ASTEROTHECA MERIANI (BRONGN.) STUR AND ITS SPORES FROM THE UPPER TRIASSIC OF LUNZ (AUSTRIA)

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ABSTRACT

This paper deals with the morphological study of *Asterotheca meriani* (Brongn.) Stur, a species of ferns from the Upper Triassic of Lunz, Austria, well preserved in the form of carbonaceous crust on the shales. The frond is bipinnate. Pinnules are longer than broad and the venation is typically of *Pecopteris* type. Synangia are circular, borne intramarginally, comprising 4 sessile sporangia in close cohesion at the anterior end but slightly apart at the apical end. Spores are bilateral, circular to oval in polar view and indisputably show a longitudinal (monolete) slit, slightly bent in the middle. The spore exine is thick and finely granulose.

INTRODUCTION

FOR the last few decades the study of plant microfossils, especially the spores and pollen grains from the sedimentary strata such as shales and coals is being increasingly pursued. These spores and pollen grains are not only of academic interest but are also of significant applied value such as in the dating of strata and their stratigraphical correlation. But dispersed and isolated as these minute plant organs are, they provide little scope for the study of such interesting aspects as their phylogeny. To enable this, lately investigations are being increasingly carried out to describe the *in situ* spores from fructifications whose systematic position is more or less well established. Such studies are of immense value in not only that they supply the necessary clues for better classification and taxonomy of the dispersed spores but also provide us a better understanding of the general floral composition represented by the *Sporae dispersae* for floristic speculations.

The results of investigations reported in this paper pertain to *Asterotheca meriani* (Brongn.) Stur and its *in situ* spores.

MATERIAL AND METHODS

Several pieces of fronds of *Asterotheca meriani* preserved as compressions on a dark grey shale were collected by one of the authors (BHARDWAJ) from near Lunz a. See (Austria) in 1954.

Horizon — *Lunzer Schichten*, Upper Triassic.

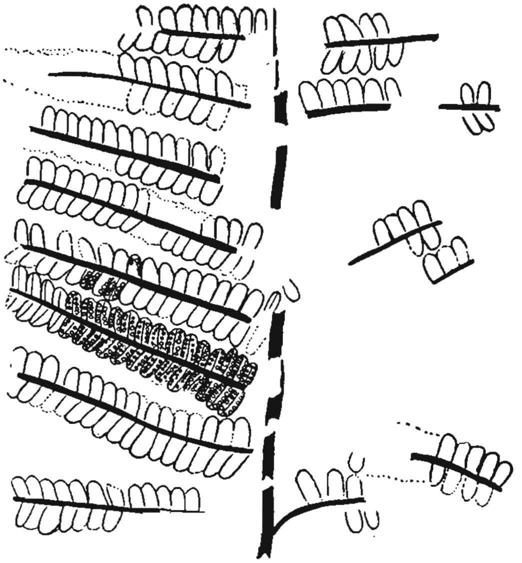
The compressions were examined under strong reflected light. The transfer preparations were made following Walton's transfer method (WALTON, 1923) and studied under strong reflected light. The synangia were picked up with the help of a needle from the transfers and treated separately with commercial nitric acid for about 24 hours. Then the oxidized products were washed with water and followed by a treatment with 10 per cent potassium hydroxide solution for 4 hours. After several washings with water, till the residue was free from alkali, the spores thus recovered were mounted in Canada balsam. For the recovery of the cuticles, the organic crust in the transfers was separated with the help of xylol and passed through alcohol to bring it to water. This organic crust was subsequently macerated in the usual manner. But the cuticles could not be recovered as they probably disintegrated on the addition of alkali.

DESCRIPTION

Asterotheca meriani (Brongn.) Stur

(For synonyms *see* KRASSER, 1909, p. 32)

Leaf — Text-fig. 1 represents the middle part of the lamina. Some other blocks give an idea of its upper part but nothing is known about the basal part. Though *Asterotheca meriani* appears to have had a large frond, nothing can be exactly stated about its length from this evidence. All the specimens examined are fully fertile and not even one sterile pinnule has been observed so far. Midrib of the pinna is broad and conspicuous. The pinnules are borne laterally, $\pm$ opposite to each other along the midrib (PL. 1, FIGS. 1, 2). Each pinnule is spathulate with a broadly rounded apex and a wide base. The midrib in each pinnule is distinct and subtends lateral veins which are once forked. Beyond the point of bifurcation they slightly curve out and then run parallel to each other up to the end of the margin (PL. 1, FIG. 3). The structure of the cuticle is not known.



TEXT-FIG. 1 — A part of the frond of *Asterotheca meriani* showing the arrangement of pinna and pinnules. × ½.

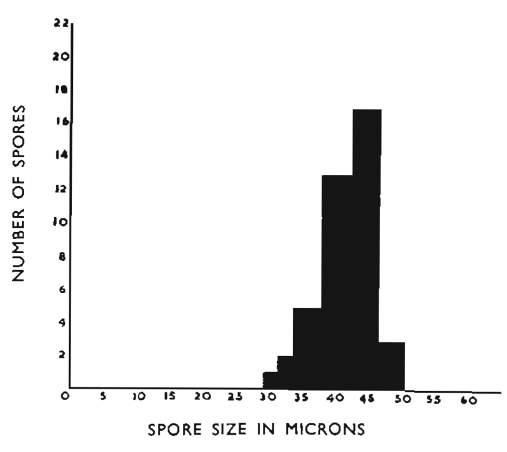
Several efforts were made to recover the cuticle by maceration but to no avail. It seems that the cuticle in this species is too thin and delicate to withstand chemical treatment.

Synangium — The easily noticeable circular, pustular swellings or pits indicate the position of synangia (PL. 1, FIGS. 2, 3). These are borne in two rows on each side of the midrib (PL. 1, FIGS. 4a, 4b). Generally they are situated on the veins, in close proximity to the margin of the pinnule. The synangia may be obliquely pressed (PL. 1, FIG. 4a) largely due to the effect of lateral pressure during fossilization or vertically pressed (PL. 1, FIG. 4b). The base of the synangium is broad but it gradually narrows upwards (PL. 1, FIG. 5). Invariably in each synangium 4 sporangia are present, each of which has a broad base and a narrowed apex. The structure of the sporangial wall could not be made out even in the partially macerated sporangia. This is probably due to the destruction of the sporangial walls during maceration. Thus nothing comparable to the annulus cells has been detected.

The sporangia from the basal, middle and top portions of the pinnae were separately macerated. In some pinnae the spores were uniformly mature but in some others, quite immature spores, which were held in firm union and could hardly be separated from each other (PL. 2, FIGS. 6, 7), were found.

Spore — In polar view the spores are more rounded than oval. In lateral view the proximal side appears slightly flattened but the distal side is deeply arched. The mature spores show a significant range of variation in size within the same sporangium (PL. 2, FIG. 9).

The spores measure on an average 42 μ but they vary in size from 29·4 to 50 μ (TEXT-FIG. 2). Most of the spores are sized 37·8-46·2 μ. The exine is finely granulose (PL. 2, FIG. 13). In top focus each granum is white, surrounded by a darkened hallow. In low focus the hallow becomes bright which together with the adjacent ones appears as a reticulation, evidently negative in character (PL. 2, FIGS. 10, 15, 17, 18) but which can easily be confused with true reticulate ornamentation. The exine is ±2 μ thick in optical section. Each spore shows the presence of a monolete mark which may be open (PL. 2, FIG. 10) or closed. The latter, in polar view, is slightly bent in the middle just as in a bow (PL. 2, FIGS. 8, 11, 12, 18-20). Occasionally a slitted arm has been seen to arise from the median bend in the monolete slit, at ± right angles to it, resulting in the formation of a pseudotrilete mark (PL. 2, FIGS. 9, 13-15). It is apparent that this third slit is secondary in nature, arising presumably as a consequence of flattening during fossilization. In partly, laterally compressed spores the monolete slit is closed, hair thin and the median bend is not clearly evident (PL. 2, FIGS. 16, 21, 23). The ends



TEXT-FIG. 2 — Histogram depicting the range of variation in the size of the spores in *Asterotheca meriani*.

of the slit are not bifurcated. The slit measures on an average 26 μ varying from 20 to 30 μ. One of the spores (PL. 2, FIG. 25) shows 4 arcuate lines, opposite to each other. These are the marks of tetragonal compression while the spore was in a tetrad condition. These marks are obliterated in a matured, free spore.

DISCUSSION

Our observations described above enable us to invoke discussion on a number of aspects relating to the systematics of *Asterotheca* Presl., and its spores.

It is apparent from the nature of fronds as well as the synangium that our specimens refer to a typical member of the genus *Asterotheca*. The synangium, which is by far the most diagnostic, is intramarginal and sessile with the four constituent sporangia fused in the lower part but separated in the apical region. It has also been observed by us that in fossil condition the synangia, if vertically flattened, are disc-like, but if obliquely flattened, they are more or less cylindrical in one and the same pinnule. As observed by us, the sporangia are cylindrical yet devoid of any stalk which, even if present, must have been negligibly small so as to escape detection. In spite of the fact that cylindrical synangia and sporangia in the opinion of some authors (ANDREWS, 1943) answer more to the circumscription of the genus *Scolecopteris* Zenker, the absence of synangial stalk has led us to decide in favour of *Asterotheca*. As regards the problem of the taxonomic status of *Scolecopteris* which has been included by Hirmer (1927, p. 576) as well as Radforth (1942) in *Asterotheca* but contested by Andrews (1943), we are inclined to support the former contention, although our specimens tend to show a combination of characters, i.e. cylindrical synangia and their sessile condition, each of which are separately diagnostic of the two contending genera. However, we reiterate Andrews' (1943, p. 436) remark that the range of variation in the structure of the synangia in *Asterotheca* (incl. *Scolecopteris*) tends to be unduly large for a single genus. As the value of the chief diagnostic features for the genera *Asterotheca* and *Scolecopteris* separately has been questioned in view of such forms as show a combination of the characters of both, it is preferable to maintain only the combined genus for the time being till its monographic revision can bring forth new basis for its subdivision.

The spores of *Asterotheca meriani* are typically monolete. In some other species the spores are described to be trilete, e.g. in *A. parallela* (Kid.) Rad. (RADFORTH, 1942) or *Scolecopteris radforthii* Andrews (ANDREWS, 1943). From the description of spores given by Radforth, it is apparent that the spores examined by him were immature. What he has interpreted as a triradiate ridge (RADFORTH, 1942, PL. 1, FIG. 6-t) could as well be the monolete slit with the median bend similar to the one so clearly established in our spores. Although Andrews (lcc. cit.) states that the spores of *S. radforthii* display a triradiate commissure, he has unfortunately not given any photograph to enable us to support his observations. Prima facie the evidence of a trilete spore occurring in *Asterotheca* is questionable. It seems that the spores studied by these authors were immature not enabling them to conclude precisely on the nature of the slit. However, if Andrews' observations are based on mature spores, it will be apparent that his species, which unquestionably refers to the diagnosis of *Scolecopteris*, differs from the species of *Asterotheca* by having trilete spores.

As far as observed by us the spores of *A. meriani* are all of one kind, i.e. monolete. Such spores which could, if cursorily examined, be held as trilete have also been shown to be monolete, the third slit having arisen secondarily as a crack arising from the median bend in the monolete slit. This observation also raises some doubt in the authenticity of records where the monolete and trilete spores are said to have been found occurring in the same sporangium. If, however, these records are proved to be true, it will be all the more interesting to know how the monolete or trilete spores of such sporangia tend to vary in their structure and organization from the spores of those plants which produce only either of the types of spores.

Among the genera of *Sporae dispersae*, the spores of *A. meriani* answer to the circumscription of *Latosporites* Pot. & Kr. (1954). Potonié (1956) surmises *Latosporites* to belong in part or full to Calamitales of Sphenopsida. Potonié's opinion is based on the figures of spores from the fructifications of Calamitales described by Reed (1938). On the scrutiny of Reed's figure (REED, 1938,

FIG. 18) it became apparent that those spores could only be referred to *Laevigatosporites* and not to *Latosporites*. Thus *Latosporites* contains spores of *Asterotheca* and maybe of some other closely allied genera as well.

Now the question arises, to what group in the plant kingdom can *Asterotheca* be referred? Kidston (1924-25) thought that *Asterotheca* in general should be regarded as a Pteridosperm. On the other hand, both Bower (1908, p. 521) and Scott (1920, pp. 253, 254) have opined that the synangial structure in *Ptychocarpus* (which has a synangium of very much the *Asterotheca* type) shows marattiaceous affinities and so also thinks Radforth (1942) that *Asterotheca* can be tentatively considered a marattiaceous fern. Hirmer (1930) has shown that *Asterotheca truncata* represents an intermediate type between other species of *Asterotheca* and *Crossotheca*. The latter genus is well known to be pteridospermous. From the general morphology of the frond studied by us there is no evidence to support one or the other view on this controversial issue. In the spores, but for the nature of the monolete slit, especially the median bend in it, nothing is relevant to this question. A slit exactly similar, i.e. with a median bend is characteristic of the spore genus *Schopfipollenites* Pot. & Kr., or the microspores of Medulloseae (RENAULT, 1896, *Dolerotheca* or *Dolerophyllum*; HALLE, 1933; FLORIN, 1937; SCHOPF, 1949 — *Whittleseya*). Thus the spores of *A. meriani* and the microspores of Medulloseae agree only in the nature of the slit but differ in size (the latter being 5-10 times bigger) and in the presence of folds and ridges in the latter. The organizational similarity in the spores of *Asterotheca* and *Whittleseya* is evidently superficial and hardly suggests that the former genus might have been pteridospermous. Further it is well known that pteridospermous leaves possess thick cuticles which are easily recoverable by maceration of their compressions whereas in *Asterotheca meriani* the leaf cuticle is not recoverable. Thin and delicate cuticle is a characteristic of fern fronds. It is apparent that *Asterotheca*, in spite of the organizational congruity of its spores to the microspores of *Whittleseya*, should preferably be regarded as marattiaceous. The similarity of the slit in *Latosporites* and *Schopfipollenites* appears to have resulted due to parallel evolution.

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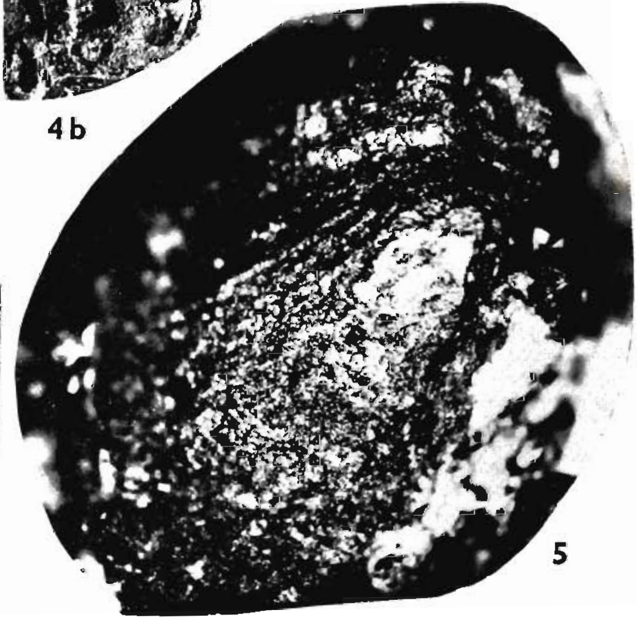

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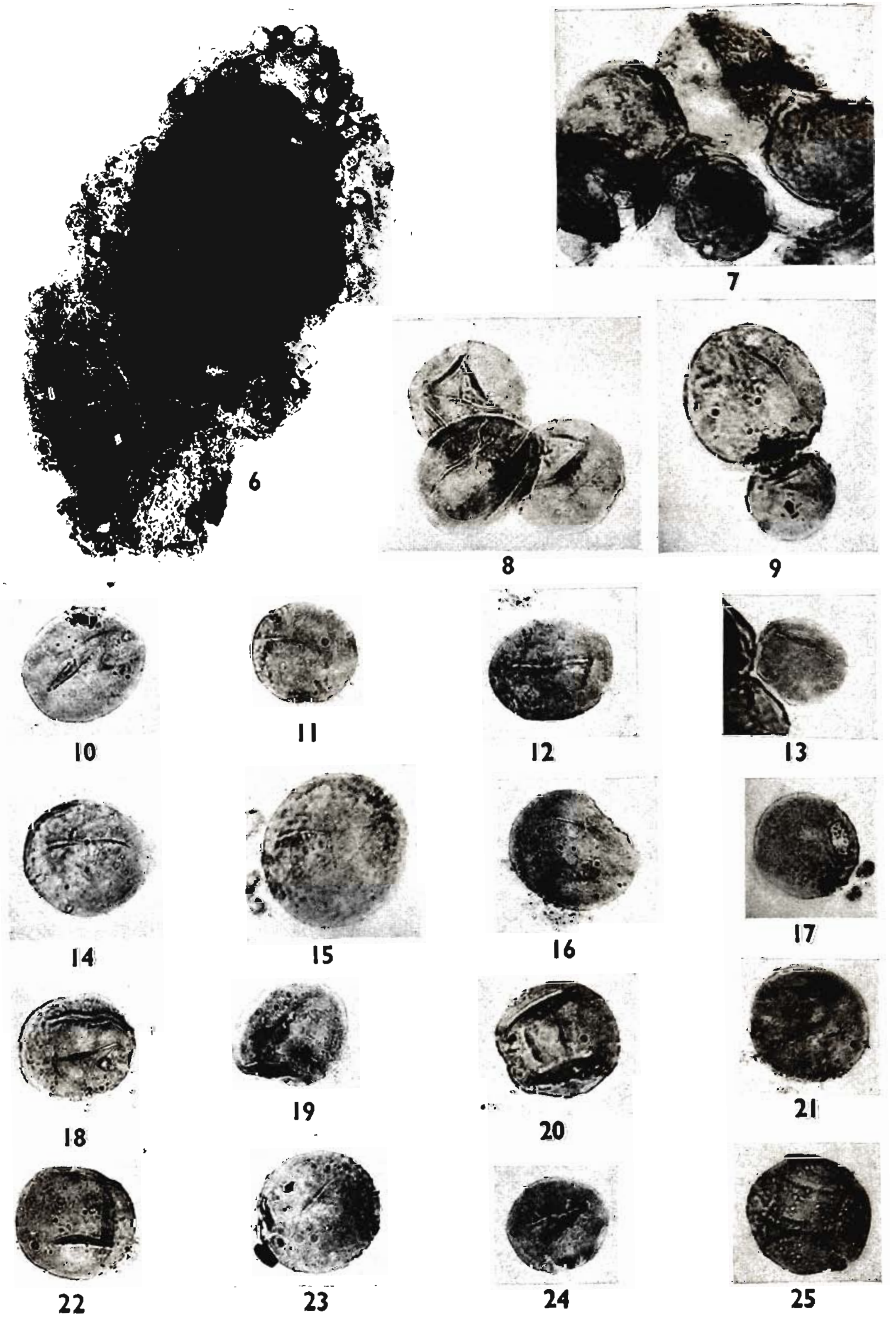
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EXPLANATION OF PLATES

Plate 1

1. Parts of pinnae showing thick midrib and the position of the pinnules. × 1.

2. A part of a pinna in Fig. 1 magnified to indicate the position of the synangia. Note the round pustular swellings or pits. × 3.

3. A portion of a pinna. Pinnules showing the *Pecopteris* type of venation. × 5.

4. a & b. Transfer preparations of the fertile pinnules showing the circular, vertically pressed and elongated, obliquely flattened synangia, respectively. × 7.

5. One synangium showing its four constituent sporangia which are slightly apart at the apical end. × 90.

Plate 2

6. A mass of immature spores from one sporangium. × 110.

7. Some spores isolated from the spore mass. × 500.

8, 11, 12, 18-20. Spores in polar view. Note the longitudinal monolete slit which is slightly bent in the middle. × 500.

9, 13-15. Spores showing a third arm originating from the median bend in the monolete slit at right angles to it. × 500.

10. Spore showing an open monolete slit. × 500.

16, 17, 21-23. Spores laterally compressed with a closed, hair thin slit. × 500.

25. A spore showing the four arcuate lines of tetragonal compression. × 500.