# Possible fossil *Sporae dispersae* of Hepaticae and Anthocerotales in the fossil record

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The paper attempts to find the characters which can distinguish the spores of Hepaticae and Anthocerotales from iso- or micro-spores of pteridophytes and pollen grains of gymnosperms and angiosperms for the indentification of possible fossil *Sporae dispersae* of bryophytes reported from different geological horizons. The problem was approached by looking for characters in fossil spores which are (i) exclusively bryophytic, (ii) prevailingly bryophytic, and (iii) closely matching characters of in situ spores of fossil bryophytes in a first hand comparison. Our account also takes into consideration the *Sporae dispersae* which were described or suspected by previous workers as those of bryophytes but which could equally well belong to pteridophytes.

**Key-words**—Palynology, Adherent tetrads, Pseudocolpus, Hepaticae, Anthocerotales.

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## साराँश

### अश्मित हिपेटिसी एवं ऐंन्थोसिरोटेल्स के सम्भाव्य विकीरित बीजाणु

दिव्य दर्शन पन्त एवं रीता सिंह

इस शोध-पत्र में उन विभेदी लक्षणों को खोजने का प्रयास किया गया है जिनके आधार पर हिपेटिसी एवं ऐंन्थोसिरोटेल्स के बीजाणुओं की टेरीडोफ़ाइटीयों के सूक्ष्मबीजाणुओं तथा अनावृतबीजी एवं आवृतबीजी पौधों के परागकणों से पहचान की जा सके। ये लक्षण विभिन्न भूवैज्ञानिक संस्तरों से उपलब्ध ब्रायोफ़ाइटी पौधों के सम्भाव्य अश्मित विकीरित बीजाणुओं के अभिनिर्धारण में सहायक सिद्ध होंगे। उक्त समस्या हेतु अश्मित बीजाणुओं में विद्यमान लक्षण प्रेक्षित किये गये हैं जिन्हें (i) वस्तुतः जो ब्रायोफ़ाइटी हैं, (ii) प्रचलित ब्रायोफ़ाइटी, तथा (iii) अश्मित ब्रायोफ़ाइटीयों के स्वस्थाने बीजाणुओं से घनिष्ठतम् मिलते-जुलते लक्षणों की श्रेणी में विभक्त किया गया है। इसी शोध-पत्र में उन विकीरित बीजाणुओं का भी अध्ययन किया गया है जिनको कि शोध-कत्ताओं ने ब्रायोफ़ाइटीयों का वर्णित किया है अथवा संदेह व्यक्त किया है लेकिन ये टेरीडोफाइटीयों के भी हो सकते हैं।

AFTER the discovery of hepatic thalli in British Carboniferous rocks (Walton, 1925, 1928), the time range of this group was further extended up to the Devonian by Hueber (1961) who reported *Hepaticites devonicus* from Onteroa Red Beds of North America which is now renamed as *Pallavicinites devonicus* (Hueb.) Schuster (see Schuster, 1966). There are also a few problematic fossils which have been reported from the Lower Devonian. One of these was referred by Andrews (1960) to *Sporogonites* Halle and it shows a thallus-like carbonaceous mass below a number of parallel subadjacent, unbranched erect stalks. If unbroken they terminate in ovoid spore sacs containing spores ca 20-25 μm in diameter. No details of the spore characters are available. Andrews believed that the stalked sporangia had arisen from a common thallus. Dixon (1927) has referred this fossil to *Andreaea*. As the spores in the spore sacs are not accompanied by elaters, the attribution of this fossil to Hepaticae becomes doubtful (see Krassilov & Schuster, 1984). Schuster (1966) has accordingly referred the genus to an order of its own, the Sporogonitales.

Another fossil of the same kind called *Lyonophyton* was described by Remy and Remy (1980) from. Rhynie Chert bed as having as "independent and possibly autotrophic gametophyte which is of approximately equal size and shape with the sporophytes from the same beds" This fossil is described as having a cup-shaped gametophore with lobed margins. Remy and Remy (1980) have compared it with *Horneophyton* on the basis of its anatomy as well as the morphology of fertile parts and they have further suggested that *Lyonophyton rhyniensis* seems to be "the gametophyte of a plant representing an evolutionary stage previous to the separation of land plants into bryophytes and higher land plants." Till recently all other Devonian forms which had a central strand were included among the pteridophytes. In fact, one of these called, *Rhynia major* was regarded as one of the best known Devonian pteridophytes but a recent renaming of this form as *Aglaophyton* by Edwards (1986) is based on his claim that its central strand lacks secondary wall thickenings in the longitudinal cell walls. According to him it consists of cells having uniformly thick walls and he raises doubts about its being a vascular plant suggesting that it had a bryophytic level of organisation (Taylor, 1988). However, the observations of Edwards, on this form, which is otherwise quite like *Cooksonia* and *Rhynia gwynne vaughanii* need confirmation before they can be accepted particularly when they are based on the negative evidence of thickenings.

Beside the above two forms, there are some other uncertain Devonian bryophyte-like genera, called *Protosalvinia* Dawson, *Parka decipiens* Lang and *Steganotheca*. Out of these, *Protosalvinia* is reported from the Upper Devonian Black Shales of east-central U.S.A. and its detached sporiferous organs usually show once forked branches which are approximately 2-5 mm in width and appear to have been borne on a thalloid plant body. The forks of the thallus show sporocarp-like structures, each containing a single tetrad of 4 large spores (? megaspores) ca 200 μm in the cavity of inner tissues. The affinities of *Protosalvinia* are uncertain. It has been assigned to the algae by White and Stadnichenko (1923) but Kidston and Lang (1924) believed it to be intermediate between the algae and lowermost vascular plants. Kräusel (1941) created a new intermediate class, the Algomycetes, between algae and fungi. Arnold (1954) observed that "it had evolved to a level comparable to that of the bryophytes" but at the same time he contradicted himself by saying that there was no apparent reason for classifying it with the bryophytes. Lacey (1969) thought that *Protosalvinia* could be compared with *Riccia*-like bryophytes which were reported by Walton (1949) and Hueber (1961) from the Carboniferous but sporogonia of *Riccia* differ from those of *Protosalvinia* in having a number of tetrads of smaller spores instead of a single one of large spores. Stewart (1983) is of the opinion that *Protosalvinia* does not fit well into any group of extant plants. The shales in which *Protosalvinia* has been found suggest a shoreline (littoral zone) where the environment was transitional between that of water and terrestrial plants and the plant shows a combination of characters of both the habitats. He further suggests that *Protosalvinia* was probably "caught in act" of evolving into a plant which was becoming adapted for living in a desiccating environment.

*Parka decipiens* is another Lower Devonian plant having a flat thallus-like body whose surface was covered by flattened disc-shaped structures with numerous cutinized spores ca 28-34 μm in diameter. The thallus is parenchymatous in nature (Lang, 1937). The affinites of *Parka* too are uncertain, it has an alga-like thalloid body and cutinized spores like those of land plants (see Walton, 1953).

The third uncertain fossil *Steganotheca* shows a plant compression which is comparable with *Cooksonia* in having terminal sporangia on dichotomously branched axes but their central strands lack tracheids so that it could be compared with bryophytes instead of pteridophytes.

The above reports of megafossils beginning with Lower Devonian make it at once likely that some of the dispersed miospores described by different authors from the beds of different geological ages beginning with strata of this period could even belong to bryophytes. Indeed, after Walton discovered undoubted structurally preserved bryophytes in the Carboniferous, he suggested to Knox (1939) that she should look for spores of bryophytes among fossil *Sporae dispersae*. However, she only mentioned some fossil spores (see Knox, 1939; figs 41-51) which were broadly comparable with those of some living bryophytes like *Anthoceros chilensis, Moerckia hibernica, Anthoceros punctatus, Riccia crystallina, R. beyrichiana, R. fluitans, Fossombronia angulosa* and *Plagiochasma subplana*.

To the best of our knowledge the next paper dealing with bryophytic spores was published by Lundblad (1954) when she created a new form genus based on the dispersed united spore tetrads *Ricciisporites tuberculatus* Lundblad from the Jurassic of Scania and attributed them to Ricciaceae but later thought that its affinity was dubious (Lundblad, 1959). Krassilov and Schuster (1984) find that *R. tuberculatus* can be compared with a sphaerocarpalean tetrad more closely.

In her account of Upper Mesozoic microfloras from south-eastern Australia, Dettmann (1963) compared some fossil miospores with those of some extant and fossil bryophytes, e.g., *Foraminisporis dailyi* (Cookson & Dettmann) Dettmann has been compared with the spores of *Phaeoceros bulbiculosus* (Brotero) Prosk., *Foraminisporis wonthaggiensis* (Cookson & Dettmann) Dettmann with spores of *Notothylas breutelli* Gottsche, *Rouseisporites reticulatus* Pocock, with spores of *Riccia beyrichiana* Hampe and *R. canaliculata* Hoff. and *Couperisporites tabulatus* Dettmann with spores of *Naiadita lanceolata* Buckman as described by Harris (1939). Among other *Sporae dispersae*, Mehra (1974) compared some spores described as *Leisphosphaera rotunda, Uniporata torosa, Phosphosphaera obscura* by Pichova (1967) from the Early Cambrian of south east Siberia with those of extant *Lophocolea* and *Jungermannia* which are presently found in wet tropical forests. Mehra (1974) merely expressed surprise at the resemblance of the smooth exined fossil and living spores.

Some other authors like Gray (1985), Richardson (1985), Pflug and Reitz (1987), Richardson and Ioannides (1973) have offered compelling evidences to suggest that a few sporomorphs of Early Silurian and Mid-Ordovician age which occur in the form of monads, diads, and tetrads were produced by bryophytes. However, most other authors discount the existence of fossil bryophytes or their spores during Cambrian, Ordovician or Silurian times due to the absence of any authentic macrofossils of bryophytes or land plants in rocks of these ages.

Even in the rocks where macrofossils of bryophytes have been reported, no serious attempt has been made lately to look for possible bryophytic *Sporae dispersae*. In fact, in this connection Miller (1984) is of the opinion that in comparison with macroscopic fossils, dispersed bryophytic spores have received little organized study, although they are probably abundantly represented in certain sedimentary environments. To fill up this lacuna the present study has been undertaken.

## CHARACTERS OF HEPATIC AND HORNWORT SPORES

Before we deal with our study of bryophytic spores we have to point out that in the present article which deals only with the fossil spores of Hepaticae and Anthocerotales, we have left out the fossil spores of foliose hepatics and mosses since limitations of space do not permit us to deal with the spores of these plants in a single article. We hope to cover this aspect at a later stage.

We may also mention that in our search for fossil *Sporae dispersae* of hepatics and hornworts we have first attempted to find out characters, which can distinguish the spores of these groups from the iso- and micro-spores of pteridophytes and pollen grains of gymnosperms or angiosperms. To enable us to do so we began our work by making a first hand study of the spores of some living forms of Indian Hepaticae and Anthocerotales as well as published accounts of spores of the extant members of these groups besides looking for possible bryophytic spores in published literature of fossil *Sporae dispersae*. As a result we can categorically state that colpate and porate pollen grains (microspores) of living gymnosperms and angiosperms differ radically from the spores of bryophytes and pteridophytes. The only exceptions are the pollen grains of pteridosperms, like *Potoniea* Halle (1933), *Crossotheca hoeninghausii* Brongnt., *C. hughesiana* Kidston (Wodehouse, 1935), *C. sagittata* (Arnold, 1947) which show proximal trilete marks besides distal colpi and the pollen grains of *Dolerotheca*, which have a biarmed proximal monolete with a vestigeal third arm and also colpi on the distal side (Schopf, 1949). Disaccate pollen grains of *Abies nobilis* too are reported to show proximal triletes (Wodehouse, 1935). Pant (1954) has even mentioned some angiospermous pollen grains like those of *Trapa* and some Liliaceae which show apparent trilete marks.

However, bryophytic spores are most closely comparable with those of pteridophytes whose isospores and microspores are usually trilete and more or less similar in size. In trying to look for distinctions, between spores of these two groups and for the identification of fossil *Sporae dispersae* of bryophytes from those of pteridophytes we concluded that the problems could be approached in three ways. Firstly by looking for exclusively bryophytic characters of spores which are not found in the spores of Pteridophyta, Gymnospermae and Angiospermae. Secondly, we may try to find out characters of spores which are prevailingly found in spores of living bryophytes and occur only rarely in other plants. Thirdly, we may identify bryophytic fossil *Sporae dispersae* by comparing them first hand with figures, photographs and descriptions of similar looking in situ spores of fossil bryophytes or those of extant bryophytes.

Our account also takes into consideration the *Sporae dispersae* which were described or suspected by previous workers as those of bryophytes. These are mentioned in Table 1 against the names of comparable living forms.

## CATEGORICAL DISTINCTIONS MARKING OUT BRYOPHYTIC SPORES

Among the categorical distinctions which mark out bryophytic spores from those of pteridophytes (and other land plants) we may mention:

1. The peripheral flanges of some bryophytic

**Table 1—Possible fossil bryophytic *sporae dispersae***

| FOSSIL SPOROMORPHS | AUTHORS ATTRIBUTING AFFINITIES | AGE & LOCALITY | COMPARABLE EXTANT FORMS |
|---|---|---|---|
| **Family—Fossombroniaceae Evs.** | | | |
| Fig. 50, Knox, 1939 (Pl. XLI, fig. 50) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Fossombronia angulosa* (Fig. 12) |
| **Family—Pallaviciniaceae Migula emend. Schuster** | | | |
| Fig. 44, Knox, 1939 (Pl. XL, fig. 44) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Moerckia hibernica* (Fig. 10) |
| *Couperisporites tabulatus* (Dettmann, 1963; Pl. XXI, figs 12-19; fig. 6c) | Dettmann, 1963 | Upper Mesozoic of South Australia | Fossil spores of *Naiadita lanceolata* (Buckmann) Harris |
| **Family—Sphaerocarpaceae Cavers** | | | |
| *Aequitriradites* (Del. & Sprum.) Cookson & Dettmann, 1961 | Dettmann, 1963 | Upper Mesozoic of Eastern Australia | Spores of modern Sphaerocarpaceae |
| *Coptospora striata* Dettmann, 1963 (Pl. XX, figs 1-5) | Dettmann, 1963 | Upper Mesozoic of South Australia | *Geothallus tuberosus* Campbell |
| **Family—Targioniaceae Endl.** | | | |
| *Echimonocolpites rudae* Hamm. & Garc. D. M. Dez. 1965<br>Potonié, 1970 (Taf. 15, fig. 168) | Present authors | Eocene, Tibu Area, Colombia | *Cyathodium aureo-nitens* |
| **Family—Aytoniaceae Cavers** | | | |
| Fig. 51, Knox, 1939 (Pl. XLI, fig. 51) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Plagiochasma subplana* (Fig. 22 a,b) |
| *Aequitriradites spinulosus* Cookson & Dettman (Dettmann, 1963; Pl XXII, figs 1-13) | Present authors | Upper Mesozoic of Eastern Australia | *Plagiochasma intermedium* Lindenb. et Gott. |
| *Aequitriradites verrucosus* Cookson & Dettmann | Present authors | Upper Mesozoic of Eastern Australia | *Plagiochasma intermedium* Lindenb. et Gott. |
| *Perotriletes granulatus* Couper, 1953 (Pl. 3, figs 28, 29) | Present authors | Jurassic of New Zealand (very rare) | *Reboulia hemispherica* |
| **Family—Marchantiaceae (Bisch.) Endl.** | | | |
| *Hamulatisporis hamulatis* Krutzsch, 1959 (Potonié, 1966; Taf. 4, fig. 50) | Present authors | Eocene of Geiseltal, Lutel, Germany | *Marchantia palmata* |
| **Family—Ricciaceae Dumort.** | | | |
| Fig. 47, Knox, 1939 (Pl. XLI, fig. 47) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Riccia crystallina* (Fig. 28) |
| Fig. 48, Knox, 1939 (Pl. XLI, fig. 48) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Riccia beyrichiana* (Fig. 26) |
| Fig. 49, Knox, 1939 (Pl. XLI, fig. 49) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Riccia fluitans* (Fig. 27) |
| *Camptotriletes corrugatus* (Ibrahim) Potonié & Kremp, 1954 (Taf. 7, fig. 25) | Present authors | Palaeozoic of West Germany | *Riccia* sp. |
| *Lapposisporites lapposus* Visscher (Potonié, 1970; Taf. 4, fig. 33) | Present authors | Permian of Netherlands | *Riccia curtisii* |
| *Quadrisporites horridus* Hennelly (Hennelly, 1958, Pl. V, figs 6, 7) (Potonié & Lele, 1959, Pl. 1, fig. 26-36) | Present authors | Permian-Triassic Transition of New South Wales, Australia; Carbo-Permian, India | *Riccia perssonii* Khan |

*Contd.*

**Table 1—Contd.**

| FOSSIL SPOROMORPHS | AUTHORS ATTRIBUTING AFFINITIES | AGE & LOCALITY | COMPARABLE EXTANT FORMS |
|---|---|---|---|
| *Tigrisporites hallensis* Klaus, 1960 (Potonié 1966, Taf. 4, fig. 51) | Present authors | Triassic Salsburg, Germany | Spores of Ricciaceae |
| *Perotriletes pseudoreticulatus* Couper, 1953 (Pl. 3, fig. 30) | Present authors | Jurassic of New Zealand | *Riccia canaliculata* |
| *Schizosporis reticulatus* Cookson & Dettmann, 1959 (Dettmann, 1963; Pl. XXVI, figs 20, 21) | Present authors | Upper Mesozoic of Eastern Australia (Dettmann, 1963), Upper Neocomian beds of Canada (Pocock, 1962) | *Riccia discolor* L. et L. |
| *Cooksonites variabilis* Pocock, 1962 (Dettmann, 1963; Pl. XXI, figs 8-11) | Dettmann, 1963 | Valanginian-Barremian strata of Canada (Pocock, 1962) Upper Mesozoic of S.E. Australia (Dettmann, 1963) | Modern spores of Ricciaceae |
| *Rouseisporites reticulatus* Pocock, 1962 (Dettmann 1963, Pl. XXIII, figs 4-9; Potonié, 1966, fig. 6d) | Dettmann, 1963 | Barremian-Lower strata of Canada (Pocock, 1962), Aptian-Albian and Turonian beds of Siberia (Samoilovitch *et al.*, 1961). Upper Mesozoic of Eastern Australia (Dettmann, 1959, 1963). | *Riccia beyrichiana* Hamper and *Riccia canaliculata* Hollm. |
| **Family—Anthocerotaceae Dum.** | | | |
| Fig. 45, Knox, 1939 (Pl. XLI, fig. 45) | Knox, 1939 | Carboniferous, productive Coal Measures of Fife | *Anthoceros chilensis* (Fig. 30) |
| Fig. 46, Knox, 1939 (Pl. XLI, fig. 46) | Knox, 1939 | Carboniferous, Productive Coal Measures of Fife | *Anthoceros punctatus* (Fig. 29) |
| *Pseudogravisporites reticulatus* Visscher, 1966 (Potonié, 1970, Taf. 7, fig. 70) | Present authors | Lower Permian of Netherlands | *Phaeoceros laevis* |
| *Foraminisporis dailyi* Dettmann, 1963 (Pl. XIV, figs 15-18) | Dettmann, 1963 | Upper Mesozoic of South East Australia | *Phaeoceros bulbiculosus* (Brotero)<br>*Notothylas breutelli* Gottsche |
| *Foraminisporis wonthaggiensis* (Cookson & Dettmann) Dettmann, 1963 (Pl. XIV, figs 15-18) | Dettmann, 1963 | Upper Mesozoic of South East Australia | *Notothylas breutelli* Gottsche |
| *Anthocerisporis europas* Krutzsch, 1963 (Tafel 3, figs 1-8) | Krutzsch, 1963 | Oligocene-Miocene Germany | *Anthoceros* |
| *Anthocerisporis bohemicus* Krtz. & Pacl. (Krutzsch, 1963; Tafel 4, figs 1-7) | Krutzsch, 1963 | Oligo-Miocene | *Anthoceros* |
| *Foraminisporis granoverrucatus* Krtz. & Pacl. (Krutzsch, 1963; Tafel 2, figs 1-8) | Krutzsch, 1963 | Upper Oligocene | *Anthoceros tuberculatus* |
| *Foraminisporis zonaloides* Krutzsch, 1963 (Tafel 1, figs 1-6) | Krutzsch, 1963 | Miocene ? | *Anthoceros* spp. |
| *Rudolphisporis rudolphi* (Krtz.) Krtz. & Pacl. (Krutzsch, 1963; Tafel 9, figs 1-7) | Krutzsch, 1963 | Lower Miocene N. Bohemia | *Anthoceros* cf. *punctatus* |
| *Rudolphisporis saetosus* (Pflanzl.) Krtz. (Krutzsch, 1963; Tafel 10, fig. 7) | Krutzsch, 1963 | Oligocene, Bohemia | *Anthoceros* cf. *punctatus* |
| *Rudolphisporis torgauensis* Krtz. (Krutzsch, 1963; Tafel 10, figs 1-6) | Krutzsch, 1963 | Middle Oligocene, Bohemia | *Anthoceros* cf. *punctatus* |

*Contd.*

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|---|---|---|---|
| *Saxosporis duebenensis* Krtz. (Krutzsch, 1963; Tafel 5, figs 1-8) | Krutzsch, 1963 | Lower Miocene, Germany | *Phaeoceros laevis* subsp. *carolinianus* |
| *Saxosporis gracilis* Krtz. & Pacl. (Krutzsch, 1963; Tafel 6, figs 1-6) | Krutzsch, 1963 | Oligo-Miocene, Germany | *Phaeoceros laevis* subsp. *carolinianus* |
| *Phaeoceros* Form A, B, C (Jarzen, 1979; Pl. VI, figs 1-8) | Jarzen, 1979 | Upper Cretaceous | *Phaeoceros laevis,* Form A resembles to fossil spores of *Baculatisporites pseudoprimarius* Krtz. & Thiergart and *Ceratosporites couliensis* Srivastava |

spores like *Riccia, Plagiochasma, Reboulia* which show pores near their trilete laesurae These pores are not at all comparable with the germ pores of angiospermous pollen and possibly they never function like them. Flanges are present in some pteridophytic spores but none of them shows such pores although pores of a different kind are found in the spores of some species of *Asplenium* like *A. abyssinicum* which reportedly shows a prominent granular perine with circular or oval non-sculptured areas sometimes replaced by large perforations (see Nayar, 1964) but the size, shape and position of these perforations are not figured and therefore it was not possible for us to compare these spores with the porate spores of Hepaticae whose position and number is characteristic for a particular species.

2. Among other exclusive bryophytic characters we may mention the occurrence of permanently adherent spore tetrads like those of *Cryptothallus* Malmb., *Sphaerocarpos* Ludwig where the tetrads are tetrahedral and in some species of *Riccia* (Mich.) L. like *R. curtisii* James and *R. perssonii* Khan where the tetrads could also be bilateral. No doubt the microspores of some species of *Selaginella*, viz., *S. estrellensis* Hieron and *S. delicatissima* are also dispersed in tetrads but they are clearly different from the spores of the bryophytes in being enclosed in a common wall (see Tryon & Tryon, 1982, p. 821 822). The pollen grains of some angiosperms, e.g., Ericaceae, Mimosaceae, Droseraceae, Sapindaceae and others (see Erdtman, 1952) are also jugate but they are typically colpate and aperturate while the jugate microspores of bryophytes are neither colpate nor aperturate. Moreover, the jugate tetrads of bryophytes have generally larger elements (ca 55 to 60 $\mu$m), whereas the jugate pollen grains of the above angiosperms are very small.
3. Mature spores of many hepatics become alete (although they are arranged in tetrads in the young condition), e.g., spores of *Treubia* Goeb., *Fossombronia* Raddi, *Sewardiella* Kash., *Calycularia* Mitt., *Riccardia* Raddi, *Monoclea* Schust., *Targionia* L., *Cyathodium* Kunze., *Conocephalum* Necker, *Exormotheca* Mitt., *Dumortiera* Reinw., *Riccia billardieri* Mont. & N., *R. discolor* L. & L., *R. melanospora* Kash., etc. Such spores are categorically absent in pteridophytes except in modern *Equisetum*, whose spores have peculiar hygroscopic elaters.
4. A characteristic proximal depression is present between two folds in spores of *Cyathodium* as reported by Mehra and Sood (1969) and Mehra and Sokhi (1972). However, such a depression cannot be regarded as a colpus since a true colpus has never been observed in the spores of thalloid Hepaticae and in Anthocerotales. The term colpus sensu Faegri and Iversen (1950) is typically applied to a thinner area of the exine on the distal side from where the germ tube generally emerges and sometimes ectexine may even be absent in the region of a colpus.
5. Non-adherent monolete spores produced in bilateral tetrads are typically absent among hepatics but as mentioned in (2) above, bilateral spores are found only in *Riccia curtisii* and *R. perssonii* (Khan, 1955) although in these they occur in permanently adherent tetrads.
6. Complete absence of megaspores among the species of bryophytes. These are present in some pteridophytes and theoretically also in all seed plants.

## IDENTIFICATION OF *SPORAE DISPERSAE* OF FOSSIL HEPATICAE

Out of the categorical distinctions which are mentioned above, we have only come across sporomorphs having characters (2) and (4) among hitherto described fossil *Sporae dispersae*. We find character (1) consisting of pores in the flange near the ends of trilete laesurae, is present only in *Rouseisporites reticulatus* Pocock. These spores have been compared by Dettmann (1963) with the spores of *Riccia beyrichiana* Hampe and *Riccia canaliculata* Hoff. but we find that such pores are also present in *Riccia cruciata* Kash. Accordingly, we can assign *Rouseisporites* to Hepaticae with certainity (Text-fig. 1 O, P).

Among earlier reported sporomorphs joined tetrads (character 2), the first spore of this kind was reported by Erdtman (1954) from the Rhaetic-Liassic of north-west Scania who provisionally referred them to *Tetrasulcites magna*. As quoted by Lundblad (1959) "Erdtman thought that sulcate grains of a similar type have not been encountered in recent plants. Slightly similar pollen types occur in certain monocotyledons and monocotyledonoid dicotyledons. However, it would be preposterous to base any conclusions regarding the affinities of '*Tetrasulcites*' on such grounds." In the same year Lundblad (1954) also found similar spores and referred them to *Ricciisporites tuberculatus*. She also gave a detailed diagnosis and on the basis of her studies, attributed them for the first time to bryophytes (Ricciaceae) but later (Lundblad, 1959) thought that their affinities were uncertain though Krassilov and Schuster (1984) find that *R. tuberculatus* can be compared to sphaerocarpalean tetrads more closely but on the basis of our observations we think that it is more closely comparable to the spore tetrads of *Riccia curtisii* (see Pl. 1, figs 1-4) than those of sphaerocarpalean spores.

A third permanently joined tetrad of the same kind called *Tetrapterites visensis* Sullivan & Hibbert 1964 is described from the Lower Carboniferous shales in the Menai Straits, Caernarvonshire. This tetrad is about 200 μm in diameter and it is enclosed by a non-cellular membrane which has a tetrahedral shape and possesses a large wing like expansion near each of its four apices. Subsequently on the basis of scanning electron microscopic studies Hibbert (1967) found that the enclosing membrane of spore is highly ornamented with anastomosing ridges. Sullivan and Hibbert (1964) compared *Tetrapterites* confidently with the mature spores of *Sphaerocarpos* Ludwig whose spores remain adherent in tetrads even after liberation (see Text-fig. 1 M, N). Though these spores are not found in situ, their possible bryophytic nature cannot be denied firstly since the earliest authentic liverworts are known from the Upper Devonian and secondly, since unusual type of spore tetrads called *Tetrapterites* Sullivan & Hibbert occur in beds of Menai Straits, Caernarvonshire. As pointed out by Lacey (1969) these could even belong to a fragmentary thalloid bryophyte which had been mistaken by Walton (1928) as minute pinnules of a pteridosperm genus *Rhodea* Presl. Lacey thought that these thalloid fragments could be part of a *Riccia*-like plant which was the parent plant of *Tetrapterites*. Thirdly, as already discussed by Lacey the Sphaerocarpales are themselves possibly represented by *Naiadita* Buckman from as far back as the Rhaetic of Britain and that genus also has large spores which sometimes persist in tetrads and sometimes separate out but always show a prominent flange on each member of the tetrad. In the occasional separation of members of tetrads into monads and their occasional persistence in tetrads *Naiadita* seems to be comparable with *Haplomitrium gibbsiae* (Steph.) Schuster (see Schuster, 1984) and *Riccia frostii* (our unpublished findings).

Potonié (1970) in his synopsis of *Sporae dispersae* has described *Lapposisporites lapposus* Visscher from the Permian of Netherlands as having united spore tetrads but these differ reportedly from *Ricciisporites tuberculatus* in the absence of a distal "sulcus". We observed that these sporomorphs closely resemble the spore tetrads of living *Riccia curtisii* James (see Text-fig. 1E, F). Without reference to the previous accounts of united fossil tetrads by Erdtman (1954), and Lundblad (1954, 1959) another similar fossil sporomorph was described by Hennelly (1958) as *Quadrisporites*

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## PLATE 1

1, 2. *Ricciisporites tuberculatus* Lundblad : Spore tetrads showing distal sulcus.

3. *Riccia curtisii* James : Permanently joined spore tetrads × 1000.

4. *Sphaerocarpos donnellii* Aust. : Joined spore tetrad.

5. *Densoisporites* : A spore tetrad with one missing spore × 500.

6. *Lundbladispora* : Tetrad showing isobilateral arrangement of spores × 500.

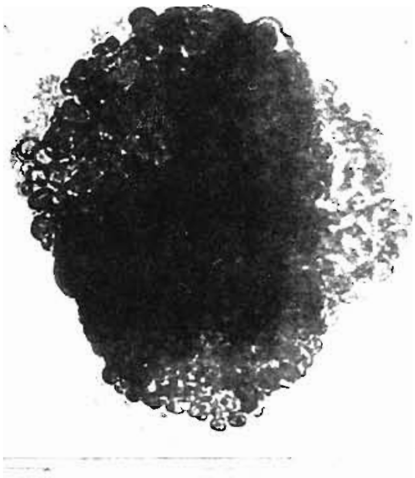
6-10, 14, 15. *Quadrisporites horridus* Henn. : Isobilateral joined spore tetrads × 250.

11-13. *Tetrahedraletes* cf. *T medinensis* Gray *et al.* : Permanently joined isobilateral tetrads of spores.

12. Conventional tetrahedral arrangement of spores in a tetrad × 1000.

16, 17 *Riccia perssonii* Khan. : Permanently joined isobilateral and cruciate spore tetrads.

1, 2. after Lundblad, 1954; 4, after Schuster, 1984; 7-10, after Potonié & Lele, 1959; 11-13, after Gray *et al.*, 1986; 14, 15, after Hennelly, 1958).



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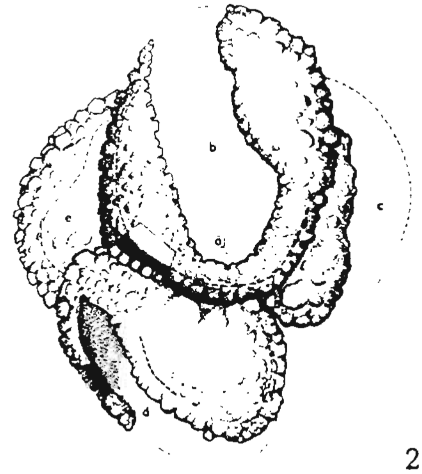

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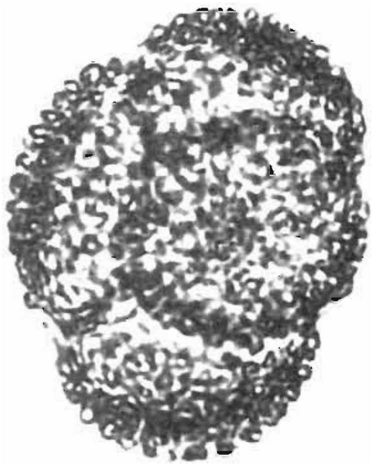

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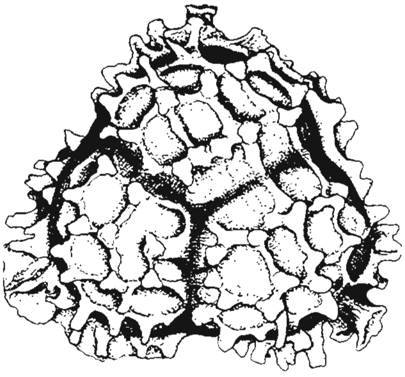

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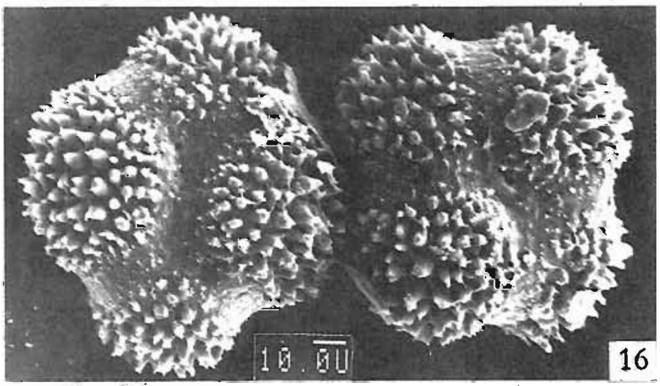

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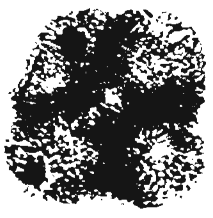

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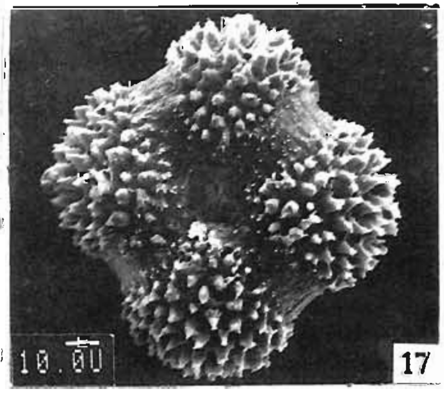

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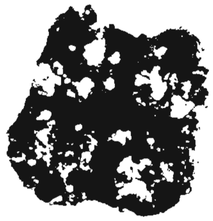

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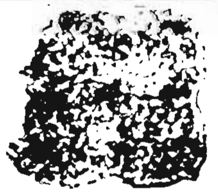

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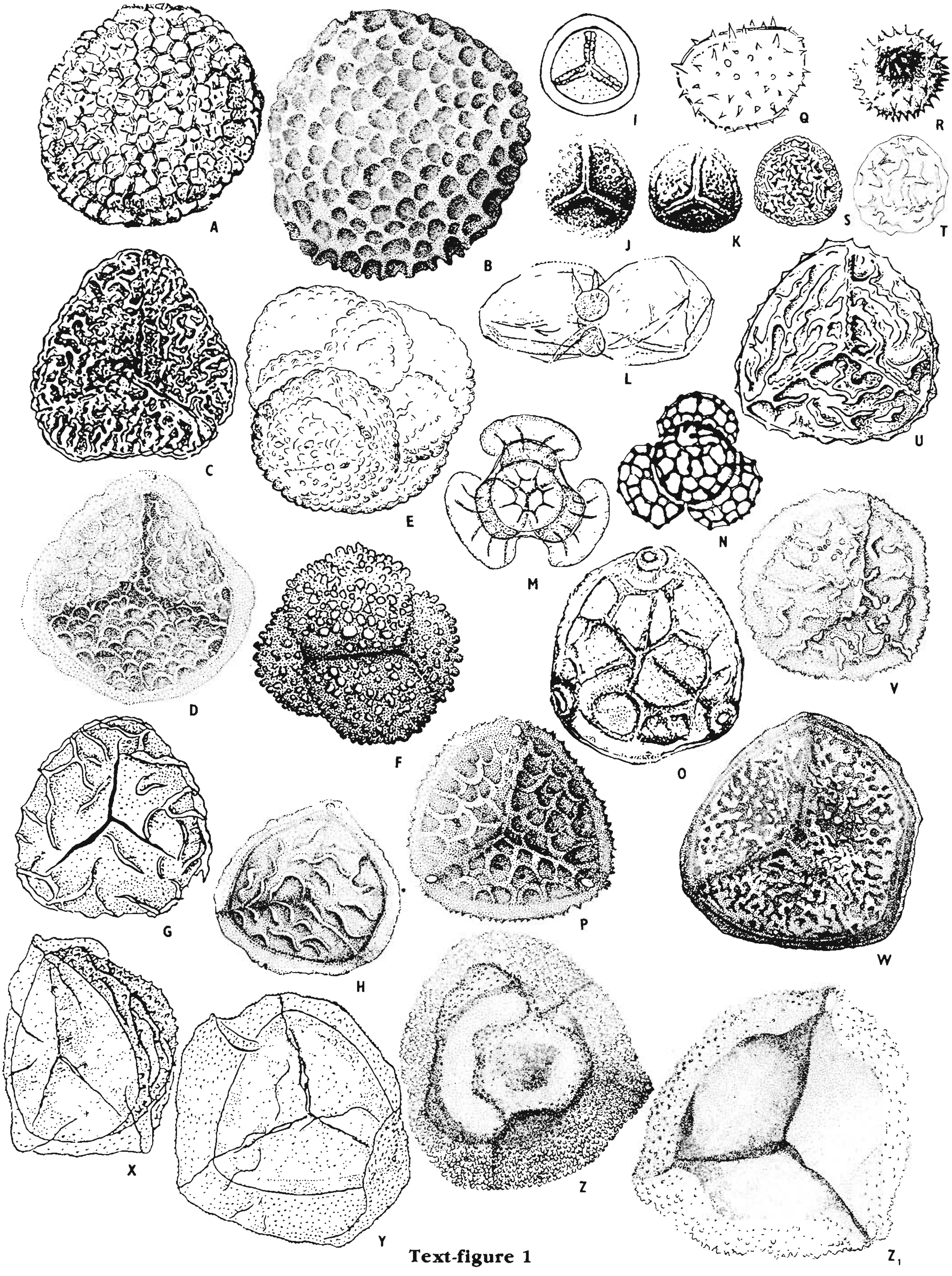
**PLATE 1**



**Text-figure 1**

*horridus* from the Permian-Triassic transition of New South Wales, Australia (Pl. 1, figs 14, 15). Shortly afterwards Potonié and Lele (1959) gave an emended diagnosis of the same species from Talchir beds and South Rewa Basin (Carbo-Permian age) of Indian Peninsula. These authors neither compared their *Quadrisporites horridus* with previously described adherent fossil tetrads nor with spores of living bryophytes which have permanently adherent tetrads even though their *Quadrisporites horridus* (Pl. 1, figs 7-10) is closely similar to tetrads of *Riccia perssonii* Khan (see Pl. 1, figs 16, 17).

Unlike the above dispersed adherent spore tetrads which are comparable with the united spore tetrads of bryophytes, Chaloner (1958) reported tetrads of *Didymosporites* having two large and two small spores enclosed in a common membrane which are attributed to *Stauropteris burntislandica* (see Text-fig. 1L). Other spore tetrads which are joined by tubular connections are also reported in some extant pteridophytes and angiosperms including some Indian species of *Isoetes* L. described by Pant and Srivastava (1962) and by Goswami and Khandelwal (1973) in *Ophioglossum costatum* and *O. vulgatum* L. Wodehouse (1935) had earlier mentioned a report of the occurrence of similar pollen grains by Stout (1918) in some angiosperms like *Cichorium intybus*. The intines of such spores are continuous through tubular connections and they have a single continuous protoplast. Pant and Srivastava (1962) suggested that the occurrences of occasional joined spores may have been caused by the nonseparation or incomplete separation of individual spores of a tetrad due to meiotic irregularities caused by hybridity.

The presence of the so-called "sulcus" in Lundblad's *Ricciisporites tuberculatus* remains uncertain since the wall of the distal depressed area in the joined fossil grains has never been shown to have a thinner wall like that of a sulcus, as defined by Kremp (1965), wherefrom germination takes place although some of the living hepatics have alete spores, viz., *Riccia* (mich.) L., *Cyathodium* Kunze, *Targionia* L. which bear a proximal concavity but that too has not been shown to be meant for germination, although germinal furrows have been reported in most of jungermannialean spores by Miyoshi (1966).

Among spores of bryophytes and pteridophytes we can also distinguish two other kinds mentioned below:

## Spores having characters more common in Bryophytes but rare in Pteridophytes

Among such spores reticulate ornamentation seems to be more common in bryophytes than tuberculate, verrucate or echinate sculpturing particularly among hepatics, whereas the spores of pteridophytes are more commonly echinate, verrucate and tuberculate and less commonly reticulate except in the families Lycopodiaceae, Sphenophyllaceae and Ophioglossaceae. Echinate spores of bryophytes like *Cyathodium* Kunze are characterised by having a proximal concavity. As far as we can gather from our own study of spores and from previously published accounts fragmentimurate (broken muri) too are prevailingly more common in bryophytes but rare in pteridophytic spores although they have been sometimes reported in spores like those of *Lycopodium cernuum* L., *L. serpentinum* Kunze and in *L. volubile* Frost.

## Spores having characters rare in Bryophytes but more common in Pteridophytes

Among spores of this kind are those having "Crassimarginate" and "incrassate" trilete laesurae with thickened lips or unsculptured ridges which

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**Text-figure 1—A,** *Schizosporis reticulatus* (Cookson & Dettmann) Dettmann : Alete spore showing reticulate ornamentation; **B,** *Riccia discolor* L. & L. : Alete reticulate spore × 500; **C,** *Tigrisporites hallensis* Klaus; **D,** *Riccia* sps. : Spore showing irregular reticulations × 500; **E,** *Lapposisporites lapposus* Visscher. : Joined spore tetrad; **F,** *Riccia curtisii* James : Permanently joined tetrad of spores × 500; **G,** *Perotriletes pseudoreticulatus* Couper; **H,** *Riccia canaliculata* Hoffm. : Spore showing rugulate ornamentation × 500; **I,** *Pseudogravisporites reticulatus* Visscher; **J,** *Phaeoceros laevis* (L.) Prosk. : Spore showing margin around trilete mark × 500; **K,** *Phaeoceros himalayensis* Kash. : Spore × 500; **L,** *Didymosporites scottii* Chal. : Spore tetrad showing two small and two large spores; **M,** *Tetrapterites visensis* Sullivan & Hibbert. **N,** *Cryptothallus mirabilis* Malmb. : Spore tetrad; **O,** *Rouseisporites reticulatus* Pocock; **P,** *Riccia cruciata* Kash. : both spores (O, P) showing pores in the flange × 500; **Q,** *Echimonocolpites rudae* Hamm. & Garc. O. M. Dez. : Echinate spore showing a colpus-like depression; **R,** *Cyathodium aureo-nitens* (Griff.) Mitt. : Spore showing a proximal concavity and echinate exine sculpturing × 500; **S,** *Hamulatisporis hammulatus* Krtzch.; **T,** *Marchantia polymorpha* L. : Distal surface of a spore; **U,** *Camptotriletes corrugatus* (Ibrahim) Potonié & Kremp : Trilete spore fragmentimurate sometimes anastomosing; **V,** *Riccia fluitans* L. : Spore showing fragmentimurate exine × 500; **W,** *Riccia frostii* Aust. : Spore × 500; **X, Y,** *Perotriletes granulatus* Couper; **$Z, Z_1$,** *Plagiochasma intermedium* Lindeb. & Gott. : Distal and proximal surface of a spore showing granulate flange. (**A, C, M, O, S,** after Potonié, 1966; **E, I, Q,** after Potonié, 1970; **L,** after Potonié, 1960; **N,** after Schuster, 1984; **U,** after Potonié & Kremp, 1954; **G, X, Y,** after Couper, 1953.)

occur commonly in pteridophytes (Erdtman, 1952; Harris, 1955) but these are seldom reported in any bryophytes, the only spores which have a slightly ridged trilete are those of *Phaeoceros himalayensis* Kashyap and *P laevis* Prosk.

Apart from the characters mentioned above as categorical or otherwise for distinguishing bryophytic spores from those of other land plants one of the most reliable methods of referring a particular fossil sporomorph to a bryophyte should be first hand comparison of spores of living bryophytes with a fossil sporomorph as has been done among others by Knox (1939), Dettmann (1963), Nagy (1968), Jarzen (1979) and Krutzsch (1963).

## IDENTIFICATION OF *SPORAE DISPERSAE* OF FOSSIL HEPATICAE AND ANTHOCEROTALES

On the basis of the above mentioned categorical and prevalent distinctions between the spores of pteridophytes and bryophytes we found that dispersed fossil spores like *Camptotriletes corrugatus* (Ibrahim) Potonié & Kremp 1954 described from the Permo-Carboniferous beds of Germany resemble living spores of *Riccia fluitans* L. and *Riccia frostii* Aust. in having broken muri (fragmentimurate) forming incomplete reticulations (Text-fig. 1 U—W). *Echimonocolpites rudae* Hamm. & Garc., D. M. Dez (see Potonié, 1970) which are described from the Eocene of Columbia are quite like those of present day *Cyathodium aureo-nitens* (Griff.) Mitt. because they have echinate exine and a concavity on one side (Text-fig. 1 Q, R). The following spores resemble spores of living forms noted against each of them *Hamulatisporis hamulatus* Krutzsch (see Potonié, 1966)—*Marchantia polymorpha* L. (Text-fig. 1 S, T), *Perotriletes granulatus* (see Couper, 1953)—*Plagiochasma intermedium* Lindenb. & Gott. and *Reboulia hemispherica* Raddi (Text-fig. 1 X-$Z_1$), *Perotriletes pseudoreticulatus* (Couper, 1953)—*Riccia canaliculata* Hoffm. (Text-fig. 1 G, H), *Pseudogravisporites reticulatus* Visscher (Potonié, 1970)—*Phaeoceros himalayensis* Kashyap and *P. laevis* (L.) Prosk. (Text-fig. 1 I-K) and *Tigrisporites hallensis* Klaus Nov. resemble spores of *Riccia* sp. in their size and ornamentation (Text-fig. 1 C, D).

*Aequitriradites verrucosus, A. spinulosus* Cookson & Dettmann and *Schizosporis reticulatus* Cookson & Dettmann (see Dettmann, 1963) which are reported from the Upper Mesozoic of Eastern Australia can be compared with the spores of the *Plagiochasma intermedium* Lindenb. (Pl. 2, figs 1-6) and with the spores of *R. melanospora* (Pl. 2, figs 7-9) (see Gupta & Udar, 1986) respectively and also with spores of *R. discolor*—Text-fig. 1A, B (determined by Dr K. R. Bapna and collected from Mt. Abu, Rajasthan, India).

## IDENTIFICATION OF BRYOPHYTIC FOSSIL *SPORAE DISPERSAE* WITH SIMILAR LOOKING IN SITU SPORES OF FOSSIL BRYOPHYTES

The only definitely known in situ spores of fossil bryophytes which have been described so far are those of *Naiadita lanceolata* (Buch.) Harris 1939; *Hepaticites discoides* Douglas 1973; *H. nidpurensis* Pant & Basu 1978; *Notothylacites filiformis* Nemjec & Pacltova (see Krassilov & Schuster, 1983) and *Notothylites nirulai* Chitaley & Yawale 1980 which range in age from the Triassic to the upper-most Cretaceous or Eocene. The characters of most of the above in situ spores are rather generalised and it is difficult to compare them with any bryophytic spores but a fossil sporomorph, *Couperisporites tabulatus* Dettmann is closely comparable with in situ spores of *Naiadita lanceolata* (see Dettmann, 1963).

The occurrence of *C. tabulatus* in the Triassic of Australia lends support to its relationship with

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## PLATE 2

1, 2. *Aequitriradites verrucosus* (Cookson & Dettmann) : Spores showing distal surface × 500.

3, 4. *Aequitriradites spinulosus* (Cookson & Dettmann) : Proximal and distal surface of spores showing spinules × 500

5, 6. *Plagiochasma intermedium* Lindeb. et Gott. : Proximal and distal surface of a spore showing spinulate ornamentation × 500.

7, 8. *Schizosporis reticulatus* (Cookson & Dettmann) : Spore showing polar reticulate view × 250.

9. *Riccia melanospora* Kash. : Alete spore with reticulate ornamentation × 600.

10. *Phaeoceros laevis* (L.) Prosk. : Spore showing proximal surface × 500.

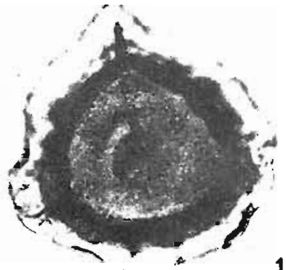
11. *Phaeoceros himalayensis* Kash. : Proximal surface in spore × 500.

12-15. *Foraminisporis wonthaggiensis* (Cookson & Dettmann) Dettmann : Spores showing proximal and distal surfaces of spinate spores × 500.

16, 17, 21-23. *Notothylas breutellii* Gottsche. : Spores showing spinulate and verrucate ornamentation × 500.

18-20. *Foraminisporis dailyi* (Cookson & Dettmann) Dettmann : Proximal and distal surface of a spore × 500.

(1-4, 7-8, 12-23. after Dettmann, 1963; 9. after Gupta & Udar, 1986).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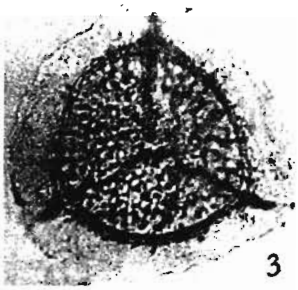
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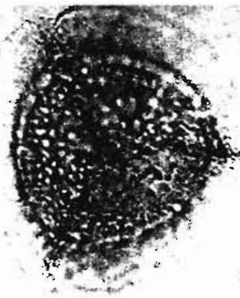
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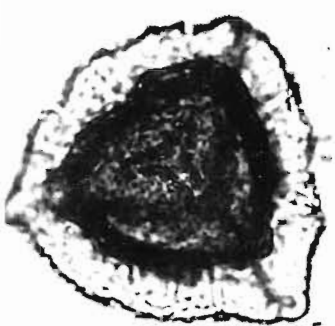
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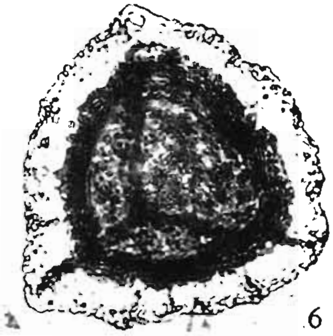
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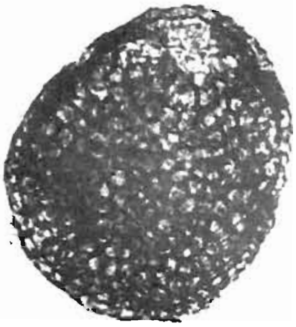
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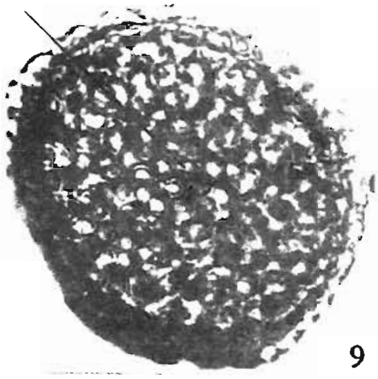
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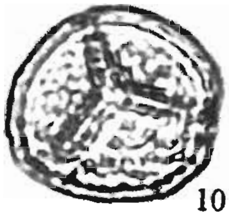
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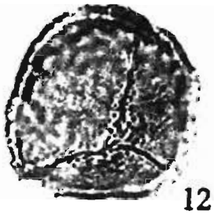
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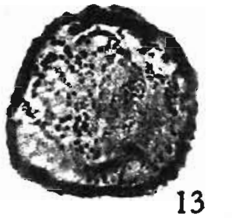
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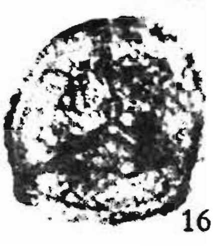
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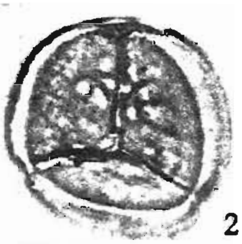
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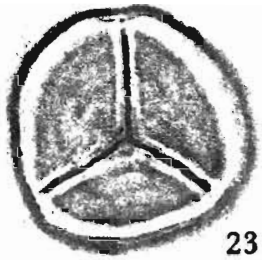
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PLATE 2

*Naiadita* and it may suggest that *Naiadita* or allied plants also existed in Australia.

## DISCUSSION AND CONCLUSIONS

Our comparative study of the spores of extant bryophytes and other land plants enables us to say that fossil *Sporae dispersae* of bryophytes can be placed into three broad categories: (i) spores which can be categorically recognised as belonging to bryophytes on the basis of the presence of characters which are indubitably different from those of other land plants, (ii) spores which can be assigned to bryophytes with some uncertainity on the basis of more frequent occurrence of their characters in bryophytes and less so in other land plants, and (iii) spores which may belong to bryophytes but cannot be distinguished from those of other land plants, because of the presence of characters which occur equally frequently in all land plants but some of them could belong to bryophytes. Although we know it for certain that land plants had come into existence during the Upper Silurian and Lower Devonian and the earliest plants attributable to Bryophyta are also recognised from the Lower Devonian, as far as *Sporae dispersae* are concerned, categorically distinguishable spores of the group have not been reported from the Silurian-Devonian time.

The present geological agewise search of fossil bryophytic spores shows that the first categorically distinguishable bryophytic miospores of the type represented by permanently adherent jugate tetrahedral tetrads are traceable up to the Middle Ordovician of North America and Saudi Arabia, Late Ordovician and Early Silurian of Ghana, Czechoslovakia, North America and Libya from where Gray (1985) reported some obligate tetrads of *Tetrahedraletes*. Thereafter such tetrads under the name *Tetrapterites vissensis* are reported from Lower Carboniferous by Sullivan and Hibbert (1964). Spores of this generalised type are also reported from Carbo-Permian beds of India by Potonié and Lele (1959) and from the Permian-Triassic transition beds of New South Wales in Australia by Hennelly (1958) as *Quadrisporites horridus*, similar spore tetrads were later described by Visscher, 1966 (see Potonie, 1970; Tiwari & Meena, 1988) under the names *Lapposisporites lapposus* and *Paralundbladispora* from the Permian of Netherlands which are reportedly different from the earlier described jugate tetrads of *Ricciisporites tuberculatus* (Lundblad, 1954, 1959) from Rhaeto-Liassic beds of north-west Scania. Visscher mentions that *Ricciisporites* differs from *Lapposisporites* in the presence of a distal sulcus.

Playford (1965) called jugate tetrads having laevigate exine by the name *Lundbladispora* and Banerji and Maheshwari (1975) described similar spores from Panchet beds (Triassic) under *Decisporis variabilis*; Tewari and Meena (1988) now assigned spores of the same kind to *Lundbladispora* Playford and *Densoisporites* Weyland & Krieger emend Dettmann, whose ornamentation was reportedly diverse. However, this is not discernible from their photographs although the occurrence of crusiate and tetrahedral tetrads not reported by these authors, can be easily made (see Pl. 1, figs 5, 6). Seemingly unaware of the publications of Gray (1985) and others on the abundance of obligate jugate tetrads in Pre-Triassic strata, Tewari and Meena (1988) quoted Heslop-Harrison (1973) to visualize "a situation (which) appears to have arisen during the Early Triassic times" where they said that the enzymic reaction for the separation of spores "fails due to some reasons or the other" and leads to "a condition where a number of tetrads will remain intact and consequently no individual spore gets released". The fact of the existence of jugate tetrads in Ordovician, Silurian would push back the supposed failure of reaction at least by about 250 m.y. in time but we are unable to understand the seemingly fashionable necessity of quoting Heslop-Harrison (1973) and his enzymic mechanism to explain the occurrence of obligate tetrads in the Early Triassic.

Leaving aside the above digression into the enzymic explanation, we may sum up our information on the above mentioned permanently united tetrads of variously named spores as indicating that bryophytes having such generalised forms of spores may have come into existence as early as the Middle Ordovician or Silurian and thereafter continued to exist during the Devonian, Carboniferous, Permian, Triassic and Liassic times.

At this stage it is necessary to point out that the occurrence of similar jugate pollen and spore tetrads in angiosperms and *Selaginella* cannot be used as an argument to weaken the evidence for the occurrence of bryophytes in the above mentioned strata since beside such spores of these plants being radically different from those of bryophytes, on the basis of the fossil record of angiosperms it would be wrong to imagine that jugate tetrads of spores occurring from Ordovician to Jurassic times could belong to that group. Even their attribution to heterosporous pteridophytes like *Selaginella* would seem to be equally unlikely unless it is supported by associated megaspores. On the contrary, even though we could assign jugate tetrads from Pre-Cretaceous to Mid-Ordovician, to bryophytes on the basis of the presence of fossils of this group in such beds or in slightly later ones, it would be difficult to assign Cretaceous and Post Cretaceous jugate tetrads to bryophytes with certainity since very similar jugate tetrads occur in the angiosperms which had come into existence.

Although bryophyte-like jugate spores have not been recorded in strata after the Liassic, the cosmopolitan occurrence of bryophytes producing such spores at the present time suggests that future research on *Sporae dispersae* of strata after the

**Table 2—Fossil spores attributable to Hepaticae and Anthocerotales through Geological Times**

| ERA | | PERIOD | EPOCH | FOSSIL SPOROMORPHS |
|---|---|---|---|---|
| **Cenozoic** | | Quaternary | Recent | |
| | | | Pleistocene | |
| | | Tertiary | Pliocene | |
| | | | Miocene | _Baculatisporites pseudoprimarius_ Krtz. & Thier.; _Foraminisporis zonaloides_ Krtz.; _Rudolphisporis rudolphi_ Krtz.; _Saxosporis duebensis_ Krtz. |
| | | | Oligocene | _Bohemiasporis vaclavensis_ Krtz. & Pacl.; _Anthocerisporis europaeus_ Krtz.; _A. bohemicus_ Krtz. & Pacl.; _Ceratosporites couliensis_ Srivastava |
| | | | Eocene | *_Echimonocolpites rudae_ Hamm. & Garc. D. M. Dez.<br>*_Hamulatisporis hamulatis_ Krutzsch |
| | | | Palaeocene | |
| **Mesozoic** | | Cretaceous | Upper | *_Schizosporis reticulatus_ Cookson & Dettmann |
| | | | Lower | _Phaeoceros_ Form A; _Phaeoceros_ Form B; _Phaeoceros_ Form C Jarzen (1979); _Aequitriradites_ sps. (Del. & Sprum.) Cookson & Dettmann; *_A. verucosus_, *_A. spinulosus_ (Cookson & Dettmann; _Cooksonites variabilis_ Pocock; _Coptospora striata_ Dettmann; _Couperisporites tabulatus_ Dettmann; _Foraminisporis dailyi_ Cookson & Dettmann; _Foraminisporis wonthaggiensis_ Cookson & Dettmann; *_Rouseisporites reticulatus_ Pocock |
| | | Jurassic | Upper | |
| | | | Middle | *_Perotriletes granulatus_ Couper; *_Perotriletes pseudoreticulatus_ Couper |
| | | | Lower | |
| | | Triassic | Upper | _Ricciisporites tuberculatus_ Lundblad, *_Tigrisporites hallensis_ Klaus; _Lundbladispora_ Playford; _Densoisporites_ Weyland & Krieger emend Dettmann; _Verrucosisporites_ Ibrahim emend. Smith _et al._; *_Quadrisporites horridus_ Hennelly |
| | | | Middle | |
| | | | Lower | |
| **Palaeozoic** | | Permian | Upper | |
| | | | Lower | _Lapposisporites lapposus_ Visscher; *_Pseudogravisporites reticulatus_ Visscher |
| | CARBONIFEROUS | Pennsylvanian | Upper | *_Quadrisporites horridus_ Hennelly |
| | | | Middle | |
| | | | Lower | *_Camptotrilites corrugatus_ (Ibrahim) Potonié & Kremp |
| | | Mississippian | Upper | Un-named _Sporae dispersae_ by Knox (1939) |
| | | | Lower | _Tetrapterites visensis_ Sullivan & Hibbert |
| | | Devonian | Upper | |
| | | | Middle | |
| | | | Lower | _Tetrahedraletes medinensis_ Gray _et al._ |
| | | Silurian | Upper | Trilete cutinized spores |
| | | | Lower | _Tetrahedraletes medinensis_ Gray _et al._ |
| | | Ordovician | Upper | _Tetrahedraletes_ cf. _T. medinensis_ Gray _et al._ |
| | | | Lower | |

*Fossil spores which have been attributed here for the first time.

Liassic may also yield remains of such spores.

In this connection Gray (1985) has suggested that these earliest jugate tetrads could belong either to any one or any combination of the following—protobryophytes, protohepatics or hepatics unrelated to the later trilete spore producers or to common ancestors for bryophytes' and vascular plants. On the contrary, Schuster (1966), Crum (1972) and Hébant (1977) have suggested that the similarities between these fossil spores which are jugate and those of some extant bryophytes, are two great to be due to parallel evolution. We agree with the latter viewpoint and believe that the occurrence of joined spores of *Tetrapterites-Quadrisporites* type in the rocks of Middle Ordovician age indicates that out of our two groups of plant amphibians—Bryophyta and Pteridophyta, the Bryophyta seem to have come into existence earlier and that even in plants of this group perhaps hepatics like *Riccia* or *Sphaerocarpos* appeared before the foliose forms. If in addition to this evidence the fossil history of early pteridophytes continues to remain traceable only up to the Upper Silurian, as it is at present, it would suggest that there would be no question of assuming that the bryophytes have evolved from pteridophytes as some authors have suggested. Indeed, the historical evidence of permanently joined tetrads of *Riccia*- and *Sphaerocarpos*-type being traceable up to the Ordovician could strongly militate against the Reduction Theory of bryophytes or the ideas about their thallose forms having arisen from foliose forms.

Another type of categorically distinguishable *Sporae dispersae* of bryophytes which show reticulate sculpturing and an equatorial flange having pores flanking the distal end of trilete laesurae like those of modern *Riccia, Plagiochasma* and *Reboulia*, are shown here to go back only up to Upper Mesozoic (Lower Cretaceous) where they are exemplified by *Rouseisporites reticulatus* (see Pocock, 1962; Samoilovitch *et al.*, 1961; Dettmann, 1959, 1963) and thus it is fairly clear that plants of Marchantiales like those mentioned above had also come into existence in the Lower Cretaceous or Upper Jurassic if not earlier. A search of their existence in subsequent strata is also likely to be fruitful.

The third kind of categorically determinable bryophytic *Sporae dispersae* which are alete and reticulate like those of many species of modern *Riccia*, viz., *R. billardieri, R. crispatula, R. discolor, R. gangetica* and *R. melanospora* include *Schizosporis reticulatus* described from the Upper Mesozoic of Australia (Cookson & Dettmann, 1959; Dettmann, 1963) and Upper Neocomian beds of Canada by Pocock (1962). Spores of this kind have not been reported in any pteridophytes.

Coming to the second category of *Sporae dispersae* which can be doubtfully assigned to bryophytes are alete echinate spores having a concavity on one side like those of modern *Cyathodium aureo-nitens*. This category includes dispersed spores which have been reported from the Palaeocene of Columbia as *Echimonocolpites rudae* by Hammen and Garcia de Mutis (1965) but we need to look for spores of this kind in earlier or later strata.

Presently our knowledge of the spores of the earliest plants attributed to the bryophytes occuring in Upper Silurian or Lower Devonian strata, is rather scanty but if the spores of these plants are represented in the *Sporae dispersae* of these times (see Gray, 1985; Richardson, 1985; Richardson & Ioannides, 1973; Gensel & Andrews, 1987) they seem to belong to the third category of bryophytic spores which are indistinguishable from those of other land plants.

The sporomorphs which have been attributed to the bryophytes indicate their lineages, viz., Metzgeriales, Sphaerocarplaes, Marchantiales and Anthocerotales which can be traced back in geological time up to the Middle Ordovician (see Table 2) but such sporomorphs have not so far been reported in any earlier strata.

Among the sporomorphs which have been compared with those of extant forms of bryophytes, the largest number are *Riccia*-like suggesting that such forms have been in existence not only for a long time but had also been fairly common. Another fact which is emphasized by this study is our uncertainty about the origin of bryophytes and the evolution of their various lineages in geological time. These problems can be solved only by further work on the fossils of the group.

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