ON TWO STRUCTURALLY PRESERVED BRYOPHYTES FROM THE TRIASSIC OF NIDPUR, INDIA

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ABSTRACT

The paper describes thallose gametophytes with an attached sporogonium under the name *Hepaticites nidpurensis* sp. nov. and detached leaves resembling those of modern *Sphagnum*, called *Sphagnophyllites triassicus* gen. et sp. nov.

INTRODUCTION

INDUBITABLE proof of the existence of bryophytes during Palaeozoic times was first brought forth in 1925 by Walton's discovery of structurally preserved members of the group in the Carboniferous rocks. Since then, a large number of undoubted bryophytic remains have been reported from various ages ranging from Devonian to the Tertiary-Quaternary. However, as far as we know up to date, the only reports of fossil bryophytes from Gondwanaland countries are those of Lundqvist (1919), Dolianiti (1948), Saksena (1947, 1958), Clifford and Cookson (1953), Medwell (1954), Gupta (1956), Townrow (1958), Mehta and Goswami (1960), Singhai (1964), Jain and Delevoryas (1967) and Anderson (1976).

Among these reports, the first two describe impressions of thallus-like remains called *Marchantites* from Lower Gondwana beds. Their structure is unknown and they are even suspected to be roots of *Lithorhiza tenuirama* (Pant, 1958).

Another Lower Gondwana fossil recovered in maceration residues and named *Capsulites gondwanensis* was described as a moss capsule by Saksena (1947, 1958). According to Pant and Nautiyal (1960) it is almost certainly a macerated seed of *Platycardia* or *Pterygospermum* type, with its nucellar cuticle enclosed in the inner cuticle of integument (minus outer cuticle) when viewed upside down so that the chalazal hole was taken to be the stomium of the capsule and the micropylar canal was regarded as the seta.

Some other bryophytic fossils from Gondwanaland are of Tertiary and post-Tertiary age. Among these are three sporophytic fossils called *Muscites yallournensis* by Clifford and Cookson (1953), a *Notothylas* type of sporogonium reported by Gupta (1956) and *Shuklanites deccanii* described by Singhai (1964), while Mehta and Goswami (1960) have reported thallose remains under the name *Hepaticites kashmiriensis*. Gametophytic fossils of some thallose forms were reported by Medwell (1954) from the Jurassic and Jain and Delevoryas (1967) and Anderson (1976) from Triassic beds as *Thallites* sp.

The only previous works which deal with the Triassic Gondwana bryophytes of South Africa are those of Townrow (1958) and Anderson (1976). Out of the two authors, Townrow reported a thallose fossil under the name *Hepaticites cyathodoides* and some foliose remains called *Muscites guescelini*. Anderson, in addition to describing a species of *Thallites*, also transferred the fossil of *H. cyathodoides* to *Marchantites*.

In contrast fossil bryophytes of northern regions are more numerous and better known and the northern Triassic beds have yielded such well-preserved fossils that it has been possible to assign them to genera like *Ricciopsis*, allied to modern *Riccia*, *Marchantites* resembling *Marchantia* and *Muscites* allied to the present-day mosses. In fact the best known fossil bryophyte, *Naiadita lanceolata*, also comes from the Triassic beds of England.

MATERIAL AND METHODS

Shales of possible middle Triassic age containing compressed fragments of stems, leaves, seeds, synangia, spores and bryophytes were collected from the cuttings of Gopad River by the side of the village Nidpur, Sidhi District, Madhya Pradesh, India. None of the bryophytes could be

recognized on the rock surface but carbonaceous remains were extracted in bulk macerations of the rock sample in hydrofluoric acid. All the fossils have been mounted in canada balsam.

OBSERVATIONS

Hepaticites nidpurensis sp. nov.

Diagnosis — Plant thalloid, thallus about 1 mm wide, dorsiventral, apex notched with apically dichotomising lobes, margin somewhat irregular, centre of thallus many cells thick, margin membranous and only one cell thick. Thallus showing attachment of numerous rhizoids on ventral side, rhizoids more crowded near apex, simple, smooth-walled. Air chambers and air pores and other structural details of thallus not seen. Thallus bearing at apex a distally attached globose to oval sporogonium, 0·8 mm long and 0·7 mm wide, not embedded in thallus tissue but attached dorsally to the thallus by a narrow tapering base. Spores numerous, round, 32 to 49 μ in diameter, trilete. Exine with obscure reticulations. Elaters absent.

Holotype — Specimen no. 40,651 of D. D. Pant Collection, Botany Department, Allahabad University, India.

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

DESCRIPTION

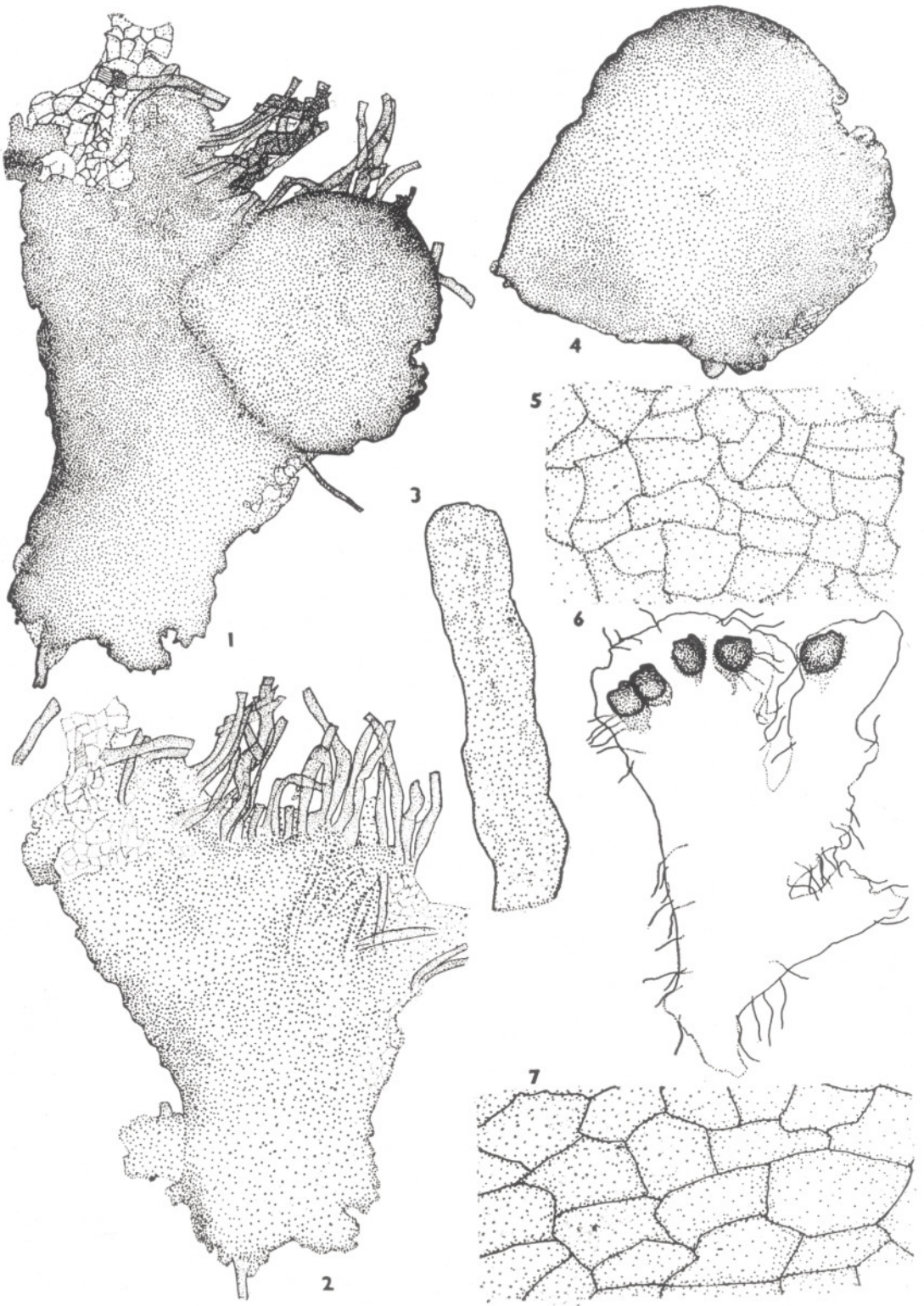
The species is based on several pieces of thalli but a single specimen showed the attached sporogonium (Pl. 1, fig. 1; Text-fig. 1). The terminal portion of the thallus has a distinct notch indicating that the growing point was situated in a depression. The thallus is abruptly broken at its basal extremity either due to decay before fossilization or during the process of extraction. The epidermal cells of the lamina are visible due to natural maceration only at certain points on the thallus (Pl. 1, fig. 2; Text-fig. 2). The cells are thin-walled and rectangular to isodiametric 45×33 μ (Text-fig. 5). The rhizoids seem to originate from cells which are of somewhat darker colour than the other cells of the thallus (Pl. 1, fig. 4). The apical rhizoids become clearly visible only after detaching the sporogonium. The rhizoids are 16 to 32 μ wide, smooth-walled and simple, i.e. without any cross-walls or branching (Pl. 1, fig. 3; Text-fig. 3). The distal ends of the rhizoids are broken and their full length is indeterminable. The sporogonium was attached at the apex of a lobe of the thallus by its pointed wedge-shaped proximal end. A seta is absent but the narrow end of the sporogonium could have been attached to a seta and a foot. The wall of the sporogonium consists of a hyaline membrane without any cellular outlines. The apex of the sporogonium is broken and perhaps the dehiscence took place there.

COMPARISON AND DISCUSSION

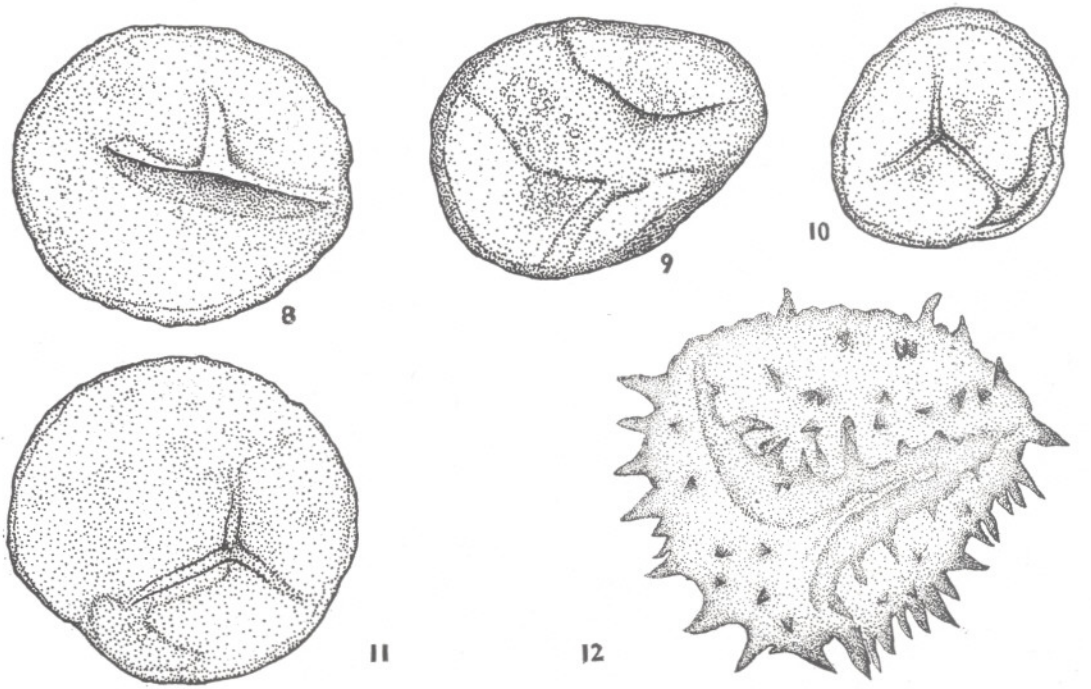
Not only is *H. nidpurensis* the first undoubted thallose bryophyte to be reported from India but it is also the oldest hepatic to be found in this region being described from the Middle Gondwana beds. An earlier report of a similarly compressed thallose fossil, *H. kashmiriensis*, was made by Mehta and Goswami (1960) from the Karewas (Pleistocene) of Kashmir. The bryophytic character of this fossil is, however, doubtful since as described its rhizoids (? hairs) could have been one-celled or multicelled and its sporophyte and spores too are unknown. Indeed one could even suspect that it could be a thallus or compressed organ of unspecified nature.

Nevertheless, two petrified sporogonia have been reported from the Deccan Intertrappeans of Mohgaon Kalan by Gupta (1956) and Singhai (1964). Out of these, the fossil sporogonium called *Shuklanites deccanii* Singhai is better known. The size of *S. deccanii* and its spores are similar to those of the sporogonium of *H. nidpurensis* but as reported *S. deccanii* differs in having a well-differentiated foot and capsule which contains not only spores but also 'elaters (pseudoelaters)'. The spores of *H. nidpurensis* are, however, slightly different and their surface shows obscure reticulations (the spores of *S. deccanii* are reportedly smooth-walled).

The report of *H. nidpurensis* from the Triassic beds of Gondwanaland is of special importance, since the known fossil record of



TEXT-FIGS. 1-7



TEXT-FIGS. 8-12 — *H. nidpurensis* sp. nov. **8-11,** variously compressed spores obtained after teasing the sporogonium, each showing a proximal trilete. 40,651 × 940. **12,** *Cyathodium tuberosum.* Proximal view of a spore showing spinous exine × 1000.

Pre-Tertiary liverworts with the exception of *Naiadita lanceolata* Harris (1938) from the Rhaetic of England, is devoid of fertile structures.

In comparing *H. nidpurensis* with other species of liverworts reported from different parts of the world it would appear to be best comparable with *Marchantites cyathodoides* (Townrow) Anderson, another Gondwana species, also reported from the Triassic beds of South Africa and originally known as *H. cyathodoides.* However, the sporophyte of *M. cyathodoides* is unknown and therefore only the gametophytes of the two species can be compared. The thalli of both species have similar form and size, rectangular to isodiametric cells and rhizoids. As described by Anderson (1976) the gametophyte of *M. cyathodoides* shows indications of midrib, air chambers, ventral scales and rhizoids which enabled Anderson to remove this species from *Hepaticites* and place it in *Marchantites.* Due to their dark colour the internal details of the gametophytes of *H. nidpurensis* are imperfectly known and no ventral scales or internal ribs can be seen. Although the similarity of the thalli of *M. cyathodoides* and *H. nidpurensis*

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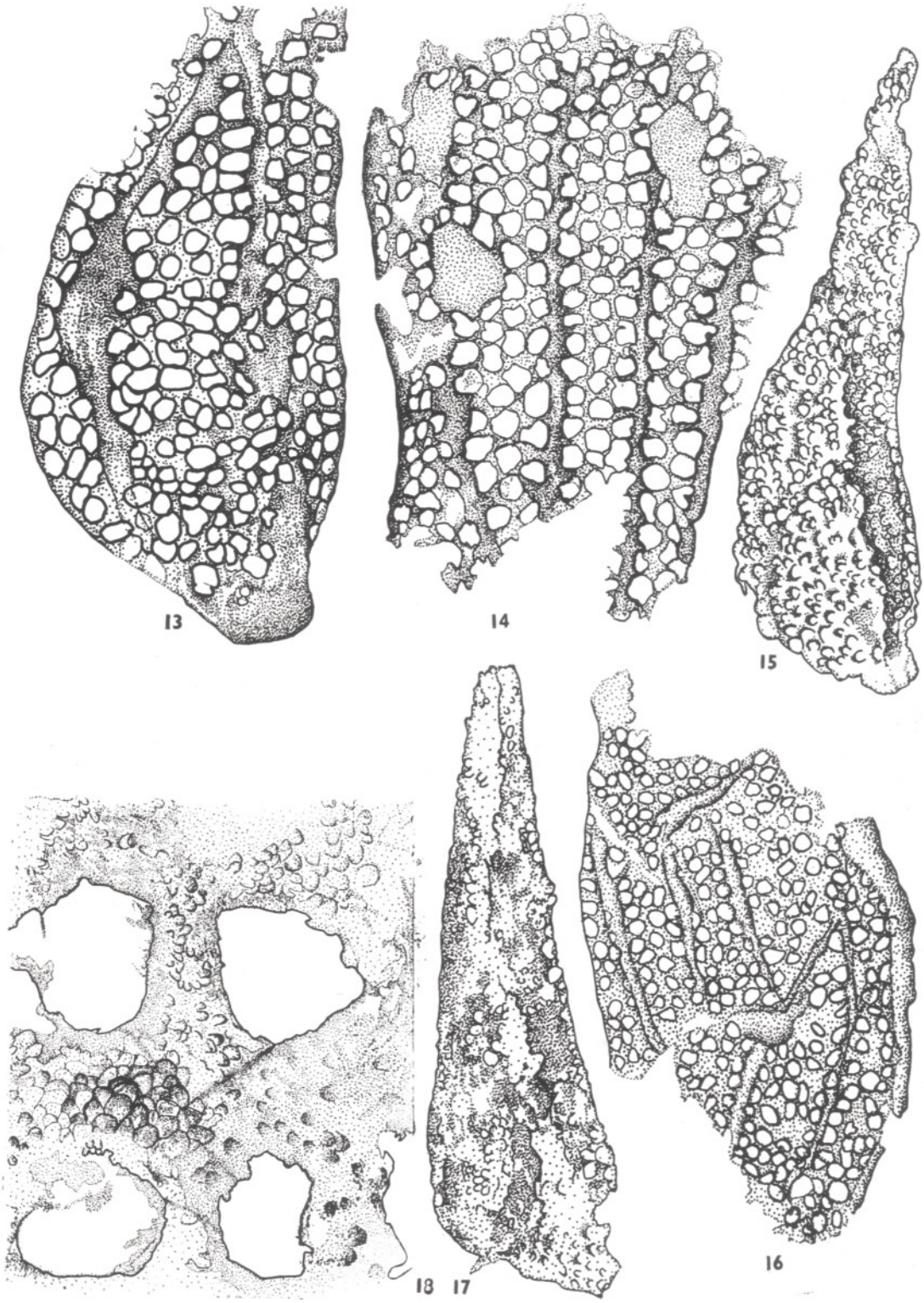
TEXT-FIGS. 1-7 — *Hepaticites nidpurensis* sp. nov. **1,** Holotype. Thallus showing rhizoids and a dorsally attached sporogonium. 40,651 × 66. **2,** thallus in fig. 1, seen after removal of sporogonium. The notch between the two lobes represents the growing point × 72. **3,** a single rhizoid showing aseptate and smooth walls. 40,651 × 500. **4,** the detached sporogonium showing a tapering base and an apical opening. Outlines of spores are visible along the margin of the sporogonium. 40,651 × 86. **5,** rectangular to polygonal cells of the thallus. 40,651 × 250. **6, 7,** *Cyathodium tuberosum.* 6, thallus showing apical dorsal sporogonium and rhizoids × 10. **7**, polygonal cells of the thallus × 250.



TEXT-FIGS. 13-18

creates a suspicion in our mind that the internal ribs, air chambers and scales could have been present even in the thalli of *H. nidpurensis*, we are presently unable to assign them to *Marchantites* since as pointed out by Harris (1942) the name *Marchantites* should be "restricted to hepatics agreeing with *M. sezannensis* Brongniart, the type species, in which marchantiaceous air chambers, ventral scales and reproductive organs have been demonstrated." The sporophyte of *H. nidpurensis* is also not closely comparable with that of any known Marchantineae and therefore we prefer to retain our species under the non-committal genus *Hepaticites*.

The question which arises next is whether the present material should be assigned to *Thallites* or to *Hepaticites*. According to the original diagnosis of Walton (1925) thalli which can be distinguished from thallose material of algae, pteridophyte and other groups of plants should alone be included under *Hepaticites* and other fossil thalli should be called *Thallites*.

If we had to classify only the thalli in the present material, we would have included them in *Thallites* since the presence of rhizoids is not enough to characterize them as bryophytic; thalli with rhizoids occur in algae, e.g. *Fritschiella* and pteridophytes, e.g. prothalli of *Equisetum* and ferns but the presence of an attached sporophyte in a thallus enables us to assign our thalli with certainty to *Hepaticites*.

While discussing the affinities of *H. cyathodoides*, Townrow had compared it with extant *Cyathodium* and had succeeded in finding a number of similarities. The much smaller thalli of *H. nidpurensis* can be compared with those of modern *Cyathodium* only in their general form (details of air-pores, ventral scales etc., are lacking in *H. nidpurensis*). Its sporophytes also seemingly resemble those of *Cyathodium*. In order to make a detailed comparison between the fossil and living sporogonia we made a first hand study of the sporophytes of local *C. tuberosum* and we find that the sporogonia of both forms have a similar position on the thalli and their size and oval form are also similar although a foot and a seta are not seen in the fossil form (the sporophyte of *Cyathodium* shows a clearly demarcated foot & seta). Sporogonial walls in *H. nidpurensis* and *Cyathodium* are similarly membranous but that of *Cyathodium* shows clearly marked cell outlines (these are absent in *H. nidpurensis*). In order to find out whether the absence of cellular outlines and a peristome-like layer could have been caused by chemical treatment of the fossil specimen, we treated some sporogonia of *Cyathodium* with HF in exactly the same manner as we used for the extraction of the fossil thalli. The membranous walls of the living sporogonia remained unchanged. However, maceration of the same sporogonia in dilute nitric acid obscured all cellular details except those of the thick-walled peristome-like cells. It is therefore possible that natural maceration during fossilization could have obscured the cellular details in the fossil sporogonium. Further, as a result of acid treatment the foot and the seta started resembling the tapering proximal end of the sporogonium of *H. nidpurensis*. If the apical rupture in the sporogonium of *H. nidpurensis* represents apical dehiscence it would be a further point of resemblance between the two sporogonia. Differences between the sporogonia of *Cyathodium* and *H. nidpurensis* consist of (a) the absence of an involucre around the sporogonium of *H. nidpurensis* (the sporogonia of *C. tuberosum* are enveloped in a perianth), and (b) the absence of elaters in the sporogonium of *H. nidpurensis* (they are present in *C. tuberosum*). The spores are, however, trilete in both the cases but their sculpturing is different —

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TEXT-FIGS. 13-18 — *Sphagnophyllites triassicus* gen. et sp. nov. **13-17,** detached acostate leaves showing broad base and a tapering apex. Figs. 13, 14 and 16 are views under transmitted light while figs. 15 and 17 are under incident light. The round to polygonal hyaline cells appear raised like tuberculate growths under incident light. Dark lines seen in figs. 13, 14 and 16 are possibly caused by folding. 13, holotype. 40,604 × 45; 14, 40,605 × 30; 15, 40,601 × 26; 16, 40,603 × 26; 17, 40,602 × 26. **18,** portion of a leaf highly magnified to show the chloroplast-like dots in the photosynthetic cells. In fig. 18, part of an obscure partition between photosynthetic cells is also seen. 40,606 × 520.

the spores of *H. nidpurensis* have a smooth exine with obscure reticulations but those of *C. tuberosum* are spinous.

In view of the above differences any idea about a close relationship between *H. nidpurensis* and *Cyathodium* is ruled out and it may be the same with *H. cyathodoides*. However, the fossils could still belong to the same wider alliance of thallose bryophytes as *Cyathodium*.

In its lack of a foot and seta and also in the absence of elaters the sporogonium of *H. nidpurensis* is even more closely comparable with that of *Riccia*. However, the sporogonium of *H. nidpurensis* is pear-shaped, with a prolongation at the proximal end and its tip projects well beyond the thallus while the sporogonium of *Riccia* is perfectly globose and completely embedded in the thallus tissue.

Genus — *Sphagnophyllites* nov.

Diagnosis — Leaves detached, acostate, sessile, lamina unistratose showing cells of two kinds: hyaline cells bound by meshes of brown cells.

Type Species — *Sphagnophyllites triassicus* n. sp.

The genus *Sphagnophyllites* is made for *Sphagnum*-like acostate fossil leaves which show meshes of brown cells (which are comparable with the chlorophyllose cells) around hyaline cells. A sirgle species is presently included in the genus.

Sphagnophyllites triassicus n. sp.

Diagnosis — Leaves obovate, lanceolate to acicular when folded, 3·8 mm long to 2·5 mm wide, margins entire. Hyaline cells isodiametric, rounded to polygonal, 0·1 mm in diameter. Hyaline cells sometimes showing simple oblique partitions and surrounded by 4-6 brown cells. Brown cells 88 μ long ×43 μ wide. Cross-walls between darker cells rarely seen and oblique. Darker cells showing a large number of dark brown rounded chloroplast-like bodies, 10 μ in diameter.

Holotype — Specimen no. 40,604 of D. D. Pant Collection, Botany Department, Allahabad University, India.

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

DESCRIPTION, COMPARISON AND DISCUSSION

The present material consists of eight detached but almost complete leaves besides several smaller fragments.

The shape of the leaves is variable but they often appear acicular or oblong due to folding.

When examined under unilateral incident light, the surface of the leaf appears uneven with a large number of short tubercles with intervening meshwork of depressed areas. When the same leaves are mounted in canada balsam and examined under the microscope in transmitted light they show a number of hyaline areas and bounding brown meshes corresponding with the tubercles and depressions respectively of the unilateral incident light view. Some of the hyaline cells also show simple septa comparable with the thickenings in the walls of hyaline cells of *Sphagnum* leaves. The meshes formed by brown cells show a large number of dark brown oval or rounded bodies which at first sight appear like papillae, but careful observation shows that they often overlap each other and fine focussing confirms that they lie inside the wall. Accordingly, we presume that they represent chloroplasts like those found in the chlorophyllose cells of *Sphagnum*. Our belief in the chloroplast nature of these bodies is strengthened by the reported occurrence of chloroplasts inside the cortical cells of *Rhynia* (Kidston & Lang, 1917), chromatin-like granules in calcified sphenopsid spores (Baxter, 1950, 1964), starch grains in the endosperm of fossil seeds (Pant & Srivastava, 1963) and nuclei and chromosome-like structures in silicified fern sporangia (Vishnu-Mittre, 1967).

The brown meshes generally lack cross walls, but occasionally an oblique partition may be clearly seen. The partitions correspond with the partitions in the chlorophyllose cells of *Sphagnum*.

The present leaves of *Sphagnophyllites* therefore resemble those of *Sphagnum* not only in their external form, e.g. in having similar raised and depressed areas, but also in their microscopic details.

A peculiar feature of some leaves is the occurrence of a number of parallel or anastomosing darker lines formed by rows of darker coloured brown cells. There is less regularity in their arrangement and we believe these are artifacts caused by folds or crumples in the leaves during fossilization.

The present unistratose, acostate leaves could also be compared with those of the foliose Jungermanniales, some acostate Bryales like *Schistostega*, *Ephemerum* and *Hedwigia* and some Sphagnales. However, the occurrence of two kinds of cells, viz., the hyaline and chlorophyllose, rules out their assignment to any of the above two groups.

Sphagnum-like shoots from beds earlier than the Triassic were reported by Neuburg (1956, 1960) from the Lower and Upper Permian deposits of the Petchora, Kuznetsk and Tunguska Basins, Angarida, U.S.S.R. The three species (*Junjagia glottophylla*, *Vorcutannularia plicata* and *Protosphagnum nervatum*) also possess two kinds of cells — the so called chlorophyllose (photosynthetic) cells and the hyaline water holding cells. A photograph of *Junjagia glottophylla* (see Neuburg, 1960, pls. 59, 60, figs. 2, 4 respectively) seems to show even some chloroplast-like rounded bodies inside the darker coloured mesh work, but her descriptions do not mention them. All the above mentioned Russian forms differ from modern *Sphagnum* in having a midrib and occasional vague indications of lateral nerves. The presently described material does not show any costae or lateral nerves and therefore are quite different from the Russian forms. Parallel and anastomosing ribs seen in some leaves appear to be artifacts rather than nerves since they do not show a many-cell thick costa.

Arnold (1932, 1947), Reissinger (1952), Straus (1952) and Abramova and Abramova (1962) have reported undoubted leaves of *Sphagnum* from Mesozoic, Tertiary and Quaternary deposits, in the various parts of the world. However, the closest comparison with our species is offered by Reissinger's (1952) specimens, the Cretaceous, Tertiary and Quaternary sphagna described by the other authors seem to be so closely comparable with modern forms that they have been actually referred to some of the living species of the genus. Reissinger (1952) described authentic leaves and spores of *Sphagnum* from the Liassic (Lower Jurassic) of Nuremberg in Bavaria. The size of the Indian leaves is larger, those of Reissinger (1952) being 880 μ × 200 μ.

Not only does the present species constitute the first report of a fossil resembling *Sphagnum* from any Triassic beds but it is also the first such fossil to be reported from India. However, some Triassic shoots, called *Muscites guescelini* by Townrow (1958) from the Triassic beds of South Africa, seem to show similar leaves and we suspect that the presumed thick walls of cells in this species are actually chlorophyllose cells and the cell lumina are hyaline cells (cf. Townrow 1958, p. 9, fig. 3C). On the basis of these findings it appears that *Sphagnum*-like plants were well represented not only as early as the Triassic but were also fairly widely distributed in Gondwana countries.

Another fossil moss which shows a superficial resemblance with *Sphagnophyllites* is *Diettertia montanensis* Brown and Robinson (1974) from the Lower Cretaceous of Montana. Both have unistratose, acostate leaves, dark spots in the angles of some of the marginal and apical cells (like the chloroplasts of the present Indian species) and no alar cells. All the same the leaf cells in *D. montanensis* are elongate to hexagonal and not isodiametric like the hyaline cells of *S. triassicus*.

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EXPLANATION OF PLATES

PLATE 1

Hepaticites nidpurensis sp. nov.

1. Thallus showing dorsally attached sporogonium and rhizoids. 40,651. × 66.

2. Thallus seen after removal of sporogonium. A naturally macerated portion of the thallus on the left hand side shows thin-walled epidermal cells. 40,651. × 72.

3. An aseptate smooth-walled rhizoid. 40,651. × 500.

4. A naturally macerated portion of the thallus highly magnified to show the epidermal cells. The broken end of a rhizoid is seen lying by the side of its point of attachment. 40,651. × 360.

5. A pear-shaped sporogonium showing its tapering base and the dehisced wall on the wider distal side. 40,651. × 115.

PLATE 2

H. nidpurensis sp. nov.

6. A bunch of spores obtained by dissecting the sporogonium. 40,651. × 500.

7-10. Variously compressed spores showing a proximal trilete. 40,651. × 940.

Sphagnophyllites triassicus gen. et sp. nov.

11-13. Detached leaves seen in incident illumination in figs. 11 and 12 and transmitted illumination in fig. 13. 11, 40,602. × 26; 12, 40,601. × 26; 13, 40,603. × 26.

PLATE 3

S. triassicus gen. et sp. nov.

14, 15. Leaves as seen in transmitted light. Rows of photosynthetic cells occasionally appear as dark lines possibly due to folding. 14, 40,605. × 30; 15, 40,604. × 45.

16. Enlarged view of a portion of leaf showing hyaline and photosynthetic cells. Some of the hyaline cells also show the characteristic spiral thickenings in the form of faint partitions (*p*). 40,601. × 130.

17. Further magnified view of leaf in fig. 16, showing the chloroplasts in the photosynthetic cells. 40,601. × 520.

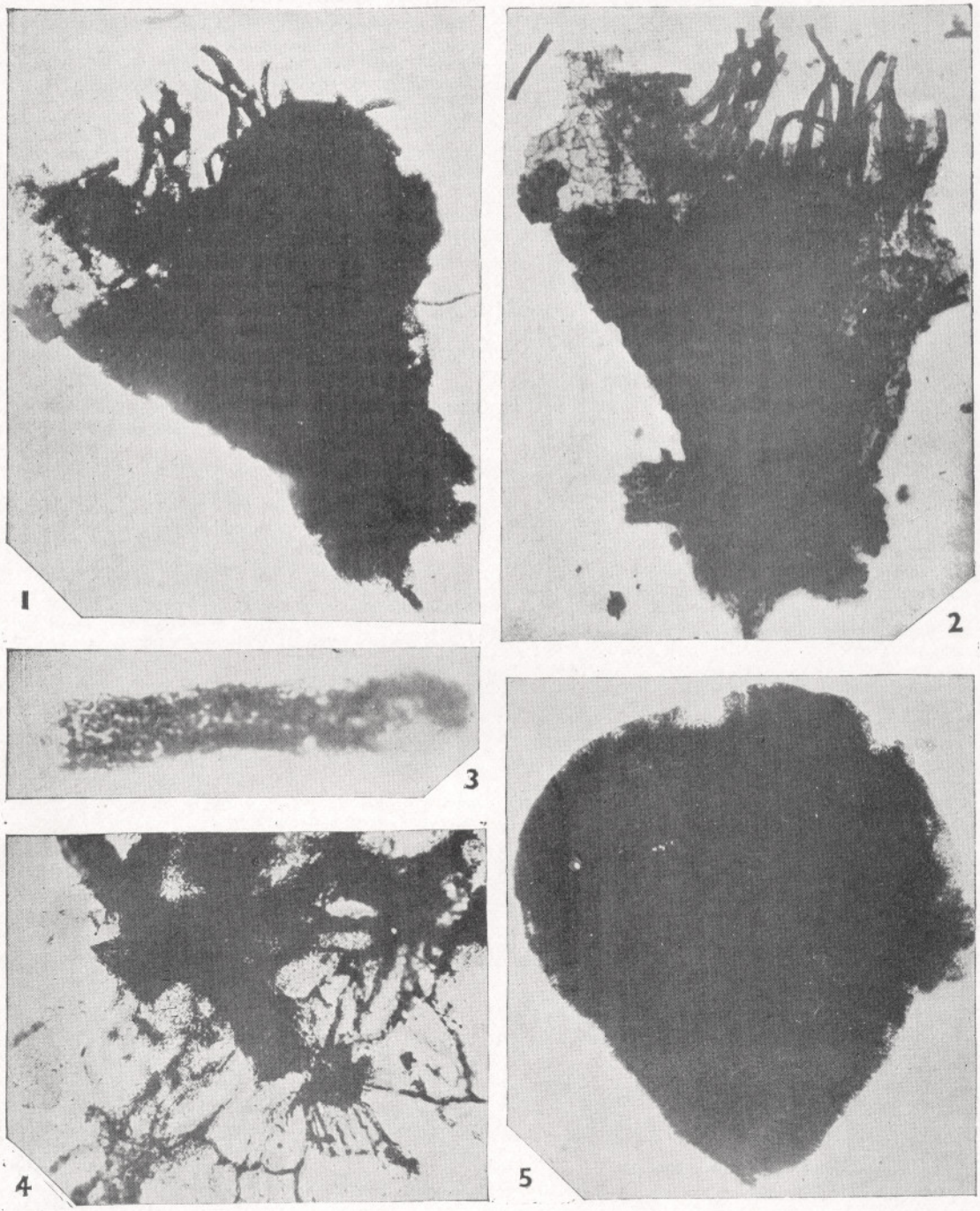
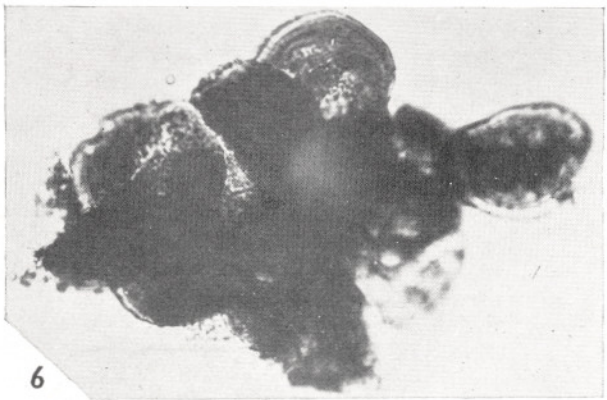
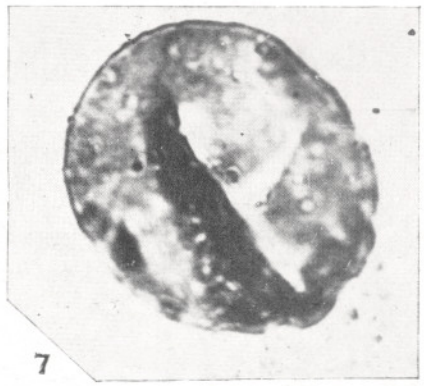
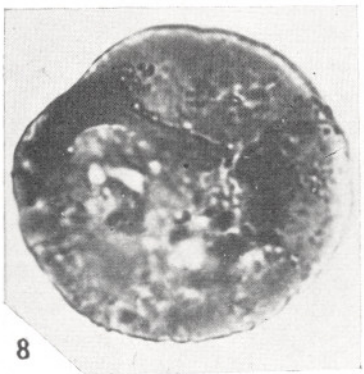
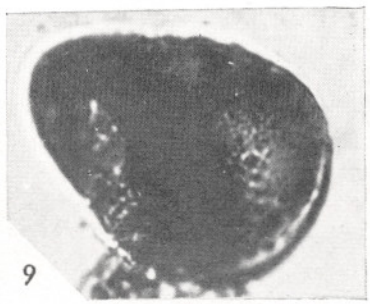


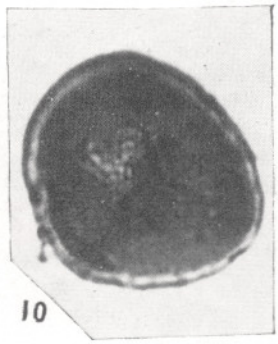
PLATE 1











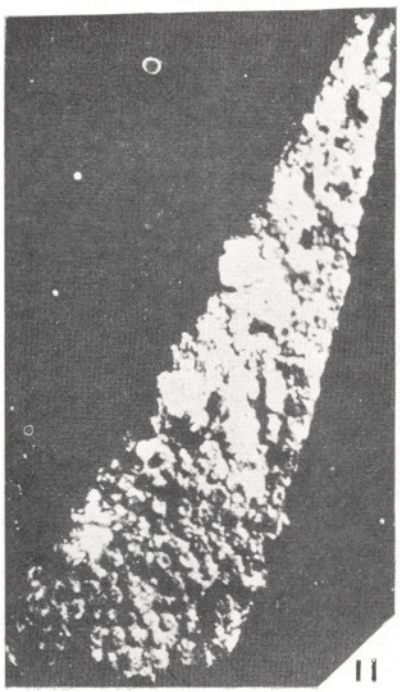
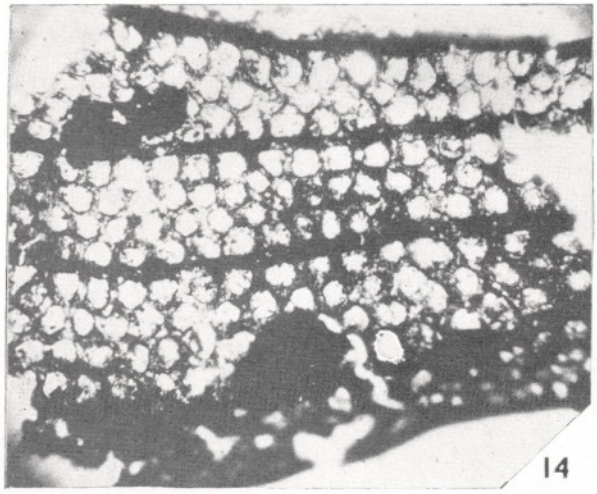
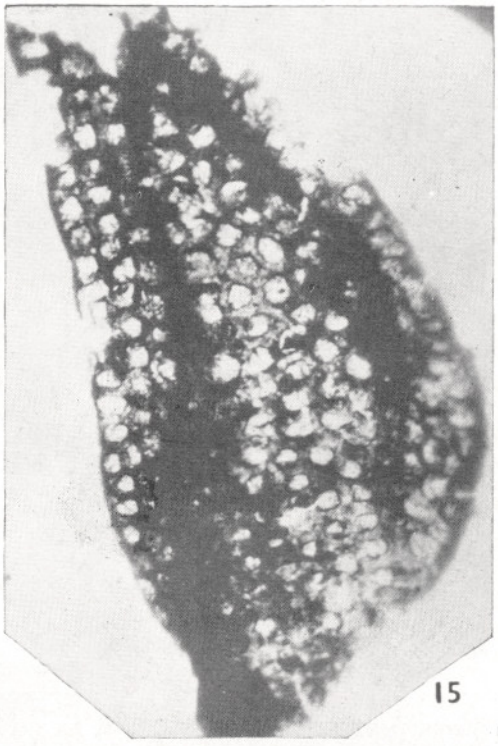
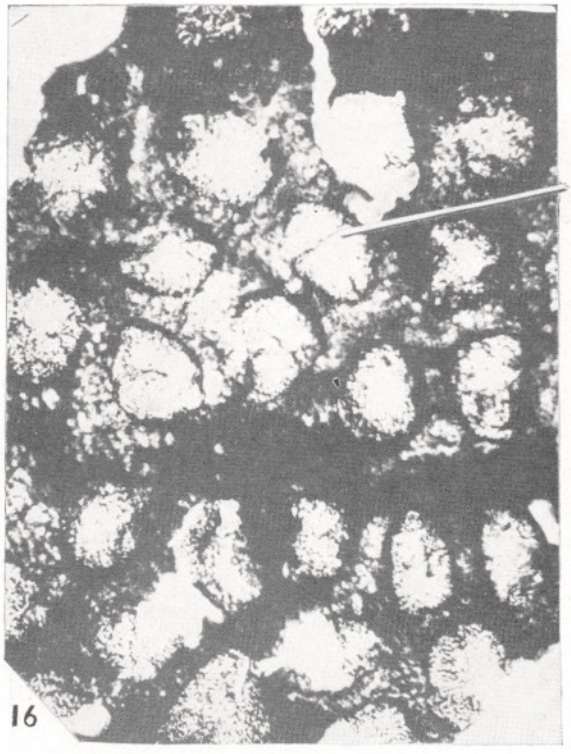


PLATE 2







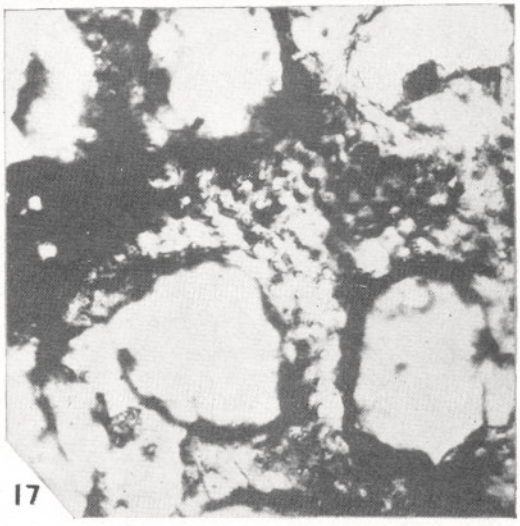


PLATE 3