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Fossil flora (*Costatheca* and *Spermatites*) from the Upper Maastrichtian Deccan Intertrappean Beds of India

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Abstract: *Costatheca* and *Spermatites* are recorded from the Maastrichtian Deccan Intertrappean Beds of Mohgaon-Kalan and Padwar, Madhya Pradesh, India. These forms are found in association with typical Late Maastrichtian palynological species of aquatic pteridophytic sporomorphs namely, *Azolla cretacea, Ariadnaesporites* sp., *Gabonisporites vigourouxii* and angiospermic pollen *Aquilapollenites bengalensis.* Specimens of *Spermatites* are compared with the megasporangium of *Azolla pinnata.* It is observed that the indusium of *A. pinnata* resembles *Spermatites* in shape, size and ornamentation. The views of other scientists regarding the affinity of *Costatheca* and *Spermatites* have also been discussed.

Key words: Deccan Intertrappean, Late Cretaceous, *Costatheca, Spermatites.*

Introduction

Miner (1932, 1935) investigated the Upper Cretaceous coals of Western Greenland and amongst other forms reported *Chrysotheca* and *Spermatites* — presumably seed cuticles of angiosperms. Later, Binda & Nambudiri (1983) and Friis (1985) changed the name of *Chrysotheca* to *Costatheca* as the previous name was already occupied for Chrysophycean algae. These two genera were later found to be of stratigraphic importance as they are confined to Cretaceous strata. Schemel (1950), Binda (1968), Gunther & Hills (1972), Collin (1973), Binda & Nambudiri (1983), Knobloch (1986) and Kovach & Dilcher (1988) studied these two genera and commented on their morphology and affinity. Batten & Zavattieri (1996) extensively studied Miner's material of these two genera, critically assessed the various species and provided detailed descriptions.

The two genera were described and recorded only from the Northern Hemisphere until Sahni et al. (1999), reported them as casts from the Maastrichtian Lameta Formation near Jabalpur, India. Kar & Singh (1986: pl. 12, Fig. 5) illustrated a *Spermatites*-like specimen from the Cretaceous Mahadek Formation of Meghalaya. However, it was designated as ?anther type-1. The present paper includes descriptions of *Costatheca* and *Spermatites* represented in the Maastrichtian Deccan Intertrappean Beds of Madhya Pradesh (India) and discusses about their probable affinities.

Material and methods

Costatheca and *Spermatites* were collected from the Deccan Intertrappean Beds of Mohgaon-Kalan and Padwar (Chhindwara District and Jabalpur District respectively, Madhya Pradesh, India) (Fig. 1). At Mohgaon-Kalan, the intertrappean bed was observed by Kar & Srinivasan (1998) in an unlined water well situated 0.5 km west of the village (79°11′E, 22°1′N). The intertrappean bed is about 1 m thick and is sandwiched between two basaltic flows (Fig. 2). The lower sediment is made up of buff-coloured, hard chert of 0.25 m thick with occasional wood fragments; it is overlain by green shale of 0.25 m thick containing fresh water pelecypod. The upper bed consists of carbonaceous shale of more or less the same thickness. Kar & Srinivasan (1998) described typical Late Cretaceous palynomorphs including aquatic pteridophytes like *Azolla cretacea, Ariadnaesporites* sp., *Gabonisporites vigourouxii* and angiosperm namely, *Aquilapollenites bengalensis* from this shale. *Costatheca* and *Spermatites* were also examined from this unit.

The palynological investigation of Padwar Intertrappean Bed was carried out by Prakash et al. (1990) and Sahni et al. (1996). In a dug out abandoned well at Padwar, Kar et al. (1998) detected two layers of trap, one layer of volcanic ash and two intertrappean beds in the well. They divided the palynological assemblage recovered from this well into a lower *Aquilapollenites bengalensis* Zone and an upper Algae dominant Zone. The former zone is also very rich in *Costatheca* and *Spermatites* and most of the specimens illustrated here come from this horizon (Fig. 3). The samples were macerated in commercial HNO_3 followed by a wash in 5% KOH solution and passed through a 400 meshed sieve. The residues were collected and the slides were prepared with polyvinyl alcohol solution and when dried mounted in Canada balsam. The slides and stub studied are deposited at the repository of the Birbal Sahni Institute of Paleobotany, Lucknow.

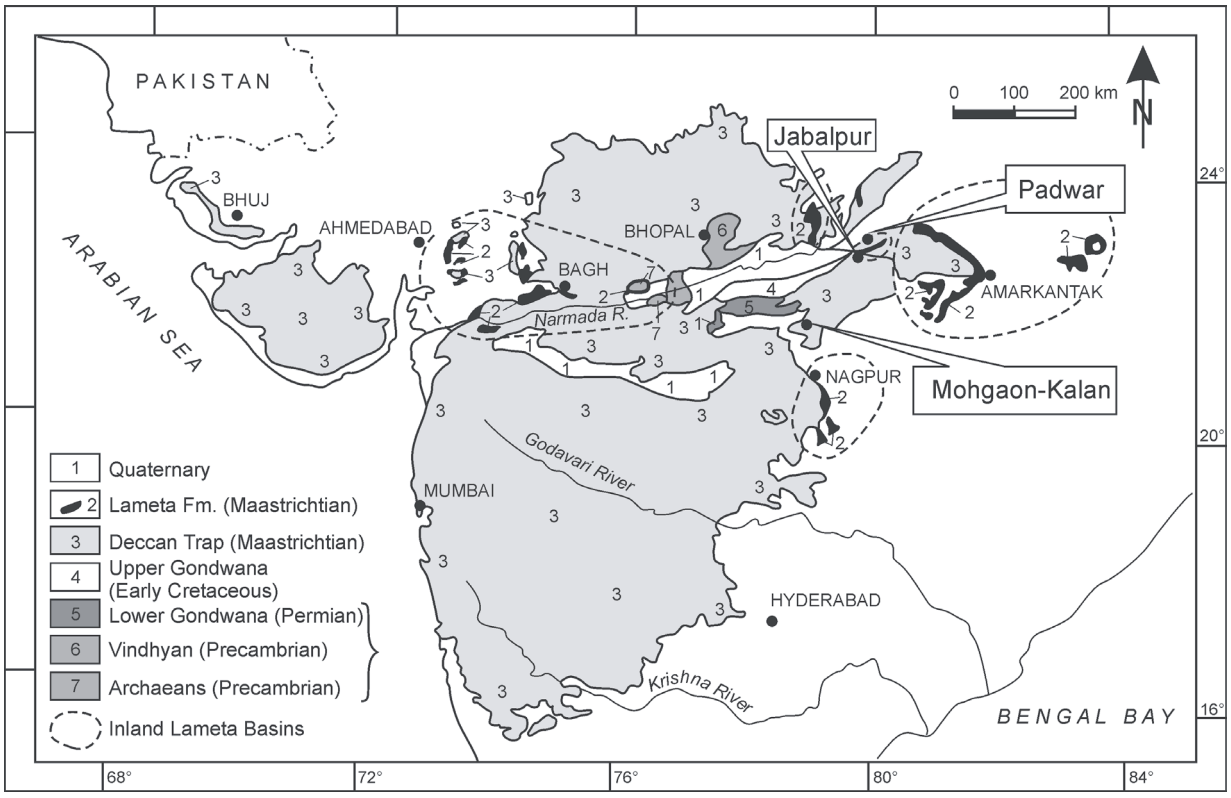

Fig. 1. Geological map showing the localities of Mohgaon-Kalan and Padwar in Madhya Pradesh.

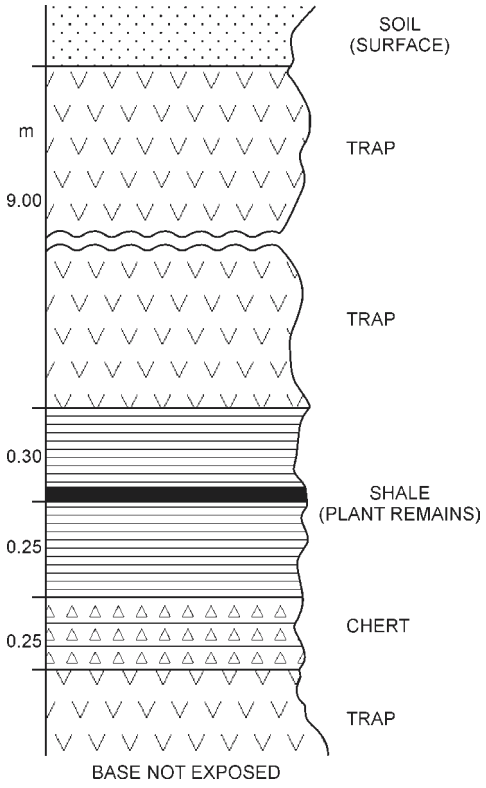

Fig. 2. Lithological profile of unlined water well at Mohgaon-Kalan, Chhindwara District, Madhya Pradesh. Lower 0.25 m shale bears *Costatheca* and *Spermatites.*

Systematic description

Genus: *Costatheca* (Miner) Hall, 1967.
Type Species: *Costatheca diskoensis* (Miner) Hall, 1967, p. 1298, Figs. 1–3

Costatheca sp.
Fig. 4.1,2

Locality: Mohgaon-Kalan, Chhindwara District, Madhya Pradesh.

Horizon: Deccan Intertrappean, Maastrichtian, Late Cretaceous.

Description: The specimens are oval with more or less equally broad lateral ends. The size range is 594–704 × 321–378 µm. The specimens are adorned with two distinct ribs, they are 2–3 cells thick, parallel to longer axis. The cells on remainder of the surface are transversely oriented, irregular in size and shape, 6–10 µm thick. The margin of the cells is thin and muri are up to 3 µm thick.

Comparison: The species described here resembles *Costatheca diskoensis* (Miner) Hall (1967) in size range and general organization; however, *C. diskoensis* has 6 vertical ribs whereas the present specimens have only two. *C. dakotaensis* (Miner) Hall (1967) has pronounced midribs and transverse cellular outlines while *C. levis* Vangerow (1954) has more or less psilate cell wall.

Number of specimens studied: Four. Sample No. H2, 5a; Sample No. Pad. 1.1, Sample No. Pad. 2.2.

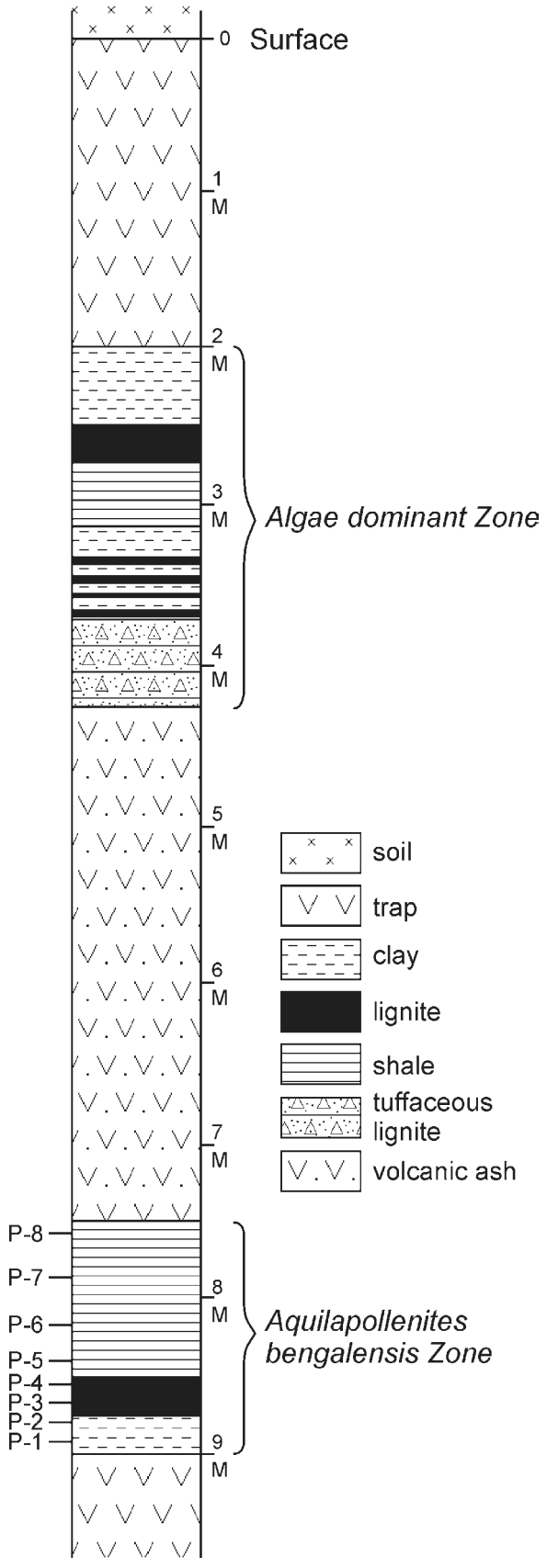

Fig. 3. Lithological profile in an abandoned dug out well at Padwar, Jabalpur District,0 Madhya Pradesh. Samples Nos. P2–P8 contain *Costatheca* and *Spermatites.*

Genus: *Spermatites* Miner, 1935.
Type Species: *Spermatites ellipticus* Miner, 1935.

Spermatites ellipticus Miner, 1935, p. 609, Pl. 19, Fig. 46
Fig. 5.1–5

Locality: Padwar, Jabalpur District, Madhya Pradesh.

Horizon: Deccan Intertrappean, Maastrichtian, Upper Cretaceous.

Description: The specimens are oval-elliptical in shape; the size is very variable, ranging from 432–825×250–270 µm. The apical part is mostly cutinized, generally forms a cap with protruding end (Fig. 5.1,5), cutinized layer may be dissolved due to maceration. The lower part of the specimens when detached forms a circular opening, the marginal cells of this area may also be cutinized. The cell walls have two layers — the outer wall is thin and mostly laevigate while the inner layer is thick and reticulate in structure; cell walls are 1–12 µm thick. The meshes are arranged parallel to longer axis, squarish-rectangular in outline and up to 2 µm thick.

Comparison: The specimens described here as *Spermatites ellipticus* Miner (1935) closely resemble those figured by Miner (1935, pl. 19, Fig. 46) in oblong-elliptical shape, square-rectangular cells and presence of apical cap. *S. arcuatus* Miner (1935) is easily distinguished from *S. ellipticus* Miner (1935) by its bean shape. *S. elongatus* Miner (1935) is oblong-elliptical in shape and *S. orbicularis* Miner (1935) is oval-subcircular in disposition. The characteristic feature of *S. polyporous* Miner (1935) is its lateral position of the chalazal orifice.

Number of specimens studied: Twenty seven. Sample Nos. Pad. 2.2, Pad. 1.3, Pad. 4.5, Pad. 6.2, Pad. 7.2, Pad. 8.6.

Discussion

Since their introduction *Costatheca* and *Spermatites* attracted the attention of a number of paleobotanists. They were thought to be algal (Deák & Combaz 1967), bryophytic (Arnold 1932), pteridophytic (Vangerow 1954), pteridospermic (Harris 1954), angiospermic (Miner 1935; Binda 1968 etc.) and even animal in origin (Tiffney 1983). It is obviously very debatable and we would take *Spermatites* first because it is better known.

Deák & Combaz (1967) thought that *Spermatites* could be an alga resembling *Polysiphonia* because their morphological characters broadly resemble each other. Arnold (1932) postulated that *Spermatites* might be an antheridium of bryophyte. Miner (1935) refuted this assumption stating that amongst the present day bryophyte no comparable form is known.

Vangerow (1954) thought that *Spermatites* might be related to some aquatic pteridophytes. Batten & Zavattieri (1996) recovered many heterosporous pteridophytes namely, *Arcellites disciformis, Ariadnaesporites ariadnae, Minerisporites borealis* and others, along with *Costatheca* and *Spermatites* and other palynomorphs. Rao (1935) observed that the cells of the upper part of the indusium in megasporangium of *A. pinnata* become hardened and lignified so that when the lower part has decayed these dark coloured cells remain as a conical cap at

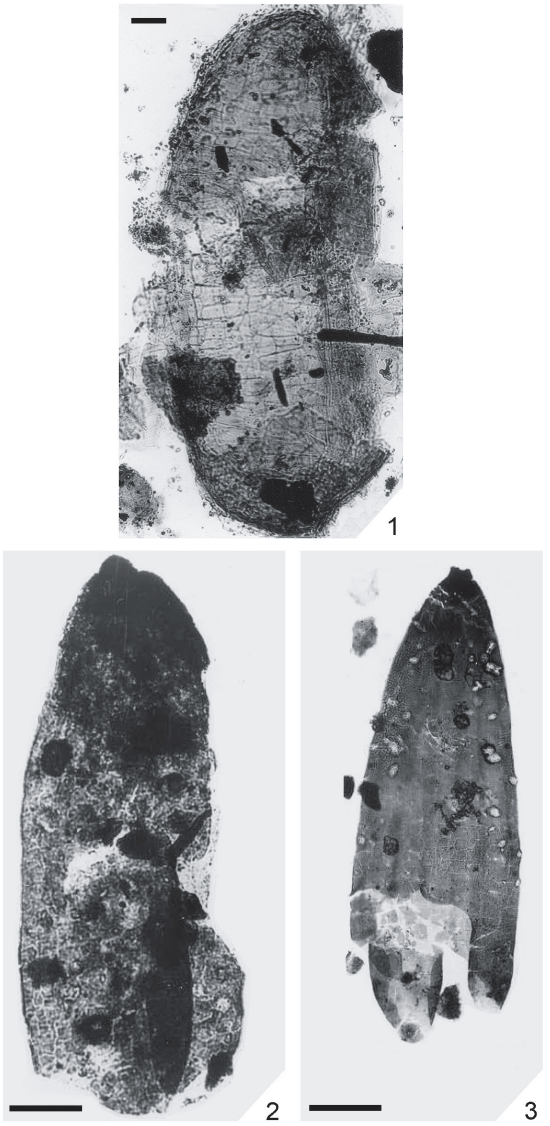

Fig. 4. 1, 2 — *Costatheca* sp. Sample No. H2, Slide No. 1, U61; Sample No. Pad. 2, Slide No. 3. **3** — *Costatheca diskoensis* (Miner) Hall, 1967. Sample No. Pad. 2, Slide No. 3, V45/1. All scale bars = 0.1 mm.

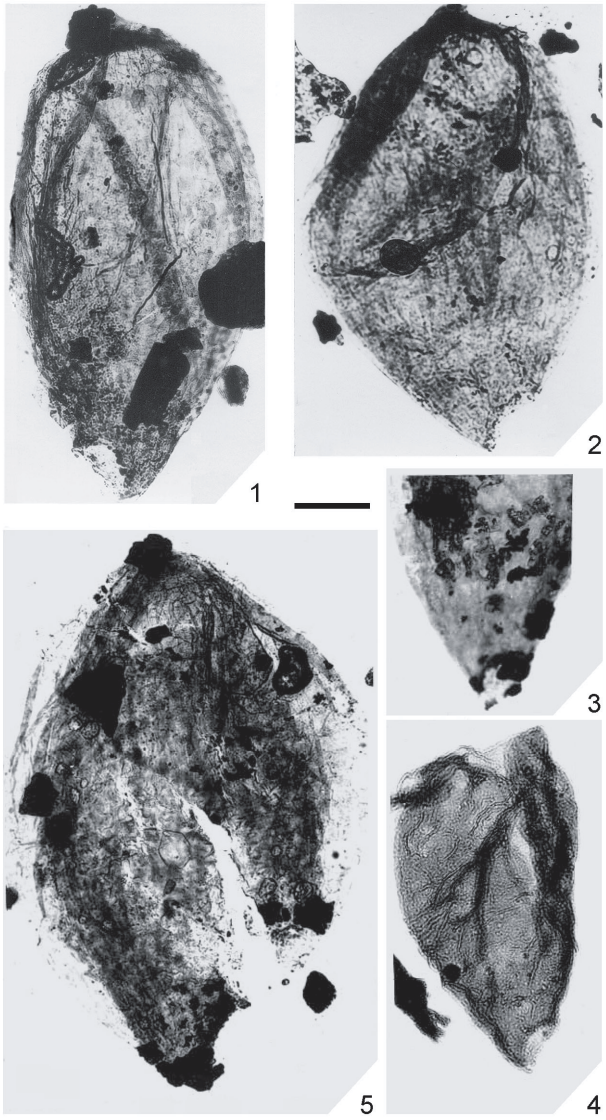

Fig. 5. 1–5 — *Spermatites ellipticus* Miner, 1935. Sample No. Pad. 2, Slide No. 3, R49; Sample No. Pad. 2, Slide No. 3, G23/4; Sample No. Pad. 2, Slide No. 3, R49; Sample No. Pad. 2, Slide No. 3, Q31; Sample No. Pad. 2, Slide No. 2, Q53. Scale bar = 0.1 mm.

the top of the spore. Microscopic study of the plants reveals that the indusium of *A. pinnata* which is the outer covering of the megasporangium, very much resembles the genus *Spermatites* in shape, size and ornamentation. The cutinized cap is very similar to the micropylar end of seeds and consists of closely spaced convoluted cell walls forming a cap, which may be extended to a stalk of varying length (see also Tryon & Tryon 1982; Tryon & Lugardon 1991). Hall & Peake (1968) also mentioned that the cap of *Spermatites* somewhat resembles the cap of present day *Azolla.* The indusium generally dissolves when the megasporocarp is mature except for the apical part. In the abortive megasporocarp the indusium does not dissolve and when fossilized may form *Spermatites*-like bodies (Fig. 6.1,2).

The sporophylls in *Azolla filiculoides* are always the lowest leaves on the branch (McLean & Ivimey-Cook 1951). The sporophyll has two lobes, the lower lobe divides early into two at the apical part where the sori develop. The indusium grows out as a ring-wall below the sorus and covers it completely except for a micropyle-like opening at the top. Von Goebel (see McLean & Ivimey-Cook 1951, p. 550) remarked that this type of indusium resembles very much an integument surrounding the ovule of a seed plant. No wonder that the aborted indusium of *Azolla* in the fossil condition could apparently be regarded as an angiospermic seed. The SEM photograph of the megasporangium of *A. pinnata* (Fig. 6.3) is broadly comparable to *Spermatites* sp. illustrated by Batten & Zavattieri (1995: Fig. 2C) recovered from the Campanian sediments of Alberta, Canada.

Harris (1954) observed that the isolated nucellar cuticles of the pteridosperm *Caytonia* approximates *Spermatites* in morphology. The nucellus has a thick and strong cuticle and in both micropylar and chalazal regions the cells become small

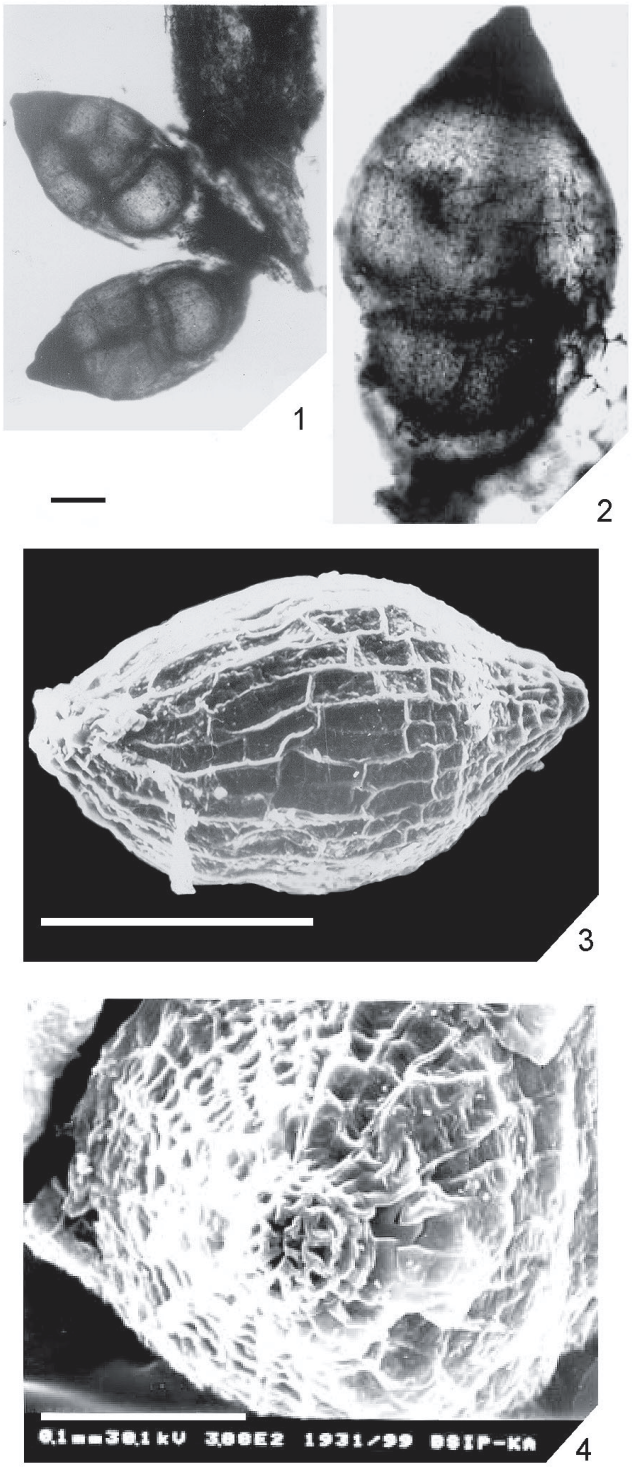

Fig. 6. 1, 2 — Indusium of *Azolla pinnata* R. Brown with megasporangium. Scale bar = 0.1 mm. **3** — SEM of indusium of *Azolla pinnata* R. Brown showing cap and reticulation. Scale bar = 0.5 mm. **4** — Cap of the same in SEM. Scale bar = 0.5 mm.

and isodiametric. The chalaza has a small circular hole and the micropylar end is occasionally raised. However, the megaspore membrane in most of the modern gymnosperms is generally heavily cutinized and according to Batten & Zavattieri (1995) *Spermatites* has no such thickening.

The reproductive structures of *Archaefructus* described by Sun et al. (1998, 2002) from the Jurassic sediments of China apparently resemble *Caytonia* in gross morphological characters. But is easily distinguished by its closed carpels along an adaxial stigmatic crest; in *Caytonia* it is not conduplicate. Besides it has bisaccate pollen whereas in *Archaefructus* the pollen are non saccate and monosulcate.

Binda (1968), Binda & Nambudiri (1983) and Nambudiri & Binda (1991) contemplated that *Spermatites* resembles the seed of *Juncus.* Kovach & Dilcher (1988) also endorsed this view and commented that the thin outer cuticular layer of seed of *Juncus* is comparable to some specimens of *Spermatites.* They, however, pointed out the stratigraphic disparity between the two as no form of *Juncus* is known from the Upper Cretaceous sediments. Huang & Dilcher (1988) remarked that the two layers that are seen in most specimens of *Spermatites* may be interpreted as representing the two integumentary layers typical of angiosperms ovules in seeds. In *Archaeanthus linnenbergeri* Dilcher & Crane (1984) *Spermatites*-like seeds or aborted ovules isolated by maceration of a follicle fragment have strongly cutinized pointed tips and rounded bases with a circular perforation. These were interpreted by them as micropylar and chalazal ends respectively.

Batten & Zavattieri (1995) however, observed that *Spermatites* must be regarded as a heterogenous taxon because it comprises a variety of plant groups. Most of the *Spermatites* are devoid of morphological characters that could be compared to the extant species of angiosperms. Before them, Gunther & Hills (1972) and Spleeman & Hills (1980) regarded *Spermatites* as well as *Costatheca* as merely plant remains of uncertain affinity. Batten & Zavattieri (1996) commented that the disappearance of *Spermatites* at the end of the Cretaceous seems to be more apparent than real as the associated megaspores and angiosperms do not disappear. Considering all these facts they concluded that at present the evidence is equivocal to assert that *Spermatites* were derived from herbaceous angiosperms inhabiting hydrophyllous environments.

Costatheca sp. described here is, however, different from the indusium of *Azolla pinnata* as cells other than the longitudinal ribs are transversely oriented. Knobloch (1986) observed that shape, number of ribs and external character of *Costatheca* is very variable. Miner (1935) postulated that *Costatheca* resembles Jungermanniales of bryophyta. Vangerow (1954) thought that it could be a spore sac. Tiffney (1983) suggested that *Costatheca* could be an insect egg. Batten & Zavattieri (1995) opined that some *Costatheca* could be insect eggs because the cuticles of some insect eggs are very similar to *Costatheca.* Knobloch (1981) thought that this genus is not angiospermous in origin. Binda & Nambudiri (1983), however, assumed that *Costatheca* could be related to the seeds of Butomaceae of angiosperms.

Conclusions

Costatheca and *Spermatites* are known from wide geographical regions with a limited stratigraphic range. Most of the workers think *Spermatites* is an angiospermic seed while a few assume it of gymnospermic or pteridophytic in origin.

Since it grew in aquatic environments, the external morphology of the diverse organisms could have developed more or less similar forms in response to the same kind of adaptation. Hence *Spermatites* could very well be a heterogenous complex comprising different entities.

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