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MESOZOIC LYCOPODS AND FERNS FROM THE BUREJA BASIN

BY

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With 11 plates and 1 figure in the text

Abstract

Lycopods *Lycopodites macrostomus* sp. nov. and *Synlycostrobus tyrmensis* gen. et sp. nov. (leafy shoots, cuticles, strobili, spores) and ferns *Osmunda diamensis* (SEW.) comb. nov., *Klukia tyganensis* KRASSIL., *Dicksonia concinna* HEER (= *Coniopteris burejensis* (ZAL.) SEW.), *D. arctica* (PRYN.) comb. nov. and *Cyathea tyrmensis* (SEW.) comb. nov. (leaf morphology, indusia, sporangia, spores) are described from the Late Jurassic — Early Cretaceous strata of the Bureja basin. Thermophilous ferns came from the southern localities about 50° North suggesting a rather steep temperature gradient. Fertile shoots of *Synlycostrobus* resembled the compound strobilus of conifers evidencing the high evolutionary potential of the Mesozoic lycopods. *Osmunda* probably originated in the Siberian province. Most species of *Coniopteris* had bivalvate (not cup-shaped) indusia as in *Dicksonia* or *Cibotium*. In the Cyatheaceae, indusia probably evolved from hemitelioid to cyatheoid.

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Introduction

1976 was a centennial year for paleobotany in Siberia and the Amurland. Initial work of OSWALD HEER (1876) based on the collections furnished by F. B. SCHMIDT in 1859, not only brought to light the fossil floras of northern Asia, but also challenged a widely held belief in universal homogeneity of Jurassic vegetation and climate. Localities situated in the upper reaches of the Bureja River proved to be the most representative sample of the temperate Jurassic and Early Cretaceous vegetation. HEER described 17 species, among them *Dicksonia* (several species), *Adiantites* and *Asplenium*. These ferns had been redescribed by ZALESSKY (1904) and SEWARD (1912). The latter author assigned HEER's *Dicksonia* and *Adiantites* to a single species *Coniopteris burejensis* (ZAL.) SEW., while "*Asplenium*" was transferred to *Cladophlebis* and then to *Raphaelia*. He added also a few fern

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species from the Tyrma River (tributary of the Bureja), *Sphenopteris tyrmensis* SEW. among them. VACHRAMEEV & DOLUDENKO (1961) have listed 28 species of ferns, most of them the leaf-species of *Cladophlebis* and *Sphenopteris*. They distinguished as many as five species of *Coniopteris*. DOLUDENKO has described spores of *Coniopteris* (practically identical in all "species") and other Dicksoniaceous ferns. I attempted more detailed survey of the spore-bearing structures which led to taxonomic changes and revealed some evolutionary trends among Mesozoic ferns. Lycopods, hitherto unknown in the Bureja locality, are represented by two very distinctive species.

Stratigraphy

Stratigraphy is given in VACHRAMEEV & DOLUDENKO (1961) and KRASSILOV (1973a, b). Rich fern localities belong in the Talynjan Formation of the Callovian or Callovian-Oxfordian age and the Tyrmian beds of the Tithonian-Berriasian age. The best preserved material came from two classical localities: (I) the outcrops of Talynjan Formation near the mouth of Umalta, first described by HEER and (2) the outcrops of Tyrmian beds on the right bank of the Tyrma, made known by SEWARD. *Osmunda ("Raphaelia") diamensis* and *Dicksonia concinna ("Coniopteris burejensis")* are dominant in (1) while *Klukia tyganensis* and *Cyathea tyrmensis* are abundant in (2). These localities yielded also the remains of lycopods.

Younger strata are moderately rich in ferns. *Dicksonia concinna* is common in the Soloni Formation (Valanginian) and is replaced by *Dicksonia arctica* in the overlying beds of Barremian and Aptian age. *Osmunda diamensis* and *Dicksonia arctica* are stratigraphically important species in the Bureja basin and adjacent territories.

Description

Genus *Lycopodites* LINDLEY & HUTTON (non BRONGNIART)

Lycopodites macrostomus sp. nov.

Pl. 1, figs. 1—14

Diagnosis: Shoots isophyllous, axis up to 1 mm thick, forking regularly at 45—50° at intervals of 4—6 mm. Leaves ligulate, arising spirally, obliquely spreading, imbricate. A leaf in the angle of dichotomy absent. Leaves lanceolate, about 3 x 0.7 mm, base expanded, clasping the axis, apex long, acuminate, margin entire or toothed. Teeth sparse, 1—2 — celled. Midrib prominent, straight, filling the apex or extending only two thirds of the leaf. Epidermal cells irregular-rectangular, about 65—70 x 30μ, with sinuous walls forming longitudinal or oblique rows. Stomata scattered all over the leaf surface, elliptical, about 45μ long. Hypodermal fibres parallel to the midrib or diverging from it at a narrow angle.

Holotype: 514—155. Pl. 1, fig. 2.

Description: The holotype (Pl. 1, fig. 2) is a branching shoot with imbricate leaves. Its counterpart was transferred from the rock surface yielding fragments of leafy axes and isolated leaves. Leaves variable, 1—3 mm long, typically lanceolate, tapering gradually to an acuminate apex, but sometimes mucronate or contracted just above the base and awl-shaped (Pl. 1, fig. 12). Leaf margin mostly entire. Among 40 cleared leaves only 5 show marginal teeth. These are sparse, irregular, formed by one to two marginal cells. A single specimen shows a rather large distal tooth (Pl. 1, fig. 7) suggesting unequal dichotomy of the apex. In many cleared leaves, a minute protuberance (ligule) is seen just at the base of a midrib (Pl. 1, figs. 8—10). Fibres run parallel to the midrib or diverge from it obliquely, stretching along the cell rows. Stomata scaterred over both sides, mostly avoiding ligular pit, tending to form irregular groups of three to four, longitudinal or oblique. Concentration of stomata per leaf variable: leaves 1.0, 1.5, 2.0 and 3.0 mm long showed 12, 10, 33 and 26 stomata respectively.

Remarks: The ligule suggests Selaginellean affinity, but the shoot morphology, the absence of a leaf at the point of dichotomy and the epidermal characters are more similar to those in *Lycopodium*. This species resembles *Lycopodites falcatus* (HARRIS, 1961) in the epidermal characters, however the shoot morphology is different.

Locality: 514, Bureja near the mouth of its tributary Umalta River.

Age: Late Jurassic, Callovian.

Genus *Synlycostrobus* gen. nov.

Diagnosis: Fertile shoots bearing strobili laterally in the axils of bracts at each node or alternating with occasional leaves. Stalks of strobili fused with the bracts. Strobili unisexual, microsporophyll apices forked, sporangia adaxial, borne singly, protected by upcurving arm of sporophyll apex and a heel of adjacent sporophyll. Microspores numerous, trilete.

Type species: *Synlycostrobus tyrmensis* sp. nov.

Remarks: Strobili of this plant are like miniature *Lycostrobus*, but the dichotomy of sporophyll apices is more pronounced than in any other lycopod save the Devonian *Protolepidodendron*. "Inflorescences" bearing strobili laterally in the axils of bracts are unique among lycopods. Sterile shoots of the type species (see below) are like those of *Selaginella*. Hetospory is suspected, but not proved.

Synlycostrobus tyrmensis sp. nov.

Pl. 3, figs. 15—30, Pl. 2, figs. 31—36

Diagnosis: Sterile shoots presumably creeping. Main axis stiff, ribbed, branching monochasially in one plane, with lateral leaves only. Leaves on branches in four ranks with two rows of lateral leaves about 2.2 x 1.3 mm and two rows of much smaller dorsal leaves. Leaves ligulate. Fertile shoots, or "inflorescences", probably erect, up to 20 mm long, bearing unisexual strobili fused by their stalks to subtending bracts. Sporophylls about 20 per strobilus, apically forked. Sporangia single in a cavity formed by sporophyll arms, shed at maturity. Spores trilete, nearly globose 20—22μ in diameter, granular.

Holotype: 550—589, Pl. 2, fig. 22.

Description: Reconstruction of this plant is conjectural because sterile and fertile parts were not found intact. However occasional leaves in the fertile shoot are like lateral leaves of the sterile shoots. Separation of sterile and fertile parts suggests that they were not in the same plane: the sterile shoot was probably prostrate and the fertile one erect, breaking off under pressue.

Sterile shoots: There are fragments of unbranched stems 1 mm thick, straight, ribbed, apparently rigid, bearing widely spaced leaves (Pl. 2, figs. 20—21). Leaves on these stems are spreading like lateral leaves on branches. Branching axes are about 0.5 mm thick, giving off lateral branches at intervals of 5—6 mm, changing direction at the points of branching. Lateral branches up to 20 mm long, forking repeatedly at intervals of about 2 mm, those on the acroscopic side more profusely branched. A leaf in the angle of a dichotomy is constantly present.

Lateral leaves alternate, arising at 75°, oblong-ovate, acute, base slightly emarginate or cordate, typically 1.5 mm long, 0.8 mm broad, but in larger shoots up to 2.2 x 1.3 mm. Dorsal leaves ovate or semicordate, spreading more obliquely, sometimes obliterated. Transfer preparations of dorsal leaves show ligula as a small process at the base, about 250μ long (Pl. 3, fig. 31). Epidermal cells small, rectangular, with straight walls. Large rectangular mesophyll cells are seen in cleared leaves.

Fertile shoots: The best specimen (holotype) is 25 mm long. Axis 0.4 mm thick, twisting, bearing two rows of alternate strobili at intervals of 4 mm. Strobili arising at each node, but those in the lower part of a shoot alternate with a few leaves. Strobili borne in the axils of subtending bracts though they appear adaxial (epiphyllous) on bracts to which they are fused with their stalks. Bracts narrow, acute, curved, about 3 mm long. Stobili about 5 x 1 mm, elongate, apex rounded, axis very slender, bearing about 20 sporophylls attached spirally at a right angle. Sporophylls consisting of a proximal horizontal part about 0.4 mm long, bearing a single adaxial sporangium, and a distal part divided into two arms of unequal length diverging at 150—180°: the one shorter, pointing downward (heel) and the other longer, curved upward and overlapping the heel of adjacent sporophyll. Sporangia are, thus, enclosed in a cavity formed by the sporophyll arms.

Another fertile axis on the same slab bears more bulky strobili 2 mm long, some of them with empty sporangial cavities (Pl. 2, fig. 25). Sporangia have been shed from the fertile shoot shown in Pl. 2, fig. 28. The axis is strongly twisted, bearing empty strobili and two sterile leaves. Strobili 5 mm long, their axes also twisted in a zig-zag manner, sporophylls subopposite, widely spaced, not overlapping.

Sporangia elliptical, about 400μ long, wall scabrate (Pl. 3, fig. 32). Spores numerous (not exactly counted, but more than 200 per sporangium) trilete, nearly globose, amb rounded, mean diameter 20—22μ. Spore wall two-layered. Outer layer densely covered with spherical granules about 0.2μ in diameter. Inner layer smooth, with weakly developed trilete mark (Pl. 3, fig. 33). Outer layer rather loose, usually folded. Occasional spores with a smooth protuberance, probably germinated.

Megaspores, associated with fertile shoots: A megasporangium containing four megaspores and numerous isolated megaspores, all of the same kind, were obtained by bulk maceration of the *Synlycostrobus*-bearing rock slabs. Megaspores 150—220μ in diameter, amb rounded-elliptical, contact facets flattened. Trilete ridges prominent, straight or slightly sinuous, arms of unequal length, reaching two thirds of the spore radius. Ridge slopes verrucate. Arcuate ridges not developed. Exine verrucate on both surfaces of the spore. Verrucae of variable outline, spherical, bluntly conical or baculate, more crowded on the proximal surface, often fused and forming arcuate or sinuous ridges. Mesosporium (inner sac) from one half to three quarters of the spore body in diameter (Pl. 4, figs. 37—43).

These megaspores resemble *Triletes anodios* HARRIS from the Yorkshire Jurassic (HARRIS, 1961).

Locality: 550, Tyrma River near Alanap.

Age: Latest Jurassic or Lowermost Cretaceous (Tithonian-Berriasian).

Genus *Osmunda* L.

Osmunda diamensis (SEWARD) comb. nov.

Pl. 5, figs. 44—52, Pl. 6, figs. 53—59

Asplenium whitbiense: HEER, 1876, p. 94, Pl. 22, figs. 4d, 9c.
Asplenium whitbiense var. *tenue:* Ibid., p. 95, Pl. 16, fig. 8.
Cladophlebis haiburnensis: SEWARD, 1912, p. 10, Pl. 1, fig. 7, Pl. 2, fig. 10.
Raphaelia diamensis: VACHRAMEEV & DOLUDENKO, 1961, p. 75, Pl. 6, fig. 5, Pl. 27, fig. 1, Pl. 28, fig. 1, Pl. 30, fig. 4.

Description: Whole overground rosettes of leaves are occasionally preserved on the large slabs of mudstone (Pl. 5, fig. 44). Leaves dimorphic. Sterile leaves bipinnate, rachis proximally 10 mm wide, lower pinnae short, drooping. In the middle of a leaf pinnae about 120 mm long, pinna rachis grooved, with minute pits suggesting hairs. Basal pinnules inclined towards the rachis, other pinnules arising at about 70° in katadromic order. The form of pinnules variable. "Typical" pinnules about 10—12 x 5—6 mm, tongue-shaped, straight or slightly curved, obtusely pointed, base contracted, margins entire or slightly lobed. Distal pinnules triangular, acute, not contracted at the base. Aberrant pinnules linear, oblanceolate, deeply lobed, or even divided into narrow, forking, single-veined segments (Pl. 5, fig. 46). This form of pinnules was not previously recorded. Veinlets forking twice or (in smaller pinnules) once.

The leaf cuticle show cells of irregular shape with sinuous walls (Pl. 5, fig. 52). Stomata on the lower side only, ellipticle, about 45μ long, oriented along the veinlets, mostly arranged in groups of 2 to 5, adjacent stomata in a group often contiguous.

Fertile pinnules about 7 x 1 mm, straight or slightly curved with completely reduced lamina (Pl. 5, fig. 47). Sporangia globose, about 0.7 mm in diameter, attached by a short stalk, crowded. Cleared sporangia show a large rounded basal cell about 130μ in diameter and elongate cells 110—150μ long radiating from it. Cell walls ridged. A group of thickened cells (annulus) are placed laterally, about half-way between the stalk and the apex, 2—3 cells high. Thickened cells short, polygonal. Dehiscent sporangia split into two valves joined by the annulus.

Spores spherical, about 60μ in diameter, amb rounded, trilete mark distinct, laesure simple, straight, reaching to the amb. Distal surface spinulate. Spinules up to 5μ long, acuminate or bluntly pointed, mostly independent, but occasionally fused. Proximal surface verrucate or regulate.

Remarks: This fern was at first identified with the Yorkshire species "*Asplenium*" *whitbiense* (HEER, 1876) or *Cladophlebis haiburnensis* (SEWARD, 1912). The "typical" form was then placed in a separate species *Raphaelia diamensis* SEW. and became familiar under this name, especially to the Russian paleobotanists, while the names *Cladophlebis haiburnensis*, *C. whitbiensis* and *C. williamsonii* were continuously applied to leaves with pinnules not (or less conspicuously) contracted at the base. The Yorkshire leaf-species available for comparison be-

long to *Todites* (I believe this to be true also for *Cladophlebis haiburnensis*, because I have collected fertile pinnae of *Todites* associated with this leaf type in the Kamenka locality of Ukraine, unpublished). *Todites* was not hitherto recorded from Siberian localities. VASSILEVSKAJA & PAVLOV (1970) recognized the Osmundaceous affinity of "*Raphaelia*" *diamensis* and argued that SEWARD was hardly justified in his treatment of this Siberian fern as a congener of the poorly known Late Cretaceous *Raphaelia* from Aachen. They proposed the new generic name *Osmundiella*. However the more structural details come to light the more certain it becomes that "*Raphaelia*" *diamensis* is a species of *Osmunda*. It is similar to *Osmundopsis sturi* (RACIB.) HARRIS in many characters, but the annulus is lateral as in *Osmunda*, and not apical as in *Osmundopsis* or *Todites*. Dimorphic leaves, the shape of sporangia and the spore wall ornamentation suggest affinity with *Osmunda (Osmundastrum) cinnamomea* L.

Locality: 514—517, Bureja River near the mouth of Umalta and many other localities in the Bureja basin.

Age: Late Jurassic.

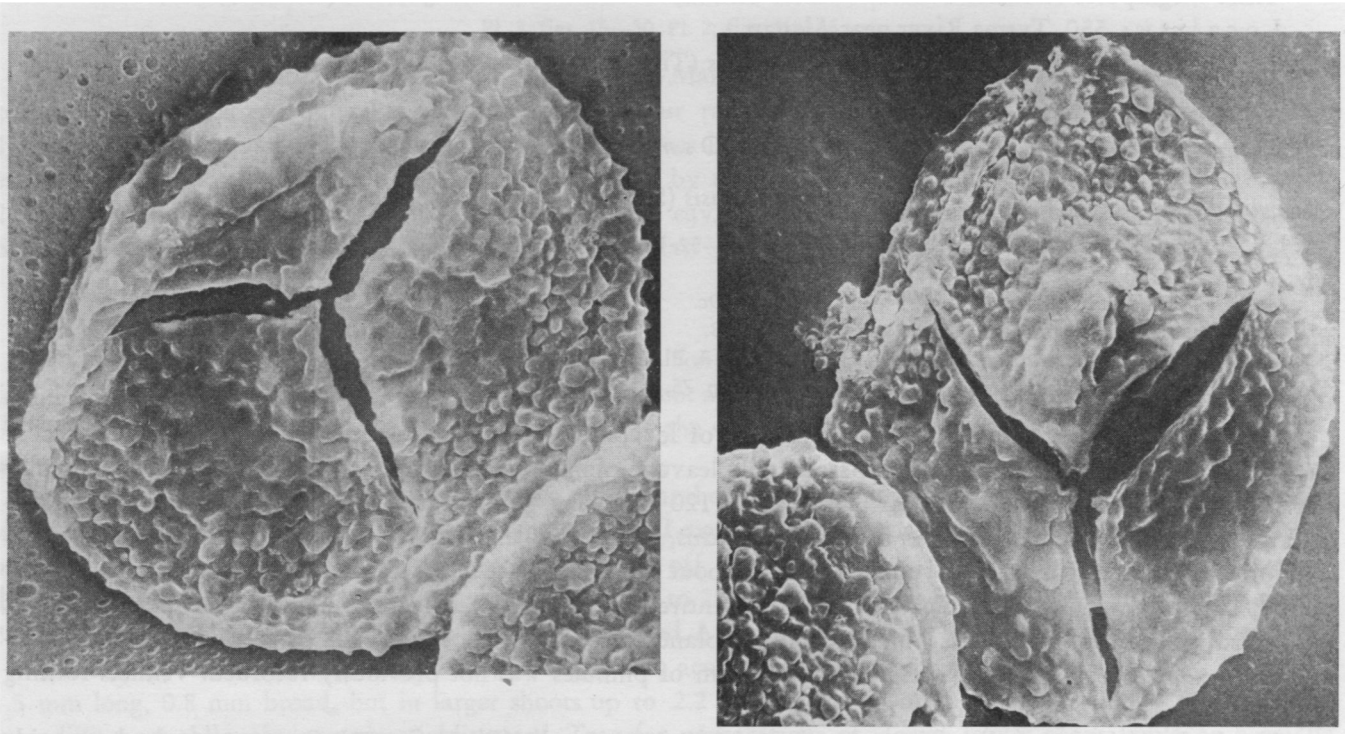

Fig. 1. *Osmunda diamensis* (SEWARD) comb. nov. Spores, proximal aspects. x 3000, SEM.

Genus *Klukia* RACIBORSKI

Klukia tyganensis KRASSILOV

Pl. 7, figs. 60—71

Klukia tyganensis: KRASSILOV, 1977, p. 130, pl. 2, figs. 1—6.

Description: Leaves up to 30 cm long, rachis slender, about 0.8 mm thick, hairless, showing a longitudinal groove which is continuous with the grooves of the pinna rachises. Pinnae arising at 45°, alternate, well spaced or slightly overlapping. Basal pinnules parallel to the rachis. Other pinnules forward-pointed, arise in katadromic order at intervals of 1/3—2 pinnule widths, connected by a narrow web. Typical pinnules linear-lanceolate, about 10—15 mm long, 1.5—2 mm broad, the base expanded or slightly contracted on the acroscopic side, the margin above the middle serrate, reflexed. Veinlets oblique, forking once or simple.

Fertile pinnules like the sterile. Sporangia in two rows about 11—12 per row, almost in contact, covering the entire pinnule save a small apical portion. Sporangia elliptical, about 0.7—0.8 mm long. Apical annulus

0.3 mm in diameter, consisting of 15 thickened cells. Spores about 240 per sporangium, spherical, mean diameter 60μ. Amb rounded-triangular, distal wall strongly convex, proximal wall moderately convex, contact facets flattened, trilete mark prominent, laesurae about three-quarters of the radius, raised, opened, bordered by a smooth membranous lip about 14μ wide. Contact facets verrucate or papillate, sculptural elements independent or fused, up to 3μ high. Distal surface ornamented with irregular reticulum extending over the equator and overhanging the ends of the trilete arms. Reticulum with rounded-polygonal or elliptical lumina 3—6μ wide. Occasional lumina subdivided by a vestigial wall. Muri broad, with sloping sides.

Remarks: This species differs from the European *Klukia exilis* (PHILL.) RACIB. (HARRIS, 1961) by longer, serrate pinnules and larger sporangia. Spores of the two species are practically indistinguishable.

Locality: 550, Tyrma River near Alanap.

Age: Latest Jurassic-Lowermost Cretaceous (Tithonian-Berriasian).

Genus *Dicksonia* L'HERITIER

Dicksonia concinna HEER

Pl. 8, figs. 72—81, Pl. 9, figs. 88—95

Dicksonia concinna: HEER, 1876, p. 87, Pl. 16, figs. 1—7.
Dicksonia saportana: Ibid., p. 89, Pl. 17, figs. 1, 2.
Dicksonia glehniana: Ibid., p. 91, Pl. 17, fig. 4.
Dicksonia gracilis: Ibid., p. 92, Pl. 17, fig. 3.
Adiantites nympharum: Ibid., p. 93, Pl. 17, fig. 5.
Dicksonia burejensis: ZALESSKY, 1904, p. 182, 192. Pl. 3, figs. 1—4, Pl. 4, figs. 1—5.
Coniopteris burejensis: SEWARD, 1912, p. 6, Pl. 1, figs. 1—5, Pl. 3, figs. 18—21.
Coniopteris burejensis: NOVOPOKROVSKY, 1912, p. 5, Pl. 1, fig. 6, Pl. 2, figs. 4, 6.
Coniopteris burejensis: VACHRAMEEV & DOLUDENKO, 1961, p. 51, Pl. 1, figs. 1—5, Pl. 2, figs. 1—4.
Coniopteris hymenophylloides: Ibid., p. 52, Pl. 3, figs. 1—6.

Description: Bipinnate leaf fragments up to 25 cm long, 9 cm broad, margins parallel for a considerable distance. Rachis 2 mm thick, grooved, hairless. Pinnae of second order linear-lanceolate, up to 12 cm long, alternate, arising at 45°, bending backward, margins of adjacent pinnae at some distance or just in contact. Pinna rachises slender, grooved, narrowly webbed. Order of branching varying from katadromic to anadromic. Two major leaf types are recognized: (I) Pinnae rather short (50—60 mm). Basal pinnules opposite or one of them (more often the acroscopic one) nearer to the rachis. Transitions from anadromic to katadromic pattern traceable within a leaf. Sterile pinnules oblique, obovate or rhomboidal, asymmetrical, decurrent, about 5—10 mm long, 3—5 mm broad, margins incised into broad lobes. Typically there are 3 acroscopic lobes and 1—2 narrower basiscopic ones. Midrib passing up to the apex, giving of about 3 pairs of forking veinlets. (2) Pinnae longer, tapering gradually to the apex, distal pinnae like the larger pinnules. Pinnules usually in katadromic order, basal pinnule on basiscopic side arising from decurrent part of a pinna rachis or just from the leaf rachis. Pinnules lanceolate or elongate-rhomboidal, acute, more or less asymmetrical, decurrent, up to 10 mm long, margin divided into 4—5 paires of lobes with sharp or minutely indented apices. Venation dense, prominent.

In both types, basal pinnules unspecialized or the basiscopic one slightly reduced An aphlebiform basal pinnule (Pl. 8, fig. 73) was observed in a single specimen only.

Fertility varies from fully fertile leaves to occasional fertile pinnae or pinnules in predominantly sterile parts. Lamina of fertile pinnules more or less reduced. Sori borne in pairs on larger acroscopic lobes and singly on the apices of other lobes (Pl. 8, fig. 75), elliptical, about 1.2—2 x 0.7—1 mm. Indusium bivalvate. Outer valve robust, appearing as the slightly modified margin of a pinnule, occasionally expanded in a leafy web. In occasional specimens (Pl. 8, figs. 76—79) sori appear superficial rather than marginal due to the abnormal expansion of the outer valve. The inner valve, or true indusium, much thinner, fragile. Margins of valves smoothly rounded. Inner valve often wanting, exposing sporangia. Receptacle knob-like, terminal on a veinlet. Sporangia numerous, attached by long stalks, of different size (250—350μ long) and presumably of different ages. Annulus nearly vertical but avoiding the stalk, consisting of 25—28 thickened cells (Pl. 9, fig. 89). Stomium rather ill-defined, composed of 6—7 flat cells. Stalk showing four cell rows.

Spores spherical, diameter 38—46μ, amb rounded-triangular, trilete mark distinct, laesurae straight or slightly arched, bordered by very thin lips, mostly shorter than the spore radius, but sometimes extending to the amb. Exine smooth.

Remarks: Two leaf forms described above have been recognized as separate species by HEER and subsequent authors. HEER (1976) placed form (I) in *Adiantites nympharum* HEER and form (2) in *Dicksonia concinna* HEER. Twenty years later ZALESSKY proposed the obviously superfluous name *Dicksonia burejensis* ZAL. for the form (2). Unfortunately, SEWARD (1912) adopted this latter name to cover both forms. Subsequent authors followed SEWARD or restricted "*Coniopteris burejensis*" to form (2), while designating form (I) as *Coniopteris nympharum* (HEER) VACHR. or *C. hymenophylloides* (BRONGN.) SEW. (VACHRAMEEV & DOLUDENKO, 1961). Several authors used *Coniopteris nympharum* sensu. VACHRAMEEV non HEER. My approach is that of a lumper, because I see no advantage in having many ill-defined species repeatedly occuring together in localities of different ages. The characters of sori, indusia, sporangia and spores are fairly constant in different leaf forms. I venture to drop "*Coniopteris burejensis*" after more than fifty years of intense usage because (I) adoption of this name violated the principle of priority, (2) inconsistent application of this name caused confusion, and (3) the original assignment to *Dicksonia* is now confirmed. The indusium of the Burejan species is composed of two unequal valves, as in *Dicksonia* and *Culcita,* while the annulus is complete, as in *Dicksonia.* Indusia of *Coniopteris* are conceived as cup-shaped. Whether this is the case or not, *Coniopteris* is primarily a name for sphenopteroid leaves with marginal sori of unknown structure.

Locality: 514, Bureja River near the mouth of Umalta (locus classicus) and many other localities in the Bureja basin.

Age: Late Jurassic and Early Cretaceous.

Dicksonia arctica (PRYNADA) comb. nov.

Pl. 8, figs. 82—87, Pl. 9, fig. 96

Coniopteris arctica: PRYNADA, 1938, p. 24, Pl. 2, fig. 8.
Coniopteris onychioides f. *gracilis:* VACHRAMEEV & DOLUDENKO, 1961, p. 55, Pl. 6, figs. 1, 2, Pl. 14, fig. 4.

Description: Leaves small, slender. Rachis up to 1 mm thick, grooved, hairless. Pinnae linear-lanceolate, about 20 mm long. Pinna rachis very slender, narrowly webbed. Pinnules arising in anadromic order. Basal pinnule on acroscopic side larger than the rest, more symmetrical, tending to lie along the rachis. Other pinnules oblique, asymmetrical. In the middle portion of a leaf pinnules about 2.5—3 mm long, deeply divided into 3—5 elongate, acute, single-veined lobes. Acroscopic lobes longer than their conterparts. Distal pinnules entire, narrow oblanceolate or linear.

Fertile pinnules mostly entire, bearing a single terminal sorus or sometimes two close sori. Indusium bivalvate, consisting of unequal valves. Outer valve thicker, expanded beyond the sorus as a fringe, conspicuous against the black sorus compression due to its lighter reddish-brown colour. Sporangia pear-shaped, up to 300μ long. Annulus complete, consisting of 24—28 cells.

Spores spherical, mean diameter 45—55μ. Amb rounded-triangular. Laesurae distinct, simple, straight, nearly reaching to the amb, often of unequal length. Exine thick, smooth.

Remarks: VACHRAMEEV & DOLUDENKO (1961) considered this fern as a form of *Coniopteris (Birisia) onychioides* VASSIL & KARA-MURZA. However in the latter species the leaves are much larger, with rigid entire pinnules arising in catadromic order. On the other hand, the Burejan fern can be safely identified with *Coniopteris arctica* from the Kolyma basin. It differs from *Dicksonia concinna* mostly in smaller dimensions of more slender leaves, more deeply divided sterile pinnules, more reduced fertile ones and more expanded outer indusial valves. Exceptional specimens of *D. concinna* mentioned above (Pl. 8, fig. 76) show fertile pinnules and indusia very similar to those of *D. arctica.* The anadromic pattern of pinnules also occures in *D. concinna.* It seems probable that the younger species, *D. arctica,* had appeared as a rare phenotype in the polymorphic population of *D. concinna.* Later its frequency had increased and it was fixed as a dominant phenotype in the Barremian time.

Locality: 521, 522, Yorek River; 543, Bureja near the mouth of Adnikan.

Age: Barremian-Aptian.

Genus *Cyathea* SMITH

Cyathea tyrmensis (SEWARD) comb. nov.

Pl. 10, figs. 99—100, Pl. 11, figs. 109—122

Sphenopteris tyrmensis: SEWARD, 1912, p. 26, Pl. 1, fig. 6.

Description: Fragments of bipinnate leaves up to 20 cm long. Rachis about 1.5 mm thick, hairy (Pl. 10, fig. 107). Pinnae liniar-lanceolate, alternate or subopposite, arising at 60—70°, their margins in contact or slightly overlapping. Pinna rachises very slender, webbed. Pinnules arising in katadromic order, at more open angle on the acroscopic side than in the opposite row. Pinnules asymmetrical, acroscopically more or less contracted, basiscopically decurrent. The following forms of pinnules are recognized: (I) Linear-lanceolate, about 10 mm long, 3 mm broad, acute, only slightly asymmetrical, with 5—6 lobes on each side (Pl. 10, fig. 99). Basal lobes with their own midribs. Lobes distally reduced to serrations. Veinlets mostly simple, substance thick. (2) Smaller, lanceolate, about 2 mm broad, asymmetrical with larger serrations on the acroscopic margin (Pl. 10, fig. 104). Veins simple, substance thick. (3) Broadly lanceolate, about 12—13 x 4—5 mm, margin incised into 5—6 lobes or teeth, basal lobes with their own midribs and 2—3 pairs of arching veinlets (Pl. 10, fig. 105—106). Veinlets forking once or simple, substance delicate, venation more clearly shown and more dense than in (1) and (2). (4), as (3) but divided into narrow single-veined segments (Pl. 10, fig. 103).

The venation is the most constant character of this fern. Midrib strong, nearly straight. Lateral veinlets thin, but conspicuous, arising at very acute angle in katadromic order, arching along the margin, predominantly simple. Only in the broader pinnules do one or two pairs of veinlets fork at a narrow angle.

The sori occur mostly in partly fertile leaves. There were probably fully fertile leaves, but the evidence is unconvincing. Fertile pinnules are of the type (1) — (3), never of the type (4). Sori typically one per lobe or tooth, supplied by a simple veinlet or by the acroscopic branch of a forking veinlet. Larger basal lobes often bearing two close and nearly contiguous sori (Pl. 11, fig. 113). Sori rounded, about 1 mm in diameter, consisting of about 10 sporangia. Receptacle elevated, globose. Many specimens with desintegrated sori show naked receptacles. Indusia are mostly fragmented in transfer preparations (Pl. 11, fig. 115). Occasional better preserved indusia meniscoid (lens-shaped) rounded-elliptical, showing obscure outlines of polygonal cells (Pl. 11, fig. 117). Sporangia pear-shaped, average length 225—240μ, with a stalk about 50μ long, consisting of four cell rows. Cells of sporangial walls rectanguloid, 30—35μ long. Annulus nearly vertical but avoiding the stalk, consisting of 20—26 thick cells and 5—7 flat cells forming rather well-defined stomium (Pl. 11, figs. 118—121).

Spores about 64 per sporangium, trilete, diameter 32—35μ, amb rounded-triangular with straight or slightly concave sides. Trilete mark prominent, laesurae straight, somewhat shorter than the spore radius, often open, with narrow border showing indistinct pits (Pl. 11, fig. 122).

Remarks: SEWARD (1912) figured sterile leaves with pinnules of the types (3) and (4), see above. These leaves resemble *Cyathea microphylla* METT., while the types (1) and (2) are more similar to *C. multiflora* SM. (see TRYON, 1976). Meniscoid indusia are believed to be primitive in the genus. Sporangia and spores are smaller than in the living tree-ferns.

Among the Mesozoic ferns, *Cyathea ordosica* (CHU, 1963) is probably conspecific, but its sporangia and spores are not known. "*Polypodites*" *polysorus* PRYN. from Primorye (KRASSILOV, 1967) is similar, but has less polymorphic pinnules, and the annuli consist of a much smaller number of cells. *Aspidistes thomasi* from Yorkshire (HARRIS, 1961) agrees with the Tyrmian species in the leaf morphology, sori, sporangia and spores and differs mainly in the recurved margins of the fertile pinnules and unicellular glands.

Locality: 550, Tyrma River near Alanap.

Age: Latest Jurassic — Lowermost Cretaceous (Tithonian-Berriasian).

Palaeoecology

Lycopodites macrostomus is a rare plant associated with very small horse-tails in the near-shore (probably semiaquatic) environment. *Synlycostrobus tyrmensis* creeping shoots are abundant, forming microsinusia with thallose hepatics. *Osmunda diamensis* is common in the flood-plain facies. The mode of preservation suggests the leaf

rosettes lying flat on the ground probably covered with snow in winter and with flood debris in spring. It can be surmised from frequent association with *Czekanowskia* in Talynjan beds that *Osmunda diamensis* dominated the lower stratum of deciduous *Czekanowskia* forests. However the decline of *Czekanowskia* forests at the end of Talynjan time apparently had not affected *Osmunda diamensis* which persisted an age/stage longer and perished at the onset of Soloni (Valanginian) time.

Dicksonia concinna is the most ubiquitious species common in various facies. It is the dominant and sometimes only plant fossil in the delta front facies. It can be suggested, that this fern was an active colonizer of new habitats and formed fern marshes on the shore of the retreating sea. It was important also in the lower strata of lowland forest with *Phoenicopsis (Stephenophyllum)* or *Elatides* as major dominants. The longer pinnule phenotype (form 2, see description above) predominated in the fern marshes whereas in the forest population form I with broader pinnules was more frequent. The supposed transition from *D. concinna* to *D. arctica* (see above) was associated with a general change of environments and vegetation in pre-Barremian time (KRASSILOV, 1973b).

The abundance of *Cyathea* in the Tyrmian locality (50° North) is in marked contrast with its extreme paucity in the Bureja basin about 140 km to the North (only two specimens were recorded near the south border of this area). KLUKIA, a key genus of the southern floristic province (BARNARD, 1973), is still common in the Tyrmian locality, but not represented at the Bureja. Tyrma is also the northernmost outpost of *Pachypteris* and *Araucaria.* These data are self-explanatory in terms of climatic zonation.

Evolutionary significance

Lycopods

Lycopodites macrostomus combines some characters of *Selaginella* (ligule) and *Lycopodium* (shoot morphology, epidermal structure). *Synlycostrobus tyrmensis* represents an evolutionary line not known among extant lycopods. The inflorescences of this plant are like a protoype of the coniferous compound strobilus. Elementary strobili partially fused with subtending bracts are analogous to the conifer seed-scale complex. It is an example of striking parallelism in remotely related groups.

Ferns

In HEER's time, most ferns had been placed arbitrarily in various extant genera on the basis of superficial resemblance in gross leaf morphology. BRONGNIART had initiated morphological classification of fossil fern leaves which, though based on characters of little taxonomic value in extant ferns (e. g., pinnule shape or venation) proved useful and was widely applied in paleobotany. Meanwile another type of classification, championed by SEWARD, was mirroring the system of extant ferns using their generic names with "ites" to make allowance for imperfection of the fossil material. HARRIS in his masterly taxonomic treatment of the Yorkshire Jurassic ferns has adopted the leaf-genera *Sphenopteris* and *Cladophlebis* for sterile leaves labeled as "unclassified", while other ferns showing sufficient diagnostic characters have been placed either in extinct natural genera, such as *Klukia, Stachypteris* and (less fortunately) *Coniopteris* or in the extant genera, e. g., *Marattia* or *Dicksonia.* Indeed, the traditional practice of adding "ites" is hardly justified when fossil species does not transgress the limits of variation seen in the living species of a genus.

Osmunda diamensis was a dominant Jurassic fern in the Siberian province while *Todites* and *Osmundopsis* were restricted to the southern province. Dimorphic leaves and the reduction of lamina in fertile pinnae probably developed independently in both lineages, the Siberian one leading to extant *Osmunda. O. diamensis* is like *Osmundastrum* in such characters as the leaf dimorphism, sporangia and spores, while the leaves are bipinnate as in *Osmunda.* It was probably close to the hypothetical common ancestor of *Osmunda* and *Osmundastrum* indicated by anatomical studies of MILLER (1971). Leaves of *O. regalis* type appear not earlier than Turonian *(O. asuwensis* MATSUO) while *Plenasium*-like fossils are recorded from the Danian (author's collection, unpublished).

Mass appearance and initial diversification of the Dicksoniaceous ferns happened not earlier than the Toarcian or Aalenian (as evidenced by fossil floras of Caucasus, Krakov and Bornholm). They reached their peak diversity in the Bajocian when the Cyatheaceae also appeared. Ferns with the marginal sori on sphenopteroid pinnules

had been placed in *Thyrsopteris, Dicksonia* or *Dennstaedtia.* The Jurassic and Early Cretaceous species were subsequently transferred into *Coniopteris,* while the Late Cretaceous species remained "*Dennstaedtia*".

Several morphological groups can be recognized within *Coniopteris:* (I) Bipinnate leaves with short pinnae and pinnules divided into single-veined lobes, as in *C. angustiloba* BRICK or *C. simplex* (LINDL. & HUTT.) HARRIS. BRICK (1937) described a rhizome bearing *C. angustiloba* leaves and proved that it was actually a very small fern. (2) Bipinnate leaves with long pinnae and (2a) basal pinnules showing filiform processes, fertile pinnules reduced, as in *C. hymenophylloides* (BRONGN.) SEW. or (2b) basal pinnules unspecialized, fertile pinnules only slightly reduces, as in "*C. burejensis*" or (2c) fertile pinnules reduced to a little more than a stalked sorus, as in *C. onychioides* VASSIL. & KARA-MURZA, and (3) tripinnate leaves with short penultimate pinnae, as in *C. murrayana* (BRONGN.) BRONGN. or *C. kirgisica* BRICK.

SAMYLINA (1972) proposed the generic name *Birisia* for the type (2c) with basal basiscopic pinnules arising from the leaf rachis. The latter is a normal condition in *Dicksonia concinna* (Pl. 8, fig. 72).

Ferns with cladophleboid pinnules had been assigned to *Eboracia, Gonatosorus (Heidenia), Disorus* and *Kylikipteris.*

Interpretation of indusia of all these genera was influenced by early comparison with *Thyrsopteris.* Indusia of *Coniopteris* were described by HARRIS as cup-shaped, though APPERT (1973) suggested that some *Coniopteris* were related to *Dicksonia* or *Culcita (Culcitites).* SAMYLINA claimed that *Birisia* was a member of Thyrsopteroideae, though no attempt was made to study the sori. In *Eboracia* and allied genera indusia are again cup-shaped and the name *Kylikipteris* is derived from "wine cup" and refers to the shape of the sori. I studied several species of *Coniopteris.* In all of them indusia were fairly constant, never cup-shaped but definitely bivalvate with equal (Pl. 9, fig. 97) or unequal valves. Thus their affinities are with *Cibotium, Dicksonia* and *Culcita* rather than with *Thyrsopteris* or *Dennstaedtia.* The Late Cretaceous species in my collection from Sakhalin (unpublished) is very much like Jurassic *Coniopteris* and belongs rather to *Dicksonia* than *Dennstaedtia.* I doubt that the Yorkshire ferns *Eboracia lobifolia* with alleged cup-shaped indusia and *Dicksonia mariopteris* with bivalvate indusia (WILSON & YATES, 1953) are specifically distinct. One can argue that in some species of *Coniopteris* indusia are still cup-shaped, but this cannot be accepted without reservation. In any event an application of the name *Coniopteris* must not depend on the interpretation of indusia. There should be at least three levels in the classification of fossil ferns: (1) for sterile leaves only, (2) for fertile leaves showing position of sori, but no details of their structure, and (3) for those showing indusia, receptacles, sporangia and spores. Such genera as *Coniopteris* belong in the second level and should remain there even when their type-species were raised to the third level: this is an advantage of parallel systems of natural, form- and organ-genera in paleobotany. In the first level, the Mesozoic Dicksoniaceous ferns can be assigned to *Sphenopteris, Cladophlebis* and *Lobifolia* while only three genera seem needed in the second level:

Coniopteris: pinnules sphenopteroid, sori lateral, or terminal, or both.
Eboracia: pinnules cladophleboid, sori lateral.
Kylikipteris: pinnules cladophleboid or much reduced and stalk-like, sori terminal.

In *Dicksonia arctica* sori are more displaced from the margin than in its putative ancestral species *Dicksonia concinna* (see above). This evolutionary line may lead to superficial sori of some Cyatheaceae as it was suggested by HOLTUM & SEN (1961): However the possibility of independent origin of indusia in the Cyatheaceae from superficial cells close to the midrib indicated by developmental studies of TRYON & FELDMAN (1975) cannot be ruled out, the more so that the early Cyatheaceae were fairly distinct from the early Dicksoniaceae. In the Bajocian *Aspidistes thomasii* (HARRIS, 1961) sori are on veinlets beyond the fork. Drawings suggest a hemitelioid indusium arising from near the midrib, as the inner lobe of the indusium in *Cyathea fulva* (TRYON & FELDMAN, 1975). In the Wealden *Aspidistes harrisii* (WATSON, 1969), fertile pinnules are reduced and strongly recurved, surrounding one to few sori as in the Far-Eastern Cretaceous species *Alsophilites nipponensis* (KRASSILOV, 1967) or extant *Alsophila gleichenioides.*

In modern classification of the tree ferns (TYRON, 1970), emphasis is placed on such characters as the structure of the petiole scales, not available in fossils. Indusial characters are claimed to be variable within a genus. However some types of indusia can be traced back to Jurassic time constantly correlating with other morphological characters.

If indusia of *Aspidistes* were hemitelioid as suggested above, then the chronological succession is from the hemitelioid type (Middle Jurassic) to meniscoid (Late Jurassic, *Cyathea tyrmensis*) and to cyathiform (Cretaceous, *Cyathea ("Gleichenites") sachalinensis* KRYSHT.) as was hypothesized by TRYON & FELDMAN (1975).

There are still many fossil ferns of Cyathean aspect with superficial sori of unknown structure. They are sometime assigned to *Polypodites*, but *Teilhardia* SEWARD seems preferable as noncommitial generic term for the second level classification.

Summary

The fossil flora of the Bureja is the most representative sample of the temperate Late Jurassic-Early Cretaceous vegetation of the Arctomesozoic realm. Major fern species of this flora are *Osmunda diamensis* (SEW.) comb. nov., *Dicksonia concinna* HEER (= *Coniopteris burejensis* (ZAL.) SEW.) and *Dicksonia arctica* (PRYN.) comb. nov., while the Tyrmian locality about 140 km to the South yielded abundant remains of *Klukia tyganensis* KRASSIL. and *Cyathea tyrmensis* (SEW.) comb. nov. The appearance of these ferns marks the southern limit of the Arctomesozoic realm.

Lycopods are described from the Burejan and Tyrmian localities for the first time. They show that evolutionary potentials of this group were still not exhausted in the Jurassic time. *Synlycostrobus tyrmensis* gen. et sp. nov. has developed "inflorescences" of the same architecture as the compound strobilus of conifers.

The Tyrmian species of *Klukia* demonstrates impressive constancy of the spore characters which are taxonomically important in the Schizaeaceae. Two evolutionary lines can be recognized within this family in the Mesozoic: (1) *Klukia-Stachypteris* with tuberculate or reticulate exine, related to *Lygodium* and (2) *Ruffordia-Schizaeopsis* with striate exine, related to *Anemia* and *Mohria*. These distinctions were ignored by REED (1947) who lumped all extinct genera in the "Klukiaceae".

The siberian province is considered as a center of origin of the genus *Osmunda*. The Mesozoic Osmundaceous genera with apical annulus, *Todites* and *Osmundopsis*, have been restricted to the southern province.

In the form-genus *Coniopteris*, indusia are mostly bivalvate as in *Dicksonia*, and not cup-shaped as in *Thyrsopteris* or *Dennstaedtia*.

In *Dicksonia concinna*, the outer indusium valve is expanded beyond the sorus and in its derivative species, *D. arctica*, sori are still further displaced from the margin. Some superficial sori might have arisen in this way, although the Cyatheaceae have been already fairly distinct from the Dicksoniaceae at the time of their appearance in the Middle Jurassic. The earliest Cyatheaceae probably developed hemitelioid indusia which were succeeded by the meniscoid form in the Late Jurassic species. The cyathiform indusia first appeared in the Late Cretaceous *"Gleichenites"*.

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Explanation of Plates

Plate 1

Figs. 1—14. *Lycopodites macrostomus* sp. nov.
- 1—3. Branching shoots. x 3 and 7.
- 4. Cleared leaf showing stomata. x 16.
- 5. Apical part of the same leaf. x 60.
- 6. Leaf showing marginal teeth. x 60.
- 7. Leaf apex with large teeth. x 146.
- 8—10. Different leaf shapes. x 60.
- 11. Leaf base. x 146.
- 12. Awl-shaped leaf. x 60.
- 13. Epidermis. x 146.
- 14. Stoma. x 395.

All specimens from locality 514, Umalta.

Plate 2

Figs. 15—30. *Synlycostrobus tyrmensis* gen. et sp. nov.
- 15—16. Branching shoots. x 3.
- 17—19. Parts of the same shoots showing lateral and dorsal leaves. x 7.
- 20—21. Lower isophyllous parts of the shoots. x 7.
- 22. Fertile shoot bearing strobili. x 3.
- 23—24. Strobili of the same shoot. x 7.
- 25—26. Another fertile shoot from the same slab. x 3 and 7.
- 27. Strobili of the shoot in the figs. 25—26. x 7.
- 28. Fertile shoot with empty strobili. x 3.
- 29—30. Strobili of the same shoot. x 7.

All specimens from locality 550, Tyrma.

Plate 3

Figs. 31—36. *Synlycostrobus tyrmensis* gen. et sp. nov.
- 31. Transfer preparation of leaves. x 60.
- 32. Sporangium. x 600, SEM.
- 33. Spore showing trilete mark on the inner exine layer. x 4000, SEM.
- 34. Spore, folded outer exine layer, x 4000, SEM.
- 35. Spore with a smooth protuberance (germinated?). x 4000, SEM.
- 36. Sculpture of exine. x 6000, SEM.

Plate 4

Figs. 37—43. Megaspores provisionally assigned to *Synlycostrobus tyrmensis* gen. et sp. nov.
37. Proximal aspect. x 180, SEM.
38. Ornamentation of the contact facets. x 500, SEM.
39. Smaller megaspore. x 180, SEM.
40—41. Megaspore showing inner body (mesosporium). x 252.
42. Distal aspect. x 180, SEM.
43. Ornamentation of the distal wall. x 500, SEM.

All specimens from locality 550, Tyrma.

Plate 5

Figs. 44—52. *Osmunda diamensis* (SEW.) comb. nov.
44. Part of a leaf rosette. x $\frac{1}{4}$. Locality 517, Umalta.
45—46. Sterile leaves. x 1. Locality 511, Tschagdamyn.
47. Fertile pinnules. x 7. Bore hole 32, Bureja.
48—49. Sporangia. x 60. Locality 515, Umalta.
50—51. Cleared pinnules showing stomata. x 20. Locality 515, Umalta.
52. Epidermis. x 60. Locality 515, Umalta.

Plate 6

Figs. 53—59. *Osmunda diamensis* (SEW.) comb. nov.
53—54. Sporangia showing lateral annulus. x 140, SEM.
55—56. Spores. x 600.
57. Distal wall ornamentation. x 10 000, SEM.
58. Spore, distal aspect. x 2000, SEM.
59. Spore, proximal aspect. 2000, SEM.

All specimens from locality 515, Umalta.

Plate 7

Figs. 60—71. *Klukia tyganensis* KRASSIL.
60. Sterile leaf. x 1.
61. Sterile pinnules. x 3.
62. Fertile leaf. x 1.
63.—64. Fertile pinnules. x 1 and 3.
65—68. Sporangia showing apical annulus. x 7 (fig. 66) and 16.
69. Spore, distal aspect. x 1500, SEM.
70. Spore, proximal aspect. x 1500, SEM.
71. Ornamentation of contact facets. x 2000, SEM.

All specimens from locality 550, Tyrma.

Plate 8

Figs. 72—81. *Dicksonia concinna* HEER.
72—73. Sterile leaves, note the position of basal pinnules on basiscopic side and an occasional aphlebiform in fig. 73. x 1.
74. Fertile pinnae. x 1.
75. Pinnule from the same specimen showing receptacles and outer indusial valves. x 7.
76. Fertile pinna with unusually expanded indusia. x 3.
77—79. Submarginal sori of the same pinnae. x 7.
80. Outer valve of indusium. x 60.
81. Two indusial valves, the inner one (above) is turned apart during preparation. x 60.

All specimen from locality 514, Umalta.

Figs. 82—87. *Dicksonia arctica* (PRYN.) comb. nov.
82. Fertile pinna. x 1.

83. Sterile pinnae. x 1.
84—85. Fertile pinnules. x 7.
86—87. Transfer preparations of sori showing expanded outer indusial valve. x 7.

Plate 9

Figs. 88—95. *Dicksonia concinna* HEER.
88. Sporangium showing stalk cells. x 300, SEM.
89. Sporangium showing complete annulus avoiding stalk. x 300, SEM.
90—91, 93. Cleared sporangia, stomium is seen in fig. 91. x 146.
92. Sorus. x 45.
94—95. Spores. x 3000 and 1800, SEM.

All specimens from locality 514, Umalta.

Fig. 96. *Dicksonia arctica* (PRYN.) comb. nov., spore. x 3000, SEM. Locality 544, Adnican
Fig. 97. *Coniopteris* sp., bivalvate indusium with equal valves. x 45. Locality 514, Umalta.
Fig. 98. Same sorus, macerated. x 69.

Plate 10

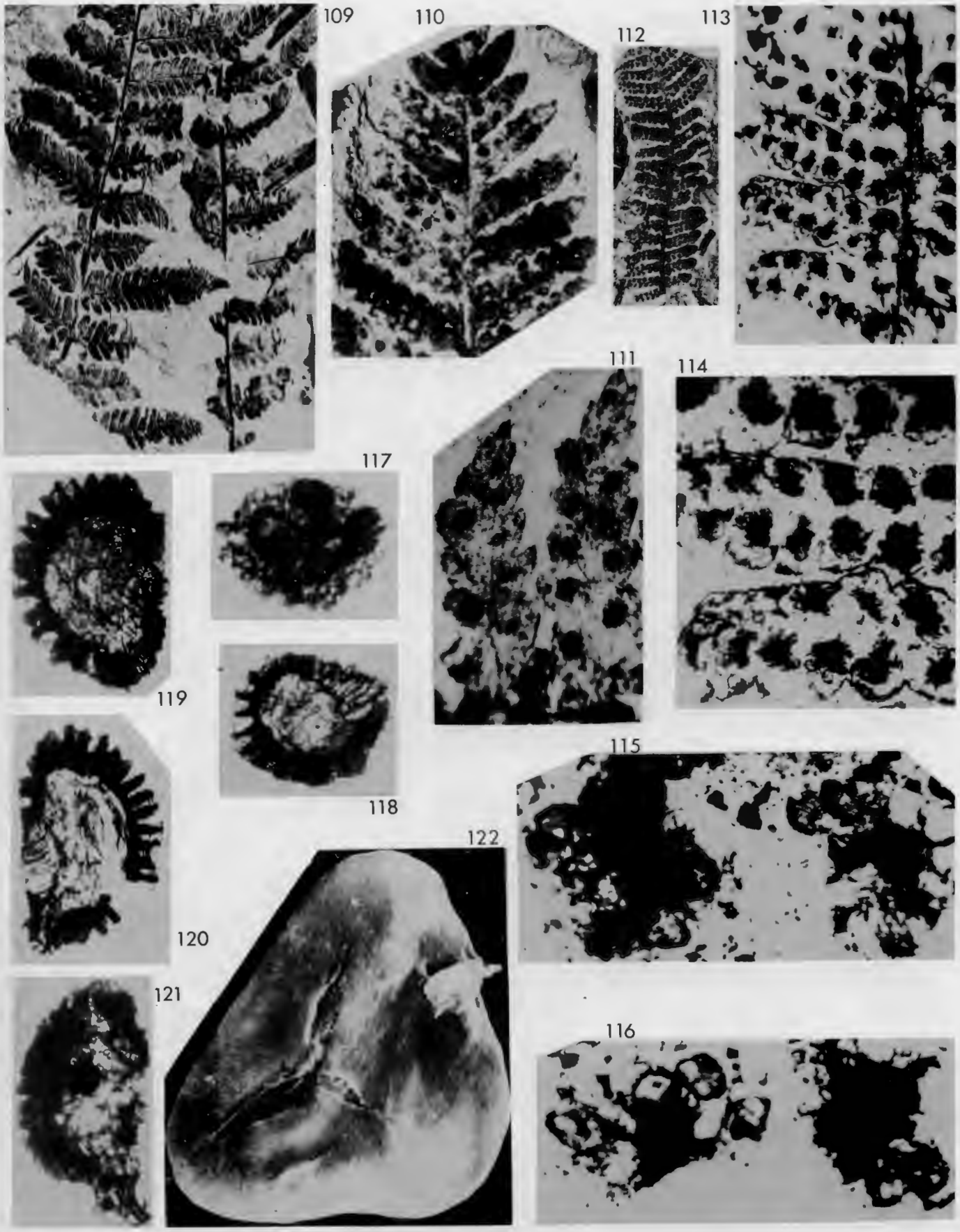
Figs. 99—108. *Cyathea tyrmensis* (SEW.) comb. nov.
99. Partially fertile leaf. x 1.
100—102. Sterile pinnae. x 1.
103—106. Different shapes of pinnules. x 7.
107. Leaf rachis showing pits. x 7.
108. Part of a rachis bearing sterile pinnae. x 1.

All specimens from locality 550, Tyrma.

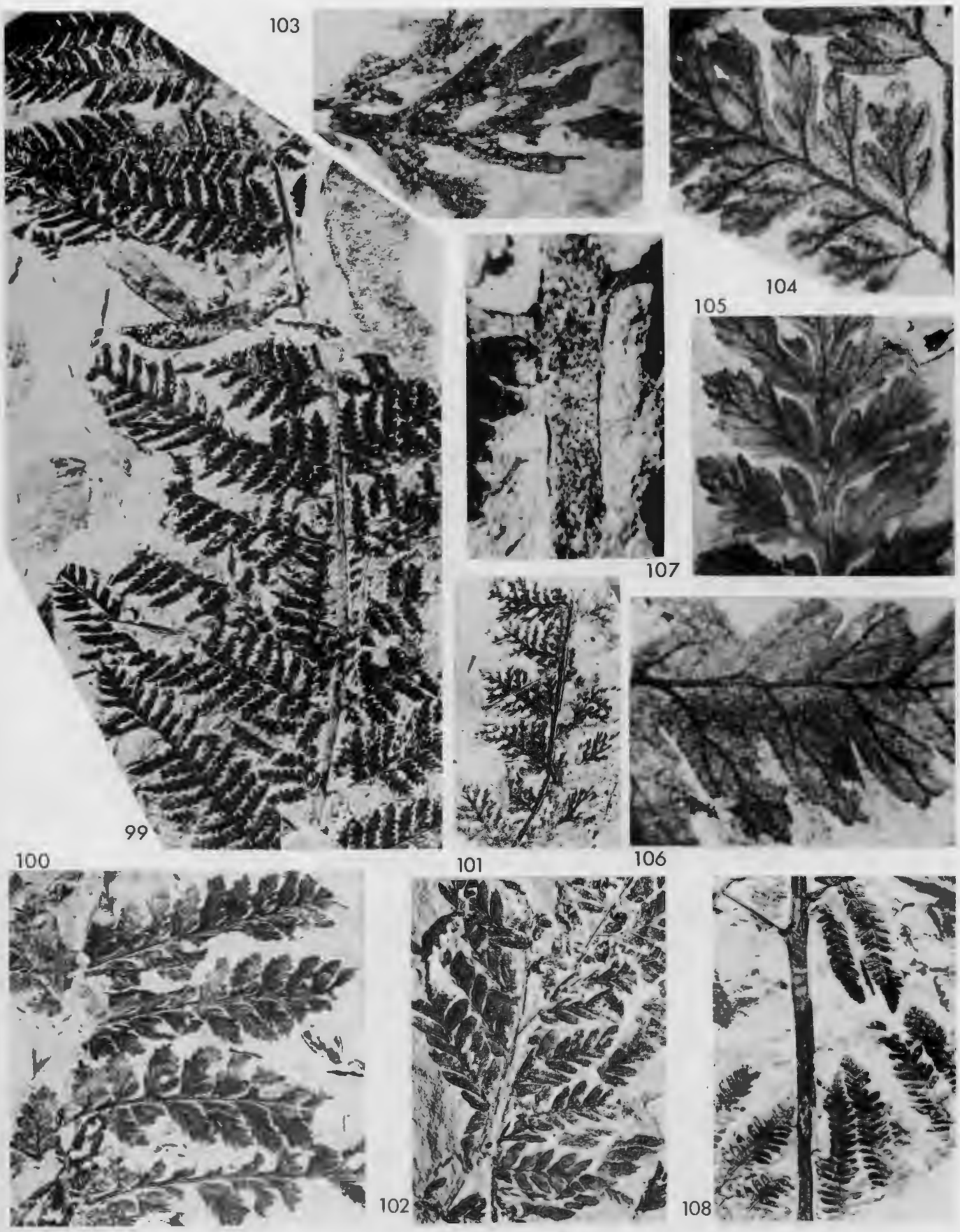
Plate 11

Figs. 109—122. *Cyathea tyrmensis* (SEW.) comb. nov.
109. Sterile pinnae. x 1.
110—111. Fertile pinnules showing sori. x 3 and 7.
112. Fertile pinna. x 1.
113—114. Transfer preparations of the same pinna. x 3 and 7.
115—116. Transfer preparations of sori showing remains of indusia. x 60.
117. Receptacle with several sporangia and meniscoid indusium. x 60.
118—121. Sporangia showing annulus and stomium. x 166.
122. Spore. x 4000, SEM.

All specimens from locality 550, Tyrma.



Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.



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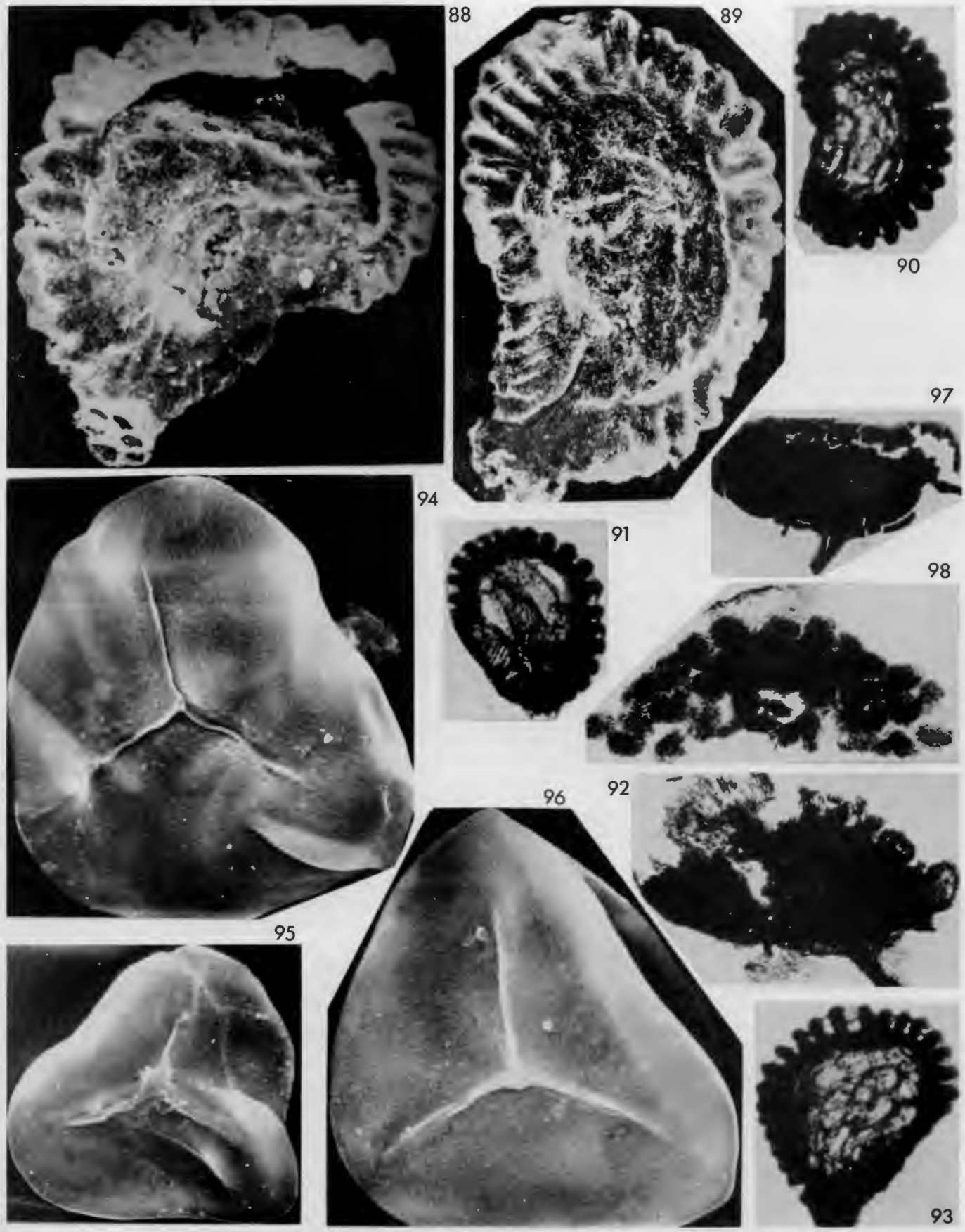
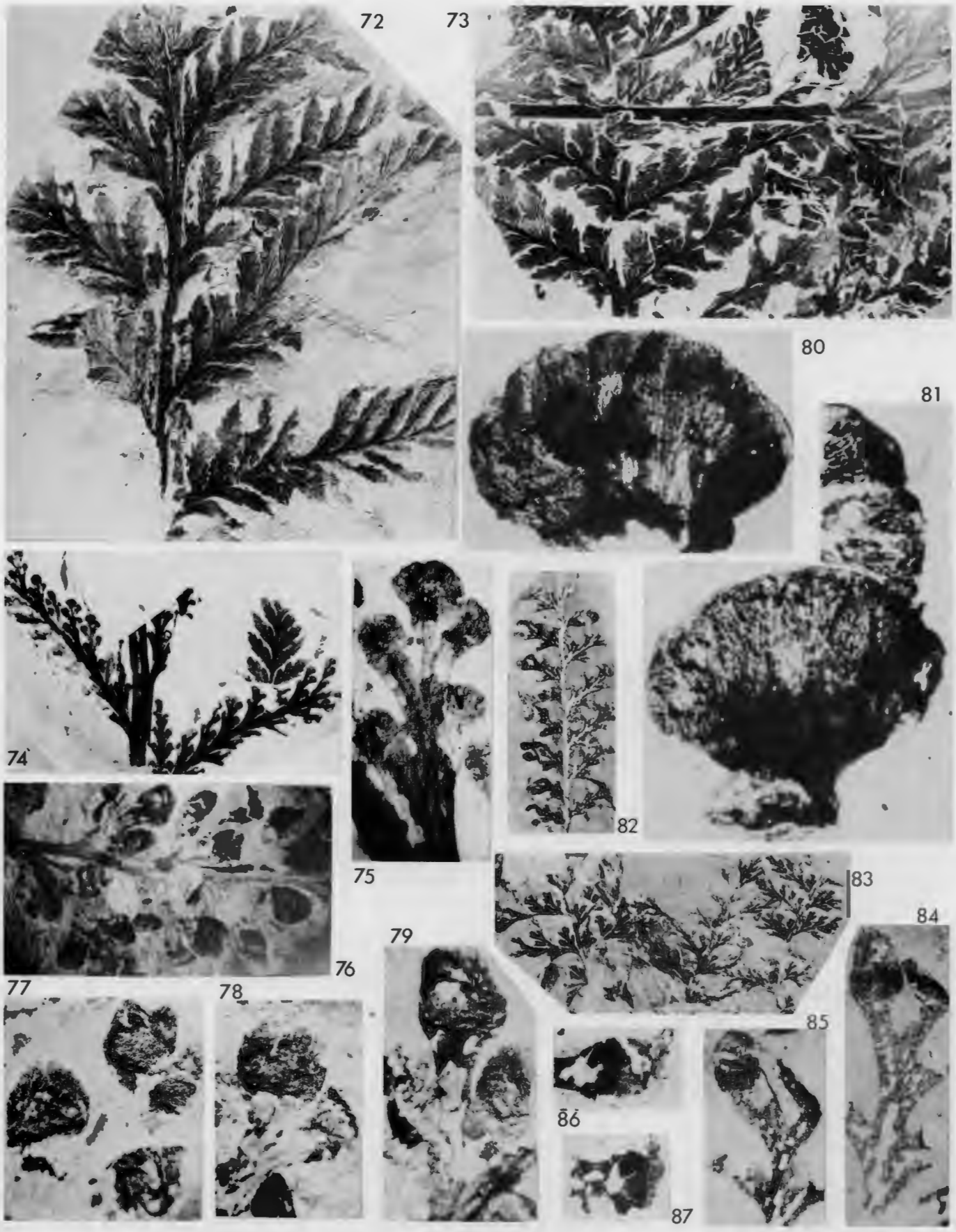
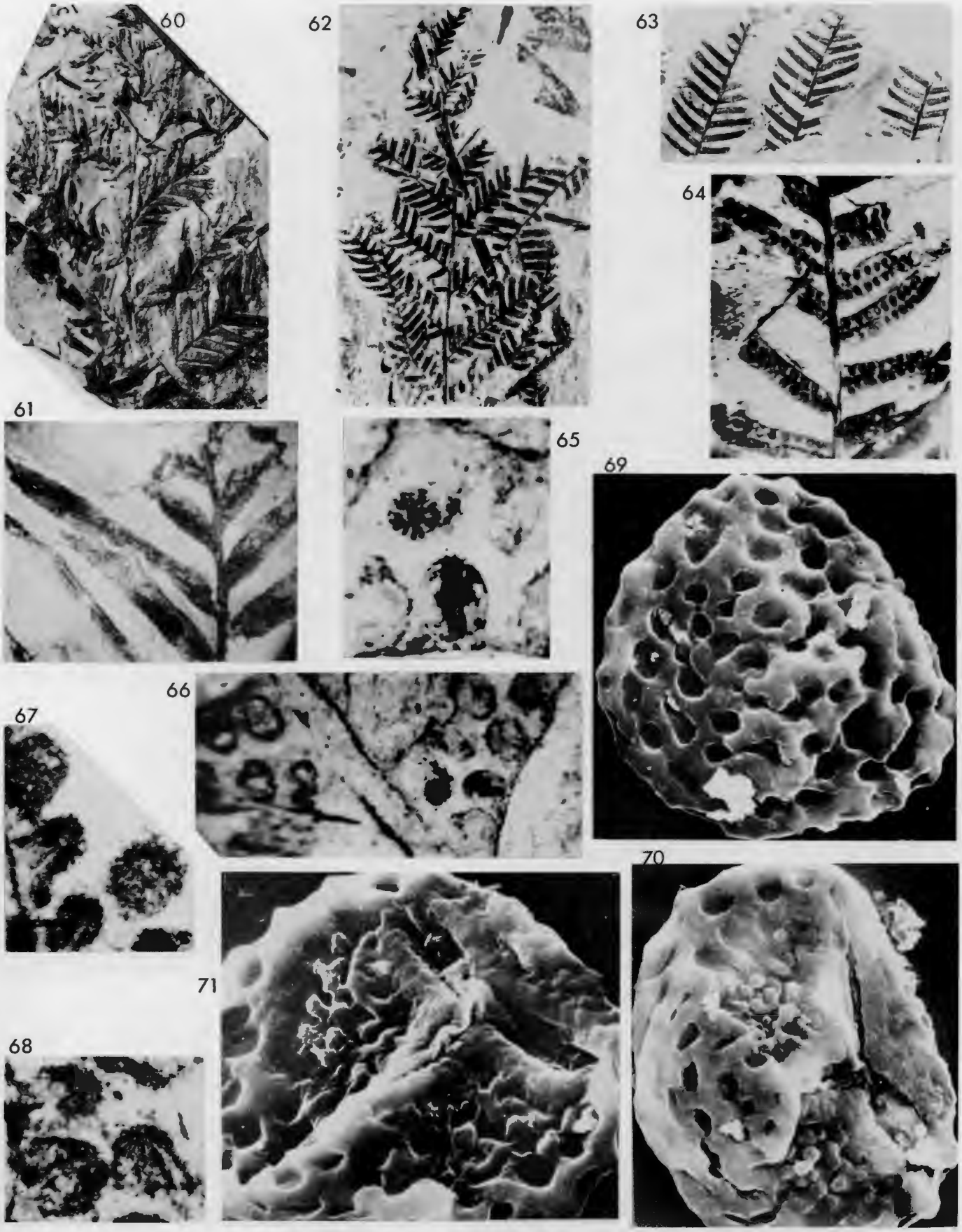


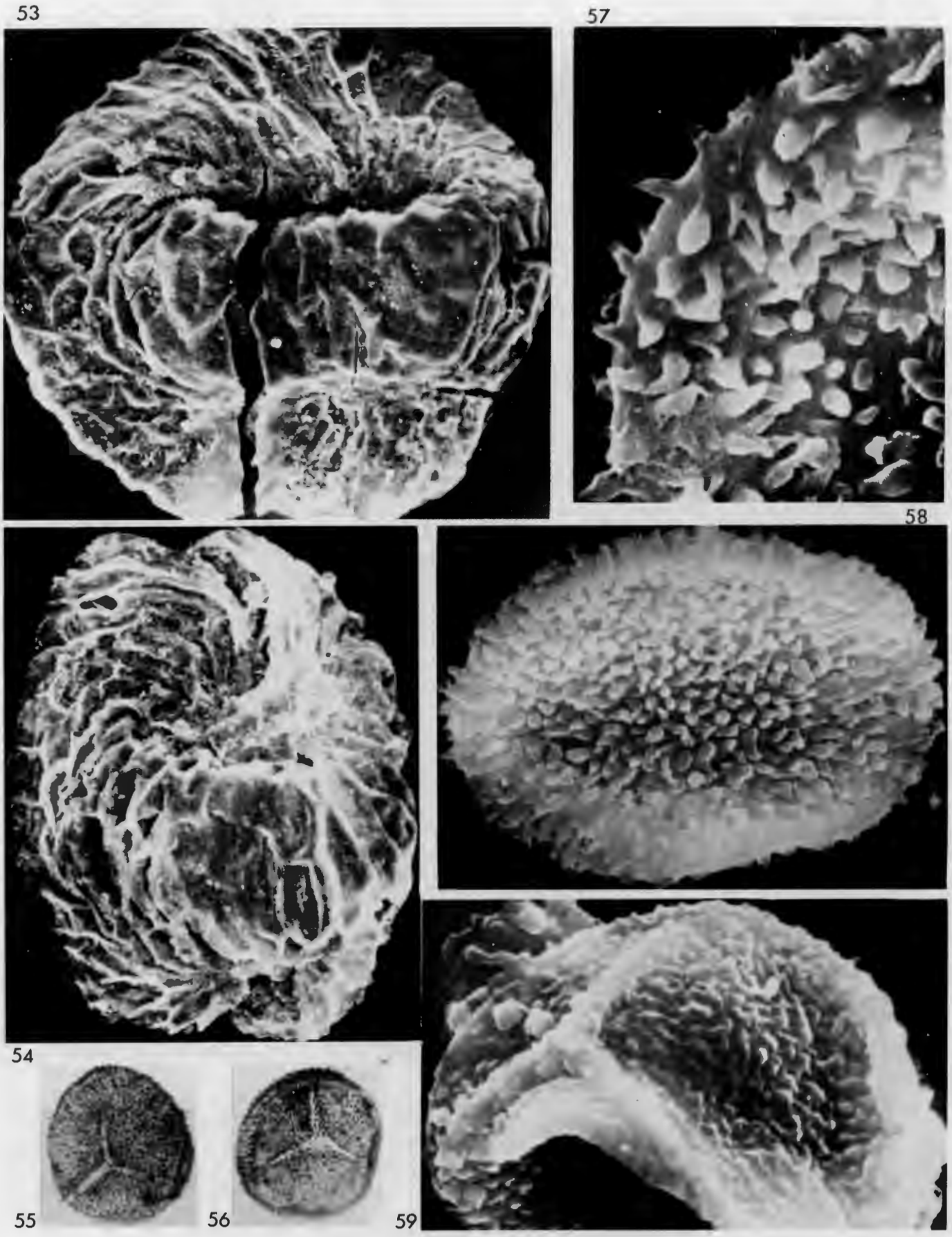
Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.



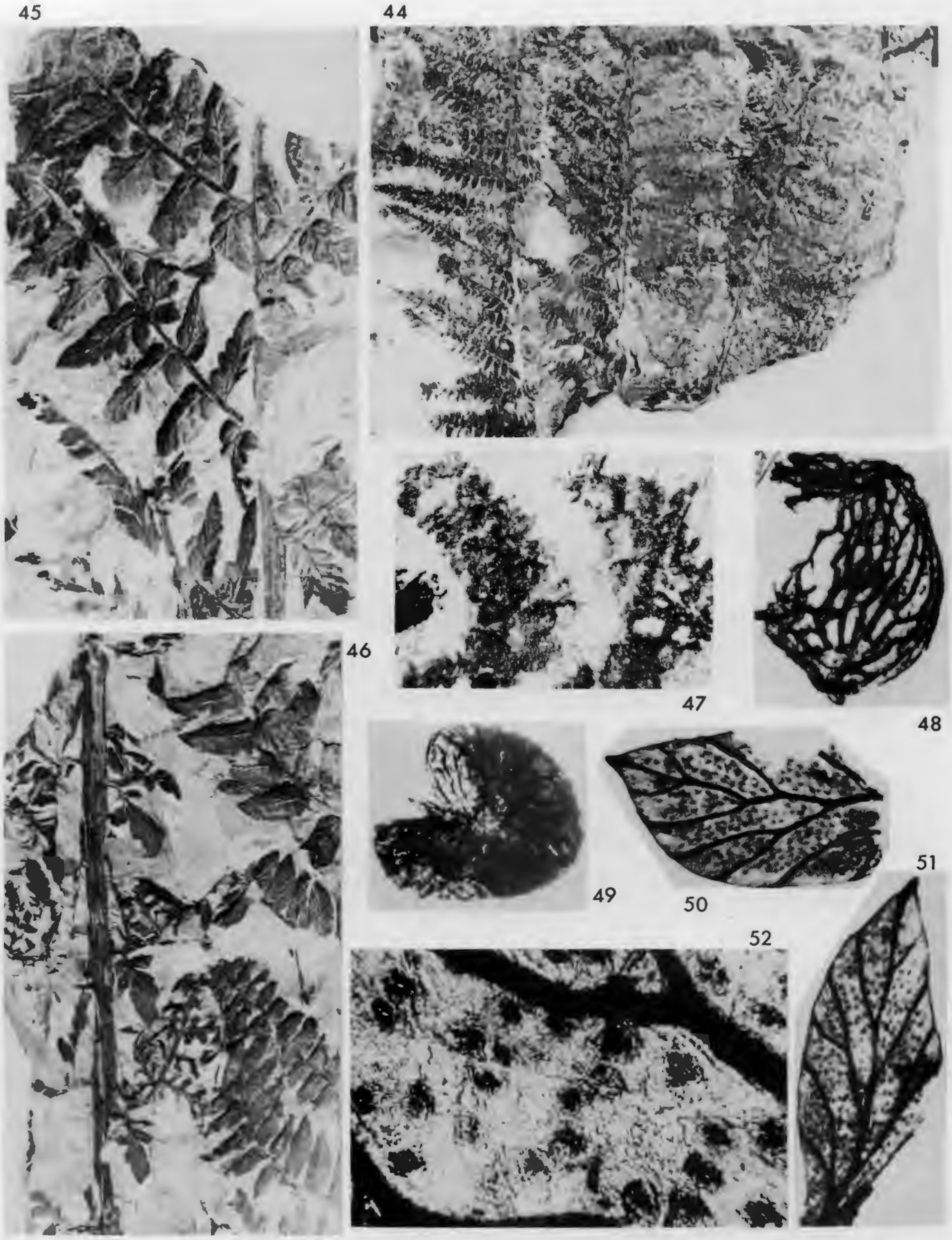
Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.



Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.



Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.



Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.

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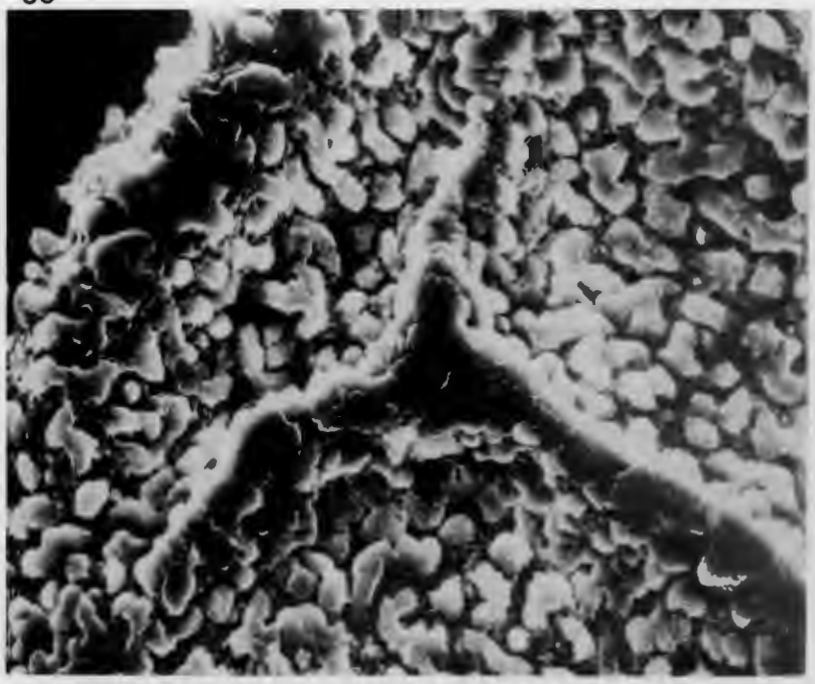

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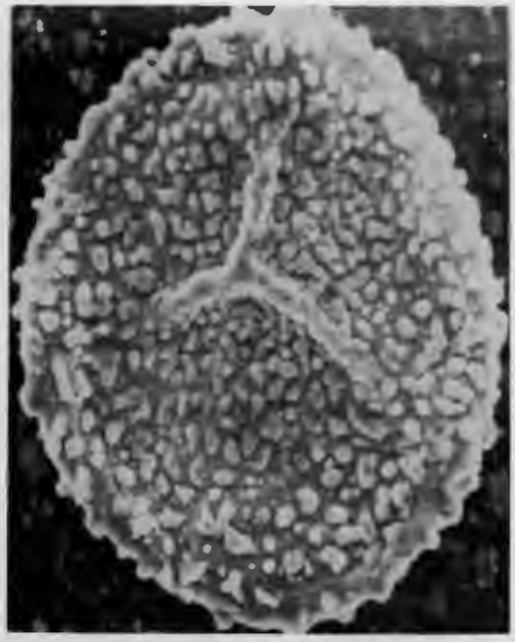

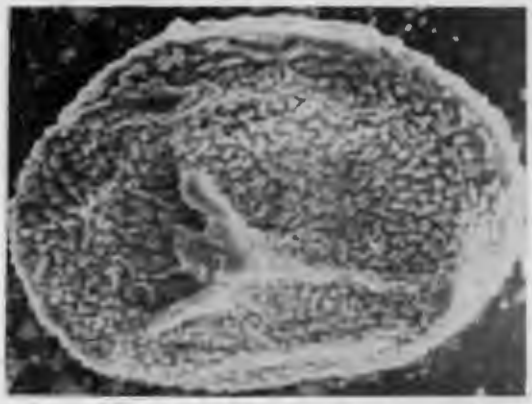

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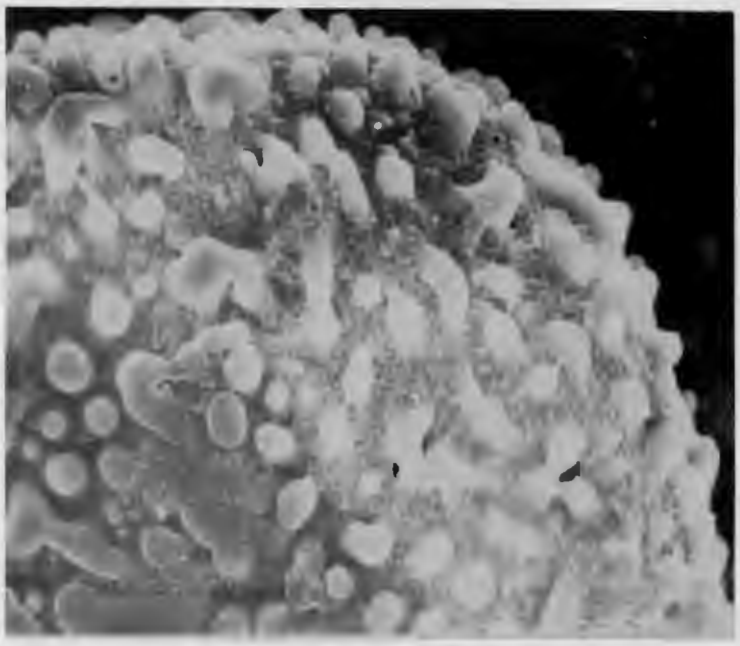

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Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.

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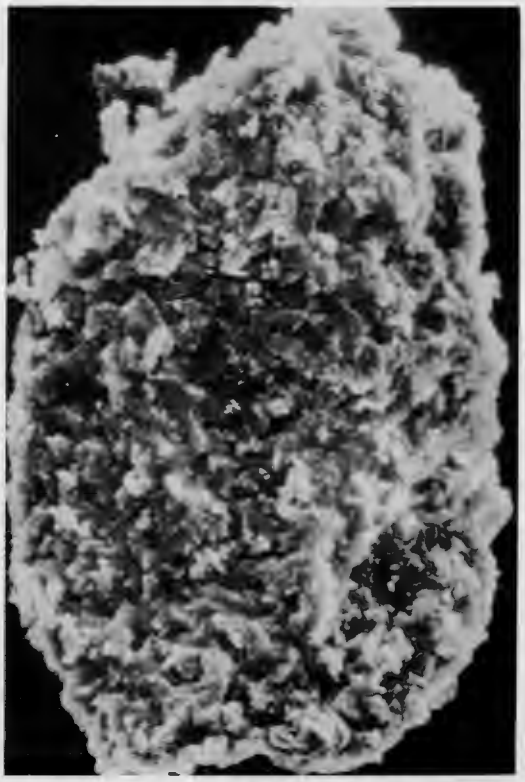

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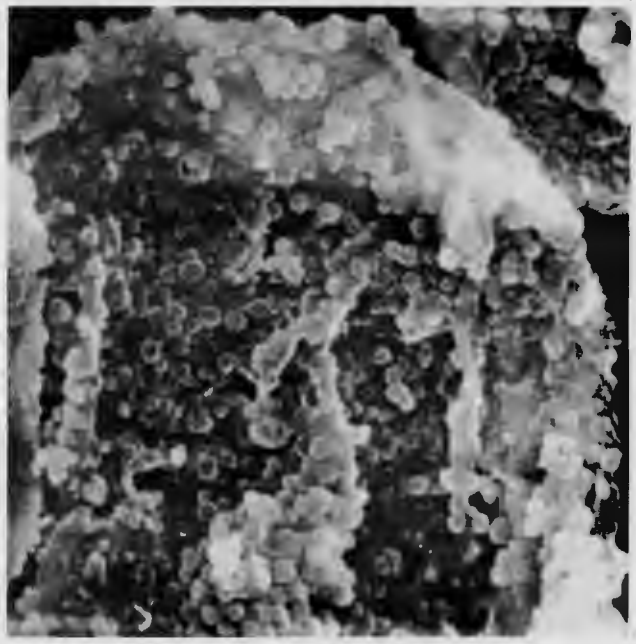

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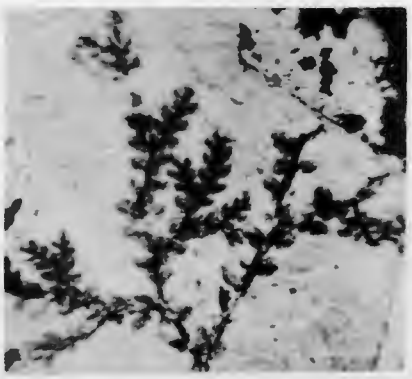
Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.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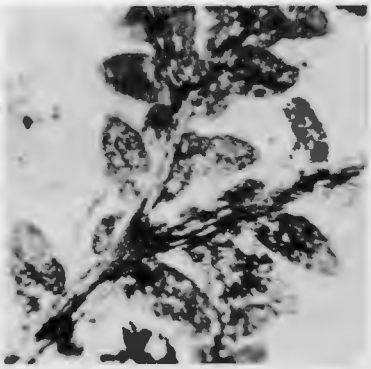
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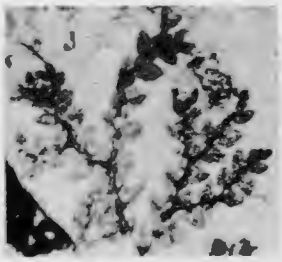
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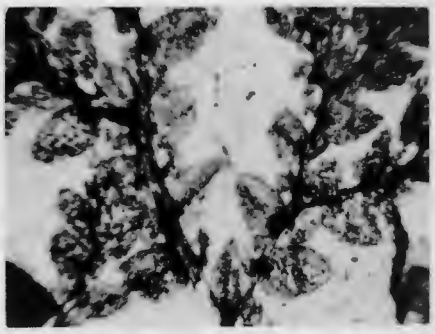
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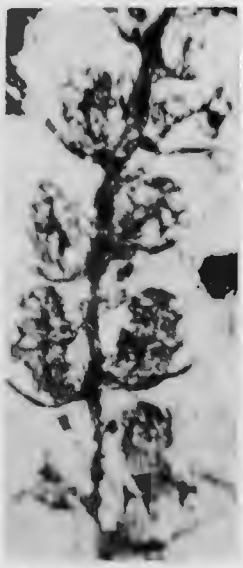
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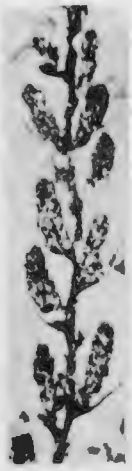
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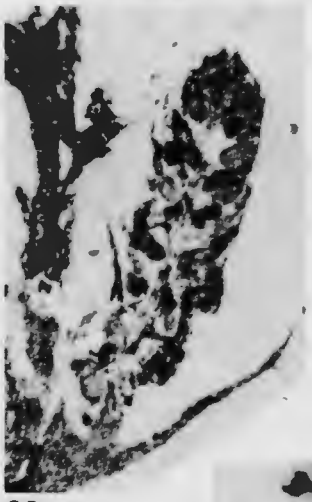
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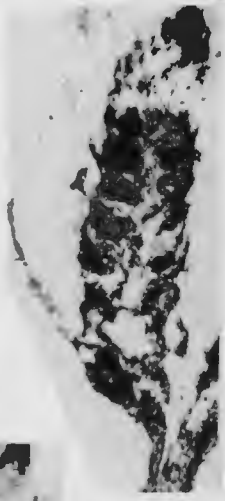
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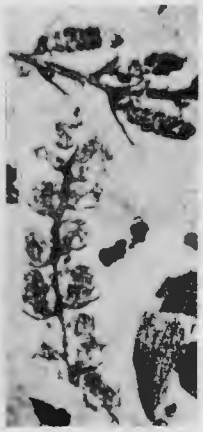
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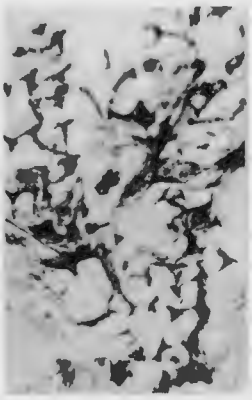
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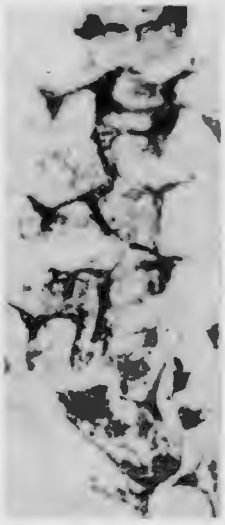
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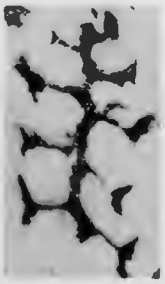
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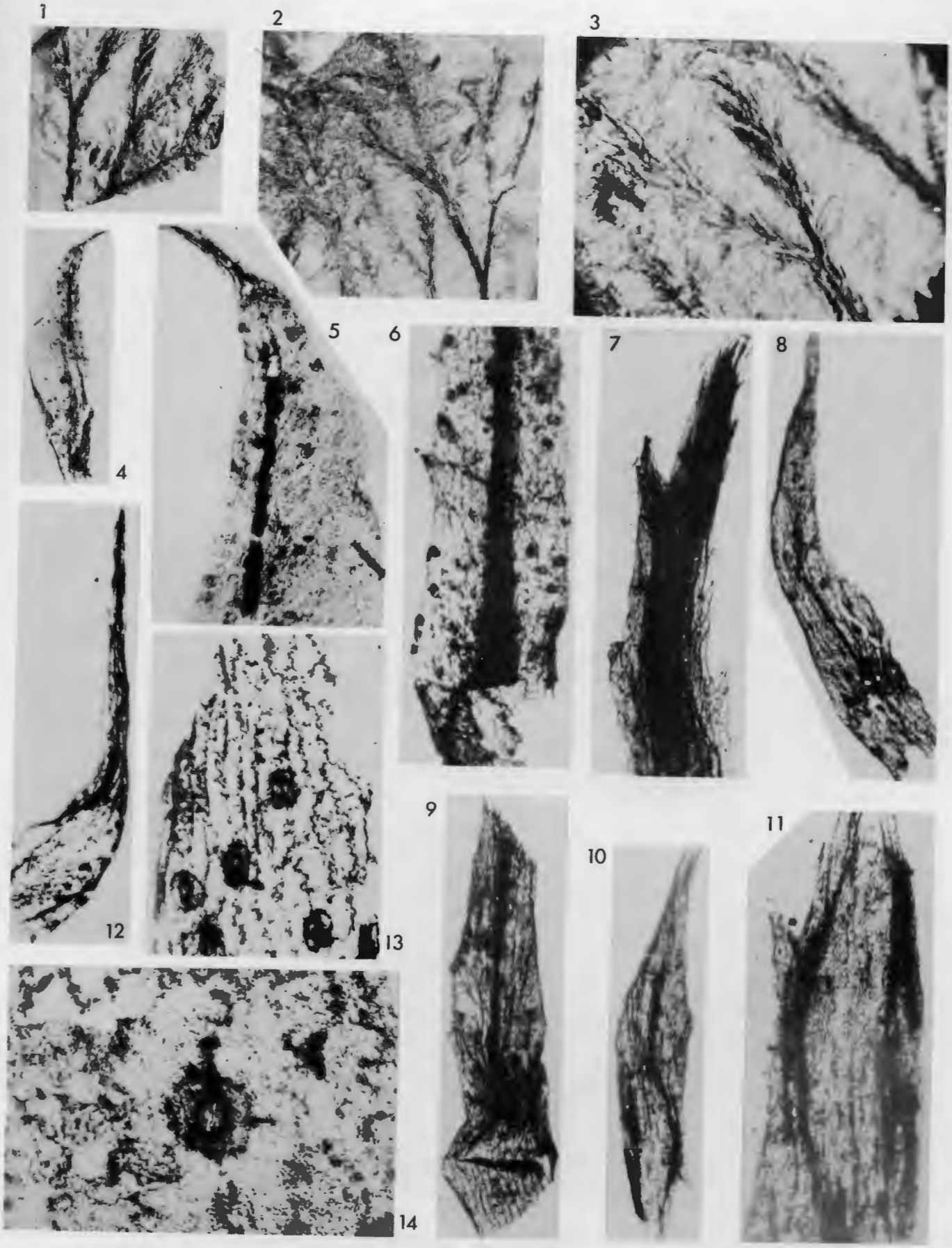
Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.



Valentin Krassilov: Mesozoic lycopods and ferns from the Bureja basin.