

Remains of Azollaceae from Late Albian of Cauvery basin and their evolutionary significance*

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The paper deals with varied remains such as megaspores, massulae with circinate, septate glochidia, massulae with barbed glochidia and microspores referable to *Azolla* and *Azollopsis* of Azollaceae from two bore wells around Kattarambakkam in South Arcot district, Tamil Nadu. A new species *Azolla pondicherriana* sp. nov. is proposed.

The palynoassemblage recovered along with the remains of Azollaceae in the maceral detritus is remarkably similar to the spore and pollen complex of the *Triporoletes reticulatus* zone of the Cauvery basin and dated as Late Albian.

The paper highlights the trends of evolution in the massulae and glochidia of Azollaceae.

Key-words : Azollaceae, Late Albian, Cauvery basin, southern India.

DURING a palynological study of the Lower Cretaceous sediments from a borewell in the Pondicherry area of the Cauvery basin in southern India, the authors have come across a good number of reproductive structures such as massulae, glochidia and megaspores referable to Azollaceae in the maceral detritus. The palynoassemblage clearly indicates a Late Albian age for these sediments. As of today, the oldest remains of Azollaceae are from the Upper Cretaceous (Campanian) of Montana, USA (Hall, 1968). The Azollaceae remains of the southern India are obviously older than the American records, and appear to be evolutionarily significant. The authors recently published an advanced note highlighting the oldest record of *Azolla* from southern India (Patil *et al.* 1995). A detailed account of these fossils of Azollaceae along with comments on their stratigraphic and evolutionary importance is presented in this contribution.

For quite a long time the water ferns *Azolla* and *Salvinia* were used to be included under a single family Salviniaceae of Salviniiales. During the recent years, however, the treatment of *Azolla* and *Salvinia* under two discrete families viz. Azollaceae and Salviniaceae is

preferred by most of the authors (Bierhost, 1971; Kubitzki, 1990)

The material consists of carbonaceous shales from a depth of 32.4 m in a borewell drilled for ground water exploration about 1.3 km west of Kattarambakkam village of Vannur Taluk (In the vicinity of Pondicherry) in South Arcot district, Tamil Nadu. The shales were subjected to customary methods of maceration for the recovery and concentration of palynofossils. Along with diverse types of spore and pollen taxa, a fairly good number of massulae and some megaspores referable to Azollaceae were also recovered.

Family-Azollaceae

Section - Filifera Hall, 1968

Genus - *Azolla* Lam.

Based upon the varied nature of the megaspore apparatus (megaspore, columella and floats) and glochidia, as of today, six discrete sections have been recognized in the genus *Azolla* viz., *Azolla*, *Rhizosperma*, *Antiqua*, *Filifera*, *Krematospora* and *Simplicispora* (Jain, 1971.) The section *Filifera*, shows massulae with hair-like glochidia broadly comparable to the perisporial hairs of

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the megaspores of *Azolla*. The glochidial tips may be inflated or circinate. Hall (1968) has mentioned only non-septate glochidia in his diagnosis of this section. As both septate and non-septate glochidia may sometimes be borne on the same massulae, the authors contend that *Filifera* should accommodate hair-like glochidia of both these categories. Megaspores referable to this section were not described by Hall (1968). However, as some information is now available in this context, the diagnosis of *Filifera* is suitably elaborated as follows:

"Megaspores spheroidal or sub-circular, highly thick-walled: wall two-layered, the outer perine light coloured, made up of thick felt of delicate hairs (tomentose); the inner darkish exine: information on floats unknown: massulae entangled in perisporial hairs as well as in dispersed condition bearing robust filamentous, septate or non-septate glochidia with tips circinate, blunt or inflated".

Azolla pondicherriana sp. nov.

Pl.1, Figs 1-6

Diagnosis: Megaspores spheroidal to sub-circular, 376-500 μm in diam., extremely thick-walled: wall two-layered, an outer well developed perine (upto 115 μm) and an inner exine; perine made up of two zones, an outer zone of thick felt of delicate, light coloured, straight or tortuous hairs (Tomentose) and an inner one of darkish densely packed hairs; exine 15-25 μm thick, in the form of dark homogeneous band; data on floats unknown; massulae entangled in perisporial hairs and also in dispersed condition, rounded to oval or irregular, 85-214 μm in long axis, 54-125 μm in short axis, surface alveolar and foamy bearing glochidia at margin; glochidia robust, 42-60 μm long, 7-10 μm broad, filamentous, many prominently circinate at apex, one or two gyres in each coil, generally septate, some non-septate and blunt-tipped; microspores 1-3 per massula (usually 1), rounded, 32-50 μm in diam., thick-walled, trilete, laesurae not quite reaching equator, surface psilate to locally granular; massulae without spores also seen frequently.

Holotype: Pl.1, Figs 1-4. Megaspore 476 μm in diam., exine 15 μm thick. From a borewell sample and

slide KP/1/3. The specific name is after Podicherry city, near the borewell locality.

The slide with the holotype is preserved in the Palaeontology Section, GSI, Southern Region, Hyderabad.

Remarks: *Azolla podicherriana* resembles *A. circinata* from the Maestrichtian of Montana, USA (Hall, 1968) in the possession of circinate glochidia. The glochidia in the American species, however, are much shorter (upto 15 μm long), narrower (1-2 μm broad) and non-septate. Further, there are many microspores per massula in *A. circinata*. As of today, the megaspores of *A. circinata* are unknown.

Genus-Azollopsis Hall, 1968

Azollopsis, another taxon referable to Azollaceae is distinguishable on the basis of the following diagnostic features viz., megaspore apparatus with tomentose perine and numerous floats imbedded in or attached to perisporial hairs; massulae with multi-hooked or barbed glochidia.

Azollopsis was originally recorded from the Upper Cretaceous (Campanian and Maestrichtian) of Montana, USA (Hall, 1968). Subsequently Jain and Hall (1969) documented a single specimen of massula referable to *A. tomentosa* from the Eocene of Montana. However, as these authors themselves hinted, this could possibly be a reworked Cretaceous specimen. *Azolla sagittifera* recorded from the Maestrichtian of the Pondicherry area in the Cauvery basin by Venkatachala and Sharma (1974) is referable to *Azollopsis tomentosa* (see Hall, 1969b).

Our preparations showed only dispersed massulae and there were no megaspores that could be referred to *Azollopsis*. Hence we have refrained from giving any specific name to the *Azollopsis* remains reported in this paper, although they seem to be different from the species already known.

Plate 1

Figures 1-6. *Azolla pondicherriana* sp. nov. (Figs. 1-4 Holotype):

- | | |
|--|--|
| <p>1. Megaspore with many massulae entangled in perisporial hairs x 100</p> <p>2. Perisporial hairs of megaspore x 400</p> <p>3,4. Two massulae from Fig. 1 enlarged. Note the circinate glochidia x 400</p> | <p>5. A dispersed massula with circinate glochidia and a microspore x 400</p> <p>6. Another dispersed massula showing circinate, septate glochidia x 450</p> |
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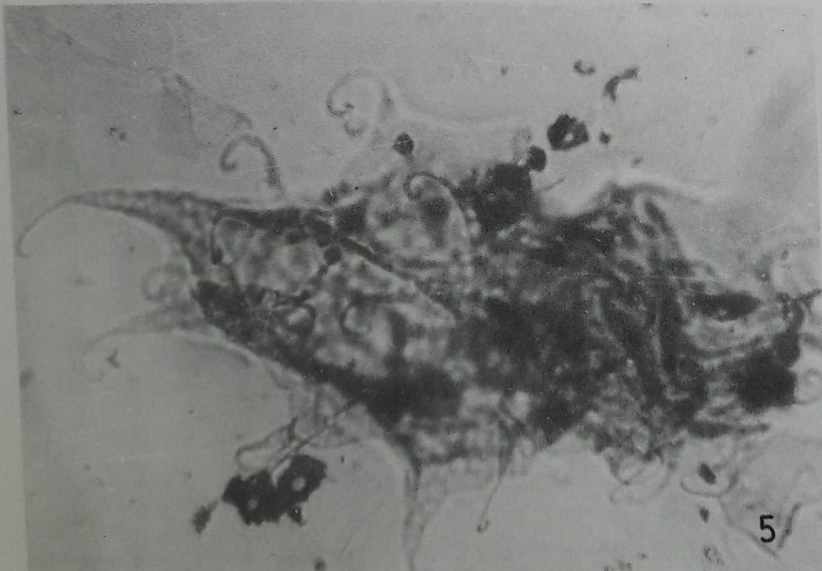
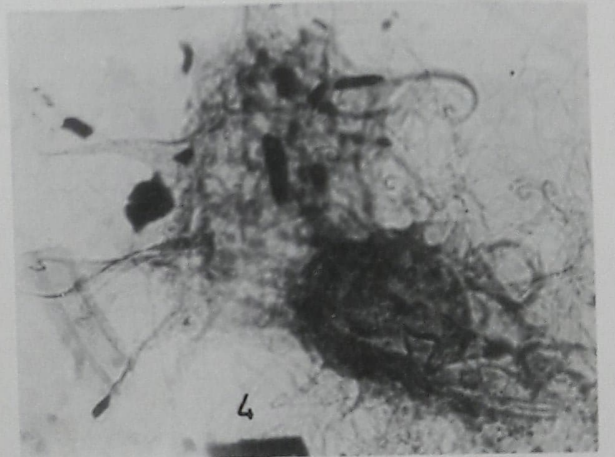
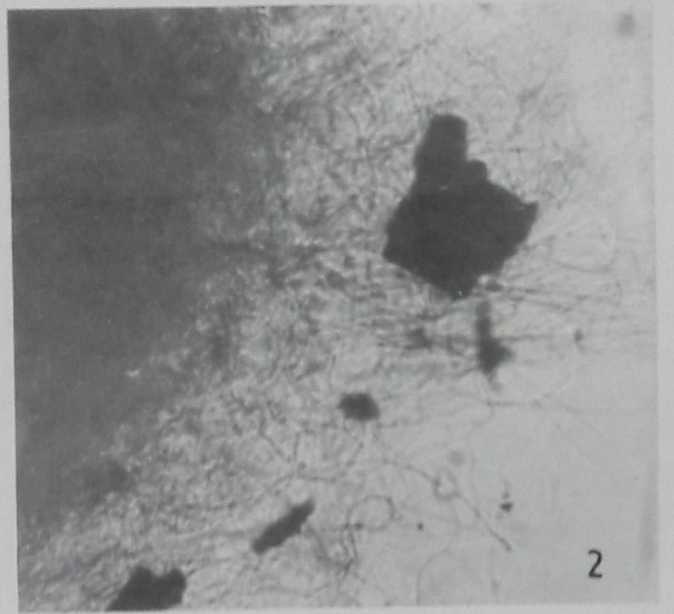
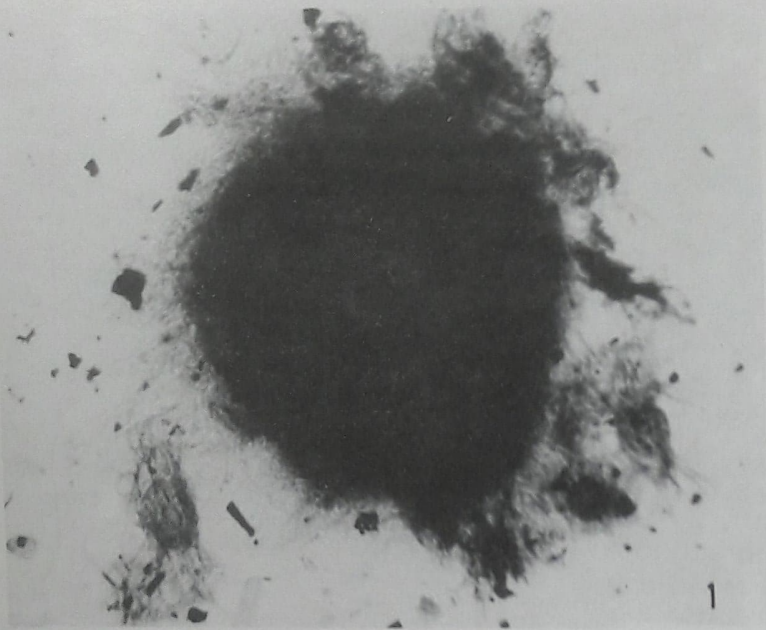


Plate 1

Azollopsis sp. Type A

Pl. 2, Figs 1-4.

Description: Massulae oval to irregular, 350-466 µm long, 175-232 µm broad, surface foamy and non-cellular, microspores 6-8 (in some upto 10) per massula, circular, 35-50 µm in diam, trilete, laesurae short; thick-walled, psilate to locally granular. Glochidia 25-40 µm long, 1.5-2.5 µm broad, bearing 4-6 retrorse pairs of barbs; barbs in two rows, non-septate, terminal barb only slightly curved.

Remarks: In the possession of higher number of spores and much smaller non-septate glochidia, the massulae of *Azollopsis* sp. Type A are easily distinguishable from those of *Azollopsis* sp. Type B.

Azollopsis sp. Type B

Pl. 2, Figs 5-8

Description: Massulae oval to often irregular, 150-250 µm long, 103-142 µm broad, surface foamy, and non-cellular, microspores 1 or 2 per massula, circular, 42-64 µm in diam., trilete, laesurae crassimarginate, not extending upto equator; thick-walled, psilate. Glochidia in limited numbers at massulae margins, 110-210 µm long (mostly 13-14 µm 10-20- µm broad (mostly 10-12), septate, prominently barbed, 6-9 pairs of barbs (flukes) in two rows, retrorse, a pair of barbs per glochidial "cell", terminal barb almost straight.

Remarks: The glochidia of *Azollopsis* sp. Type B are much larger than those of the two known species of this genus viz. *A. coccooides* and *A. tomentosa* (Hall, 1968) from the Upper Cretaceous of Montana, USA. The glochidia of *Azollopsis* sp. Type A described above are much smaller and non-septate.

DISCUSSION

The geological history of Azollaceae dates back to the Cretaceous period. The Cretaceous records of this family are referable to three genera viz. *Azolla*, *Azollopsis* and *Parazolla*. In all these taxa the megaspore apparatus is provided with floats and the massulae bear glochidia. *Azollopsis* and *Parazolla* became extinct by the end of

the Cretaceous and only *Azolla* continued in to the Tertiary and is still represented by six extant species (Kubitzki, 1990). The fossil records (Cretaceous, Tertiary and Quaternary) of Azollaceae are known from various places in N. America, Europe, Asia and Australia (Jain & Hall, 1960; Duigan & Cookson, 1959). The Cretaceous remains of this family have been documented to date only from the Upper Cretaceous deposits (Campanian to Maestrichtian) of USA, Canada and India. These include 16 species of *Azolla*, 2 of *Azollopsis* and 1 of *Parazolla* (Stanley, 1965; Hall & Swanson, 1968; Srivastava, 1968; Hall, 1969a; Snead, 1969; Jain, 1971; Venkatachala & Sharma, 1974; Baksi & Deb, 1981). The following table incorporates all the validly published taxa of Azollaceae. The list also includes the three Indian species viz., *Azolla intertrappea* (Sahni & Rao, 1943), *A. indica* (Trivedi & Verma, 1971) and *A. deccanensis* (Patil & Upadhye, 1980) recorded from the Deccan Intertrappean cherts as the Deccan traps and intertraps are now firmly dated as Late Cretaceous and not Early Tertiary ((Sahni, A. & Bajpai, 1988; Sahni, A., 1991).

Table 1. Cretaceous records of Azollaceae

Genus		Species	
I.	<i>Azolla</i>	1.	<i>Azolla intertrappea</i> Sahni & Rao, 1943
		2.	<i>A. cretacea</i> Stanley, 1965
		3.	<i>A. geneseana</i> Hills & Weiner, 1965
		4.	<i>A. montana</i> Hall & Swanson, 1968
		5.	<i>A. circinata</i> Oltz Hall in Hall, 1968
		6.	<i>A. distincta</i> Snead, 1969
		7.	<i>A. filosa</i> Snead, 1969
		8.	<i>A. bulbosa</i> Snead, 1969
		9.	<i>A. conspicua</i> Snead, 1969
		10.	<i>A. barbata</i> Snead, 1969
		11.	<i>A. lauta</i> Snead, 1969
		12.	<i>A. schopfi</i> Dijkstra, Snead, 1969
		13.	<i>A. simplex</i> Hall, 1960
		14.	<i>A. extincta</i> Jain, 1971
		15.	<i>A. indica</i> Trivedi & Verma, 1971
II.	<i>Azollopsis</i>	1.	<i>A. deccanensis</i> Patil & Upadhye, 1980
		1.	<i>Azollopsis coccooides</i> Hall, 1968
		2.	<i>A. tomentosa</i> Hall, 1968
III.	<i>Parazolla</i>	1.	<i>Parazolla heterotricha</i> Hall, 1969

Plate 2

Figures 1-4. *Azollopsis* sp. Type A

1. Massulae with barbed glochidia x 350
2. Part of massula in Fig. 1 enlarged x 800
Note the non-septate glochidia.
3. Massula with many microspores and delicate barbed glochidia x 350
4. Part of massula in Fig. 3 enlarged x 500
Figures 5-8. *Azollopsis* sp. Type B

5. Massula with robust barbed glochidia and a single microspore x 300
6. Barbed, septate glochidion of massula in Fig. 5 enlarged. Note the recurved barbs x 500
7. Another barbed septate glochidion enlarged x 500
8. Massula with a single well preserved microspore and barbed glochidion x 300

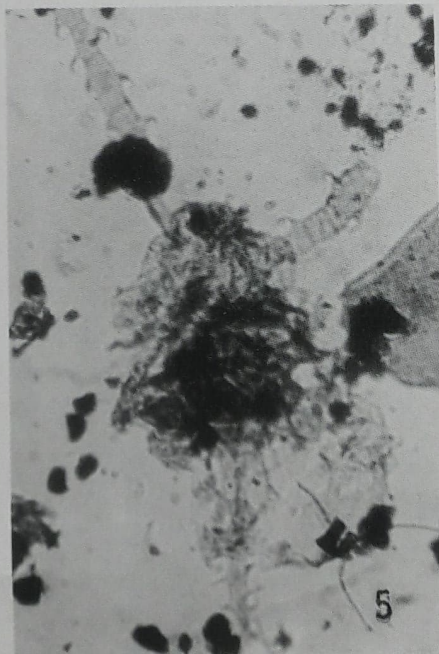
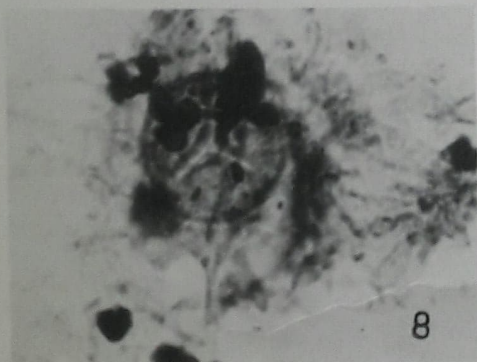
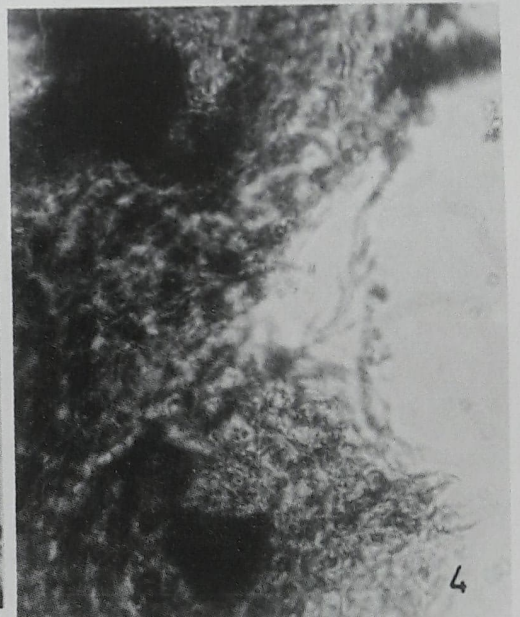
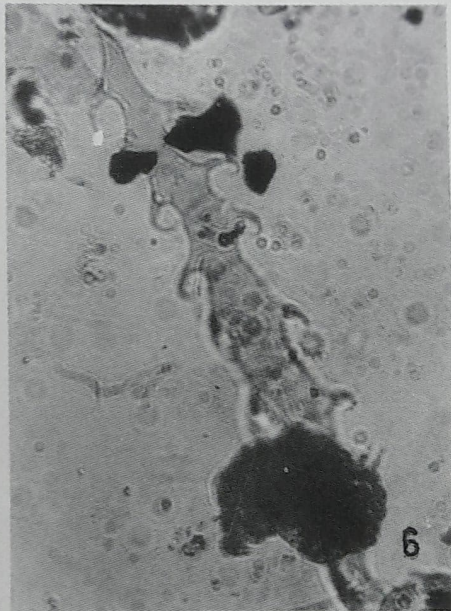
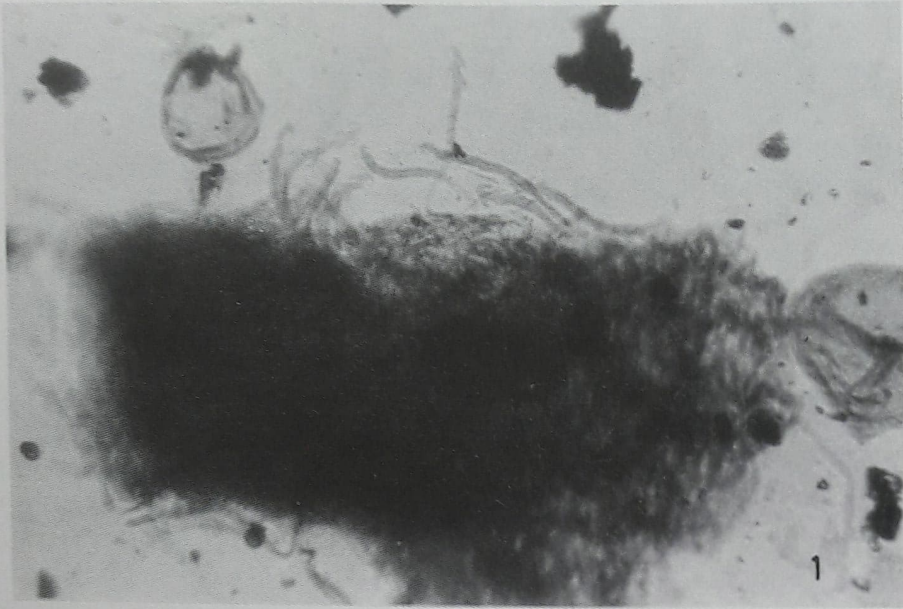


Plate 2

The carbonaceous shales which yielded *Azolla pondicherriana* and *Azollopsis* sp. Type A and Type B are dated as Late Albian on the basis of the remarkable similarity of the spore and pollen complex recovered, with the Late Albian palynoassemblages of the *Triporoletes reticulatus* Zone of the Cauvery basin in the Pondicherry area (Venkatachala & Sharma, 1974; Venkatachala *et al.* 1980). The following are the significant spore and pollen types encountered by us along with the remains of Azollaceae viz.,

Lycopodiumsporites austroclavatidites, *Biretisporites spectabilis*, *Ceratospores equalis*, *Dictyosporites speciosus*, *Crybelosporites stylosus*, *Cicatricosisporites australiensis*, *C.hallei*, *Plicifera* sp., *Coronatispora perforata*, *Contignisporites glebulentus*, *Microfoveolatisporis albertonensis*, *Foraminisporis asymmetricus*, *Schizosporis reticulatus*, *Gleicheniidites circinidites*, *Ornamentifera granulosa*, *Sestrosporites pseudoalveolatus*, *Appendicisporites tricorinitatus*, *A. distocarinitatus*, *Kraeuselisporites majus*, *Microcachryidites antarcticus*, *Triporoletes reticulatus*, *T. muricatus*, *T. radiatus*, *T. simplex*, *Tricolpites reticulatus*, *T. pannosus*, *T. crassimarginatus* and *Gothanipollis descretus*.

As the hitherto records of the earliest occurrence of Azollaceae are from the Campanian deposits of the Upper Cretaceous of North America (Hall, 1958; Jain, 1969), the Late Albian *Azolla* and *Azollopsis* from southern India constitute the oldest fossils of this family.

The massulae of the Lower Cretaceous *Azolla pondicherriana* bore filiform, circinate and essentially septate glochidia.

The massulae of the Upper Cretaceous species of *Azolla* showed various types of glochidia viz., filiform, circinate, and septate and non-septate, anchor-tipped. If the massulae of the other two Upper Cretaceous genera of Azollaceae viz., *Parazolla* and *Azollopsis* are considered, the glochidia exhibit further diversity. Thus in *Parazolla heterotricha* (Hall, 1969a) the glochidia are simple hair-like, some of them terminating in a spherical knob and in *Azollopsis coccooides* and *A. tomentosa* the glochidia are multi-hooked or barbed.

Mahabale (1963, 1974) earlier had provided an evolutionary scheme for glochidia of the extant *Azolla* on the basis of their varied morphology and structure. According to him, anchor-tipped septate glochidia are primitive and progressive reduction in the nature of glochidia resulted in the gradual disappearance of septa and hooks leading to non-septate hair-like forms as seen in the massulae of *Azolla pinnata*. The last trend in this reductional series is the total loss of glochidia them-

selves as exemplified by the aglochidial massulae of *Azolla nilotica*.

It is pertinent to note that all forms of glochidia encountered in the extant Azollaceae were already found in the Cretaceous members of this family. In addition to these, the Cretaceous taxa also showed altogether different forms of glochidia such as circinate and barbed forms which are unknown in the modern Azollaceae. Further, even the absence of glochidia was noted in the Cretaceous taxa as exemplified by *Azolla exotica* (Jain, 1971). We are of the opinion that it was during the Cretaceous period, the glochidial structures attained their maximum morphographic diversity. The evidence provided by the varied glochidia of the Cretaceous Azollaceae (*Azolla*, *Azollopsis* and *Parazolla*) clearly points towards their rapid and apparently multipronged evolution which seems to have been completed by the end of the Cretaceous.

The primary function of glochidia is to facilitate anchoring of massulae carrying microspores with the megaspore apparatus. This is done by the entanglement of glochidia with the perisporial hairs of the megaspore. Simple hair-like, or filiform circinate glochidia which are least efficient in the execution of this function should represent primitive condition and glochidia bearing hooks (anchor-tipped or barbed), constitute evolutionarily advanced types. Further, if the glochidia are homologous with the perisporial hairs of the megaspore as assumed by some workers (Eames, 1936), the most primitive glochidia would then again be represented by simple hairs similar to those of the perisporium. Such a situation is encountered in *Parazolla heterotricha* (Hall, 1969). The data now available, therefore, indicate that the anchor-tipped glochidia no more represent the primaevial condition and the evolutionary trend visualized by Mahabale (1963) becomes untenable.

The filiform, circinate and barbed glochidia have disappeared by the end of the Cretaceous. The remaining forms of glochidia, however, continued through the Tertiary and are still encountered in various species of *Azolla*. Of these, the anchor-tipped glochidia are the most commonly encountered forms both in the Tertiary and extant taxa of *Azolla*.

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