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FURTHER CONTRIBUTIONS ON THE NON-VASCULAR CRYPTOGAMS FROM THE MIDDLE GONDWANA (TRIASSIC) BEDS OF NIDPURI, INDIA — PART II

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ABSTRACT

The carbonized compressions of a filamentous fossil *Algacites oogonifera* sp. nov. and three species of bryophytes, viz., *Hepaticites riccardioides* sp. nov., *H. metzgerioides* Walton and *H. foliata* sp. nov. have been reported.

Key-words — Cryptogams, Filamentous fossil, *Algacites*, *Hepaticites*, Middle Gondwana (India).

सारांश

निदपुरी की मध्य गोंडवाना (ट्रायॅसिक) संस्तरों से श्रंसवहनी श्रपुष्पोद्भिदों पर श्रौर श्रंशदान – भाग 2.

दिव्य दर्शन पन्त एवं नूपुर बसु

एक तंतु-शैवालाश्म, ऍल्गासाइटिस ऊगोनिफ़ेरा न० जा०, के कार्बनी संपीडन तथा हरितोद्भिदों की तीन जातियाँ, हेपेटिसाइटिस रिकार्डिऑयडिस न० जा०, हे० मेट्ज़ेरौयडिस वाल्टन एवं हे० फ़ोलियेटा न० जा० अभिलिखित किये गये हैं।

INTRODUCTION

THE present paper is a continuation of our earlier work on bryophytes from the fossiliferous shales of Nidpuri, wherein we described two forms, viz., *Hepaticites nidpurensis* and *Sphagnophyllites triassicus* (Pant & Basu, 1978). Besides reporting some more bryophytes from the same beds, the present account describes, for the first time, some fragmentary, carbonaceous filamentous remains which are assigned to *Algacites* Schlotheim.

MATERIAL AND METHODS

As mentioned earlier (Pant & Basu, 1978) pieces of fossiliferous shales from the *Dicroidium* beds on the banks of the Gopad River by the side of village Nidpuri in Sidhi District of Madhya Pradesh were collected and treated with HF and the residue was thoroughly washed for sorting out the bryophytic and algal remains. Selected specimens were examined dry under unilateral incident light and subsequently mounted in Canada balsam and examined under transmitted light. Some specimens of *A. oogonifera* were also coated with gold/palladium and examined under a Cambridge S180 SEM.

OBSERVATIONS

Genus — *Algacites* Schlotheim, 1822

Algacites oogonifera sp. nov.

Diagnosis — Thallus composed of matted filaments lying parallel or crossed. Filaments tubular, almost uniformly wide, unbranched, aseptate. Surface of filaments appearing clearly tuberculate under SEM.

Holotype — No. 41303 of D. D. Pant Collection, Botany Department, Allahabad University.

Locality & Horizon — Nidpuri, Sidhi District, Madhya Pradesh, India; Triassic (Middle Gondwana).

Description — A number of fragments of *A. oogonifera* have been extracted from the rock matrix. The small pieces of the fossil are generally amber coloured and translucent enough to show the details of filaments clearly but most of the larger clumps are black and opaque revealing fewer details. When examined dry, under unilateral incident light, the mats show superimposed layers of transverse and longitudinal sheets of closely aligned tubules. As a rule the filaments of the flat mats form dense tangled masses of tubes generally running straight, but sometimes a mat may show superimposed curved and concentric filaments like those found in sections of algal stromatolites (Pl. 1, fig. 3). Individual filaments are uniformly wide throughout their entire length, measuring approximately 13 μm in width. Their ends which project beyond the mats appear jagged. Some translucent filaments seem to show vague septa or cross walls (Text-fig. 2). The surface of the translucent filaments appears fairly smooth when examined under low and high magnifications in transmitted light, but on examination under the SEM, the dry filaments show a large number of surface tubercles (Pl. 1, figs 5, 6). Similar lumps have been reported by Krumbein and Cohen (1977) as decayed slime coatings in SEM-micrographs of living filaments of *Oscillatoria*. An explanation for the presence of the tubercles only in dry specimens and not in the mounted ones is the possibility of their becoming dissolved in the mounting media, although one could even suspect that they are artifacts caused by gold/palladium coating.

A single semi-macerated translucent mat shows, here and there, almost rounded swellings in the filaments. The wall of the swellings sometimes shows a small opening and its interior is occupied by a rounded body having a minutely tuberculate surface (Pl. 1, fig. 4; Text-fig. 3). We are inclined to think that these swellings are oogonia containing oospores.

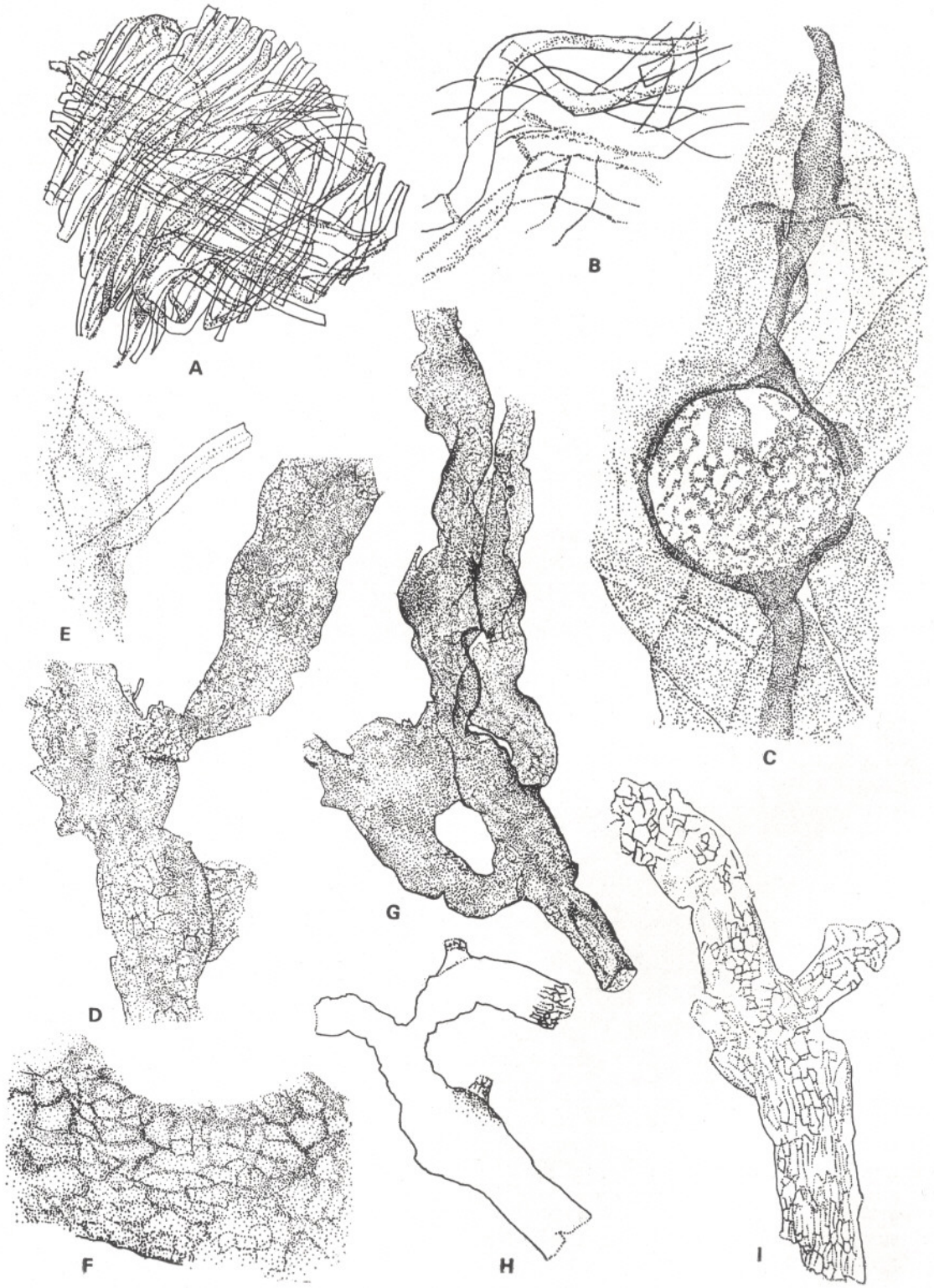
Comparison & Discussion — Even though there are abundant reports of filamentous fossils, compressed forms are rather rare, and a vast majority of them are calcareous and stromatolitic. As a result, it is not easy to find previously described form genera in which we can include the present compressed filamentous fossils. Diagenesis also creates difficulties in identifying compressed non-calcareous fossils. Indeed rarely has a compression fossil been sufficiently well-preserved to enable one to state indubitably that the source organism was actually an alga or a fungus. Earlier authors avoided the dilemma by arbitrarily referring to algae all impressions or markings on the rocks that could not be included in any particular group.

As far as we know there are only two comparable genera of filamentous fossils to which we could refer our non-septate tubular filaments, viz., *Algacites* Schlotheim (1822) and *Algites* Seward (1894). Since both the generic names have been used in the past with equal facility for impressions, casts or compressions of what are regarded as Algae *incertae sedis*, we have preferred to refer our fossils to the form genus *Algacites* which is older. Our Triassic specimens, however, exhibit oogonia-like bodies which may be cited as an evidence of their algal nature.

A. oogonifera differs from the single specimen described as *Algacites* sp. by Harris (1961), from the Jurassic of Yorkshire, in having mats of parallel, unbranched filaments without any organization into medulla or cortex (the thallus of *Algacites* sp. has repeatedly branched filaments organized into a medulla of longitudinal filaments surrounded by an ensheathing cortex of horizontal ones. Likewise *Confervites vaucherioides* described by Harris (1931) from the Lower Liassic of Greenland differs from *A. oogonifera* in having sparingly branched aseptate filaments. Further, the filaments of *Algacites* sp. and *Confervites vaucherioides* lack oogonium-like structures.

Amongst other fossils having tubes in the plant body are the nematophytes like *Nematothallus*, *Nematoplexus* and *Prototaxites* but their thalli bear two systems of wide and narrow tubes, while the tubes of *A. oogonifera* are uniformly wide.

The non-septate filaments and rounded oogonium-like bodies of *A. oogonifera* may be compared with living *Vaucheria* or *Oedogonium* but its unbranched empty filaments and intercalary oogonia (cf. *Vaucheria*) and absence of definite cross walls (cf. *Oedogonium*) make such a comparison far fetched.



TEXT-FIG. 1

Genus — *Hepaticites* Walton, 1925

Hepaticites riccardioides sp. nov.

Diagnosis — Sterile thalli smooth, often irregularly and unequally dichotomized to make thallus appear as consisting of main axes and lateral branches. Axes of various orders flattened. Main axes and lateral branches straight or slightly curved. Lateral lobes somewhat narrower but often as wide as main axis. Width of main axes 0·3 to 0·8 mm. Axes more than two layers in thickness. Thallus showing no differentiation of midrib and conducting strand. Surface cells almost uniformly polygonal all over the thallus. Rhizoids very rarely visible. Lateral branches sometimes resembling male branches of *Riccardia* and showing dark areas as in antheridial region of laterals in *Riccardia*. Reproductive structures otherwise unknown.

Holotype — No. 41402 of D. D. Pant Collection, Botany Department, University of Allahabad, India.

Locality & Horizon — Nidpuri, Sidhi District, Madhya Pradesh, India; Triassic (Middle Gondwana).

Description — A large number of thallus fragments of various sizes have been extracted from the rock matrix by maceration. Four specimens appear to show a series of recurved convergent branches forming loops (Pl. 2, fig. 9; Text-fig. 7). Rarely, the axes also show small enations. Cellular details are normally invisible in the opaque, more carbonized specimens, but naturally macerated translucent specimens show squarish to polygonal cell outlines, about 57 μm long ×35 μm broad (Pl. 2, fig. 10; Text-fig. 6). No differentiation of tissues into a midrib and lamina is visible. The margins of the thalli are more or less translucent but their middle region is more than two cell thick. Rhizoids are rarely intact but one specimen shows an attached rhizoid (Pl. 2, figs 10, 11; Text-figs 4, 5).

Although undoubted reproductive structures have not been seen, some of the dark, short, lateral branches, where even the polygonal cell outlines are not visible, appear to be closely comparable with the male branches of *Riccardia*. The dark rounded areas of such lateral branches occupy positions like those of antheridia in the male branches of *Riccardia* (Pl. 2, figs 7, 8).

Discussion & Comparison — The specific name has been given to the fossils for their close resemblance with modern *Riccardia* in being narrow, regularly and irregularly branched, and in having surface cells comparable with the surface cells of *Riccardia*. The short branches with dark areas in *H. riccardioides* also seem to be similar to the antheridial branches of *Riccardia*. Indeed the similarities between *H. riccardioides* and modern *Riccardia* are so close that we could have assigned the fossil thalli to the same genus but since structural details are imperfectly known and undoubted reproductive parts and sporogonia of the fossil form are unknown we have preferred to assign them to the genus *Hepaticites*.

Two other forms closely comparable in size and structure with *H. riccardioides* are *Thallites willsii* and *Hepaticites langii* reported by Walton (1925, 1949) from the Carboniferous of England. The habit and structure of the thalli of both the above forms, according to Walton (1925) parallels that of modern *Aneura* and *Riccia*. However, *T. willsii* differs from *H. riccardioides* in lacking rhizoids altogether while in *H. langii* rhizoids occur in groups (a single specimen of *H. riccardioides* shows a solitary rhizoid).

A comparison of our fossils may also be made with some *Riccardia pinguis*-like thalli described by Krassilov (1973) under "Undetermined Hepaticeae" from the Late

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TEXT-FIG. 1 — **A-C.** *Algacites oogonifera* sp. nov.; **D-G.** *Hepaticites riccardioides* sp. nov. **A.** A mat showing criss-cross running filaments, no. 41304 × 95. **B.** Magnified view of a few filaments from a different specimen showing cross walls or septa, no. 41305 × 225. **C.** Highly magnified view of oogonium-like body showing tuberculate oospore and lateral opening, no. 41306 × 990. **D, G-I.** Thalli of *H. riccardioides*. **D.** Thallus showing a small rhizoid, no. 41402 × 26. **G.** No. 41405 × 48. **H.** No. 41407 × 35. **I.** No. 41409 × 48. **E.** Rhizoid in fig. D, further magnified × 288. **F.** A portion of fig. D, further magnified to show surface cells × 63.

TEXT-FIG. 2

Jurassic to lowermost Cretaceous deposits of Tyrma River. However, the thalli reported by Krassilov (1973) are wider (ca. 2·5 mm) than ours (ca. 0·6 mm) and their structural details are unknown.

Hepaticites metzgerioides Walton, 1928

Emended Diagnosis — Dorsiventral thallus differentiated into lamina and dichotomously branched midrib. Midrib several cells thick. Cells of midrib longitudinally elongated, about ten times as long as broad. Wing one cell in thickness and up to twentyfive cells wide on either side of midrib. Cells of wing almost isodiametric, 52 μm long × 22 μm broad, 4-8 angled, thin-walled and bearing unicellular smooth-walled, curved or straight hairs, trigones absent. Undulate margin of wing forming lobes. Reproductive structures unknown.

Holotype — No. 41436 of D. D Pant Collection, Botany Department, University of Allahabad, India.

Horizon & Locality — Nidpuri, Sidhi District, Madhya Pradesh, India; Triassic (Middle Gondwana).

Description — Among other bryophytes a few fragmentary remains of thalli referable to *H. metzgerioides* Walton were observed in maceration residues of the fossiliferous shales from Nidpuri. Most of the specimens have thalli with translucent yellow coloured wings showing transverse rows of polygonal cells and fragments whose middle regions are intact show a dark coloured opaque midrib with vaguely discernible longitudinally elongated cells. The cells of the wing around the conducting region seem to form a complete sheath so that here the thallus also appears to be more than one cell thick. A single specimen shows a forked midrib indicating that the thallus, which is only partially preserved, was dichotomously branched (Pl. 2, fig. 13; Text-fig. 12). The width of the wing is variable. In a specimen, where the apical end is broken, the wing is 15-25 cells in width. Wings of other specimens are narrower being less than fifteen cells wide. Two specimens with intact wings show marginal lobes (Pl. 2, fig. 15; Pl. 3, fig. 17; Text-figs 14, 15). In well-preserved wings two sets of cellular outlines representing both upper and lower surface of cells are visible. The surface walls of most cells of the wing show long or short hair-like papillate outgrowths arising by the side of anticlinal walls and directed over the adjacent cells as in the extant species of *Metzgeria* (Pl. 3, fig. 18; Text-fig. 16). When such hair-like growths are compressed over cells of the lamina they appear as if they are projecting into the lumina of cells. Similar structures (hairs) are clearly seen in the photographs given by Walton (1928, pl. XII, fig. 5) although they are not mentioned in the text.

Discussion & Comparison — Lack of scales and rhizoids in our thalli would have normally pointed towards their inclusion in the form-genus *Thallites* Walton (1928) but we assign them to *Hepaticites* because (i) they closely resemble thalli of *Hepaticites metzgerioides* figured by Walton (1928), (ii) distinctive structures like the hairs on our specimens are seen even in Walton's photographs of *H. metzgerioides* (see pl. XII, fig. 5), and (iii) the hairs of living *Metzgeria* from which the specific designation *H. metzgerioides* was derived are exactly like the hairs of our thalli. We have not observed rhizoids on our thalli but according to Frye and Clark (1937) "the line between hairs and rhizoids in this genus is not clear".

Except for lacking associated fungal mycelia our Triassic fossils closely resemble the Carboniferous thalli of *H. metzgerioides* Walton. However, we do not attach any taxonomic significance to the absence of fungal mycelia in our fossils.

The specimens of *H. metzgerioides* reported by Oshurkova (1965) from the Car-

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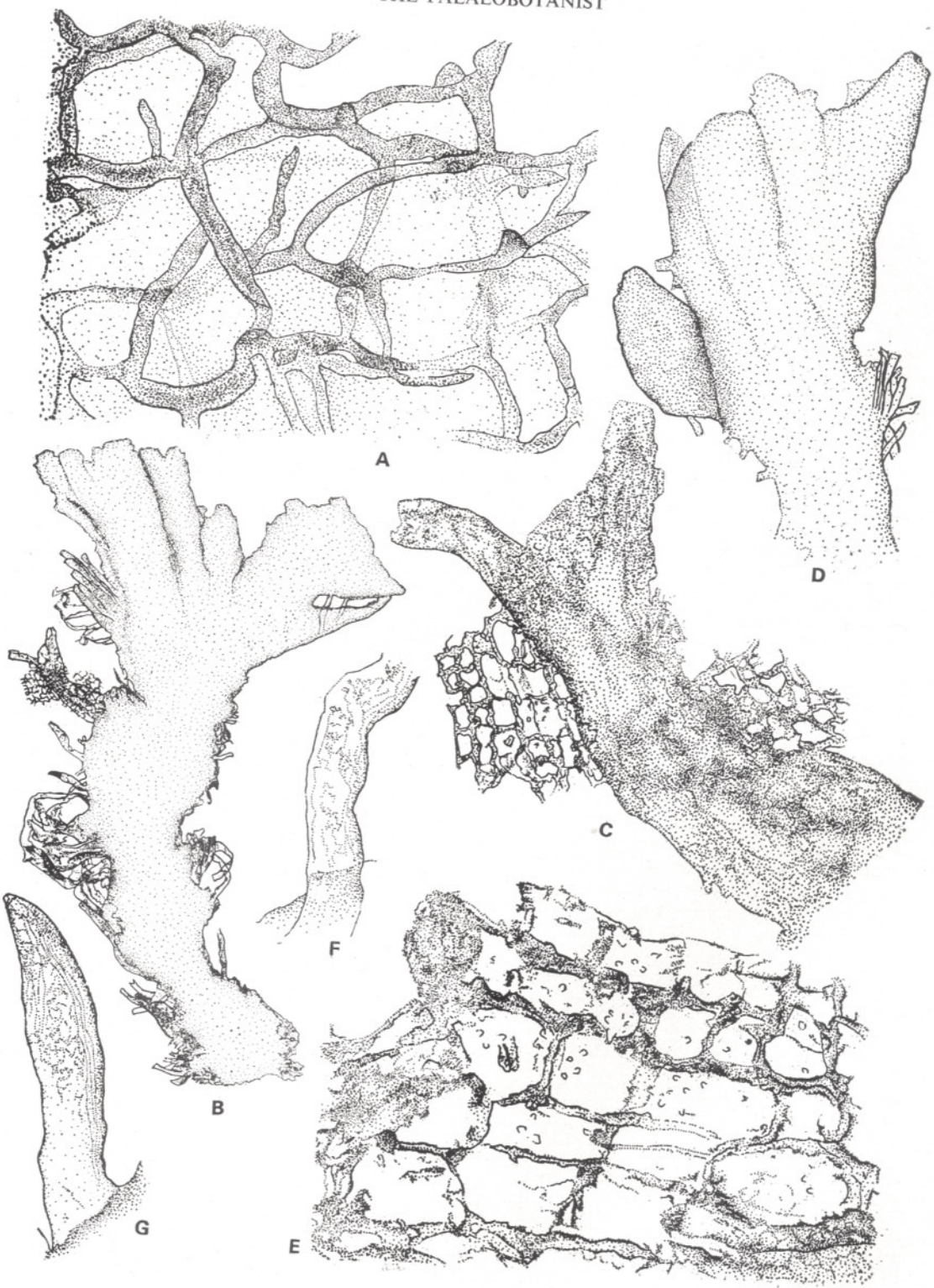
TEXT-FIG. 2 — **A.** *H. riccardioides* sp. nov.; **B.** *Riccardia* sp.; **C-F.** *Hepaticites metzgerioides* Walton. **A.** Thallus with dichotomising lateral branch, no. 41408 × 50. **B.** A branch of thallus showing polygonal surface cells × 33. **C.** Holotype — showing dichotomising midrib with fragments of lamina attached on either side, no. 41452 × 47. **D.** Portion of fig. B magnified to show cells of wing. The unshaded space in the middle represents the dark midrib × 315. **E, F.** Portions of intact wings showing lobe forming tendency; **E.** No. 41455 × 60; **F.** No. 41456 × 50.



TEXT-FIG. 3

boniferous of Karaganda Basin, U.S.S.R. are too imperfectly known to be compared with our material.

Hepaticites foliata sp. nov.

Diagnosis — Thallus dorsiventral, differentiated into a central strand and marginal lamina. Lamina appearing foliose at apical end. Leafy lobes not visible in lower region. Apical leafy lobes closely imbricating. Leafy lobes 0·3×0·2 mm, costate, costae 50 μm wide at base and distantly dichotomized, lamina unistratose, cells of lamina quadrangular to isodiametric, 14 ×10 μm, having oil bodies, corners of individual cells with trigones. Rhizoids numerous, simple, 17 μm wide at base and arising ventrally from dark areas of axis; scales absent.

Holotype — No. 41601 of D. D. Pant Collection, Botany Department, University of Allahabad, India.

Locality & Horizon — Nidpuri, Sidhi District, Madhya Pradesh, India; Triassic (Middle Gondwana).

Description — A single fair-sized specimen of *H. foliata* (Pl. 3, fig. 19; Text-fig. 17) and a few small fragments of rhizoid attached shoots were extracted out of the rock matrix. The diagnosis of the species is based mainly on the Holotype. Fossilization has seemingly rendered almost all the parts of the type specimen dark and opaque but here and there a few portions have remained translucent and the structural details are based on these. The rhizoids are simple and unicellular (Pl. 3, fig. 22; Text-figs 21, 22). Some of them may appear tuberculate but fine focussing shows that the apparent tubercles are the contents of the rhizoids and that the typical peg-like thickenings are absent in the wall. The type specimen showed, at the apex, an oval, sporogonium-like body, measuring about 270×120 μm (Pl. 3, fig. 20; Text-fig. 19).

An attempt was made to macerate the type specimen in dilute HNO_3, but this resulted in the complete dissolution of several rhizoids and the only translucent leafy lobe, although the opacity of other parts remained unaffected. Maceration also failed to yield any spores from the dark, sporogonium-like oval body and we presume that this would be due to (i) the apparent sporogonium not being a sporogonium, or (ii) its being empty, or (iii) its immaturity.

Discussion & Comparison — The following characters of *H. foliata* indicate that it is a bryophyte: (i) a slender foliose axis, (ii) small sessile, costate leaves having a unistratose lamina, (iii) presence of numerous rhizoids, and (iv) presence of an apical, oval sporogonium-like body.

The presence of costate leaves would suggest that they could belong to a moss but the axis of our fossil is dorsiventral and the leaves appear to be two ranked instead of being spirally disposed on a radial axis. The rhizoids are non-septate (unicellular). Some Jungermanniales like *Herberta* and *Diplophyllum* also have costate leaves and the costae of *Herberta* may even be forked. The cells of their lamina are squarish to isodiametric with oil bodies and prominent trigones (Pl. 3, fig. 21; Text-figs 18, 20) as is common in foliose Jungermanniales (the cells of the lamina of moss leaves are elongated and rectangular). Therefore, we assign our fossil to a new species of *Hepaticites* (*H. foliata* sp. nov.).

CONCLUSIONS

Reports of fossils like *H. metzgerioides* from the Triassic of Nidpuri indicate persistence of such forms from the Carboniferous upwards although no reports of their occurrence from intermediate strata are available. Likewise, other Carboniferous Jungermanniales, eg. *Hepaticites willsii*, etc. which also seem to have persisted into the Triassic

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TEXT-FIG. 3 — **A.** *H. metzgerioides*; **B-G** *Hepaticites foliata* sp. nov. **A.** Portion of wing in fig. F of Text-fig. 2 magnified to show cells and hairs × 520. **B.** Holotype — showing numerous rhizoids, translucent leafy lobe with forked midrib (on the left), and dark apical leafy lobes, no. 41601 × 75. **C.** Leaf in fig. B, more magnified × 375. **D.** Apical part of holotype further magnified to show, on the left, a sporogonium-like body × 165. **E.** Wing of translucent leafy lobe magnified to show cells with trigones and oil bodies × 765. **F, G.** Unicellular rhizoids appearing tuberculate due to the presence of cell contents × 625.

are represented by closely allied forms like *H. riccardioides* and *H. foliata.*

The present cryptogamic assemblage suggests the occurrence of protected shady and marshy spots in the forests of Nidpuri during the Triassic times although the prevalence of the *Dicroidium* Flora may indicate a dry environment.

Altogether we have now described five bryophytes from the Triassic beds of Nidpuri and even though poor, this is the richest haul of bryophytes from any fossil flora of India. Of the few earlier reports only some like *Shuklanites deccanii* Singhai (1964) can be assigned with certainty to bryophytes while the bryophytic affinities of the remaining genera are uncertain or doubtful. However, this apparent paucity of bryophytic remains in fossils of the Indian subcontinent should in no way suggest their actual absence in our past floras. Instead, lack of intensive search for such materials could account for their general absence from other horizons.

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EXPLANATION OF PLATES

PLATE 1

Algacites oogonifera sp. nov.

1. A mat of filaments photographed under unilateral incident light, no. 41308. × 86.
2. A translucent mat showing criss-crossed filaments. Holotype, no. 41303. × 70.
3. An opaque mat showing concentric filaments, no. 41306. × 72.
4. A portion of fig. 3, further magnified to show a few peripheral translucent filaments and an oogonium-like structure containing a tuberculate body. × 600.
5. SEM photomicrograph showing tangled filaments and tubercles, no. 41309 × 260.
6. A portion of fig. 5, further magnified. × 700.

PLATE 2

(7, 9-12 — *Hepaticites riccardioides* sp. nov.; 8 — *Riccardia levieri*; 13-15 — *Hepaticites metzgerioides* Walton)

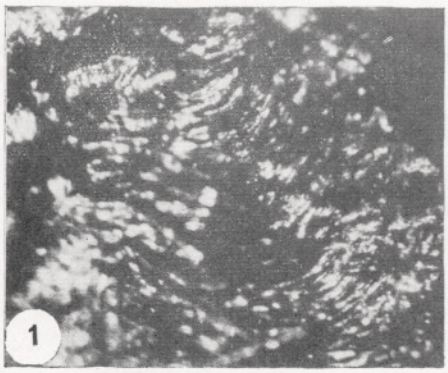
7. Thallus showing two short, dark, lateral branches. Holotype, no. 41402 × 34.
8. Thallus showing antheridial branches. × 56.
9. Specimen showing dichotomies forming loops and of almost equal width as parent axis, no. 41405 × 38.
10. Portion of fig. 7, further magnified to show surface cells. × 58.
11. Rhizoid in fig. 10, further magnified. × 230.
12. Thallus showing a young lateral branch with dichotomising apex, no. 41408. × 33.

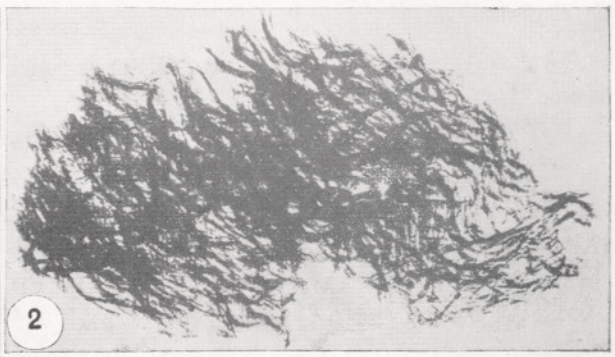
13. Thallus of *H. metzgerioides* showing forked midrib with portions of wing attached on either side. Holotype, no. 41452. × 47.
14. Photograph showing elongated cells of midrib, no. 41460. × 130.
15. Fragment of thallus showing midrib and lobed wing, no. 41455. × 60.

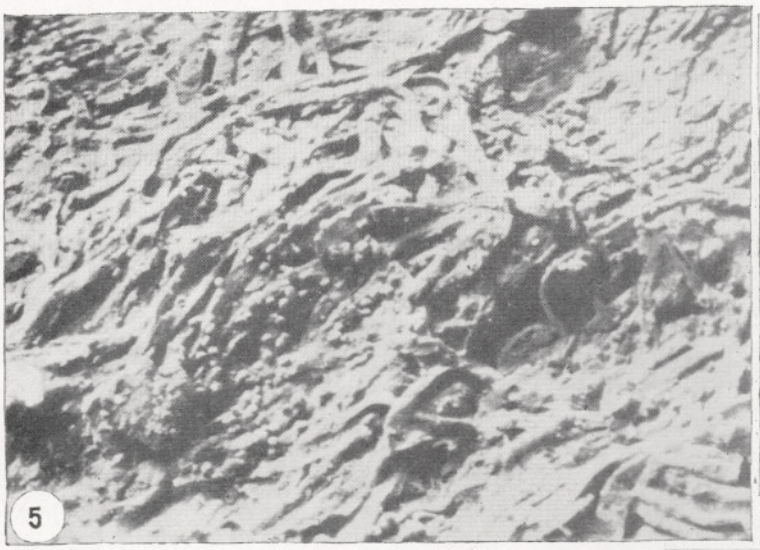
PLATE 3

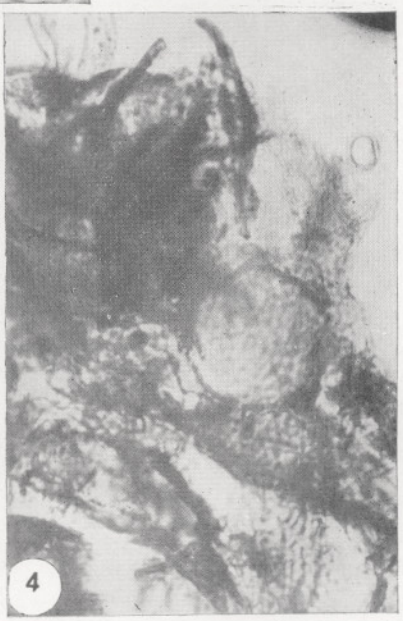
(16-18 — *Hepaticites metzgerioides* Walton; 19-22 — *Hepaticites foliata* sp. nov.)

16. A portion of fig. 13, magnified to show dark midrib and part of wing. × 210.
17. Thallus showing lobate wing, no. 41456 × 50.
18. A portion of wing in fig. 17, more magnified to show cells and hairs. × 520.
19. Plant showing rhizoids, a translucent leaf and the dark apical part. Holotype, no. 41601 × 50.
20. Apical end of fig. 19 further magnified to show exposed sporogonium-like body. × 110.
21. Lamina of translucent lobe in fig. 19, more magnified to show cells. × 900.
22. Rhizoids in fig. 19 further magnified. × 500.









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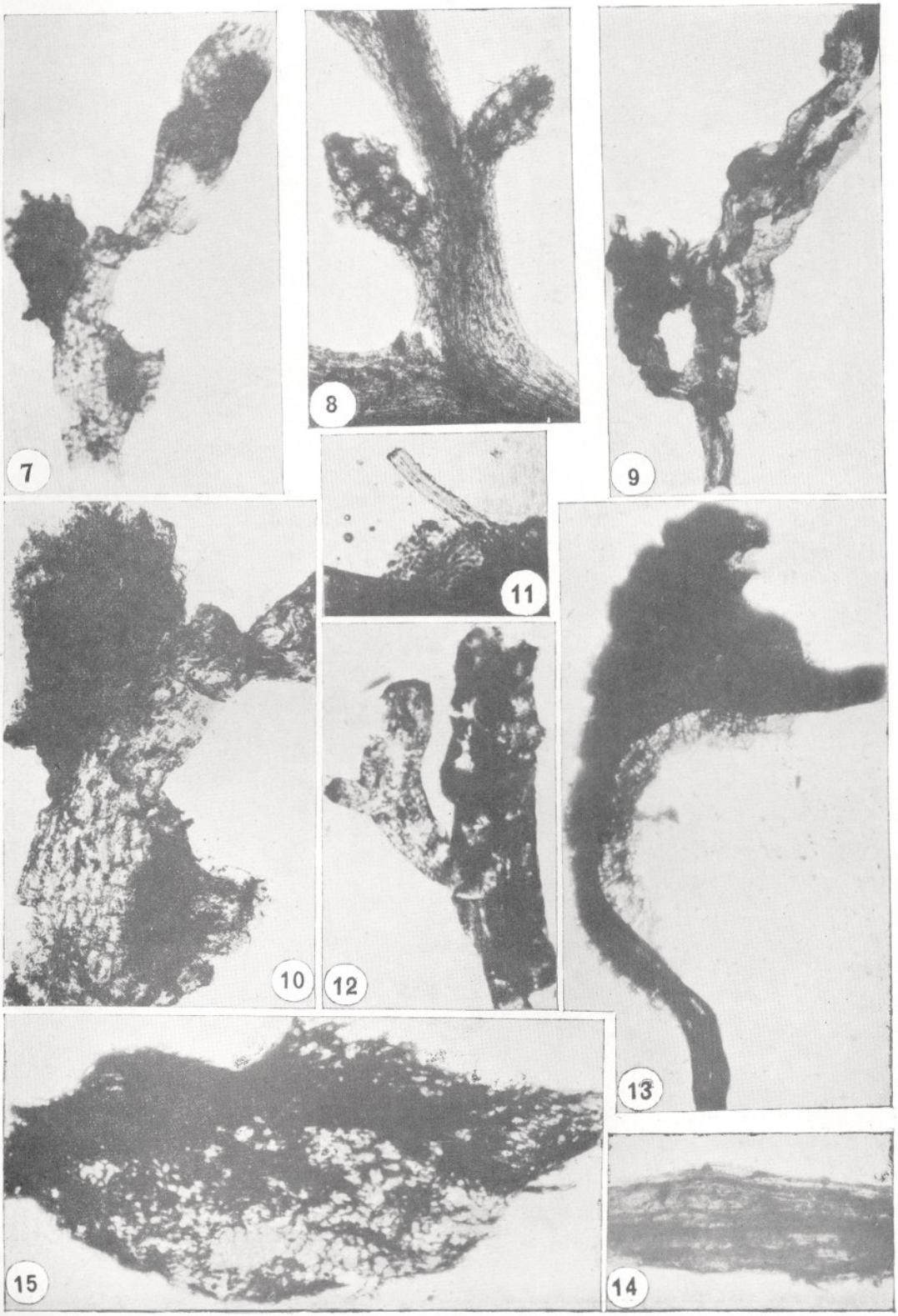
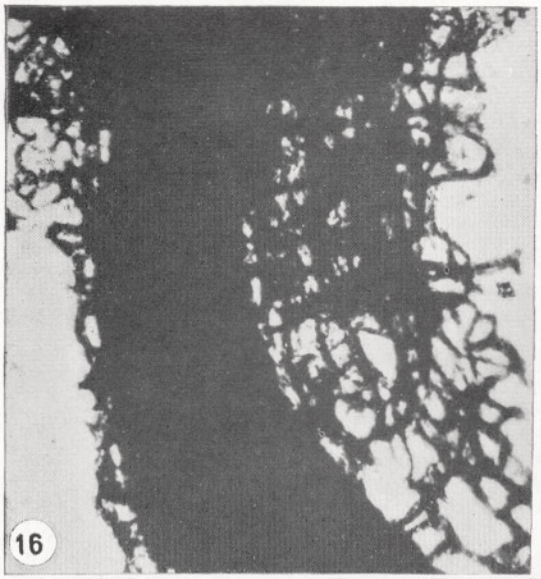
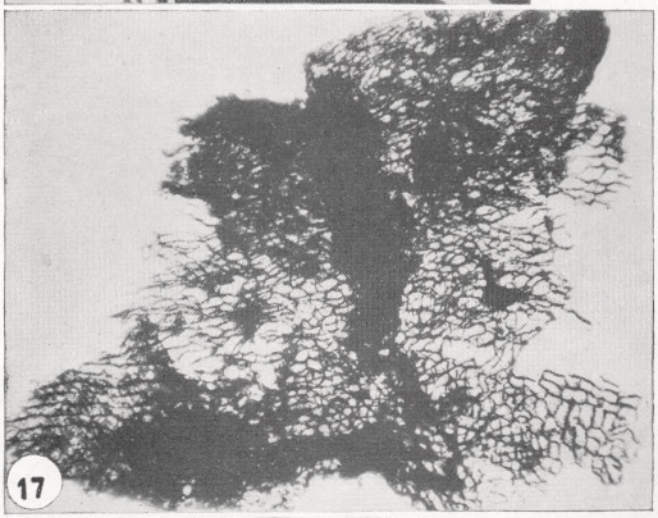
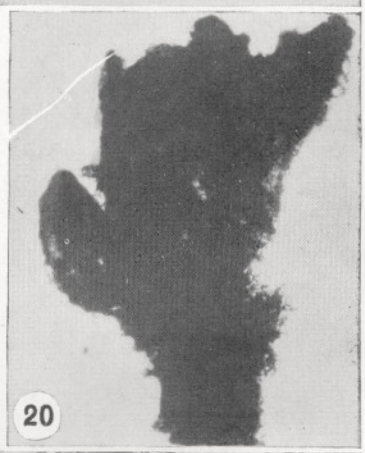


PLATE 2







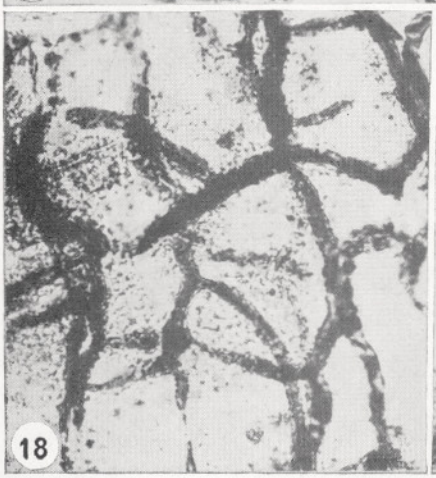


PLATE 3