Bryophytic remains from the Early Permian sediments of India

Shaila Chandra

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Bryophytic fossil remains in the Permian Gondwana formations are extremely rare. The rarity of fossil bryophytes is generally attributed to their delicate nature and small size of the plants. Fossil bryophytes so far reported are few as compared to vascular plants but they have been adequately recorded to indicate early existence of mosses and liverworts. It is also likely that bryophytes have just not been recognized in ancient sediments by palaeobotanists and they may not be so rare as are believed today. Most of the fossil specimens reported from India as bryophytes are either doubtful records or unidentifiable up to generic level. Indian Permian reports are considered doubtful while Triassic and younger records are not so meagre and are reasonably well reported.

It is for the first time a good assemblage of bryophytes has been recovered from the Early Permian sediments of India as impressions alongwith the typical Glossopteris flora. Both the groups Hepaticae and Musci are represented by newly designated form genera and species. The assemblage is represented by an indeterminate genus – *Bryothallites talchirensis*, hepatic genus – *Hepaticites umariaensis*, and three moss genera – *Talchirophyllites indicus*, *Saksenaphyllites saksenae* and *Umariaphyllites acutus*. Remarks on the naming of the fossil bryophytes, their probable possibility of preservation, spore distribution, probable habitat and evolutionary aspects also have been given and discussed.

Key-words —Impressions, Hepaticae, Musci, Early Permian, Gondwana (India).

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सारॉश

भारत के प्रारम्भिक परमियन युगीन अवसादों से ब्रायोफाइटी अवशेष

शैला चन्द्रा

परमी युगीन गोंडवाना शैल-समूहों में ब्रायोफाइटी अवशेष बहुत ही कम मिलते हैं। ऐसा सामान्यतः इनकी मृदु प्रकृति एवं आकार में छोटा होने के कारण है। उच्च वर्ग के पौधों की अपेक्षा अशिमत ब्रायोफाइटी पौधों के कम अभिलेख हैं । परन्तु इनके उपलब्ध अवशेषों से मॉस एवं सूकायों की उपस्थिति के स्पष्ट संकेत मिलते हैं। यह भी सम्भव है कि आकार में छोटा होने के कारण पुरावनस्पतिविदों का इनकी विद्यमानता की ओर कम ध्यान गया है। वैसे अभी तक अभिलिखित ब्रायोफाइटी अवशेषों में से अधिकतर या तो संदेहास्पद हैं अथवा केवल प्रजाति स्तर तक ही अभिनिर्धारित किये जा सके हैं । भारतीय परमी कल्प से प्राप्त सभी अभिलेखों का यथार्थ अभिनिर्धारण नहीं किया जा सका है जबकि त्रिसंघी एवं अल्प आयु के अवसादों से अपेक्षाकृत अभिलेखों का स्पष्ट उल्लेख है।

प्रस्तुत शोध-पत्र में पहली बार भारत के परमी कल्प से ब्रायोफाइटी पौधों के अवशेषों की सघन समुच्चय का वर्णन किया गया है। सभी अवशेष छापों के रूप में विद्यमान हैं तथा ग्लॉसॉप्टेरिस वनस्पतिजात के साथ मिलते हैं। इस समुच्चय में हिपेटिसी एवं मस्साइ दोनों ही समूह के अवशेष विद्यमान हैं । जिनमें एक न पहचाना गया *ब्रायोफिल्लाइटिस तलचीरेन्सिस*, हिपेटिसी समूह का *हिपेटिसाइटिस उमरियेन्सिस*, तीन मॉस प्रजातियाँ – *तलचीरोफिल्लाइटिस इंडिकस*, *सक्सेनाफिल्लाइटिस एक्यूटस*, *उमरियाफिल्लाइटिस एक्यूटस* नामक वर्गक सम्मिलित हैं। इसी शोध-पत्र में अशिमत ब्रायोफाइटी पौधों के नामकरण, इनके परिरक्षण, बीजाणु वितरण, स्वभाव तथा वैकल्पिक पहलुओं पर भी विवेचना की गई है।

THE existence of undoubted bryophytic remains during Palaeozoic time was first brought forth by Walton (1925) who discovered structurally preserved members of the group in Carboniferous rocks. Since then a large number of bryophytic fossil remains have been reported from various ages from all parts of the world.

The reports of fossil bryophytes from the Gondwana countries include Lundqvist (1919), Dolianiti (1948), Saksena (1947, 1958), Clifford and Cookson (1953), Medwell (1954), Gupta (1956), Townrow (1959), Mehta and Goswami (1960), Jain and Delevoryas (1967), Singhai (1973), Anderson (1976), Pant and Basu (1978, 1981), Webb and Holmes (1982), Bose and Banerji (1984), Anderson and Anderson (1985) and Banerji (1988) (see Table 1).

The first two reports on thallus-like fossil remains identified as *Marchantites* from the Lower Gondwana beds by Lundqvist (1919) and Dolianiti (1948) are suspected to be the roots of *Lithorhiza tenuirama* (Pant, 1958). *Capsulites gondwanensis* was described as a moss capsule (Saksena, 1958), later to be considered as macerated seed of *Platycardia* or *Pterygospermum* (Pant & Nautiyal, 1960). Pant and Basu (1978, 1981) reported *Hepaticites nidpurensis, H. riccardioides, H. foliata, H. metzgerioides* Walton and *Sphagnophyllites triassicus* from the Triassic beds of India recovered from a maceral residue. Bose and Pal (1982) instituted a new species *Hepaticites pantii* having a row of ventral scales on either side of the midvein from the Early Jurassic beds of Rajmahal Hills, Bihar . Banerji (1988) instituted a genus *Trambauathallites sukhpurensis* from the Early Cretaceous beds in the Kutch District, the same plant earlier described as *Hepaticites sukhpurensis* Bose & Banerji 1984. Plumstead (1966) reported for the first time an unnamed moss from the Late Permian of South Africa. *Buthelezia,* a new genus by Lacey, van Dijk and Gordon-Gray 1975 from the Late Permian beds of Natal, South Africa, is doubtfully placed under the bryophytes. Another new genus, *Dwykea goedehoopensis* Anderson & Anderson 1985 is reported from the Early Permian beds from North Karoo Basin.

Triassic Gondwanian bryophytes from South Africa were described by Townrow (1959) and Anderson (1976). Townrow reported a thallose fossil, *Hepaticites cyathodioides* and foliage remains as *Muscites guescelini.* Anderson (1976) transferred *H. cyathodioides* to *Marchantites* and also reported two species, *Thallites* sp. and *Marchantites tennantii* from the Molteno Formation.

Jain and Delevoryas (1967) reported *Thallites* sp. from the Triassic of Argentina. Miller (1979) noted an extremely well preserved moss from Antarctic beds confirming the presence of mosses in the Glossopteris flora. Smoot and Taylor (1986) instituted a genus *Merceria angustica* from the Late Permian beds of Antarctica.

Some of the other fossil bryophytic reports from Gondwana are of Tertiary and post Tertiary age. These include three sporophytic fossils called *Muscites yallournensis* Clifford & Cookson 1953, a *Notothylas* type of sporogonium reported by Gupta (1956), *Shuklanites deccanii* Singhai 1964 and thallose remains–*Hepaticites kashmirensis* Mehta & Goswami 1960. Medwell (1954) reported gametophytic remains of a thallose form from the Jurassic.

Contrast to the Gondwanian bryophytic reports, mosses are recorded in great abundance from the Permian of Angaraland. In all, there are at least 20 genera founded on very minor differences. The pioneer discoverer of mosses in the region, Neuberg (1956, 1958a, 1958b, 1960), instituted nine genera with 13 species from the Pechora, Tunkusska and Kuznetsky basins. Later, Fefilova (1978) and Ignatov (1990) instituted 10 more genera and revised some species previously described by Neuberg (see above), Meyen and Tverdokhlebov (1966) and Gomankov and Meyen (1986). All the hitherto reported bryophytes from the Russian platform obtained by bulk maceration process are structurally preserved.

Besides Angaraland, there are a few Palaeozoic mosses known from France (Renault & Zeiller, 1988; Lignier, 1914), Great Britain (Walton, 1925, 1928; Schuster, 1966), Germany (Krausel, 1958; Schuster, 1969), Sweden (Lundblad, 1959) and several minor reports from the Lower and Upper Devonian strata from all over the world.

The most complete fossil bryophyte is *Naiadita lanceolata* (Harris, 1937, 1939) from the English Rhaetic. Harris found leaves, stems, rhizoids, gemma cups, gemmae, archegonia, sporophytes and spores making *Naiadita* the best known of any almost complete fossil bryophyte.

In particular six valuable and exhaustive reviews and papers have appeared in the last three decades covering all the aspects of fossil bryophytes. Lundblad (1954) reviewed the progress in work on fossil liverworts up to that time. Afterwards Savicz-Lubitzkaja and Abramov (1959) provided a summary of the whole field of bryophytic palaeobotany. Jovet-Ast (1967) has given an extensive, detailed and up to date account of all the known fossil bryophytes. Lacey (1969) presented a geological history of bryophytes in the light of research done up to 1969. Bharadwaj (1982) gave a comprehensive account of all fossil bryophytes known up to that time. In 1982, Miller gave a detailed account of all aspects of bryophytes from the evolutionary and geographical distribution point of view.

Table 1— Geological distribution of bryophytic remains from Southern Continents

	INDIA	SOUTH AFRICA	AUSTRALIA	ANTARCTICA	BRAZIL AND ARGENTINA
QUATERNARY	*Sphagnum* Sharma 1978 from Himachal Pradesh, *Hepaticites kashmirensis* Mehta & Goswami 1960 from Kashmir, *Hepaticites* sp. Goswami 1957 from Kashmir				
TERTIARY	*Shuklanites deccanii* Singhai 1973 from Deccan Traps, *Riccia* thallus Sheikh & Kapgate 1982 from Deccan Traps, a sporogonium Gupta 1956 from Deccan Traps.		*Muscites yallournensis* Clifford & Cookson 1953 from Victoria, *Ephemeropsis* Selkirk 1974		
CRETACEOUS	*Trambauathallites sukhpurensis* Banerjee 1988 from Kutch		*Thallites* sp. A, *Thallites* sp. B, *Thallites* sp. C all by Douglas 1975 from Victoria, Several spore genera by Dettmann, 1963		
JURASSIC	*Hepaticites pantii* Bose & Pal 1982 from Rajmahal Hills		*Sphagnumsporites adnatus* Filatoff 1975 *S. tenuis* Filatoff 1975, *S. clavus* Filatoff 1975 all from Queensland, Sphagnacean type spores by Filatoff 1975 from Perth Basin, *Marchantites erectus* Medwell 1954, *M. barwoni* Medwell 1954, Several spore genera by Fefilova 1975 from Perth Basin	?*Schizolepidella gracilis* Halle 1913	

Table 1 *contd.*

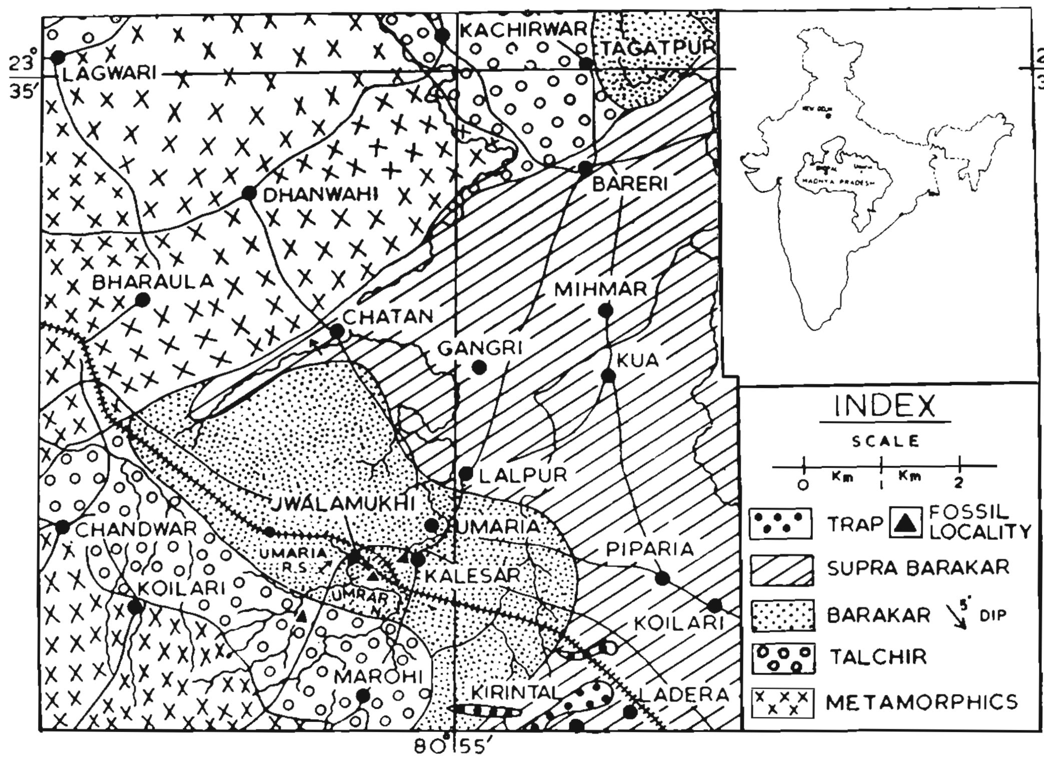
TRIASSIC	*Hepaticites nidpurensis* Pant & Basu 1978, *H. riccardioides* Pant & Basu 1981, *H. foliata* Pant & Basu 1981, *H. metzgerioides* Walton. Pant & Basu 1981 all from Nidpuri, South Rewa Gondwana Basin	*Muscites guescelinii* Anderson 1976, *Thallites* sp. Anderson 1976 both from Molteno, Karoo Basin, *Hepaticites cyathodoides* Townrow 1959 from Natal, *Marchantites cyathodoides* (Townrow) Anderson 1976, *M. tennantii* Anderson 1976 both from Molteno	Indeterminate thalloid spp. A, B & C Webb & Holmes 1982 from eastern Australia, eight undescribed liverworts by Townrow 1964 from Tasmania		*Thallites* sp. Jain & Delevoryas 1967 from Minas de Petroleo
LATE PERMIAN	?*Marchantites* (=*Lithorhiza tenuirama* Pant 1958 now considered as roots), ?*Capsulites gondwanensis* Saksena 1958 (=*Platycardia* Pant & Nautiyal 1960, now considered as seed)	?*Buthelezia mooiensis* Lacey, Van dijk & Gordon Gray 1975 from Natal		*Merceria angustica* Smoot & Taylor 1986 (permineralized)	*Marchantites* sp. Lundquist 1909 & Doianiti 1948 from Brazil, considered as roots, *Lithorhiza tenuirama* Pant 1958
EARLY PERMIAN	*Bryothallites talchirensis* gen. *et* sp. nov., *Hepaticites umariaensis* sp. nov., *Talchirophyllites indicus* gen. *et* sp. nov., *Saksenaphyllites saksenae* gen. *et* sp. nov. *Umariaphyllites acutus* gen. *et* sp. nov., all from Umaria, South Rewa Gondwana Basin	*Duykea goedehoopensis* Anderson & Anderson 1985 from North Karoo Basin			*Thallites* sp. Rigby 1969 from Sau Paulo, Brazil
EARLY CARBONIFEROUS		Probable moss by Plumstead 1966 from Transvaal			

MATERIAL AND METHODS

The fossil specimens reported in the present paper are all in the form of impressions and no carbonized crust is retained. The impressions are slightly darker in colour on greenish pale yellow muddy silty shales. The shales are full of impressions of organic material, generally with numerous small leaves of mosses. It is difficult to recognize small sized bryophytic remains on the shale. Because of the smallness of size and lack of contrast they are difficult to photograph. Therefore, to clearly show the morphographical structures, text-figures have been drawn.

In addition to the bryophytes, small leaves of *Gangamopteris* (Pl. 7, fig. 5), *Glossopteris* (Pl. 5, fig. 5), *Noeggerathiopsis* (Pl. 7, fig. 3) and equisetalean stems, alongwith numerous *Cordaicarpus* seeds (Pl. 7, fig. 4) are also noticed in the assemblage. Some unidentifiable plant and organic objects are also recognized.

The present fossil remains of bryophytes, alongwith typical Glossopteris flora, have been collected from an 8 cm thick shale bed. This shale bed is exposed in a nala near Jwalamukhi temple, situated about 2 km south-west of Umaria town in the Shahdol District of South Rewa Gondwana Basin (Map 1). The fossiliferous bed is virtually at water level and is overlain by thick (2 meters) shales of the same type but devoid of any fossils. The bryophytic fossil-bearing beds are exposed for 2-3 meters. The shales, being underwater, are difficult to collect as they are very soft and easily broken. The exact spot of the fossiliferous bed in the Umrar nala is marked on the locality map. The other exposed areas in the nala do not yield identifiable fossils.



Map 1—Geological map of Umaria, Shahdol District, Madhya Pradesh (after Hughes, 1884; Chandra & Srivastava, 1982).

PLATE 1

1. *Bryothallites talchirensis* gen. *et* sp. nov., a complete thallus of indeterminate shape. Specimen no. BSIP 37306A x 4.
2. *Bryothallites talchirensis* gen. *et* sp. nov., thallus enlarged to show irregular outlines of cells. Specimen no. BSIP 37322 x 10.
3. *Hepaticites umariaensis* sp. nov., flat, dorsiventral, dichotomously branched thallus, also note circular marking on the first left hand branch. Specimen no. BSIP 37307B x 10.
4. *Hepaticites umariaensis* sp. nov., linear wedge shaped dichotomous, smooth margined thallus, each branch with midvein. Specimen no. BSIP 37307A x 10.

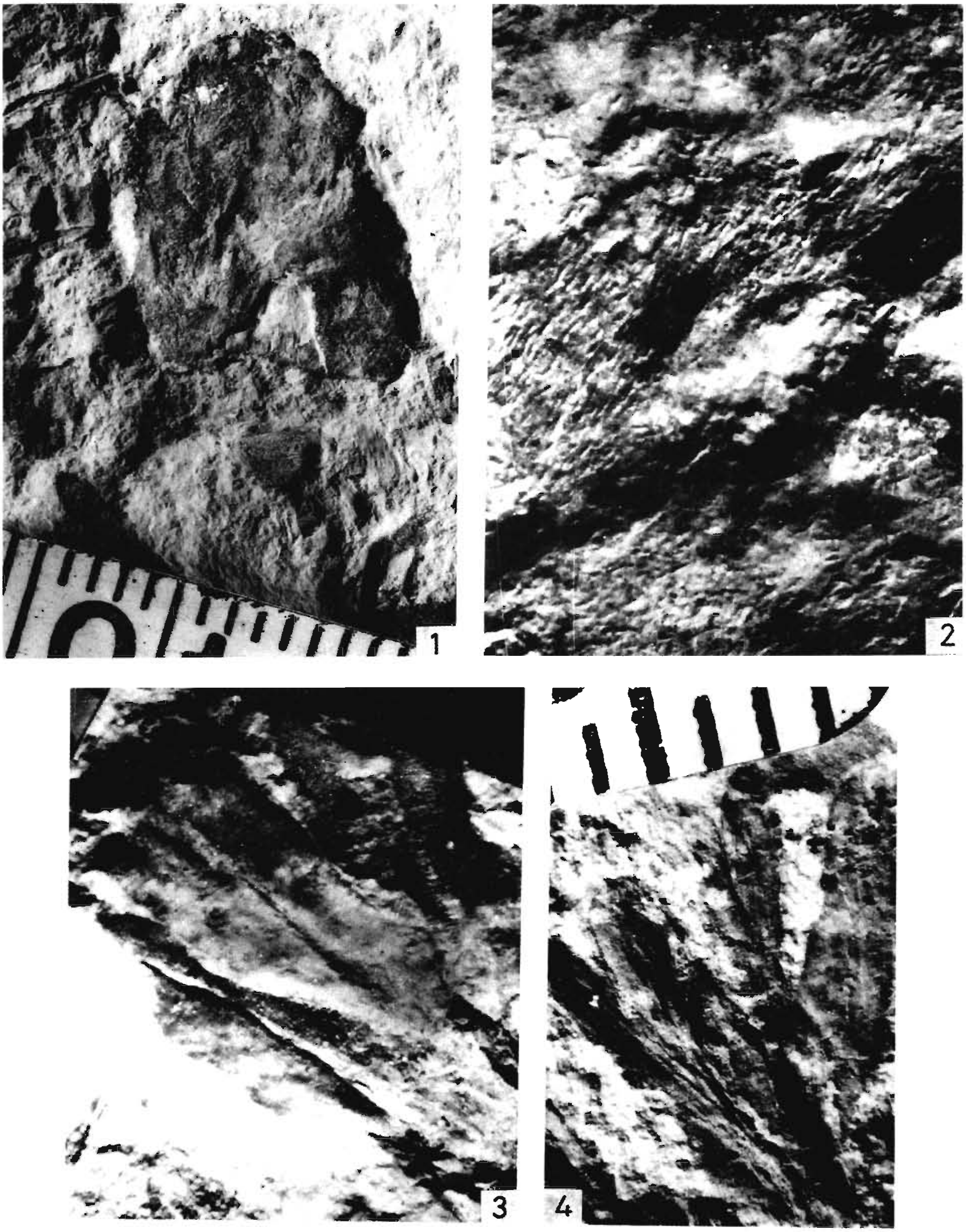
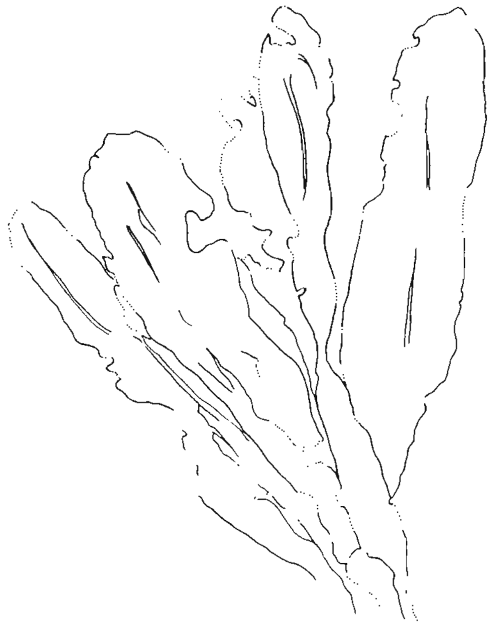
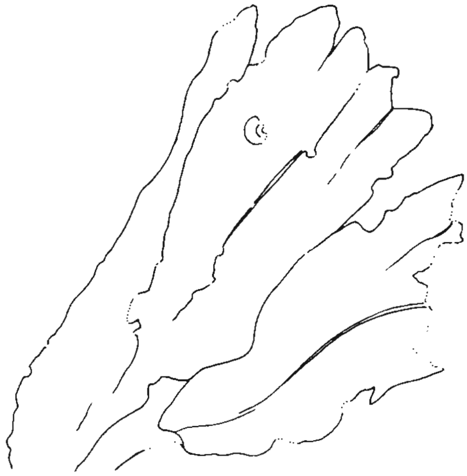


PLATE 1



Text-figure 1—*Hepaticites umariaensis* sp. nov., a flat, dorsiventral dichotomously branched thallus with smooth outer margins, each branch with a definite midvein. Specimen no. BSIP 37306A x 8.



Text-figure 2—*Hepaticites umariaensis* sp. nov., dorsiventral thallus showing dichotomy, circular marking below and ?gametangia. Specimen no. BSIP 37307B x 8.

SYSTEMATIC DESCRIPTION

Indeterminate genus—*Bryothallites* gen. nov.

Type species—*Bryothallites talchirensis* gen. et sp. nov. (Pl. 1, figs 1, 2; Pl. 2, fig. 6).

Diagnosis—Thalloid forms, indeterminate shape, cellular structures lacking details.

Holotype—Specimen no. BSIP 37306A.

Locality—Umrar Nala section, near Jwalamukhi Temple, Umaria, Shahdol District, Madhya Pradesh, India.

Horizon & Age—Talchir Formation, Early Permian.

Description—There are several thalli of 1.5-3 cm in diameter in the collection. Sometimes hair like rhizoids are also seen but details are not clearly visible. The thallus is made up of definite cells and can be seen under higher magnification. The rectangular cells are arranged longitudinally (Pl. 1, fig. 2).

Comparison—Thalloid fossils have been classified under many genera but their exact affinity is not known. One such genus is *Thallites* proposed by Walton (1925) for thalloid fossils with characters which cannot be identified as bryophyte, algae, gametophyte of ferns or equisetales. The generally accepted type species of *Thallites* is *T. erectus*, proposed informally by Walton. Its morphology was poorly known. This species was later transferred to *Hepaticites arcuatus* by Harris (1942) considering it as a definite liverwort, automatically nullifying the use of the genus *Thallites*. Later, many authors referred their specimens to *Thallites* without considering its validity. Webb and Holmes (1982), therefore proposed an informal name "indeterminate thalloid fossil" for possible algal or liverwort fossils reported from the Middle Triassic of Eastern Australia. They designated their specimens as Indeterminate thalloid fossil sp. A, sp. B and sp. C considering sp. A as an alga and sp. B and sp. C as liverworts. I think that this practice will serve no purpose and may cause problems for future workers in designating their specimens without any proper name. Therefore,

PLATE 2 ⟶

1. *Hepaticites umariaensis* sp. nov., slab showing number of dichotomously branched thalli with midveins. Specimen nos. BSIP 37307A and 37307B x 6.
2. *Hepaticites umariaensis* sp. nov., circular definite marking, ? gametangia near the forking of the thallus. Specimen no. BSIP 37315B x 20.

3, 4. Circular, definite markings supposed to be ? gametangia. Specimen no. BSIP 37324 x 40.

5. *Saksenaphyllites saksenae* gen. et sp. nov., detached sporogonium showing long seta and spathulate capsule. Specimen no. BSIP 37311 x 5.
6. *Bryothallites talchirensis* gen. et sp. nov., another irregular thallus with *Hepaticites umariensis* sp. nov. Specimen no. BSIP 37322 x 2.

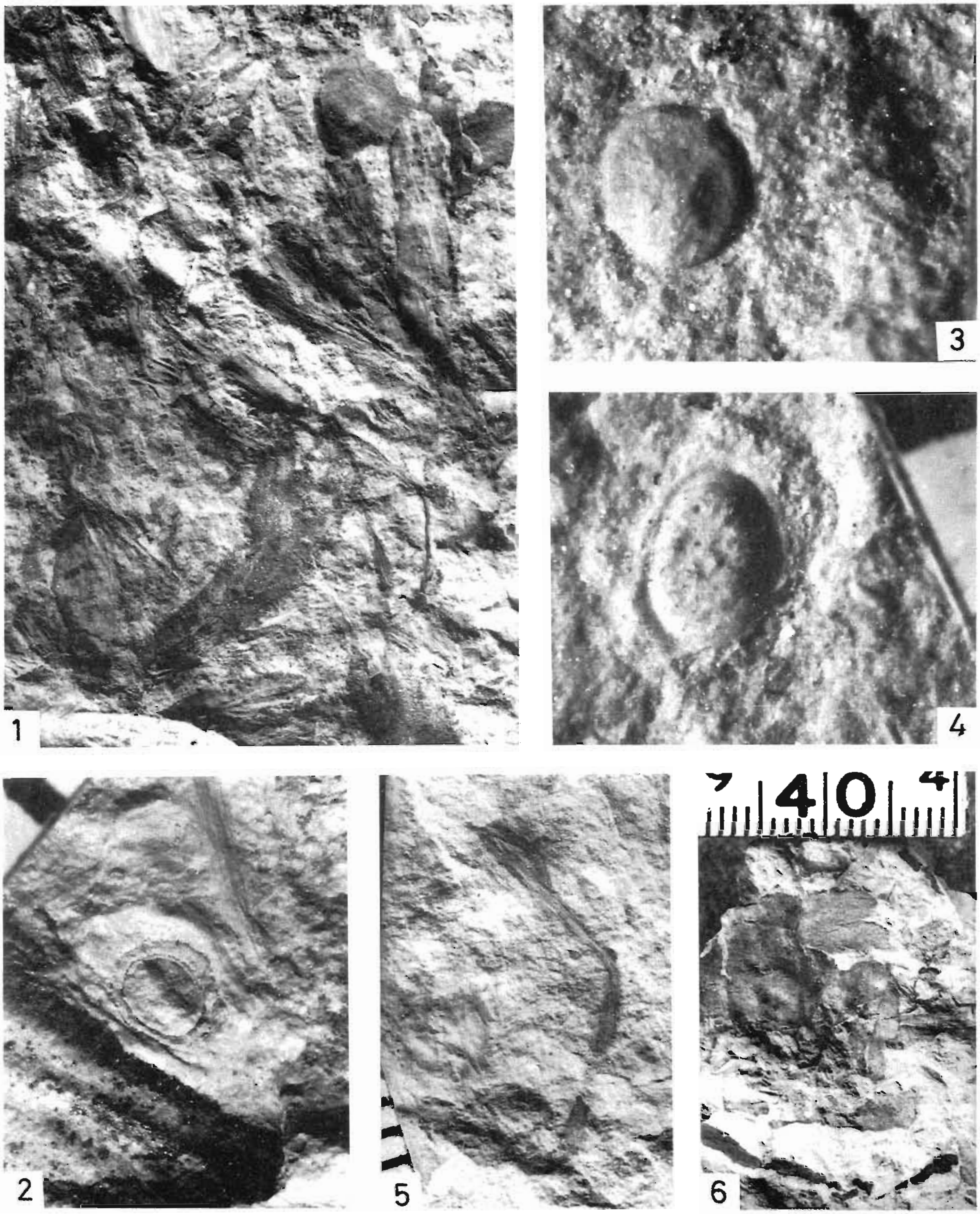


PLATE 2

those thalli which are more akin to alga should be referred to as *Algathallites* and those to bryophytes as *Bryothallites*.

Class — Hepaticopsida (Hepaticae) Rothmaler

Genus — *Hepaticites* Walton 1925

Hepaticites umariaensis sp. nov

Pl. 1, figs 3, 4; Pl. 2, figs 1-4; Text-figures 1-3

Diagnosis—Gametophyte plant thalloid impressions, prostrate, flat, dorsiventral, somewhat fleshy, dichotomously branched, dichotomy regular, each branch linear to wedge shaped with midvein, margins smooth; rhizoids, internal structures, reproductive structures unknown.

Holotype—Specimen no. BSIP 37307A.

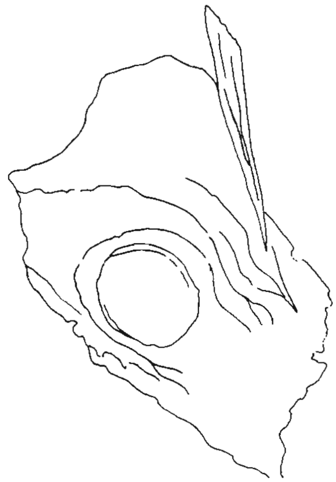
Locality—Umrar Nala section, near Jwalamukhi Temple, Umaria, Shahdol District, Madhya Pradesh, India.

Horizon & Age—Talchir Formation, Early Permian.

Description—Three distinct specimens are observed in the assemblage, though they can also be seen as ill-preserved specimens elsewhere in the shales. The thallus appears to have been made up of uniform tissue with midveins showing definite dichotomy along its length. Very thin, hair-like structures which could be rhizoids can be observed under dim light.

A circular definite marking (Pl. 2, fig. 2; Text-figure 3) is also observed near the forking region of a dichotomy. Could this be a gametangia bearing structure? Under higher magnification cellular structures can be seen, but without any definite outline.

Comparison—Walton (1925) instituted a form genus *Hepaticites* to include such fossils which resemble Hepaticopsida but cannot be assigned to any true genus, family or order. In the absence of observable internal structures, detailed comparison with other species of the genus is not possible.



Text-figure 3—*Hepaticites umariaensis* sp. nov., ? gametangia in the dichotomy of the thallus. Specimen no. BSIP 37315 x 20.

All the Late Carboniferous species, namely *H. kidstonii* Walton 1925, *H. lobatus* Walton 1925, *H langii* Walton 1925 and *H. metzgerioides* Walton 1925 and the Triassic species, viz., *Hepaticites cyathodioides* Townrow 1959, *H. oishii* Takahashi 1960, *H. nidpurensis* Pant & Basu 1978, *H. riccardioides* Pant & Basu 1981, *H. foliata* Pant & Basu 1981 are based on internal structures. A detailed comparison of known species with *Hepaticites talchirensis* is thus not possible. Therefore, a new name is designated for this Early Permian species from India. *Trambauathallites sukhpurensis* Banerji 1988 from the Early Cretaceous beds shows some superficial resemblance with *Hepaticites talchirensis*, but differs in having undulated or wavy margins of thallus.

Class—Bryopsida (Musci) Rothmaler

Genus — *Talchirophyllites* gen. nov.

Type species — *Talchirophyllites indicus* gen. et sp. nov.

Pl. 3, figs 2-5; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 6, figs 4, 5; Text-figures 4-6

PLATE 3 →

1. *Saksenaphyllites saksenae* gen. *et* sp. nov., two vegetative axes with simple, spathulate leaves. Specimen no. BSIP 37318 x 5.
2. *Talchirophyllites indicus* gen. *et* sp. nov., small, slender, erect gametophyte covered with simple leaves, lower smaller leaves and upper leaves on the axis larger. Specimen no. BSIP 37308 x 6.
3. *Talchirophyllites indicus* gen. *et* sp. nov., counterpart of 37308 x 5.

4, 5. Detached simple, smaller, lanceolate leaves of *Talchirophyllites indicus* gen. *et* sp. nov. from lower side of the axis, faint outlines of cells visible with distinct midvein. Specimen nos. BSIP 37315C x 10 and 37312B x 15.

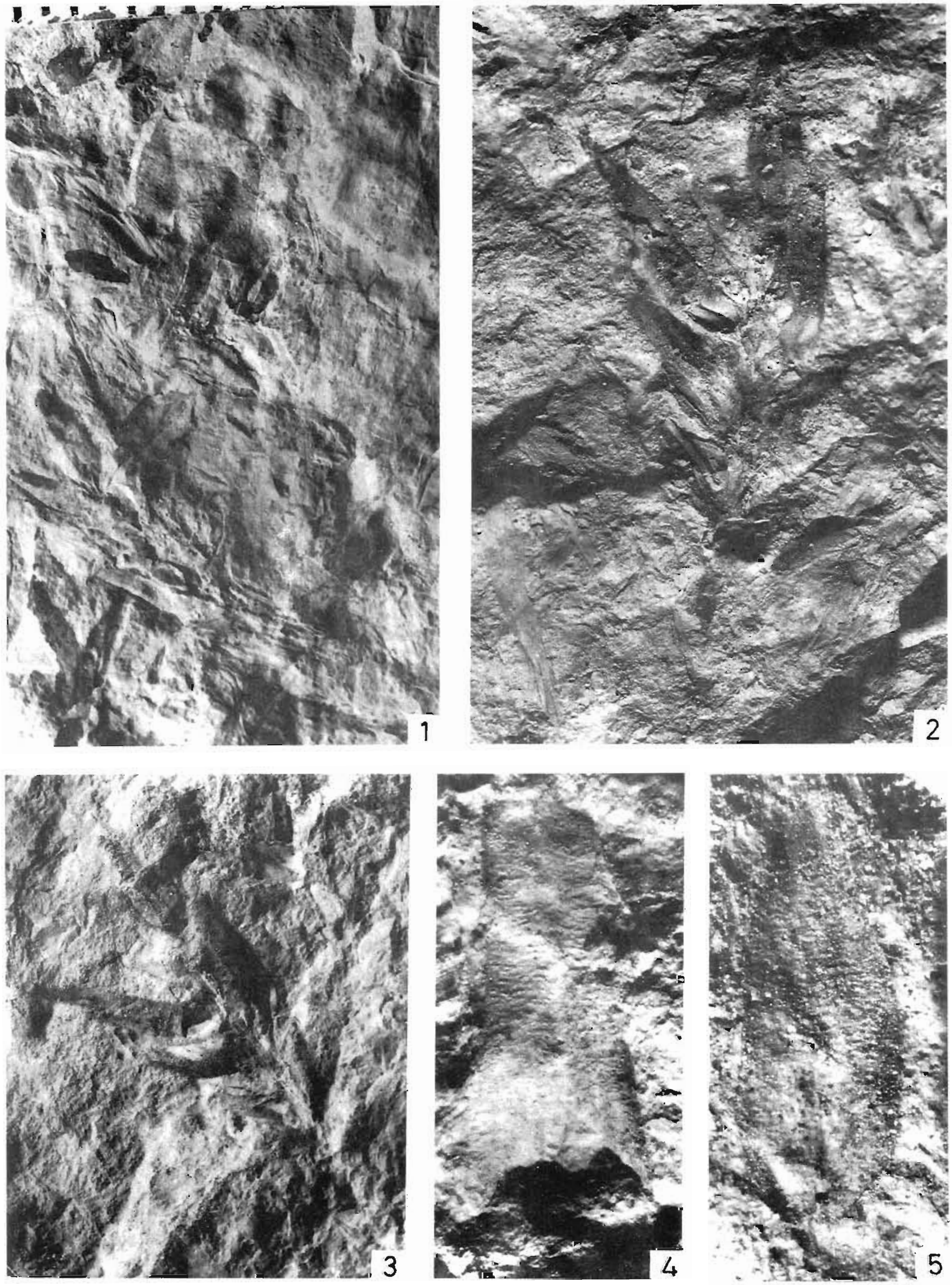


PLATE 3

Diagnosis—Gametophyte small, 1-3 cm in length, consisting of slender, erect, radial axis, covered with small simple leaves, axis branching; leaves spirally arranged, lower leaves on the axis smaller, upper leaves larger, leaves crowding at apex, sessile, lanceolate, smooth margin, attached to axis by broad base, apex pointed, each leaf with a distinct midvein.

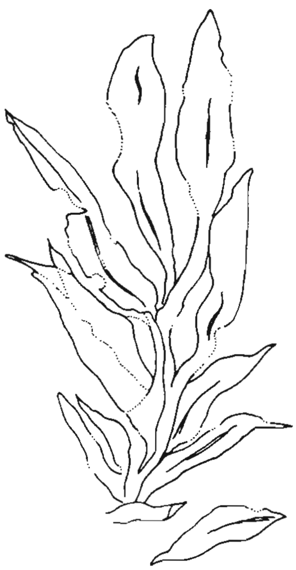
Holotype—Specimen No. BSIP 37308.

Locality—Umrar Nala section, near Jwalamukhi Temple, Umaria, Shahdol District, Madhya Pradesh, India.

Horizon & Age—Talchir Formation, Early Permian.

Derivation of name—The genus *Talchirophyllites* is named after the Indian peninsular Gondwana Formation—Talchir.

Description —There is one distinct specimen, one ill preserved specimen (Pl. 6, fig. 4) and several other detached leaves of this plant in the collection. The size of mostly complete specimen is 1.2 cm in length. Under high magnification the leaves show distinct midveins and the laminar part made up of simple cells. The size of a detached leaf is up to 8 mm in length and 1 mm in width. The leaf is attached to the axis by its complete base. Leaf-bearing axis is very thin and bears a crown of larger leaves at the tip. The shape of detached leaf is broadly lanceolate with an obtusely pointed apical end (Pl. 5, fig. 1; Pl. 6, fig. 3). The leaves appear to be one celled thick, made up of simple rectangular cells (Pl. 3, figs 4, 5). The cells along the midvein portion have thicker cell walls.



Text-figure 4 —*Talchirophyllites indicus* gen. *et* sp. nov., small gametophyte covered with simple leaves, lower older leaves smaller and upper younger leaves larger with midveins. Specimen no. BSIP 37308 x 6.

Comparison —There are at least twelve fossil moss genera reported from the Late and Early Permian beds of Russian Platform by Neuberg (1956, 1958a, 1958b, 1960) and Ignatov (1990). All the Russian fossil mosses were obtained from the macerals and are known by structural and cellular details. The major difference between *Talchirophyllites* and Russian fossil moss genera are in the manner of leaf attachment to the axis. In all the Russian fossil moss genera, the leaves are attached to the axis with their costa only and sometimes they are truly petiolated. These Russian genera are instituted on minor differences in leaf structures as is the general practice in classifying present day moss genera. Apparently *Talchirophyllites* comes closest to *Intia* Neuberg 1960 and *Uskatia* Neuberg 1960 but their finer details make them distinct forms. A close comparison between Indian and Russian forms is not possible as the cellular details are not available for *Talchirophyllites*.

Dwykea goedehoopensis Anderson & Anderson 1985, from the Early Permian beds of North Karoo Basin, is a bryophyte with midrib-less leaves. *Talchirophyllites* has distinct midveins in the leaves.

Buthelezia mooiensis Lacey *et al.* 1975 from the Late Permian beds of Natal is a complete plant placed in bryophytes with hesitation. *Talchirophyllites indicus* has smaller leaves on the lower side of the axis and the larger leaves on the upper side. Such distinction of leaves is absent in *Buthelezia*, moreover the leaves here are attached to the stem by an ensheathing broad base, ascending steeply for short distance then spreading at a wide angle, generally reflexed.

Merceria angustica Smoot & Taylor 1986 from the Late Permian beds of Antarctica is found as a petrifaction, therefore the external morphology is not known for further comparison. *Sphagnophyllites triassicus* Pant & Basu 1978, a moss from the Triassic

PLATE 4 →

1. *Talchirophyllites indicus* gen. *et* sp. nov., enlarged to show upper sessile leaves with distinct midveins and pointed apex. Specimen no. BSIP 37308 x 10.

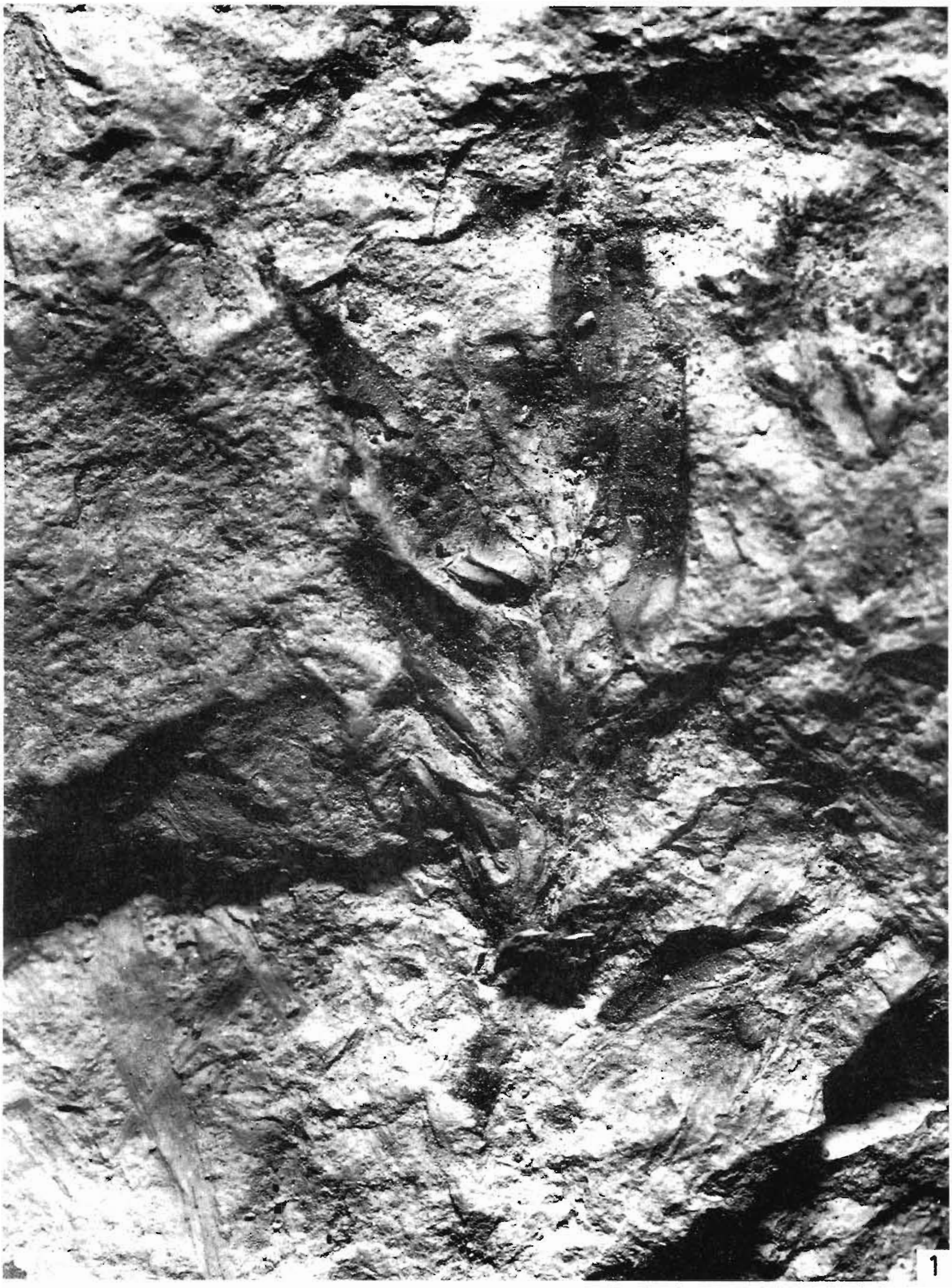
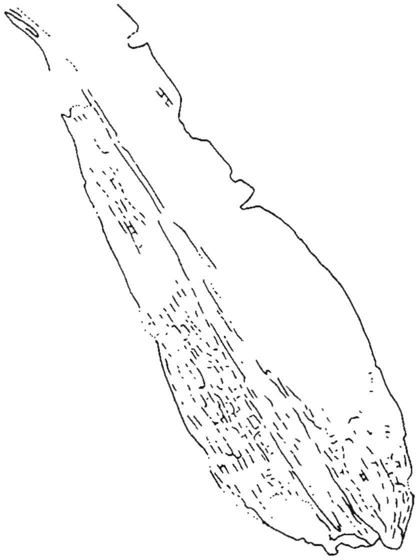
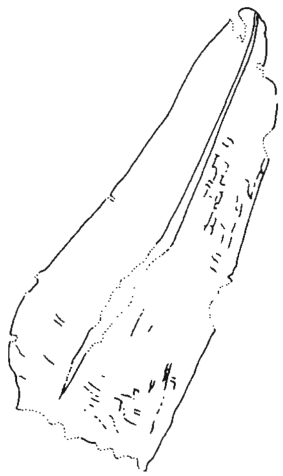


PLATE 4



Text-figure 5

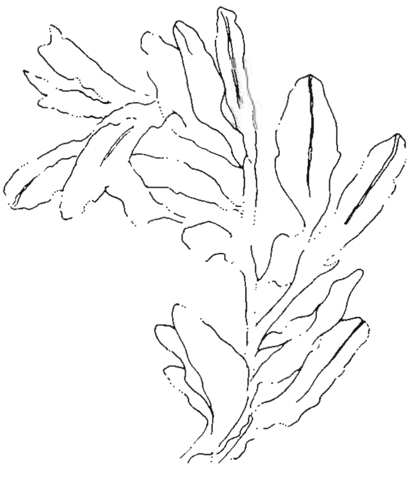


Text-figure 6

Text-figures 5, 6—*Talchirophyllites indicus* gen. *et* sp. nov., showing upper larger and lower smaller leaves. Specimen nos. BSIP 37315C and 37312B x 15.

beds of Nidpuri, South Rewa Gondwana Basin is also distinct and based on the structural details.

Talchirophyllites indicus shows some superficial resemblance with the living moss species *Atrichum pallidum* Ren *et* Card and *Poganatum aloides* (Helw) P. Beauv where lower smaller leaves are older and upper larger leaves are younger.



Text-figure 7—*Saksenaphyllites saksenae* gen. *et* sp. nov., leafy gametophytic shoot with branching. Specimen no. BSIP 37317 x 5.

In view of almost no definite record of mosses in the Early Permian beds of Gondwana, the report of *Talchirophyllites indicus* moss from the Early Permian beds of India is significant.

Genus—*Saksenaphyllites* gen. nov.

Type species— *Saksenaphyllites saksenae* gen. *et* sp. nov.

Pl. 2, fig. 5; Pl. 3, fig. 1; Pl. 5, figs 2, 3;

Pl. 6, figs 1, 2; Pl. 7, fig. 1; Pl. 8, fig. 1; Text-figures 8-10

Diagnosis—Gametophyte erect leafy stems, 1-3 cm in length; leaves spirally arranged on the axis, leaves narrow linear, obtuse tips, sessile, leaves with faint mid- veins; sporogonium consisting of capsule and seta, seta thin, long, capsule simple, spathulate broad at the tip.

Holotype—Specimen No. BSIP 37309.

Locality—Umrar Nala section, near Jwalamukhi Temple, Umaria, Shahdol District, Madhya Pradesh, India.

PLATE 5

1. Detached leaf of *Talchirophyllites indicus* gen. *et* sp. nov., showing pointed apex, broad base, lanceolate shape. Specimen no. BSIP 37308 x 20.
2,3. Detached leaves of *Saksenaphyllites saksenae* gen. *et* sp. nov., showing narrow linear shape with faint midveins an obtuse apex in fig. 3. Specimen no. BSIP 37322 x 15.
4. ?Protonema showing simple branched filaments. Specimen no. BSIP 37319 x 2.
5. An incomplete specimen of *Glossopteris* leaf with distinct midrib. Specimen no. BSIP 37313 x 2.

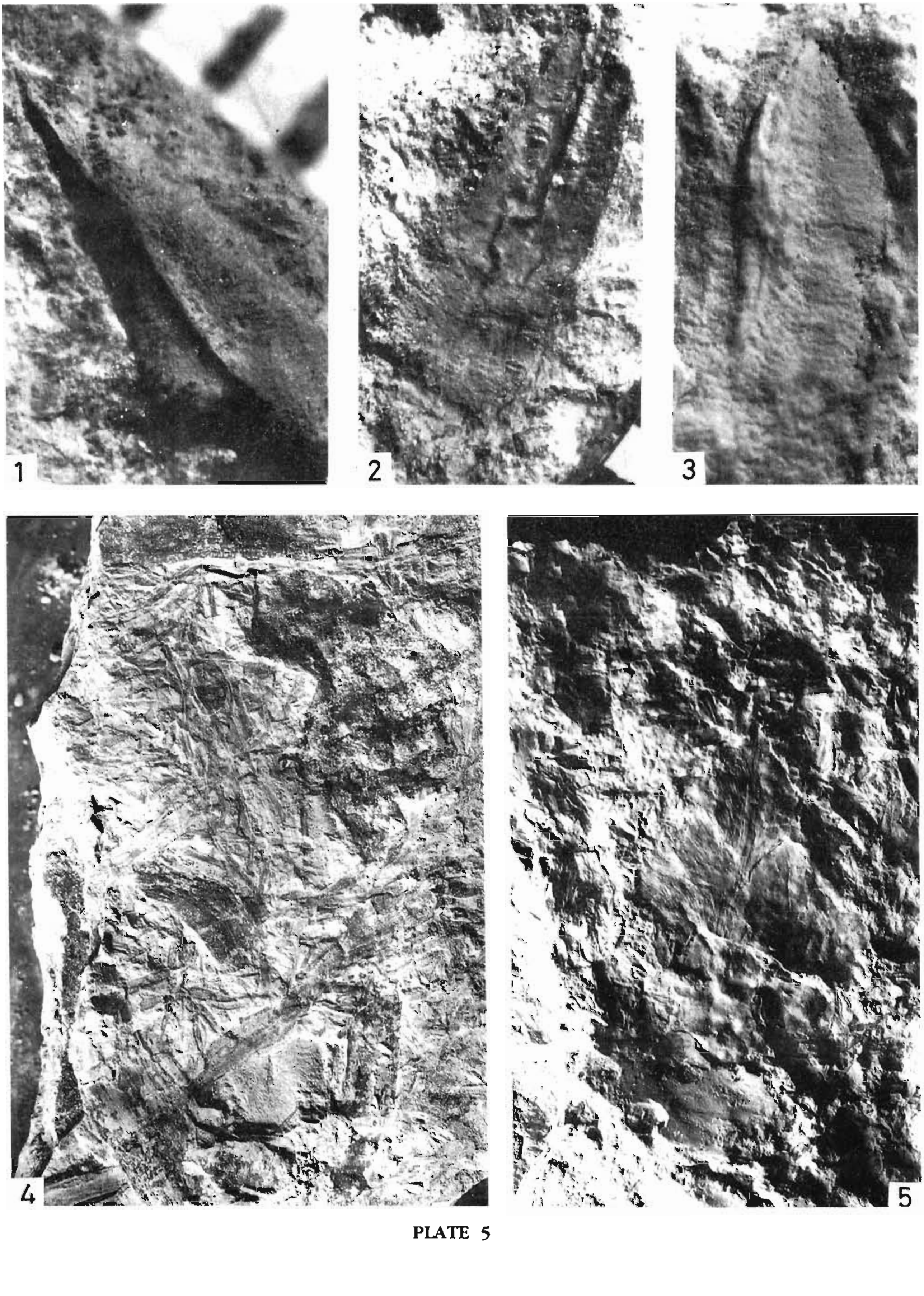
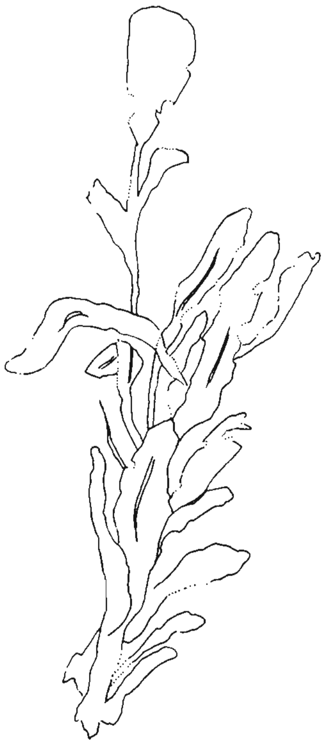


PLATE 5



Text-figure 8 —*Saksenaphyllites saksenae* gen. *et* sp. nov., gametophyte with seta and capsule. Specimen no. BSIP 37309 x 8.

Horizon & Age—Talchir Formation, Early Permian.

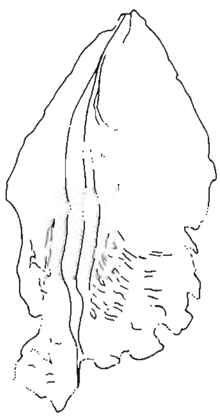
Derivation of name—The genus is named after Professor S.D. Saksena, an eminent Indian palaeobotanist, who made significant contributions towards palaeobotanical knowledge of South Rewa Gondwana Basin.

Description—There are quite a few specimens in the collection, in which one is an almost complete plant. This specimen is 2.0 cm in length. The narrow linear leaves are spirally arranged on the axis, measuring up to 5 mm in length and less than 1 mm width. A faint midvein comprising thicker cells can be noticed in each leaf (Pl. 5, figs 2, 3). The leaf lamina is made up of simple cells. The capsule measures 2 mm in length and 1 mm width and thin seta is 5 mm in length. The other details of capsule are not seen.

Text-figure 9 —*Saksenaphyllites seksenae* gen. *et* sp. nov., seta with capsule. Specimen no. BSIP 37311 x 4.

Comparison—*Saksenaphyllites saksenae* gen. *et* sp. nov. is a distinct moss plant bearing a capsule on a long seta. This is the first report of a capsule bearing moss from the Gondwana and other contemporary floras.

Saksenaphyllites saksenae differs from *Talchirophyllites indicus* in having a distinct type of leaf. As is the general practice in living mosses the generic assignment of two distinct forms has been made on leaf shape. *Saksenaphyllites* has a superficial resemblance with the living moss genus *Anoectangium bicolor* Len et Card.



Text-figure 10 —*Saksenaphyllites saksenae* gen. *et* sp. nov., a detached leaf with midvein. Specimen no. BSIP 37322 x 8.

Genus — *Umariaphyllites* gen. nov.

Type species — *Umariaphyllites acutus* gen. *et* sp. nov.

PLATE 6

1. *Saksenaphyllites saksenae* gen. *et* sp. nov., gametophyte with leafy shoots. Specimen no. BSIP 37317 x 5.
2. *Saksenaphyllites saksenae* gen. *et* sp. nov., leafy branches without sporogonium. Specimen no. BSIP 37316 x 5.
3. Detached leaf of *Umariaphyllites acutus* gen. *et* sp. nov. to show pointed apex. Specimen no. BSIP 37312C x 20.
4. *Talchirophyllites indicus* gen. *et* sp. nov., another ill-preserved specimen. Specimen no. BSIP 37320 x 15.
5. Detached leaf of *Talchirophyllites indicus* gen. *et* sp. nov. Specimen no. BSIP 37312B x 15

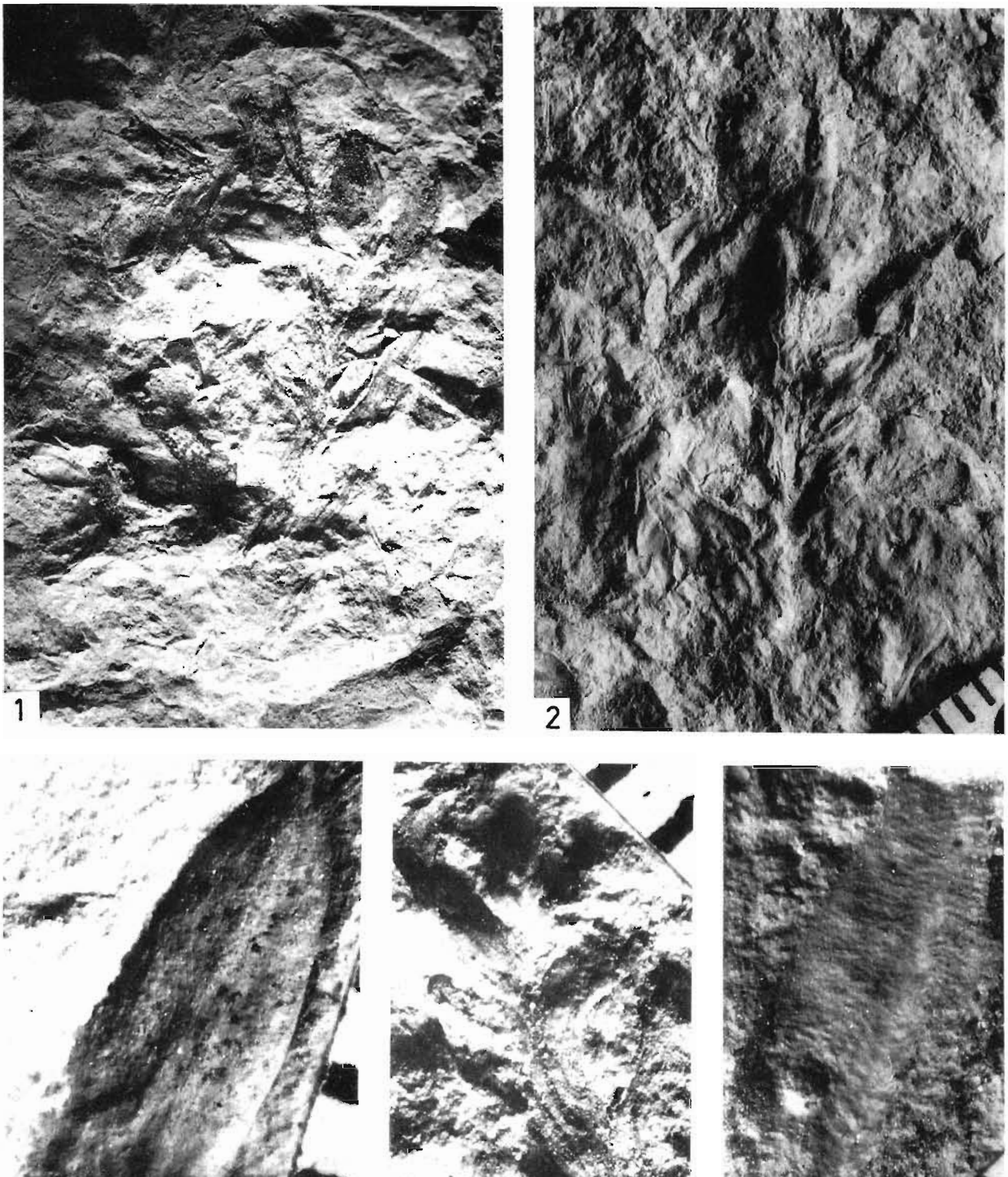


PLATE 6

Pl. 7, fig. 2; Pl. 9, figs 1-5; Pl. 10, fig. 1;
Text-figures 11- 14

Diagnosis—Gametophyte upright radial leafy shoots, leaves arranged in close spirals; near apex leaves clustered together to form a conspicuous head, leaves entire, narrow, pointed apex, broad base, indistinct midvein; sporogonium ovalish round at tips, immersed in leaves, without distinct seta.

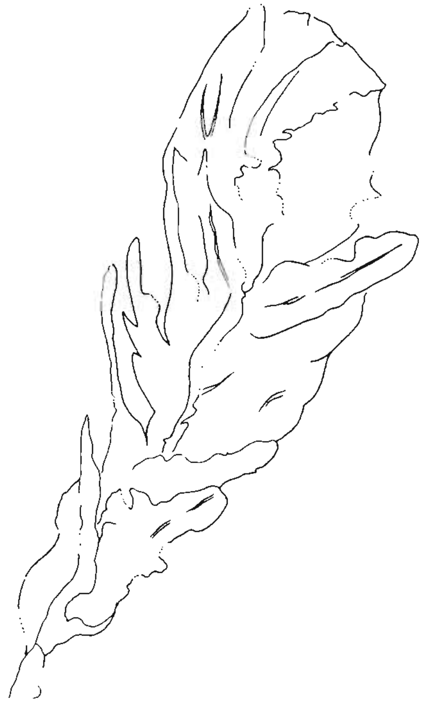
Text-figure 11 —*Umariaphyllites acutus* gen. *et* sp. nov., spirally arranged leaves with acute apex and apical conspicuous head. Specimen no. BSIP 37312A x 5.

Holotype—Specimen No. BSIP 37306B.

Locality—Umrar Nala section, near Jwalamukhi Temple, Umaria, Shahdol District, Madhya Pradesh, India.

Horizon & Age—Talchir Formation, Early Permian.

Derivation of name—The genus *Umariaphyllites* is named after the town Umaria, where the fossil locality is situated.



Text-figure 12 —*Umariaphyllites acutus* gen. *et* sp. nov., upright radial leafy shoot, leaves at the top clustered to form conspicuous head. Specimen no. BSIP 37306 x 8.

Description—There are four specimens in the collection. Average length of gametophyte is 1.5 cm. The leaves are crowded on the axis forming a conspicuous crown at the tip, covering small ovalish, round capsule. The leaves are acutely pointed, 2-4 mm in length and up to 1 mm in width. The leaves are smooth margined having a faint, indistinct midvein.

Comparison— *Umariaphyllites acutus* gen. *et* sp. nov. is distinct from *Saksenaphyllites saksenae* in two characters. There is no long, thin seta with the capsule and the leaves are different and distinct in two genera. There is no distinction in smaller and bigger leaves in *Umariaphyllites* as is found in *Talchirophyllites indicus*. The leaves of *Umariaphyllites acutus* show some resemblance with the Russian Permian moss genus *Uskatia* Neuberg 1960, but the finer details are distinctive.

PLATE 7 ⟶

1. *Saksenaphyllites saksenae* gen. *et* sp. nov., gametophyte with capsule and seta. Specimen no. BSIP 37309 x 10.
2. Detached leaf of *Umariaphyllites acutus* gen. *et* sp. nov. showing entire margin, narrow shape, pointed apex and broad base. Specimen no. BSIP 37307C x 10.
3. A small incomplete leaf of *Noeggerathiopsis*. Specimen no. BSIP 37310B x 4.
4. *Cordaicarpus seeds*. Specimen no. BSIP 37321 x 10.
5. *Gangamopteris* sp., an incomplete leaf showing typical anastomosing of secondary veins. Specimen no. BSIP 37314 x 3.

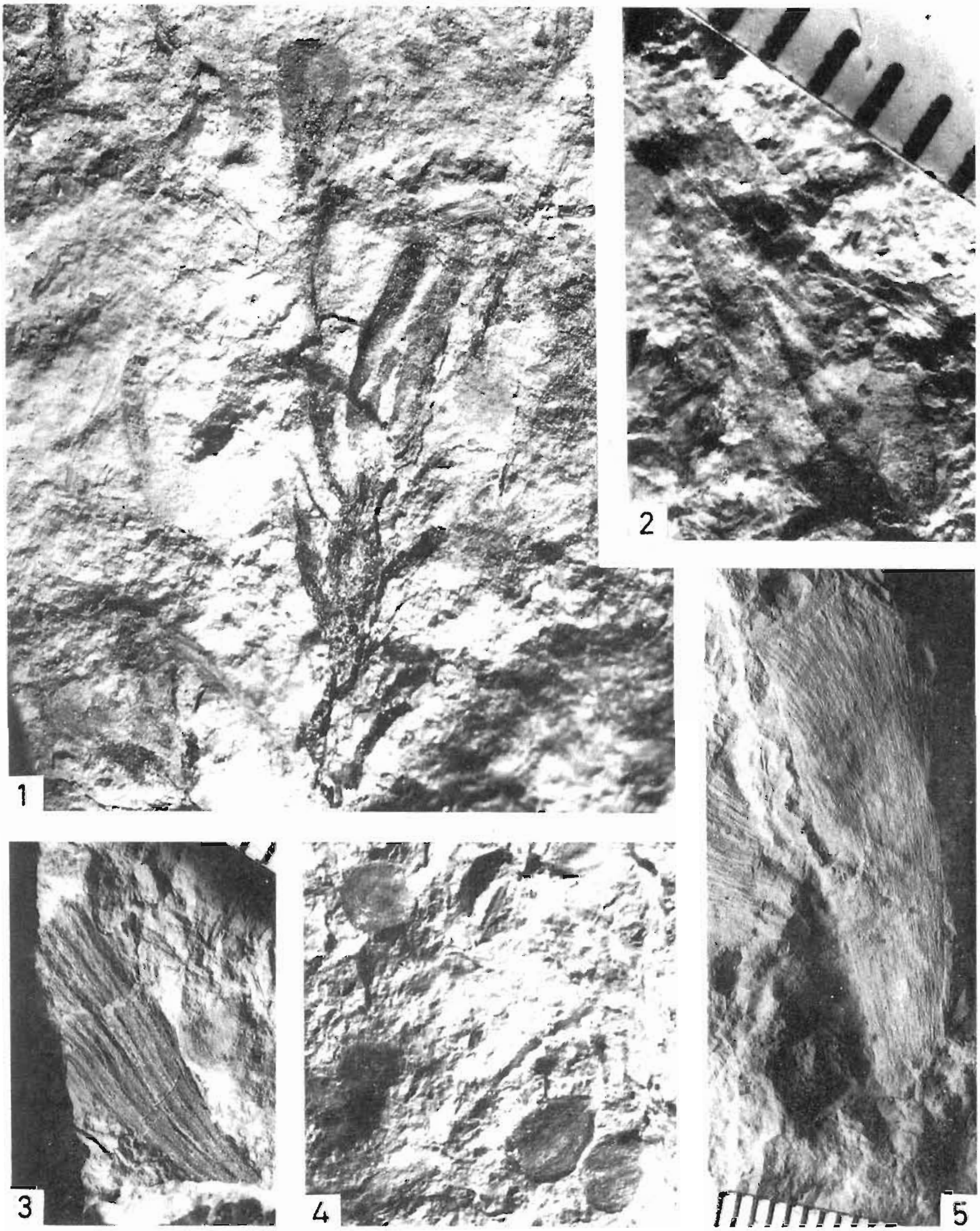
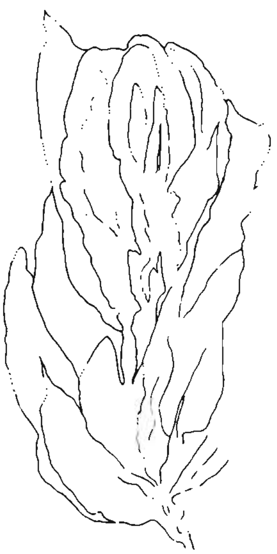
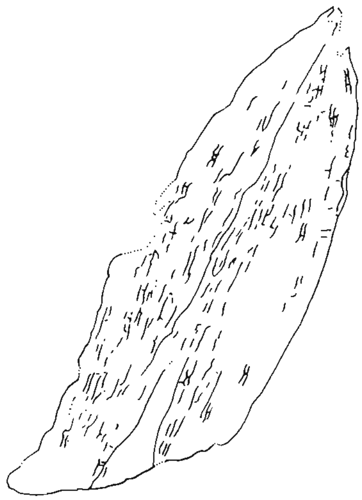


PLATE 7



Text-figure 13 —*Umariaphyllites acutus* gen. *et* sp. nov., another specimen with outline of apical capsule. Specimen no. BSIP 37310A x 8.



Text-figure 14 —*Umariaphyllites acutus* gen. *et* sp. nov., a detached leaf to show midvein and acute apex. Specimen no. BSIP 37312C x 10.

Umariaphyllites acutus superficially resembles the living moss genus *Micromitrium tenerum* (B.S.G.) Crosby which is characterised by an immersed capsule with a very short seta or without setae.

POSSIBLE VEGETATIVE PROPAGATION

The vegetative propagation in bryophytes takes place in a variety of ways such as decay of old branches, formation of adventitious shoots, tubers and gemma or gemma cups. Formation of gemmae is a prolific and specialized mode of vegetative asexual propagation in hepatics. These gemmae at the beginning of development appear to be somewhat circular, at a short distance behind the apical cells, but on account of the upward growth of adjoining vegetative tissue, they soon become the cavities, as in some thalloid hepaticae.

In one of the specimen of *Hepaticites umariaensis* (Pl. 1, fig. 3) a circular definite marking is seen just below the dichotomy of the thallus. Such simple types of gemmae as circular bodies are noted elswhere in the sediments (Pl. 2, figs 2-4). Could this be a deyeloping gemma cup or a gemma? Gemma cups and gemmae are reported as fossils from the English Rhaetic by Harris (1937-39) while reporting the most complete fossil bryophyte, *Naiadita lanceolata*. These reports of gemmae in the Early Permian and Triassic sediments indicate that bryophytes during ancient times were perhaps propagating vegetatively in the same manner as they are today.

Protonema—In most of the living mosses, protonema formation is a common feature which is considered as an intermediate stage between the spore and the adult gametophyte. The spore settles in a place where sufficient moisture and other suitable conditions exist, then begins to germinate. The endospore protrudes as one or two germ tubes which become partitioned by cross walls. The cell or cells thus cut off and form a branched filamentous, multicellular structure — the protonema. The protonema generally vanishes once the leafy shoots are formed but in some species they are persistent and continue to grow and branch as a green carpet beneath the leafy gametophore as in *Polytrichum, Schistostega* and *Ephemerum*.

In the Talchir sediments one can see many filamentous branches (Pl. 5, fig. 4) alongwith other leafy mosses. Could these be protonema branches? The structural details of these branches are not preserved, but they look to be the simplest branched filaments. The leafy moss shoots are not in organic

PLATE 8

1. *Saksenaphyllites saksenae* gen. *et* sp. nov., gametophyte enlarged to show spirally arranged leaves, sporogonium consisting of capsule and thin seta. Specimen no. BSIP 37309 x 15.

1

PLATE 8

connections with these filamentous branches. It is likely that these branches do represent the earliest protonema fossils. It is also considered that the protonema stage is a hybernating phase in the life cycle of a moss. During Talchir times the climatic conditions were not always conducive for proper plant growth, more so for delicate moss plants. It is likely that this protonema phase was helpful for the survival of the mosses during Early Permian.

DISCUSSION

The fossil remains described in this paper are the first authentic reports of Hepaticae and mossy bryophytes from the Early Permian Gondwana of India occurring alongwith Glossopteris floral remains.

The bryophytes are the simplest and small forms of terrestrial plants and differ from others as the gametophyte generation is the dominant phase in their life cycle. Absence of vascular tissue system and demonstrable cuticle in the majority of them have imposed certain restrictions on the size, and preservation of bryophytes. In spite of these restrictions they have been adequately reported as fossils from various geological formations (Table 2). Irrespective of their small size, the bryophytes today are represented by more than 25,000 species, forming reasonably dominant elements of the present day vegetation under varying ecological conditions. This is considered to be due to their remarkable protoplasmic organization which enables them to endure a wide range of ecological tolerances and to occupy niches and crevises befitting for their small size (Miller, 1980).

During Talchir sedimentation when the climatic and ecological conditions were not very hospitable even for hardy gymnospermous plants, the presence of such a large number of bryophytes and their remains is remarkable. As can be expected from their fragile nature the bryophytes cannot be transported for great distances. Therefore, it is likely that the present assemblage of bryophytes at Umaria became preserved in the fine Talchir sediments at the same place where they were growing. Small fragments of Glossopteris floral elements in the same assemblage indicate that they were transported from other site and might not have been necessarily growing with the bryophytes.

Bryophytes, in general, are considered as temperate plants (with a few tropical families) best suited for cool, wet high mountain forests or other sites where evaporation stress is low during the growing phase. The most significant underlying factor is the necessity of moisture during the reproductive stages. It can be taken as an additional supporting evidence that during the Talchir times there was enough moisture, shade and low temperature for the bryophytes to grow and reproduce. Another important factor is that the bryophytes cannot tolerate salinity so the sea must not have been in near proximity to the bryophytic site and that they were growing in and around a fresh water pool, or a stream from melting ice. The Umaria marine beds are not very far from the bryophytic locality.

CONCLUSION AND REMARKS

Inspite of the long history of research on bryophytic fossil remains, the evidence is too meagre to give support to any theory on the origin and evolution of Bryophyta. The geological history of bryophytes only indicates that they belong to an ancient group (Table 2). This state of affairs to recognise them alongwith other fossil remains of higher plants, is due to lack of a proper scheme for classification of fossil bryophytes, proper sediments for their preservation, our ability to recognize fossil bryophytic spores and their dispersal mechanism, and in general their origin and evolution. All these aspects are necessary to understand this diverse and important group of plants in fossil state.

Preservation of bryophytes as fossils—The bryophytes are devoid of true vascular tissue, lacking extensive resistant mechanical tissue with little or almost no cuticle, covering their exposed surfaces. It is therefore, difficult to expect that such diminutive plants would lend themselves to fossilization. Their

PLATE 9 ⟶

1. *Umariaphyllites acutus* gen. *et* sp. nov., upright radial leafy shoot, leaves at the tip clustered to form conspicuous head. Specimen no. BSIP 37306B x 5.

2, 4. *Umariaphyllites acutus* gen. *et* sp. nov., another specimen showing spirally arranged leaves with acute apex and conspicuous head. Specimen no. BSIP 37312A x 5.

3. *Umariaphyllites acutus* gen. *et* sp. nov., a small leafy shoot with conspicuous head at the tip, sporogonium without seta. Specimen no. BSIP 37310A x 5.

5. *Umariaphyllites acutus* gen. *et* sp. nov., an ill preserved leafy shoot. Specimen no. BSIP 37323 x 5.

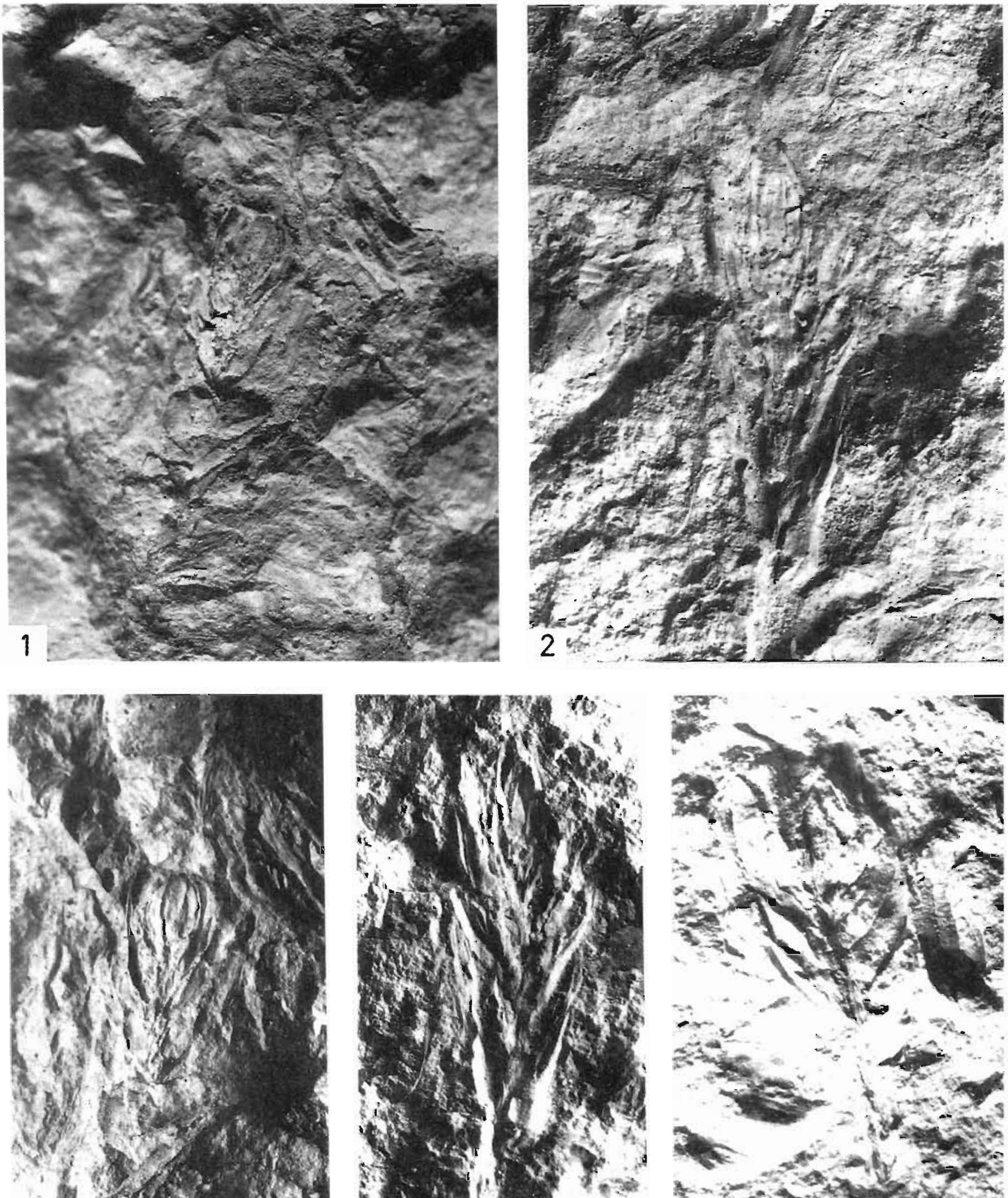


PLATE 9

delicate nature has often been quoted as the possible reason and explanation for the apparent scarcity of fossil remains of this group of plants.

Contrary to this belief, patient palaeobotanical studies during the last forty years have proved that fossil bryophytes are in fact widely distributed both geographically and geologically (Table 2) and their remains are often very well preserved, even in the oldest deposits (Table 2).

It is, therefore, clear that the chances of preservation of fossils do not always depend necessarily on the presence of resistant structures, but on the occurrence of the appropriate kind of sedimentation in the right situation andat the right time. Except for the special case of preservation in Baltic Amber all examples of well preserved bryophytes have one feature in common and this is their effective preservation in fine freshwater sediments under anaerobic conditions.

It is rather strange that bryophytes have not been recognized in the extensive studies of shales, coal-balls and petrifactions barring a few exceptions. A possible explanation could be that the shale flora mainly consist of accumulated and sometimes drifted debris of large and small vascular plants, while the bryophytes found in the shales may represent mud or soil dwelling species preserved in the original place of growth.

The most suitable lithologies for finding further fossil bryophytes probably are very fine grained deposits like clays, siltstones and shales of known freshwater origin.

Classification and naming of fossil bryophytes— Bryophytes have usually been recognized as comprising a single division Bryophyta, containing the two classes — Musci and Hepaticae and with the Anthocerotae, sometimes as a third class (Miller, 1982). Now with the advancement of knowledge this simplest, monophyletic view is considered as untenable. Most bryologists agree that at least thee divisions are correctly recognized amongst the bryophytes and the bryophytic concept represents a level of evolution paralleling roughly to the concept as undertood for algae or fungi. Further classification of these three divisions into order, family and genera depends largely on the features derived from the gametophytic and sporophytic phase .

The fossil bryophytes by and large can be classified as hepatics or musci depending on their external morphological characters and further clssification depends on the characters available in the fossil state which may or may not be preserved. Gametangia, anatomical features of leaf and stem and spores within the capsule are rare occurrence in bryophytic fossils and dealing with leaf and vegetaive shoot fragments, it is not always possible to identify eutaxa and to trace their geological history. he identification of fossil bryophytes within the system is usually based on comparison with living taxa according to the sets of subordinate characters. This has led to a common practice of instituting the form genera for fossil bryophytes as is followed for other fossil remains of vascular plants.

Fossil bryophytic spores and their dispersal— The small spores of present day bryophytes seem well suited for long distance dispersal by wind. Some mosses produce enormous spores of 10-25 μm diameter size and become airborne in light wind. Transport by sea must by ruled out because both the mature plants and spores are intolerant to sea water. Contrary to earlier belief, according to modern researches, it has been shown that bryophytic spores lacked obvious adaptation for long distance carriage due to lack of wings, etc., sparse food reserve, limited or unknown viability and questionable resistance to extreme temperatures or ultra-violet radiation (Miller, 1982). Some species are known to have water borne spores also. Gemmae, propagula, tubers, bulbils, deciduous branchlets and vaiously derived fragments are clearly of high importance for localized dissemination and spores are the only propagules with medium to long distance dispersal.

Fossilized spores having bryophytic affinity are reported from varios geological formations, but their exact affinity cannot be traced out due to their simplicity and our inperfect knowledge. Pant and

PLATE 10

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1. *Umariaphyllites acutus* gen. *et* sp. nov., enlarged to show conspicuous head and leaves arranged spirally on the axis. Specimen no. BSIP 37306B x 10.

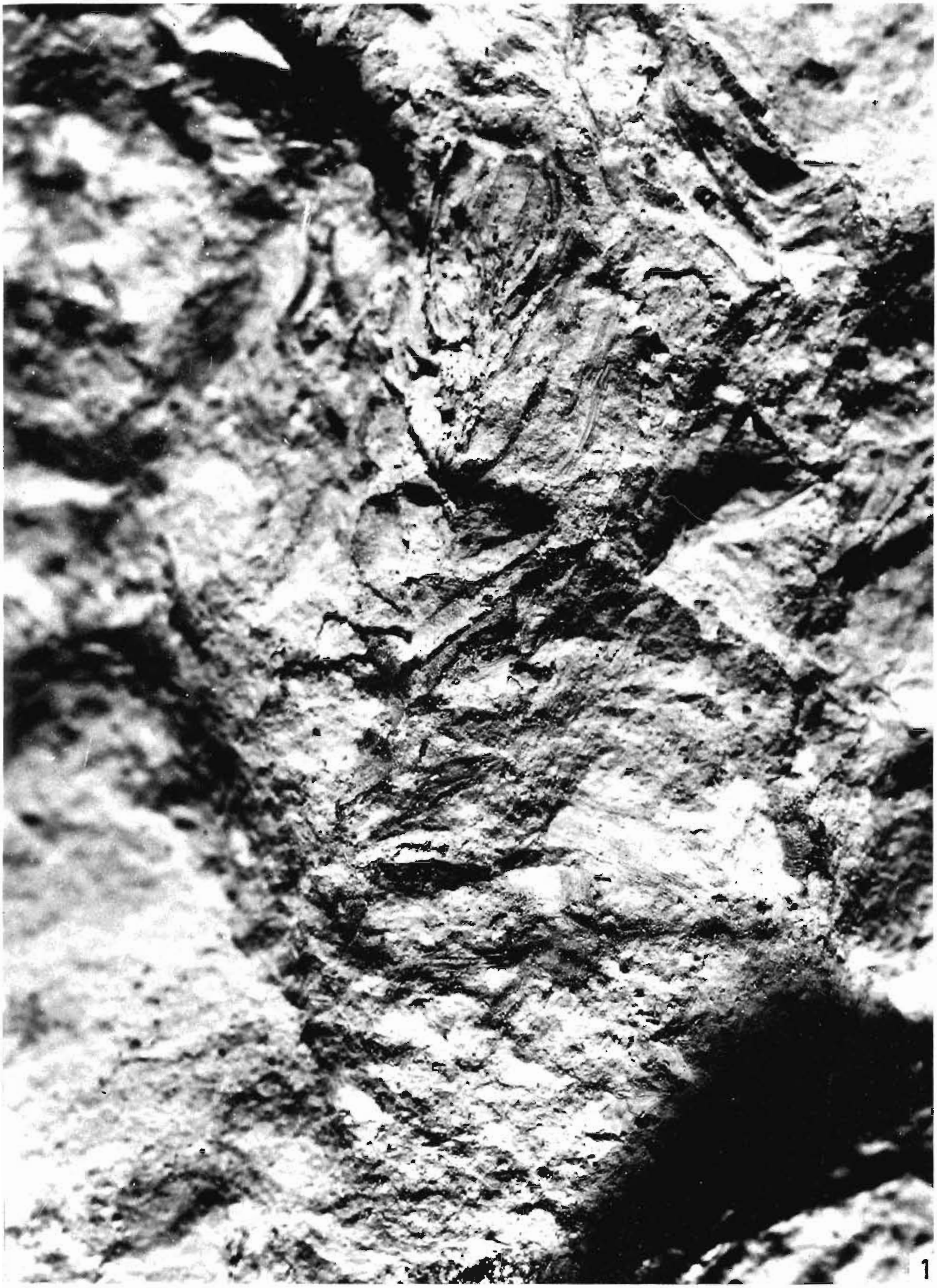

PLATE 10

Singh (1991) have tried to find the characters which can distinguish the spores of Hepaticae and Anthocerotales for identification of probable sporae dispersae of bryophytes reported from different geological horizons. Some of the rilete spores and cuticle fragments found in Silurian deposits are believed to belong to some of the bryophytic or bryophyte like plants. *Ambitisporites*, a trilete spore, is known from the Early Silurian deposits of Virginia (Pratt, Phillips & Dennison, 1978). *Sphaerocarpos*, or *Riccia*-like spore tetrad *Tetrapterides*, is known from a thalloid plant from the Lower Carboniferous of Wales and Gloucestershire (Sullivan & Hibbert, 1964; Hibbert, 1967). The Permian Gondwana spore genera, viz., *Indotriradites* Tiwari 1964, *Dentatispora* Tiwari 1965, *Jayantisporites* Lele & Makada 1972 are believed to be of bryophytic origin.

Spores, presumed to be sphagnopsid, were described from the Rhaetic strata of Germany as *Sphagnumsporites* and later were found from the Jurassic and Lower Cretaceous deposits of Queensland and Perth basins. Filatoff (1975) reported several bryophytic spore genera from Jurassic well cores in Perth Basin, Australia. In addition to *Sphagnumsporites,* the spore types, viz., *Rogalskaisporites, Polycingulatisporites, Antulsporites* and *Foveosporites*, generally belonging to Sphagnaceae types, were also reported.

Definite bryophytic spore genera *Aequitriradites* (Delcourt & Sprumont) Dettmann 1963 and *Coptospora* reported by Dettmann (1963) from the Upper Mesozoic beds of south eastern Australia and *Rouseisporites* Pocock are believed to belong to some hepatics. Kar (1990) reported three species of a supposedly bryophytic spore genus *Operculosculptites* from the Miocene sediments of Tripura, Assam. *Riccisporites* Lundblad and *Ricciaesporites* Nagy are some other hepatic tetrad spore genera from the Tertiary formations.

There are a number of simple, triradiate spore genera with a distal germinal pore distributed in various geological formations. These are generally believed to be pteridophytic in nature but it can be contemplated that many of them may turn out to be bryophytic in the course of future researches.

Various maceration techniques were used to obtain cticles and spores from the Umaria material. The results were not encouraging though some organic unidentifiable pieces were obtained.

Origin and evolution of bryophytes

On the basis of modern research in biochemistry, ultrastructure and morphogenesis of present day bryophytes, it is believed that each group had a separate origin. The fossil history, though imperfect, provides ample evidence that the bryophytes represent a level of evolution correlated with transmigration to terrestrial environments. The origin of sterile jacketed gametangia, retention of an embryo within the archegonium, absorbing and anchoring structures, adaptation to evaporative stess and perhaps most important the formation of trilete, sporopollenin spores are the major critical points to ponder.

In general, there are two classical views on the origin of bryophytes. One view considers that they have been derived from green algae, thus alien to vascular plants. The other view considers them as degenerate rhyniophytes. Evidences exist for both the points of view (Meeuse, 1967; Mehra, 1967, 1969) but generally it is expected that they have more points in common with other land plants. Photosynthetic pigments are the same, the gametangia have a common plan, the same biosynthetic pathways seem to exist in their phenolic and flavonoid chemistry (Suire & Asakawa, 1979). These authors proved that the possiblity of a direct line from algae to bryophytes is not supported by any of the chemical data. On the contrary, bryophytes seem more closely related to higher plants than to algae. Steere (1969) considered bryophytes a "dead end" group derived from the archegoniates while others (Zerov, 1966) hold to a direct algal origin. Miller (1977) considered the bryophytes as non-generate vascular plants of diverse origin. Hepatics probably derived from the same early rhyniophytic stock that lead to *Cooksonia,* while mosses seem to have originated later from early ancestors of the zosterophyllophytes (Mehra, 1969; Miller, 1982).

It is difficult to understand at present as to which group amongst the bryophytes is more primitive-hepatics or mosses, as the supposed fossil remains of both groups arose almost simultaneously in the geological past (Table 2).

Table 2— Global geological distribution of bryophytic remains

		HEPATICAE	MUSCI	ANTHOCEROTAE	SPHAGNALES
QUATERNARY	PLEISTOCENE AND HOLOCENE	5 species in four genera and two additional genera without assigning to species by Miller 1980, Nine hepatics by Partyka, 1976, Extant genera by Janssens, 1977, *Hepaticites* Goswami 1957, *Marchantia polymorpha* L. 1753, *Metzgeria furcata* (L.) Dum 1835	172 species in 82 genera by Miller 1980, 139 mosses by Partyka 1976, Several species by Janssens 1977		26 *Sphagnum* spp. by Partyka (1976), *Sphagnum* sp. Sharma 1978
TERT	NEOGENE	Hepatic spores from several countries by Van Campo (1978), Jovet-Ast & Huard (1966), Nagy (1968), *Marchantites sinuatus* Saporta 1865, *Marchantia coloradoensis* Knowlton 1930, *Plagiochila saportana* Schimper 1869, *Jungermannites cockerellii* (Howe & Hollick) Steere 1946	*Thamnites marginatus* Jaehnichen 1974, *Muscites lanceolata* Boulter 1971, 13 Species and eight genera of extant species, *Porella* sp. & 42 moss species by Kuc & Hills (1971) *Calliergon aftonianum* Kuc 1973, *Polytrichites spokanensis* Knowlton 1956, *P. aichiense* Yasui 1928, *Trachysystis flagellaris* Lundblad 1872, *T. szaferi* Szafran 1949, *Claopodium* sp. Jovet-Ast 1969, *Heterocladium squarrosulum* Jovet-Ast 1967, *Hypnodendron* sp. Jovet-Ast 1967, *Plagiopodopsis scudderi* Britton & Hollick 1915, *P. cockerelliae* Steere 1946, ?*Papillaria* sp. Jovet-Ast 1967, *Thamnium alopecurum* Jovet-Ast 1967, *Thamnium* sp. Jovet-Ast 1967, *Amblystegium schrotzburgense* Jovet-Ast 1967, ?*Muscites joursacensis* Marty 1903, *M. florissanti* Steere 1946, *Palaeohypnum arnoldianum* Steere 1946, *P. brittonae* Steere 1946, *P. brownii* Steere 1946, *P. patens* Steere 1946, *P. knowltonii* Steere 1946, *Ephemeropsis* Selkirk 1974, *Desmatodon heimii* Shchekina 1959, *Thamnites marginatus* Jaehnichen 1974	*Rudolphisporis rudolph* Stuchlik 1964	*Sphagnum* type spores by Staplin (1976)

Table 2 *contd.*

TERTIARY	PALAEOGENE	*Riccia magna* Partyka 1976, *R. riccaelliformis* Partyka 1976, *R. tenera* Partyka 1976, *Ricciites leiodorsales* Partyka 1976, *R. euricciaformis* Partyka 1976, 3 species of *Jungermannites*, extant genera of *Frullania, Phragmicoma, Lejeunea, Madotheca* (=*Porella*), *Radula Lophocolea, Jungermannia, Cephaloziella, Bazzania*, *Riccia* thallus Sheikh & Kapgate 1982, *Jungermanites eophilus* (Cockerell) Steere 1946, *J. bryopteroides* Ball 1931, *Marchantia gracilis* Saporta 1868, *M. munieri* Viguier 1907, *M. lignitica* Brown 1962, Marchantiopsid hepatics from several countries, *Marchantites sezannensis* Brongniart 1849, *M. stephensoni* Berry 1922, *M. pealei* (Knowlton) Steere 1946, *M. wardii* (Knowlton) Steere 1946, *Shulklanites deccanii* Singhai 1973	*Palaeohypnum beckeri* Steere 1972, *P. jovet-astii* Kuc 1974, *P. steere* Kuc 1974, *Dicranum, Dicranites, Dichodontium, Trichostomum, Phascum, Grimnia*, two uncertain *Muscites*, *Muscites yallourensis* Clifford, & Cookson 1953, *Pogonatum suburnigerum* Dixon 1927, *Drefanocladus* aff. *sendtneri* Partyka 1976, *Calliergon trifartum* Partyka 1976, *C. stramineum* Partyka 1976, *Muscites thudioides* Dixon 1932, *M. wilcoxensis* Wittlake 1968, *M. maycokii* Basinger & Rothwell 1947, *M. ritchiei* Basinger & Rothwell 1947, *Dicranites australis* Brown 1962, *Mnium montanense* Brown 1962, *M. rottense* Weyland 1938, *Ditrichites fylessi* Kuc 1974, *Alocommium heterostichoides* Janssens *et al.* 1979, *Ephemeropsis, Hypnites haeringianus* Ettingshausen 1853, *H. arkansana* Jovet-Ast 1967	*Anthoceros* spores by Krutzsch 1963, Partyka 1976	*Sphagnumsporites stereoides* (Pot. & Ven.) Raatz 1937, *S. australis* (Cooks.) Potonié 1956, *S. antiquasporites* Potonié 1956, *S. apolaris* Reinhardt 1961, *S. megasteroides* (Pflug) Potonié 1956, *S. concepcionensis* Takahashi 1977, Six species of *Sphagnum* by Partyka 1976, *Stereosporites stereioides* Jovet-Ast 1976
CRETACEOUS	LATE	*Marchantites yukoensis* (Hollick) Steere 1946, *M. baicalensis* Prynada 1962, *Marchantiolites blairmorensis* Brown & Robinson 1976, *Thallites* sp. A., *Thallites* sp. B, *Thallites* sp. C. all by Douglas 1973, *Jungermannites vetustior* Jovet-Ast, *J. cretaceus* Berry 1919, *Striatothallus adniconicus* Krassilov 1973, *Riccardia* and *Riccia* like thallus by Krassilov (1973)		*Notothylacites filiformis* Nemeje & Pacltova 1972	
	EARLY	*Thallites sewardii* (Berry) Lundblad 1954, *T. jimboi* Kryshtofovich 1918, *T. blairmorensis* (Berry) Lundblad 1954, *Marchantites hallei* Lundblad 1955, *Blyttia infracretacea* Saporta 1894	*Muscites lesquereuxii* Berry 1928, *Diettertia montanensis* Brown & Robinson 1974, *Yorekiella pusilla* Kassilov 1973		*Sphagnumsporites antiquasporites* (=*Stereisporites*), *S. psilatus* Couper 1953, *Sphagnum suflavum* Bolkhovitina 1959, *S. europaeum* Bolkhovitina 1959, *S. pedatiformis* Bolkhovitina 1959,

Table 2 *contd.*

					Sphagnum-like spores Phillips & Felix 1971, *Cingutriletes clavus* Hopkins & Sweet 1976, *Marsypiletes cretacea* Jarzen 1976
JURASSIC	LATE	*Schizolepidella gracilis* Halle 1913, *Cherorhiza brittae* Krassilov 1978, *Aporothallus ladyzheuskajae* Krassilov 1978, *Marchantites oolithicus* Fliche 1881, *M. barwoni* Medwell 1954, *Thallites erectus* (Leck.) Walton 1925, *T. zeilleri* (Seward) Harris 1942, *T. marchantiaeformis* (Saporta) Lundblad 1954, *T. yabei* (Kryshtofovich) Harris 1942, *T. polydichotomus* Prynada 1938, *Hepaticites pantii* Bose & Pal 1982	*Muscites fontinalioides* Krassilov 1973		*Sphagnumsporites adnatus* Jersey 1960, *S. tenuis* Jersey 1960, *S. clavus* (Balme) Jersey 1960, *Sphagnum punctaesporites* Rousel 1959, *Tricostium papillosum* Krassilov 1973, Sphagnacean type spores by Filatoff 1975, *Stereisporites psilatus* Filatoff 1975, *S. antiquasporites* Filatoff 1975, *Rogalskaisporites cicatricosus* Filatoff 1975, *R. canaliculus* Filatoff 1975, *Polycingulatisporites crenulatus* Filatoff 1975, *P. striatus* Filatoff 1975, *Antulisporites varigranulatus* Filatoff 1975, *A. clavus* Filatoff 1975, *A. saveus* Filatoff 1975, *Foveosporites moretonensis* Filatoff 1975
	MIDDLE	*Hipaticites wonnacotti* Harris 1942, *H. haiburensis* Harris 1961, *H. hymenoptera* Harris 1961, *H. arcuatus* (L. & H.) Harris 1942, *Marchantites erectus* Douglas 1973			
	EARLY	*Hepaticites plicatus* Stanislavski 1961			
TRIASSIC		*Metzgerites glebosus* (Harris) Steere 1946, *Ricciopsis iranica* Fakhr 1977, *R. florinii* Lundblad 1954, *R. scanica* Lundblad 1954, *Riccisporites tuberculatus* Lundblad 1954, *Thallites rostafinskii* Krassilov 1978, *T. uralensis* Kryshtofovich & Prynada 1933, *Thallites* sp. Jain & Delevoryas 1967, *Thallitis* sp. Anderson 1976, *Naiadita lanceolata* (Buckman) Harris 1934, *Marchantites tennantii* Anderson 1975, *M. cyathodoides* (Townrow) Anderson 1976	*Muscites quescelinii* Townrow 1959		*Sphagnophyllites triassicus* Pant & Basu 1981, *Sphagnum*-like leaves by Lacey 1969, *Sphagnumsporites apolaris* Jersey 1960

Table 2 *contd.*

SILURIC.		*Marchantiolites porosus* Lundblad 1954, *Indeterminate thalloid* sp. A, B and C by Webb & Holmes (1982), *Hepaticites solenotus* Harris (1938) *H. laevis* Harris 1931, *H. rosenkrantzi* Harris 1937, *H. amauros* Harris 1937, *H. nidpurensis* Pant & Basu 1978, *H. riccardioides* Pant & Basu 1981, *H. foliata* Pant & Basu 1981, *H. cyathodoides* Townrow 1958, *H. osishii* Huzioka & Takahashi 1960, *Hepaticites* sp. Krausel 1958			
PERMIAN	LATE		*Buthelezia mooiensis* Lacey *et al.* 1975, *Merceria angustica* Smoot & Taylor 1986, *Uskatia conferta* Neuberg 1960, *Polyssaievia spinulifolia* Neuberg 1956, *P. deflexa* Neuberg 1960, *Bachita ovata* Neuberg 1960, *Muscites uniformae* Neuberg 1960, *Bajdaievia linearis* Neuberg 1960		*Protosphagnum* sp. Meyen 1966, *Protosphagnum nervatum* Neuberg 1960
	EARLY	*Marchantites lorea* Zalessky 1937	*Intia vermicularis* Neuberg 1956, *I. variabilis* Neuberg 1956, *I. falciformis* Neuberg 1956, *I. angustifolia* Neuberg 1960, *Salairia longifolia* Neuberg 1960, *Duykea goedehoopensis* Anderson & Anderson 1985		*Junjagia glattophylla* Neuberg 1960, *Vorcutannularia plicata* Neuberg 1960
CARBONIFEROU	LATE	*Hepaticites kidstonii* Walton 1925, *H. lobatus* Walton 1925, *H langi* Walton 1925, *H. metzgerioides* Walton 1928, *Treubiites kidstonii* Schuster 1966 (=*H. kidstonii*), *Hepaticites* sp. Krausel 1958, *Blasites lobatus* Schuster 1966 (=*H. lobatus*) *Thallites willsii* Walton 1929, *T. lichenoides* Lundblad 1954, *T dichopleurus* DiMichelle & Phillips 1976	*Muscites polytrichaceus* Renault & Zeiller 1888, *Muscites bertrandii* Lignier 1914, Probable moss Plumstead 1966, *Tetrapterites* Sullivan & Hibbert 1964		

Table 2 *contd.*

S	EARLY		*Muscites plumatus* Thomas 1972		
DEVONIAN	LATE	*Pallavicinites devonicus* (=*Hepaticites devonicus*) Hueber 1961, ?*Sporocarpon* Williamson 1878, ?*Protosalvinia* Dawson 1884	?*Sporogonites* sp. Halle 1916, ?*S. yunnanensis* Hsu 1947		
	MIDDLE	?*Spongiophyton* two species by Chaloner *et al.* 1974			
	EARLY	?*Spongiophyton* Zdeboka 1979, *Thallites jiangninensis* Lixingxue 1974	?*Horneophyton Lemoigne* 1966, *Sporogonites exuberans* Andrews 1960, *Sporogonites chapmani* Lang & Cookson 1930		
SILURIAN	LATE	*Lyonophyton rhijniensis* Remy & Remy 1980, *Torticaulis transwalliensis* Edwards 1979, *Sciadophyton* sp. Remy *et al.* 1980			
	EARLY	Early tetrad spores and some questionable plant parts by Miller (1979)			
ORDOVICIAN			?*Musciphyton ramosum* Greguss 1961, ?*Hepaticaephyton simplex* Greguss 1961		
PRECAMBRIAN			?*Longfengshania* (Du) Zhang 1988		

No one has yet found unquestionable mosses or liverworts among Silurian fossils, though trilete spores and cuticle fragments are found in the shoreline deposits of Silurian age laid down some 30 million years before *Cooksonia* appeared, te oldest vascular plant presently known. Some believe that these spores do belong to some of the primitive bryophytes.

Longfengshania is an unusual fossil that was initially described as an alga, but is now taken as the earliest evidence of a hepatic bryophyte (Zhang, 1988). Although, the Precambrian age of this plant from China makes it doubtful but the specimens do share a number of characters in common with bryophytes. *Sporogonites* and *Horneophyton* both from the Early Devonian, are also considered as having bryophytic characters and designated as problematic bryophytes in several text-books of Palaeobotany.

It seems reasonable to accept that bryophytes had emerged alongwith other vascular plants by Silurian time and some of the questionable remains are indeed bryophytes. The oldest kown definite liverwort is *Pallavicinites devonicus (= Hepaticites devonicus* Hueber) from the Lower-Upper Devonian strata of U.S.A. The earliest possible fossil moss is recognised as *Muscites plumatus* from the Early Carboniferous of Gloucestershire (Thomas, 1972). It is uncertain when the first fossil hornwort occurs. Some Devonian spores are also believed to be bryophytic (Table 2).

During Permian, the bryophytes were widely distributed all over the world. Hepatics have not been strongly represented in the Permian deposits though few reports are available. Permian records of true mosses from the Russian platform by Neuburg and Ignatov and now from India are ample examples while those from the Triassic and Jurassic are well known from several places. Thallose hepatics continue to dominate the fossil records of bryophytes in the Middle and Late Mesozoic, but mosses have been reported with increasing frequency as maeration techniques improved. Krassilov (1973) reported a rich and diversified bryophyte flora in the Upper Jurassic and Lower Cretaceous, richer than in any previous period as several probable leafy liverworts and thalloid forms have been reported. Reports of fossil moss are few in the Cretaceous as compared to hepatics (Table 2).

The Palaeocene-Eocene epoch moss and liverwort fossils so far known are from North America, Russia, China, Poland, Germany and France. These confirm the presence of several species from most majr groups. Post-Pliocene fossil bryophytes can be recognized having definite affinities, with modern bryophytic plants (Table 2).

Gondwana records (Table 1) are still not sufficiently adequate and complete to throw light on the evolutionary aspects but are generally considered as primitive. Several examples from Permian, Triassic and Jurassic assemblages (Anderson, 1976; Anderson & Anderson, 1985; Townrow, 1959; Pant & Basu, 1978, 1981; Banerji, 1988; Douglas, 1973; Smoot & Taylor, 1986) from Australia, India, South Africa and Antarctica confirm that the bryophytes were well represented by major groups (Table 1). The present assemblage of Early Permian bryophytic plants alongwith the Glossopteris flora confirms that the bryophytes were well established during the early phase of the Indian Permian Gondwana. We can expect that another few years of research in this field will bring to light numerous Silurian and Devonian plants of bryophytic habit, and Carboniferous and Permian discoveries will confirm the integrity of at least major extant groups.

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