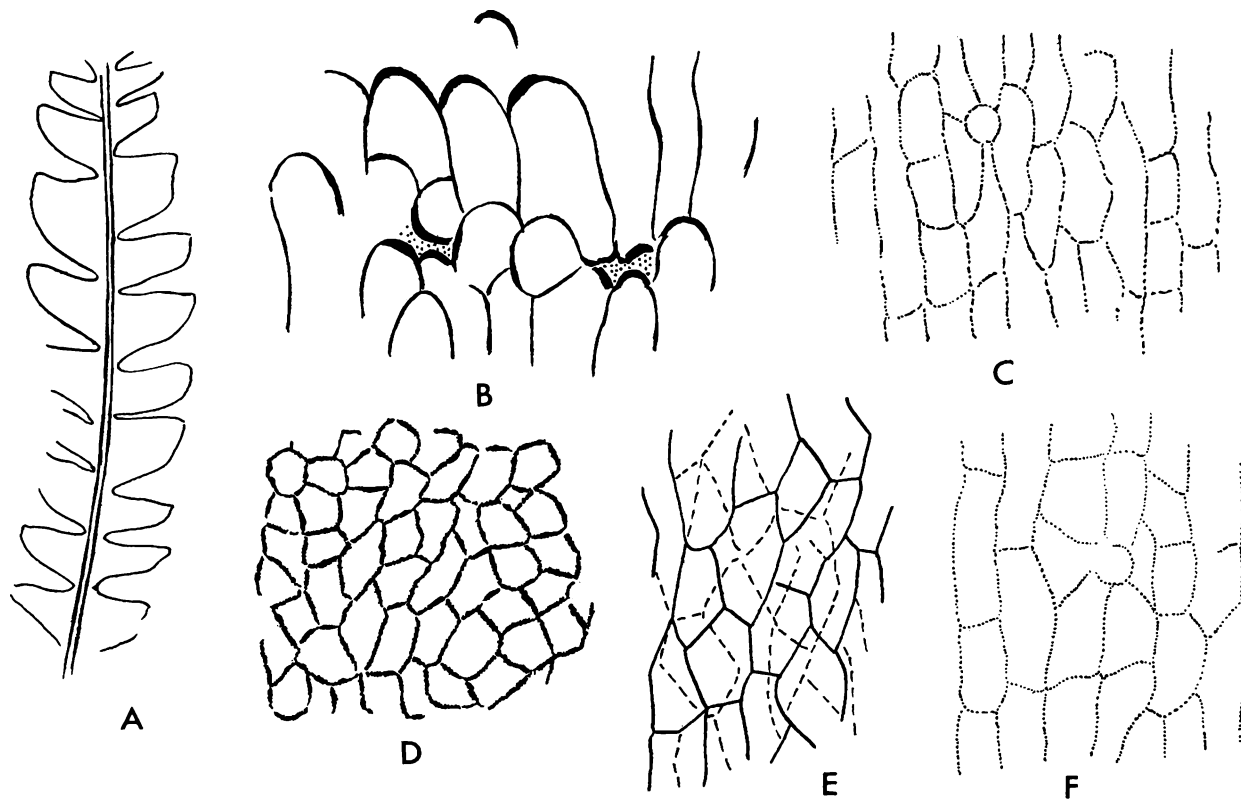
# Attribution to the same plant as *Nilssonia schmidtii* (HEER) SEWARD

The most constant associates of *Dirhopalostachys* are the gymnosperm leaf-genera *Phoenicopsis* (*Stephanophyllum*), *Pityophyllum* and *Nilssonia*. As a rule these fossils are accompanied by *Leptostrobus* fructifications and *Pityospermum* seeds, the former being attributed to *Phoenicopsis* and the latter to *Pityophyllum*. There are no resemblance between *Dirhopalostachys* and either *Phoenicopsis* or *Pityophyllum* in cuticular characters. Thus, *Nilssonia* is the most probable leaf-type of a plant with *Dirhopalostachys* gynoclads.

Among the Bureja species of *Nilssonia* the most important are *Nilssonia schmidtii* (HEER) SEWARD and *Nilssonia sinensis* YABE et OISHI. *Nilssonia schmidtii* is confined to lower horizons of the Upper Jurassic — Lower Cretaceous deposits and is associated with the *Dirhopalostachys* species described in this paper. *Nilssonia sinensis* came from upper horizons of Barremian — Aptian age containing ill — preserved fructifications of presumably *Dirhopalostachys* affinities. The upper cuticle of *Nilssonia schmidtii* agrees with the capsule cuticle of *Dirhopalostachys* in the texture, cell outlines and dimensions, appearance of the cell anticlinal walls, and trichome bases (compare figs. 57—60 and 61—62). Thus, the reasons for attribution of *Dirhopalostachys* and *Nilssonia schmidtii* to the same plant are:

- 1) Repeated association.
- 2) The absence of the other leaves which can be reasonably attributed to a plant with *Dirhopalostachys* fructifications.
- 3) Resemblance in cuticular characters.
- 4) Resemblance between *Dirhopalostachys* and *Beania* gynoclads attributed to the same plant as *Nilssonia compta* which is closely comparable with *Nilssonia schmidtii*.

In several Bureja localities the gynoclads occur in masses whereas the leaves are rather infrequent. This situation is contrary to what is known of Yorkshire localities where *Beania* fructifications are less numerous than *Nilssonia* leaves. A possible explanation is that the Siberian plant was deciduous and the gynoclads



Text-fig. 2. A—C. *Nilssonia schmidtii* (HEER) SEW. A. A leaf, x 1. B. Lower cuticle showing stomata and obliquely compressed bulging cells, x 395. C. Upper cuticle, x 166. D—F. *Dirhopalostachys rostrata* sp. nov. D. Outer seed cuticle, x 166. E. Joint cuticles of the integument interior and the nucellus, x 166. F. Cuticle of a capsule, x 166.

ripened and were shed early at the beginning of growing season whereas the leaves were shed at the end of it and, thus, have been deposited separately. This suggestion is in agreement with allegedly seasonal climate of Siberia as contrasted to the subtropical climate of Europe.

*Nilssonia schmidtii* was described one hundred years ago (HEER, 1876). However its cuticles have not been known until now. They are described below.

## Genus *Nilssonia* BRONGNIART

### *Nilssonia schmidtii* (HEER) SEWARD

Pl. 4, figs. 44—48, 50—54; Pl. 5, figs. 55—60

1876 *Anomozamites schmidtii* — HEER, p. 100, Pl. 23, figs. 2—3; Pl. 24, figs. 4—7.

1912 *Nilssonia schmidtii* — SEWARD, pp. 11, 27, Pl. 2, figs. 11, 12, 14.

1961 *Nilssonia schmidtii* — VAKHRAMEEV and DOLUDENKO, p. 96, Pl. 43, figs. 5—6.

**Description:** Leaf oblanceolate, shortly petiolate, tapering gradually towards the base, apically obtuse. A considerable part of the lamina has parallel margins. Average leaves are about 120 mm long, 26 mm wide but there are fragments of larger leaves up to 200 mm long, 75 mm wide. Segmentation varies from fairly regular to irregular — when some segments are twice as wide as the others. Four leaf types may be recognized in relation to the shape of their segments:

1) Segments short triangular with straight acroscopic and arched basiscopic margins, bluntly pointed, about 8—9 mm long, 7—10 mm wide (Pl. 4, fig. 46).

2) Segments short subtriangular to rectangular with rounded corners, about 15 mm long, 10—17 mm wide (Pl. 4, fig. 48).

3) Segments rectangular, broader than long, about 12 mm long, 15—30 mm wide (Pl. 4, fig. 47).

4) Segments long, with straight parallel margins but apex sharply pointed due to distal curving of basiscopic margin, about 35 mm long, 14—17 mm wide (Pl. 4, figs. 44, 45).

The segments are flat, with unthickened margins, occasionally notched or two-lobed. The veins are fine, mostly unforked, their concentration at the middle of segment being about 20 per cm.

The leaf is hypostomatic, the upper cuticle delicate, cells elongated, arranged in rows, about  $124\mu$  long,  $25\mu$  wide in coastal zones,  $75\mu$  long,  $31\mu$  wide between them. Occasional cells are squarish. Anticlinal cell walls are straight, faintly marked. Trichome bases are scattered mostly in the intercostal zones, consisting of rounded cell bordered by an irregular ring of 5—6 cells (Pl. 5, figs. 57—60).

The lower cuticle is moderately thin, showing clearly delimited costal and intercostal zones (Pl. 4, fig. 54) which are nearly equal in width. Costal zones somewhat raised, composed of elongated cells in regular rows. Cell walls are faintly marked. Cells are about  $31\mu$  wide, the length varies from about  $37\mu$  to  $100\mu$ . Intercostal stomatiferous zones are composed of broader cells about  $42\mu$  wide, with clearly marked anticlinal walls and bulging surface walls which often are obliquely compressed (Pl. 5, fig. 56). Cells are arranged in rows interrupted by stomata, these are scattered, well spaced, mostly longitudinal. The stomatal pit is elongated or sinuous, about  $48\mu$  long, formed by 4—6 cells, two of them polar, the other lateral. Subsidiary cells with bulging or papillate subsidiary walls (Pl. 4, figs. 51—53; Pl. 5, fig. 55). Occasional stomata are not sunken, fully exposed with guard cells  $37\mu$  long (Pl. 4, fig. 51). Trichome bases are not observed.

**Remarks:** HARRIS (1964) listed *N. schmidtii* among the specimens of unknown cuticular structure but resembling Yorkshire species *N. compta* (PHILLIPS) BROWN and *N. kendalli* HARRIS. The leaf form and segmentation in *N. schmidtii* is exactly like those of *N. kendalli* but the veins are less numerous in the former species. They differ also in cuticular characters, the lower cuticle of *N. kendalli* showing polygonal cells with flat surface walls, stomata only slightly sunken, subsidiary cells almost unspecialized, trichome bases numerous. In venation and cuticular characters *N. kendalli* is more like *N. compta* differing only in the number of subsidiary cells (four to six in *N. schmidtii* against six to eight in *N. compta*) and the absence of trichomes on the lower cuticle.

**Locality and age:** Same as for *Dirhopalostachys* (see above).



## Discussion

Several points of resemblance between the Late Jurassic — Early Cretaceous *Dirhopalostachyaceae* and mid-Jurassic *Beaniaceae* — nearly identical leaves, racemose gynoclads of similar external form, paired, inwardly pointing ovules with thickly cutinized integument — suggest genetic relations between these two groups of Mesozoic plants. I believe that the *Dirhopalostachys* capsule evolved by involution of the *Beania* “mega-sporophyll” shield borders. It is worth noting that ripe *Dirhopalostachys* gynoclads and their ovules have the dimensions of juvenile *Beania gracilis*. Thus, the transformation of *Beania* gynoclads was accomplished not only by involution and acquiring of the beak but also by acceleration of developmental stages. My suggestion is that the seasonal climate of Mesozoic northern Asia and short flowering period have been responsible for the acceleration. The carpels of some angiosperms, e. g. Hamamelidaceae might derive from *Dirhopalostachys* capsules by such steps as acquisition of a true stigma, polymerization of ovules and their corresponding modification.

The *Dirhopalostachyaceae* was certainly not the only Mesozoic group advancing towards the angiosperm level. Another angiosperm forerunner was the *Caytoniales*. They had ovuliferous spikes with many-seeded fleshy capsules which were nondehiscent and provided with a “lip” somehow related to otherwise gymnospermous pollination (THOMAS, 1925; HARRIS, 1964). The capsule wall fragments were observed in fossil coprolites of a small animal feeding on *Caytonia*. The staminate structures of *Caytoniales* were of pteridospermous nature. Their compound leaves (*Sagenopteris*) with closed venation displayed a number of angiospermous characters. Dr. HARRIS told me in a letter that stomatal structures of *Sagenopteris* were more angiosperm-like than those of other Mesozoic plants.

THOMAS (1931) suggested rather complex transformations from the *Caytonia* spike to angiosperm pistil which had been accepted with reservation by most morphologists. Recently MEEUSE (1972) demonstrated possibility of caytonialean derivation of such angiosperm groups as Berberidales having pistils without ventral suture.

The *Czekanowskiales* (Leptostrobales) recently removed from the *Ginkgoales* (which resemble them only in general leaf morphology) had rather loose racemes with many-seeded capsules dehiscent into valves. In the most advanced representatives of this group the valves were flanged by stigmatic bands (HARRIS, 1951; KRASSILOV, 1968, 1969, 1972a, b, 1973b). The episporangiate microsporophylls resembled certain type of angiosperm stamen. Thus, at least three lineages of Mesozoic plants — *Caytoniales*, *Czekanowskiales*, and *Dirhopalostachyaceae* acquired angiospermy, i. e. ovules enclosed in capsules. This acquisition excluded them from the gymnosperms despite the gymnospermous nature of their foliar and/or androecial structures. I propose the designation “*Proangiosperms*” for representatives of different lineages which combined gymnospermous characters with enveloped ovules. Various groups of the proangiosperms have been relatively advanced in some characters (e. g. the *Caytoniales* in the leaf morphology, the *Czekanowskiales* in the mode of pollination and staminate structures, *Dirhopalostachyaceae* in the capsule morphology) and primitive in the others. But all of them possessed ovuliferous capsules (I prefer this noncommittal term to both “cupule” and “carpel” where proangiosperms are concerned) with pollen-catching devices. These capsules were uniovulate or pluriovulate, dehiscent or nondehiscent (the latter character was probably related to zoochory). It appears that hypothetical hemiangiosperms of PARKIN (1923) i. e. angiosperms with “open carpels” never existed: whatever the order of appearance of angiospermous characters might have been, the closed carpels were among the earliest.

The *Gnetales* may probably be viewed as the only living proangiosperms. However the nature of their chlamys is in dispute. Teratological observations suggest its development from the perianth bracts (KENG, 1965). It is worth mentioning that occasional pollen grains in *Gnetum* do not reach the pollen chamber and pollen tubes are formed within the canal of “micropylar tube” (MAHESHWARI & VASIL, 1961; SANWAL, 1962).

Other plants not included here in the proangiosperms possibly also contributed to angiosperm ancestry. There were noteworthy points of resemblance between the *Bennettitales* and the *Compositae*. I described the cuticles of Late Jurassic disseminules with pappus presumably belonging to some bennettites but looking exactly like achense of a *Compositae* (KRASSILOV, 1973c). Several plant lineages developed various methods of seed protection alternative to that of the proangiosperms. In *Cistella* (the *Glossopteridales*, see SURANGE & MA-

HESHWARI, 1970) and *Araucaria* (Coniferales) ovules are similarly imbedded in the bracts whereas in the Pentoxylales the whole gynoclad is immersed in the receptacular tissue. According to MEEUSE (1961) the latter group may be connected with the Pandanales.

The phylogenetic role of proangiosperms was equivalent to that of Devonian progymnosperms — a polyphyletic group ancestral to genuine gymnosperms (see BECK, 1970). Both gymnospermization and angiospermization were of mosaic pattern, some categories of organs progressed more rapidly than the others. However, in contrast to proangiosperms, the vegetative parts of progymnosperms have been more advanced than their reproductive structures.

A few records of fossil stems and indirect evidence from the foliar and floral morphology indicate a tree habit of proangiosperms (see THOMAS & HARRIS, 1960 for *Nilssonina*, HARRIS, 1964, etc. for *Caytonia*). The leaves of Czekanowskiales have been clustered on short shoots, their gyno- and androclads being pendulous. Taphonomic observations suggest seasonal fall of the brachyblasts in the Czekanowskiales. Occasional records of clustered *Nilssonina* leaves have been reported from several Asiatic localities. I have found what appears to be a long shoot of *N. sinensis* with attached leaves (Pl. 4, fig. 49).

I suggested that the most advantageous adaptations appearing in a single lineage have spread among the proangiosperms by means of occasional hybridization or viral transduction of genetic material (KRASSILOV, 1973b).

The proangiosperm concept opposes rather popular idea of a single group of angiosperm ancestors emerging as small populations on tropical uplands. The proangiosperms have been widespread plants. They thrived in lowlands, along the streams and sea coasts and have been readily fossilized. In Siberian plant localities their remains outnumbered other fossils. The most advanced representatives of the group also came from these localities. It appears that the angiospermization was promoted by seasonal climate and proangiosperms reached their optimal development in the Late Jurassic-Early Cretaceous temperate forests of northern Asia which have been dominated by the Czekanowskiales and Dirhopalostachyaceae together with ginkgophytes and conifers.

### Summary

The new family Dirhopalostachyaceae described from the Upper Jurassic — Lower Cretaceous deposits of Bureja basin resembles the mid-Jurassic European Beaniaceae in the leaf characters, the gynoclad external features, and the seed structure but differs from it in having closed ovuliferous capsules instead of opened "megasporephylls". The dimensions of gynoclad lateral branches and seeds in *Dirhopalostachys* are like those of juvenile *Beania gracilis* CARRUTHERS. It is suggested that *Dirhopalostachys* evolved from *Beania* by acceleration of developmental stages, involution of seed-bearing shields and acquiring the apical capsule beak and ventral dehiscence. These transformations have been probably promoted by the seasonal climate of the Late Mesozoic northern Asia as contrasted to subtropical contemporaneous climate of Europe. The carpels of some angiosperms, e. g. the Hamamelidaceae might have originated from the *Dirhopalostachys* capsules.

The Dirhopalostachyaceae was not a single group subjected to angiospermization. This process embraced also the Caytonialean and Czekanowskialean stocks and resulted in the appearance of widespread Mesozoic proangiosperms, i. e. plants with predominantly gymnospermous features but having closed ovuliferous capsules provided with more or less advanced pollen-catching devices. The angiospermization progressing through parallel lineages of proangiosperms and affecting different organs in mosaic patterns eventually gave rise to genuine angiosperms.

It appears that the origin of angiosperms was not a single event but proceeded through at least two geological epochs involving large populations which inhabited vast territories. The Mesozoic plant assemblages have been dominated not only by pteridophytes and gymnosperms but also by proangiosperms which achieved their optimal development in the temperate forests of northern Asia.

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## Explanation of Plates

### Plate 1

- Figs. 1—17. *Dirhopalostachys rostrata* sp. nov.
- Figs. 1, 3, 7. Gynoclad compressions, locality 517. x 1.
- Figs. 2, 4—6, 10. Same from locality 510. x 1.
- Figs. 8—9. Gynoclad casts, locality 547. x 1.
- Fig. 11. Gynoclad compressions, locality 503. x 1.
- Fig. 12. Transversely split capsule showing seed from the specimen in fig. 7. x 10.
- Figs. 13—15. Capsule casts showing ventral suture and ribs, locality 547. x 10.
- Fig. 16. Capsule cast, side view, locality 547. x 10.
- Fig. 17. Internal cast of the capsule dehiscent along the ventral suture, locality 547. x 10.

## Plate 2

- Figs. 18—30. *Dirhopalostachys rostrata* sp. nov.  
Fig. 18. Dorsal aspect of the capsule showing adaxial keel and ribbed adaxial surface of the beak. x 10.  
Fig. 19. Ventral aspect of the same capsule showing ventral suture and pits. x 10.  
Fig. 20. Same, part of the seed is in focus, the other part is covered by remains of the capsule wall. x 10.  
Fig. 21. Same, part of the capsule wall is removed and the seed fully exposed. x 10.  
Fig. 22. Side view of the same capsule, part of the seed is seen below. x 10.  
Figs. 23—24. Proximal parts of stalked capsules. x 10.  
Fig. 25. Paired capsules. x 3.  
Fig. 26. Distal part of the ripe capsule. x 3.  
Figs. 27—28. Ventral aspect of the same capsule showing abaxially grooved beak. x 3 and 10.  
Figs. 29—30. Incomplete capsule with anastomosing ribs, side view. x 3 and 10.

All capsules from the same gynoclad, locality 514.

## Plate 3

- Figs. 31—43. *Dirhopalostachys rostrata* sp. nov.  
Figs. 31—35. Gynoclad compressions transferred from the rock, locality 517. x 1 (fig. 31) and 1.5 (figs. 32—35).  
Fig. 36. Capsule showing ventral suture from specimen in fig. 32. x 10.  
Fig. 37. Adnate capsules from specimen in fig. 35. x 10.  
Fig. 38. Longitudinal section of the capsule cast, locality 547. x 10.  
Fig. 39. Paired capsules, transfer preparation showing locule, locality 547. x 5.  
Figs. 40—41. Outer cuticles of the seed, locality 517. x 166.  
Figs. 42—43. Joint cuticles of the integument interior and the nucellus, the same seed. x 166.

## Plate 4

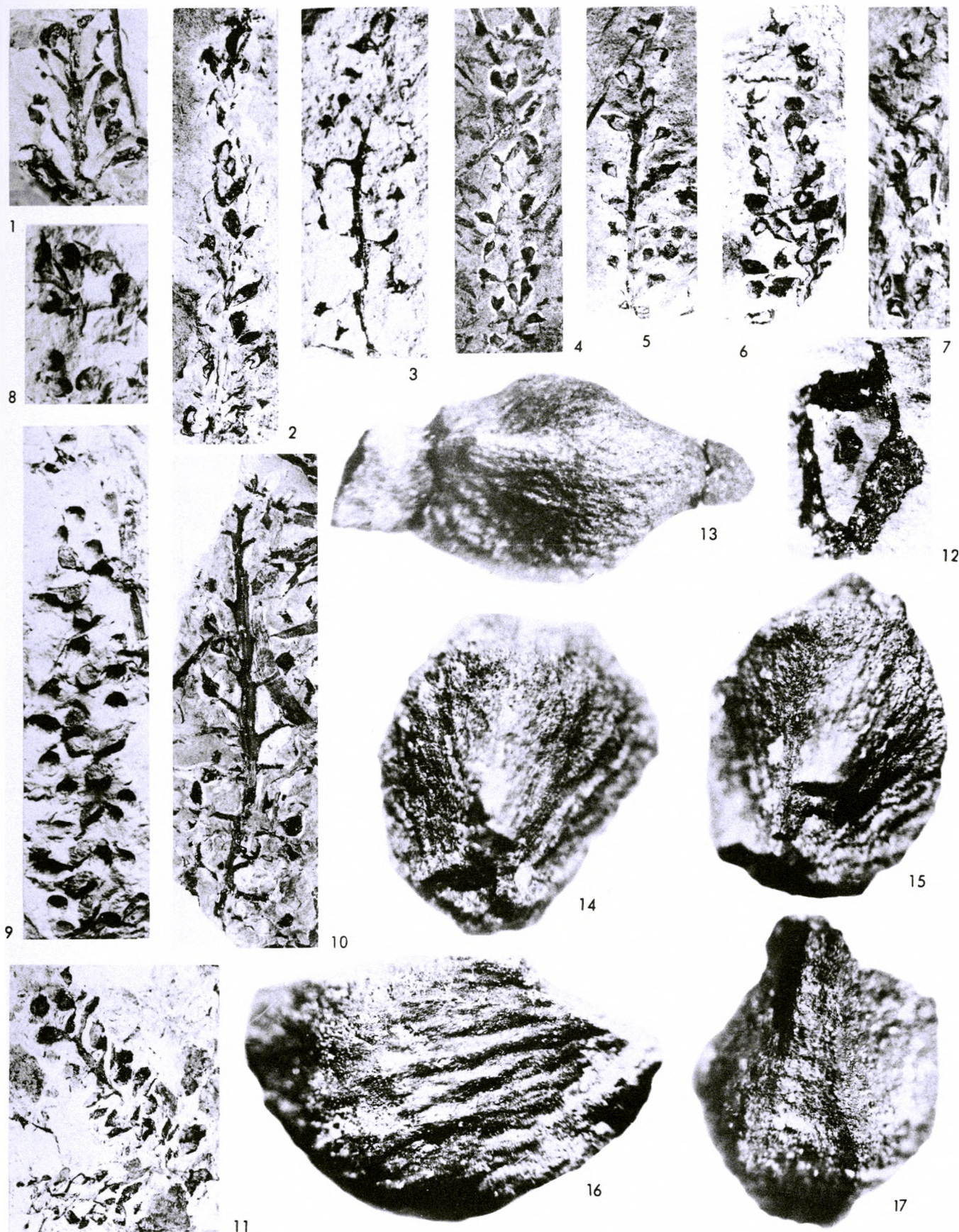
- Figs. 44—48, 50—54. *Nilssonia schmidtii* (HEER) SEWARD.  
Figs. 44—48. Leaves showing various shapes of segments, localities 508 (fig. 47), 510 (figs. 44—45), 514 (fig. 48), 547 (fig. 46).  
Figs. 50—53. Lower cuticle showing stomata and obliquely compressed bulging cells, exposed stoma is seen in fig. 51, left, locality 517. x 395.  
Fig. 54. Lower cuticle showing costal and intercostal zones. x 166.  
Fig. 49. *Nilssonia sinensis* YABE et OISHI.  
Fig. 49. Shoot fragment with two attached leaves. x 1.

## Plate 5

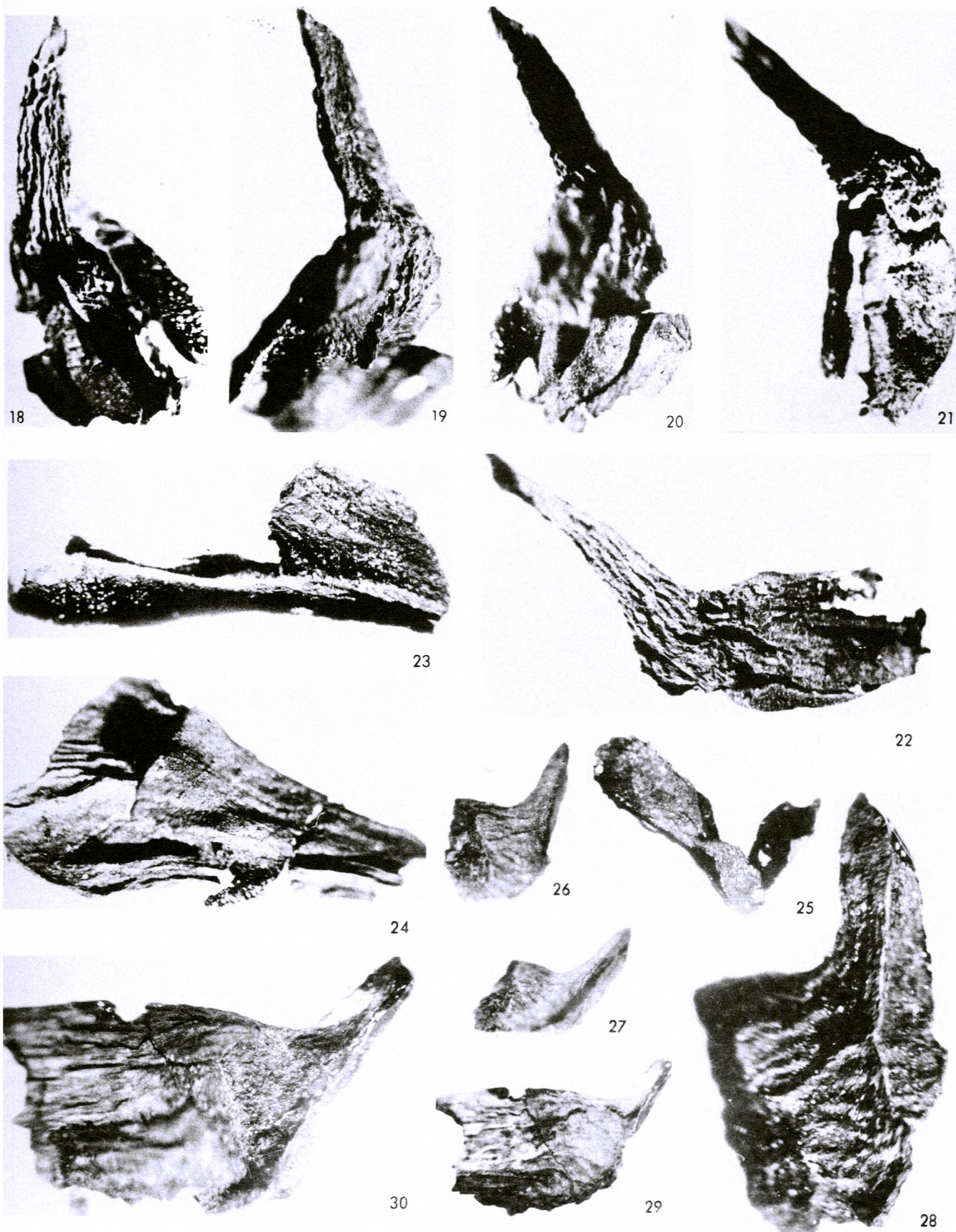
- Figs. 55—60. *Nilssonia schmidtii* (HEER) SEWARD.  
Fig. 55. Lower cuticle showing stomata with proximally bulging subsidiary cells, x 395.  
Fig. 56. Lower cuticle showing obliquely compressed bulging cells, x 395.  
Figs. 57—60. Upper cuticles, trichome base is seen in fig. 58. x 166.  
Figs. 61—64. *Dirhopalostachys rostrata* sp. nov.  
Figs. 61—62. Outer cuticles of the capsule wall. x 166.  
Figs. 63—64. Pollen grains on the capsule cuticles. x 395 (fig. 63) and 562 (fig. 64).

All specimens from locality 517.













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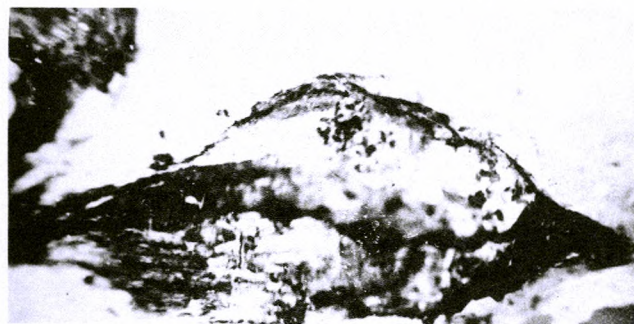
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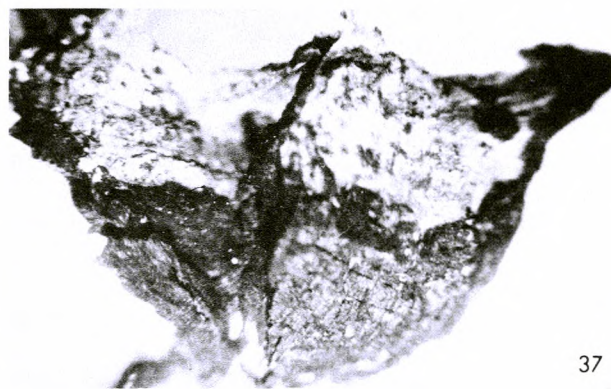
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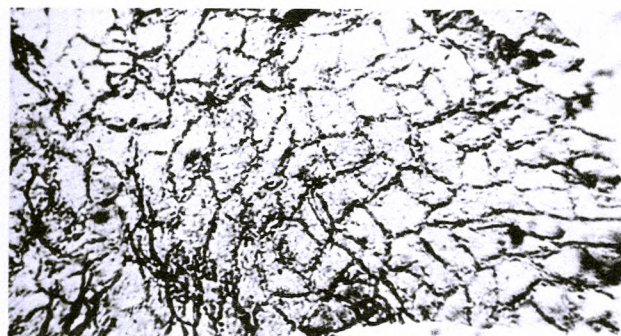
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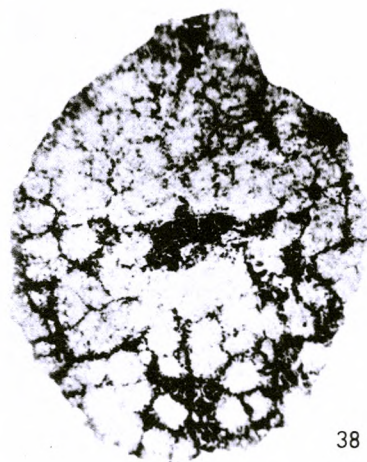
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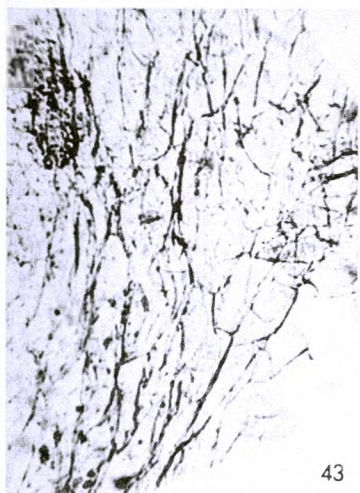
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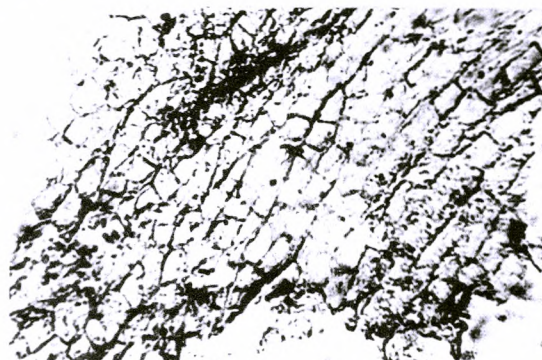
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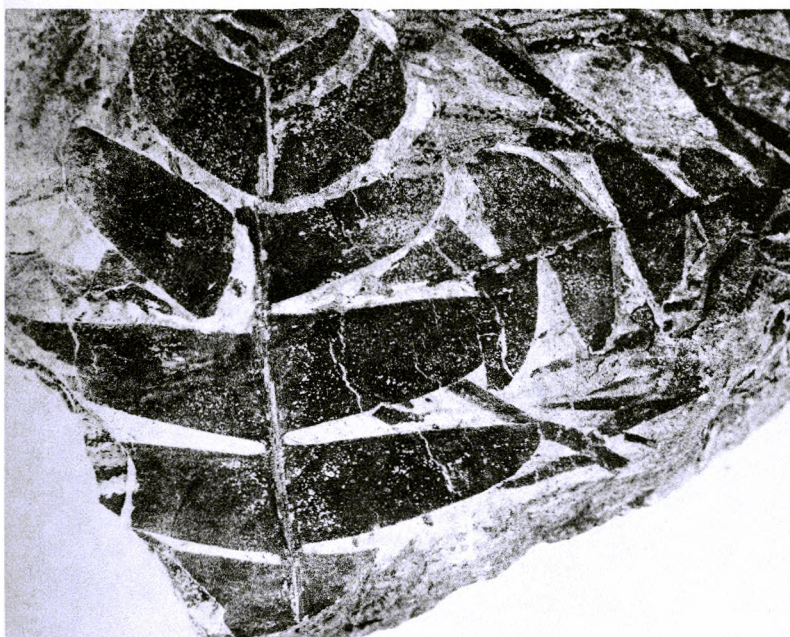


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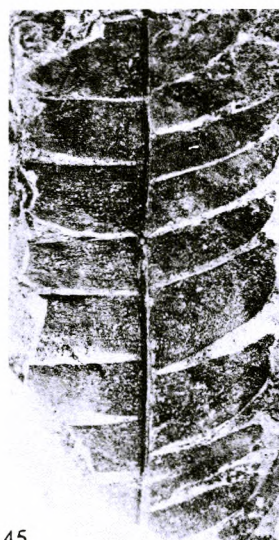


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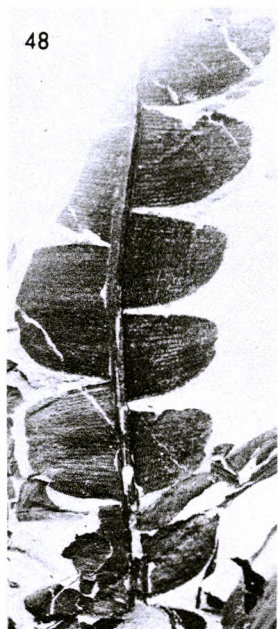
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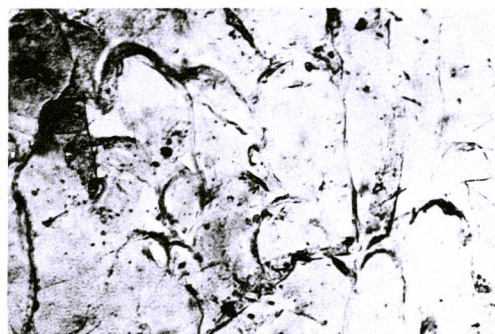
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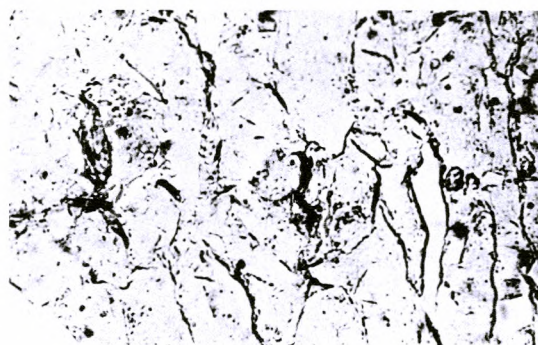
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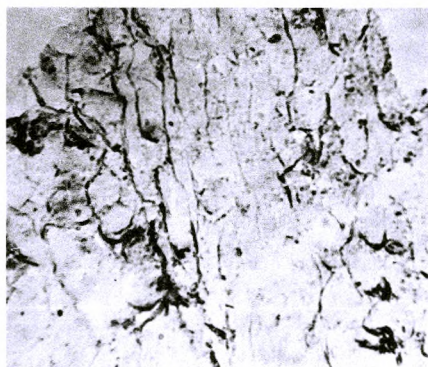
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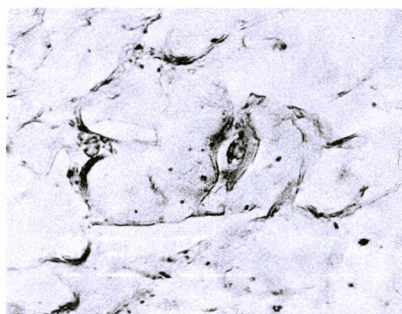
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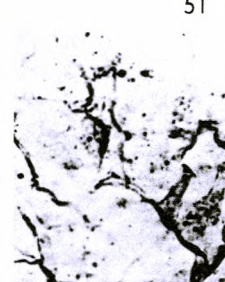
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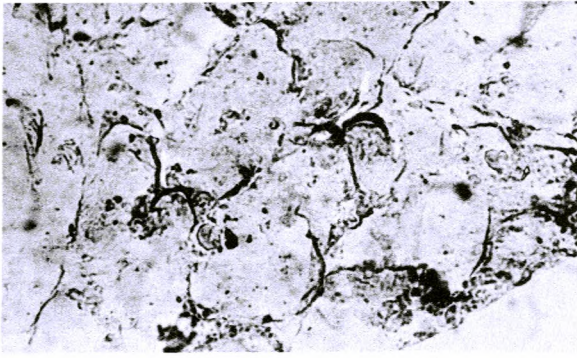


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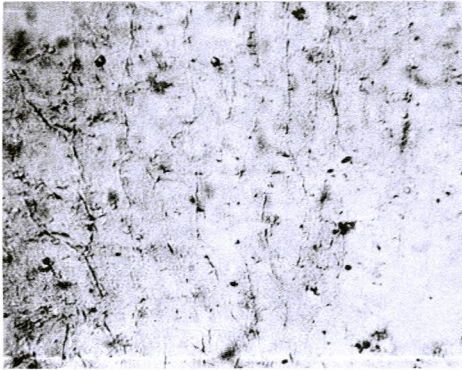




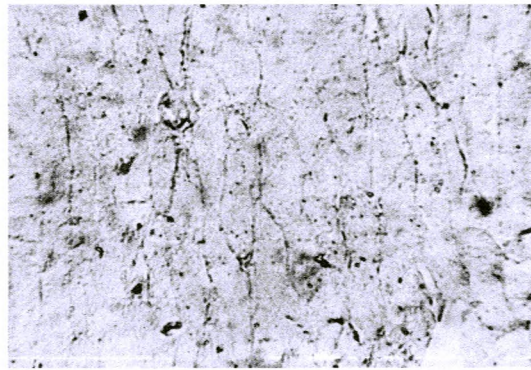
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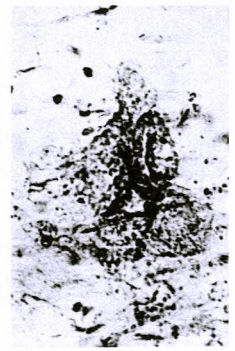
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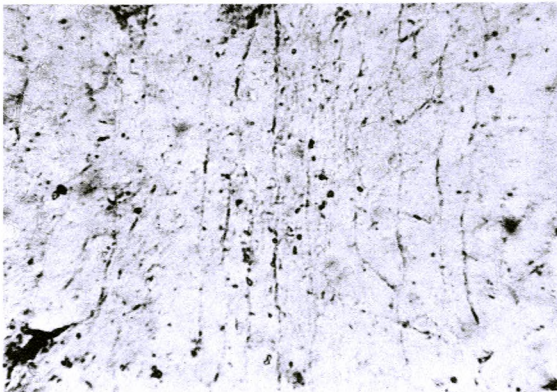
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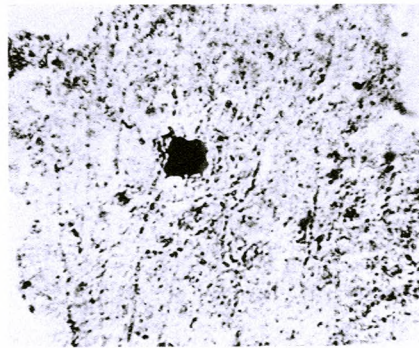
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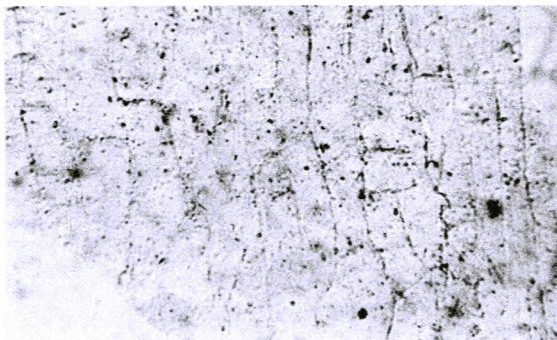
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