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WHEN Sir William Dawson described the fossil flora of southern British Columbia in 1890 (4), the name *Azollophyllum primaevum* was given to a small plant resembling the Recent water fern *Azolla*. Although Dawson was the sole author of the account in which the name was proposed, he credited it to Penhallow, who apparently had suggested it and who was responsible for the brief description. The material to which the name was applied was poorly preserved and the one figure that embellishes the description is nothing more than a crude impressionistic sketch. The figure, however, is sufficient to establish the identity of the recently discovered and herein described material from the same region.

The new material contains reproductive structures that closely resemble those of the Recent widely distributed species *Azolla filiculoides*. Although it thus turns out that *Azollophyllum primaevum* was the first fossil azolla ever described, because of the unsatisfactory description and figure, it has been ignored by most subsequent authors. The recent discovery shows that the provisional name *Azollophyllum* can be set aside and the plant designated as *Azolla primaeva* (Penhallow), comb. nov.

The source of the new material was the Allenby formation of the Princeton coal field of southern British Columbia. The azolla occurs at several places but is best preserved and most abundant in outcrops along the west side of the Smilkameen River at a place called Ashnola about 8 miles south of Princeton. The variously colored shales at this place are the products of weathered volcanic ash and contain remains of *Ginkgo,* conifers, dicotyledons, insects, and fish. The Allenby formation is tentatively regarded by Shaw (14) to be of Oligocene age.

The vegetative parts of the *Azolla primaeva* were not well preserved. They consist of fragments of leafy stems seldom exceeding 1 cm. in length, and numerous, straight, unbranched, filiform roots (Pl. I, Figs. 1–2). At places the stem and root fragments form thin mats of vegetation on the shale surfaces. The small two-lobed leaves are retained only as thin incomplete carbonaceous films, and the mode of branching is nowhere well revealed. Bodies that may be remains of sporocarps are visible here and there among the disorganized stem parts. Examination of the compressions with a lens or binocular microscope has the effect of emphasizing the poor preservation rather than bringing out morphologic features.

The best-preserved parts are the microspore massulae and the contents of megasporangia that have escaped from their respective places of origin and lie free in the matrix. Large numbers of these bodies can be recovered from the shale by treatment with hydrofluoric acid. They can then be prepared for microscopic examination by using a technique suitable for spores and other microfossils in macerated coal and shale.

The genus *Azolla* belongs to the Salviniaceae, one of two families of living ferns composing the Hydropterideae that have reverted to the water habitat. The species of *Azolla* are floating forms that under favorable conditions may completely cover the surface of the pond in which they grow. The widespread occurrence of the genus in the fossil condition, therefore, is indicative of the former presence of extensive bodies of quiet water.

A unique feature of the modern water ferns is heterospory, the production of male and female spores in separate sporangia. The only other known instances of heterospory in the fern taxon are in a few Paleozoic forms. No Mesozoic heterosporous ferns have been discovered and among the known Tertiary ferns the phenomenon is restricted to fossil members of the Salviniaceae.

In *Azolla* and the other modern aquatic ferns the mature spores are not freed completely upon maturity. The microspores of *Azolla* escape in aggregates called massulae, several of which form within a microsporangium. A massula consists of a foamy matrix that holds the microspores together and extending from the surface are tentacle-like outgrowths with anchor-shaped tips, the glochidia. The glochidia serve to attach the massulae to the released megaspore apparatuses and thus facilitate the fertilization process.

The solitary megaspore escapes from its megasporangium bearing a "swimming apparatus" which is nearly as large as the spore itself. "Swimming apparatus" is a misnomer, because Campbell (3) found that the released apparatuses do not float, but sink, at maturity. In addition to being supplied with this misnamed "swimming apparatus" the mature megaspore is surrounded by a thick perisporic layer, which is ornamented with papillate protuberances (Pl. II, Fig. 2). The papillae bear long hairlike outgrowths which entangle with the glochidia of the massulae, but in fossils these usually have been lost.

On the shale slabs bearing the *Azolla* remains the detached massulae (Pl. I, Fig. 4) and megaspore apparatuses (Pl. II, Figs. 1–2) appear as minute black dots among the stem fragments. They occur singly and in clusters of two to six or more (Pl. II, Fig. 3). The clusters consist of both types of bodies, which had come together after escape from their respective sporangia but before fossilization. The character of the clusters is clearly visible after brief treatment with Schulze's reagent.

The massulae are round, oval, or egg-shaped, amber-colored bodies which contain the microspores (Pl. I, Fig. 4). They range from 260 to 330 microns in width and 360 to 480 microns in length. Occasionally groups of freed microspores can be observed (Pl. I, Fig. 6). Some of the massulae contain what seem to be male gametophytes (Pl. I, Fig. 5). The transparent glochidia are at least 40 microns long, although the exact length cannot be determined because of the crumpled condition of the stalks. The stalks appear to be nonseptate and of nearly uniform diameter throughout their length. The rounded anchor-shaped tips are about 7 microns from one recurved tip to the other (Pl. I, Fig. 3). Individual microspores are about 20 microns in diameter. They are spherical, with smooth thin translucent walls and triradiate clefts about 4.75 microns long.

The massulae and megaspore apparatuses are about the same size. The part below the "swimming apparatus," which consists of the megaspore covered by the perisporic layer, is from 250 to 320 microns in diameter. The wall portion is about 12 microns thick. No structure was observed in the "swimming apparatus," which fits like a thimble-shaped cap over the apex of the megaspore. "Floats," of which the "swimming apparatus" of most species contains three, are not visible. This is unfortunate because the number would be useful in determining the relationship to other species of *Azolla*. Coarse papillae are present on the surface of some of the specimens (Pl. II, Fig. 2) but not on others (Pl. II, Fig. 1).

A few bodies that are obviously free megaspores of some plant are present in certain of the mounts (Pl. II, Figs. 4–5). They are nearly round and range from 160 to 184 microns in diameter. Their walls are thin and finely roughened and the slitlike rays of the inconspicuous tetrad scar are 25 to 28 microns long. These isolated spores are considerably smaller than the megaspore contained within the megaspore apparatus, even after allowance is made for the thickness of the perisporic layer. It is believed, however, that they do belong to *Azolla primaeva* and that their small size is due to their failure to germinate and to develop internal gametophytes as those that remained within the perisporic layers might have done. The possibility that some of the megaspores had undergone further development before they were fossilized is supported by the fact that some of the massulae appear to contain male gametophytes.

Paleobotanical literature contains relatively few references to fossil azollas. *Salvinia* has been mentioned more frequently. *Azolla* is sometimes referred to in connection with certain enigmatic organisms like *Sporocarpon* and *Traquaria* (Solms-Laubach, 15), but there is no evidence of any relation between them. In 1900 Zeiller (16) mentioned *Azollophyllum,* but practically all later authors have ignored it and have treated *Azolla* as unrepresented in the fossil record (Solms-Laubach, 15; Seward, 13; Hirmer, 6; Emberger, 5). Although little information was available to the earlier writers, four fossil species of *Azolla* were known by 1934. The first, *Azolla prisca,* was described by Reid and Chandler (9) in 1926 from the Oligocene of the Isle of Wight. They figured and described vegetative material, massulae, and the megaspore apparatuses. In 1927 Berry (1) named *A. tertiaria* from the Esmeralda formation of the Pliocene of Nevada, but only vegetative material was obtained. Brown (2) described a third species as *A. berry* from the Eocene Green River formation in Colorado in 1934 and in the same year Sahni and Rao (11) published their preliminary account of *A. intertrappea* from beds now regarded as of Eocene age in India. This last species has subsequently been discussed at some length (Sahni, 10; Sahni and Rao, 12). Because we can now demonstrate that *Azollophyllum primaevum* belongs in *Azolla,* Penhallow's species becomes the first fossil species to have been named.

Although the rather meager fossil record of *Azolla* goes back at least to the Eocene, it is quite likely that the genus was in existence during the late Mesozoic. All known Tertiary species show affinity with the section *Euazolla,* which is characterized by glochidia with anchor-shaped tips attached all around the massulae. All living species of this section have three floats. The Oligocene *A. prisca* has nine floats and agrees in this respect with the section *Rhizosperma,* but its glochidia are of the *Euazolla* type. The place of *A. primaeva* in the scheme cannot be determined because of the invisibility of the floats. Sahni (10) claims that *A. prisca* is transitional and a sharp distinction between the sections cannot be made. No fossil members definitely referable to *Rhizosperma* have yet been found in deposits older than the Pleistocene. On the basis of the fossil record, therefore, *Euazolla* must be regarded as the older of the two groups and *Rhizosperma* the derived one.

When *Azolla primaeva* is compared with other species, living as well as fossil, a close resemblance to *A. filiculoides* is evident. Only a partial comparison with *A. prisca* or *A. intertrappea* is feasible, because the published descriptions lack some details. For *A. prisca,* only a few measurements of reproductive structures are given and the illustrations are too small to show details satisfactorily. *A. intertrappea,* though the best preserved and most thoroughly described of any of the fossil forms, is silicified and could be studied only from thin sections. Consequently, many features such as size of the massulae and megaspore apparatuses were determined only from what could be seen in the sections. *A. berry* and *A. tertiaria* cannot be compared because of incomplete descriptions.

Present information indicates that *Azolla primaeva* is closer to *A. intertrappea,* the Indian species, than to *A. prisca,* although if the number of floats were known in *A. primaeva* the situation might be otherwise. Reid and Chandler's figures of the massulae of *A. prisca* show glochidia stalks that are rather broad, basally and throughout most of their length, but narrow rather abruptly just below the anchor-shaped tips. So constructed, the glochidia stand out like stiff bristles from the massula surface. In *A. primaeva* and *A. intertrappea* the stalks are more slender and apparently of nearly uniform diameter throughout their length. As stated, it is impossible to observe the complete stalks in our species. The megaspore apparatuses are similar in both. The two are certainly close and if more facts were known it might be impossible to maintain a satisfactory separation.

Family Salviniaceae
Genus *Azolla* Lamarck

Azolla primaeva (Penhallow), comb. nov.
(Pls. I–II)

Azollophyllum primaevum Penhallow (in Dawson) 1890, p. 77, Fig. 2; Penhallow, 1908 (8), p. 39; LaMotte, 1952 (7), p. 80 (citation only).

Age—Oligocene.

Horizon—Allenby formation.

Locality—Stump Lake (Dawson, 4; Penhallow, 8) and the Princeton coal field, British Columbia.

SUMMARY

Material recently discovered in the Princeton coal field of British Columbia shows that the plant described by Dawson in 1890 as *Azollophyllum primaevum* is a true species of *Azolla* and similar to the living water fern *A. filiculoides* and to the fossil form *A. intertrappea* of the Deccan Intertrappean Series of India. The vegetative parts are poorly preserved but detached massulae and megaspore apparatuses are abundant and readily identifiable.

The material came from the Allenby formation which is regarded as of Oligocene age.

LITERATURE CITED

1. BERRY, E. W. 1927. Flora of the Esmeralda Formation in Western Nevada. Proc. U. S. Nat. Mus., Vol. 72, Art. 23.
2. BROWN, R. W. 1934. Recognizable Species of the Green River Flora. U. S. Geol. Surv., Prof. Paper 185-C.
3. CAMPBELL, D. H. 1893. On the Development of *Azolla filiculoides*. Ann. Bot., Vol. 7, pp. 155–87.
4. DAWSON, J. W. 1890. On Fossil Plants from the Smilkameen Valley and Other Places in the Southern Interior of British Columbia. Roy. Soc. Canada Trans., Vol. 8, No. 4, pp. 75–91.
5. EMBERGER, L. 1944. Les plantes fossiles dans leurs rapportes avec les végétaux vivantes. Paris.
6. HIRMER, M. 1927. Handbuch der Paläobotanik. München und Berlin.
7. LAMOTTE, R. S. 1952. Catalogue of the Cenozoic Plants of North America through 1950. Geol. Soc. Amer. Mem., No. 51.
8. PENHALLOW, D. P. 1908. Report on Tertiary Plants of British Columbia collected by Lawrence M. Lambe in 1906 together with a Discussion of Previously Recorded Tertiary Floras. Canada Dept. Mines, Geol. Surv. Br., No. 1013. Ottawa.
9. REID, E. M., and M. E. J. CHANDLER. 1926. The Bembridge Flora. *In*: Cat. Cainozoic Plants in the Dept. of Geol. Vol. I. London: Brit. Mus. Nat. Hist.
10. SAHNI, B. 1941. Indian Silicified Plants. I. *Azolla intertrappea* Sah. & H. S. Rao. Proc. Indian Acad. Sci., Vol. 14 (6): 489–501.
11. SAHNI, B., and H. S. RAO. 1934. The Silicified Flora of the Deccan Intertrappean Series. Pt. V. *Azolla intertrappea,* sp. nov. Proc. 21st Indian Sci. Cong., 1934, pp. 26–27.
12. SAHNI, B., and H. S. RAO. 1943. A Silicified Flora from the Intertrappean Cherts round Sausar in the Deccan. Proc. Nat. Acad. Sci. India, Vol. 13, No. 1, pp. 36–75.
13. SEWARD, A. C. 1910. Fossil Plants. Vol. 2. Cambridge.
14. SHAW, W. G. The Princeton Coalfield, British Columbia. Geol. Surv. Canada, Paper No. 52–12. Ottawa.
15. SOLMS-LAUBACH, H. 1891. Fossil Botany. Authorized Eng. trans. by E. T. Henry Garnsey. Oxford.
16. ZEILLER, R. 1900. Elements de paleobotanique. Paris.

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PLATES

EXPLANATION OF PLATE I

Azolla primaeva (Penhallow) Arnold, comb. nov.

FIGS. 1–2. Vegetative fragments strewn over surface of shale slabs. Natural size.
FIG. 3. Apices of two anchor-shaped glochidia. × 750.
FIG. 4. Free massula. × 130.
FIG. 5. Small massula containing bodies resembling male gametophytes. × 185.
FIG. 6. Mass of free microspores. × 380.

PLATE I

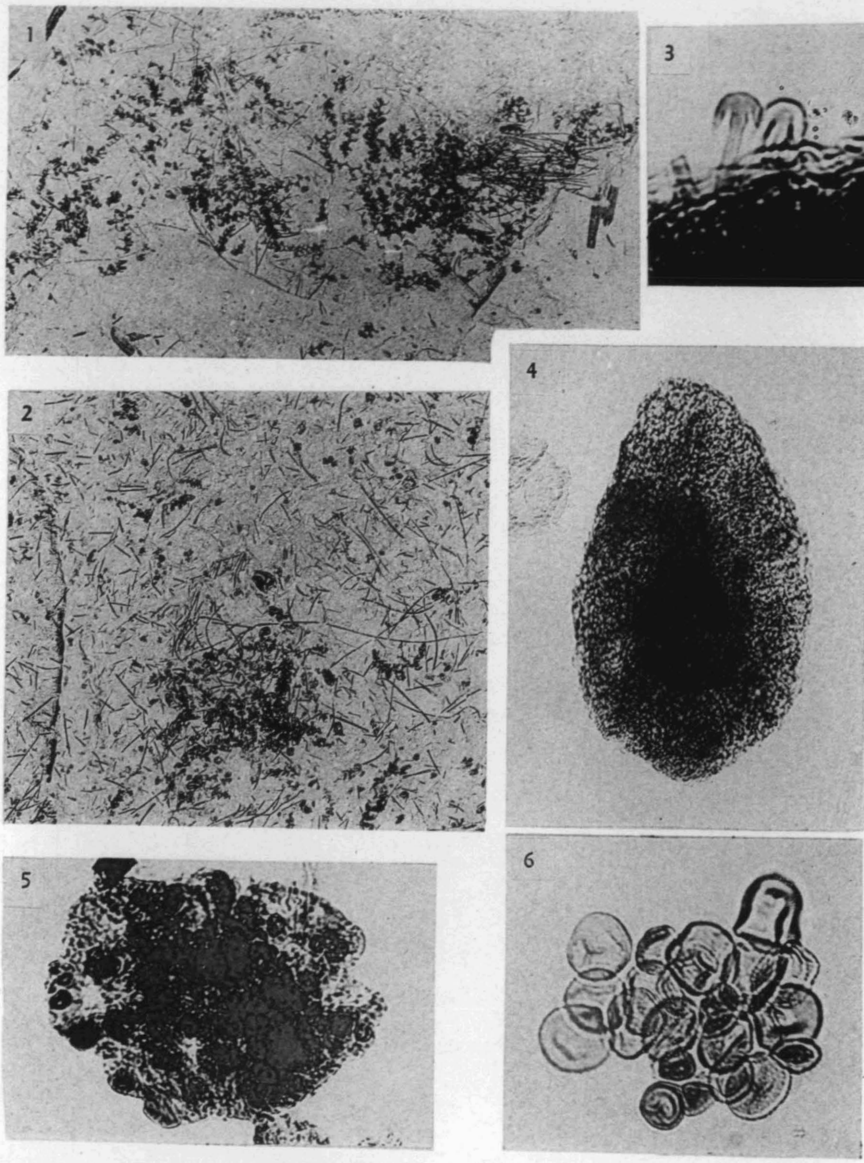
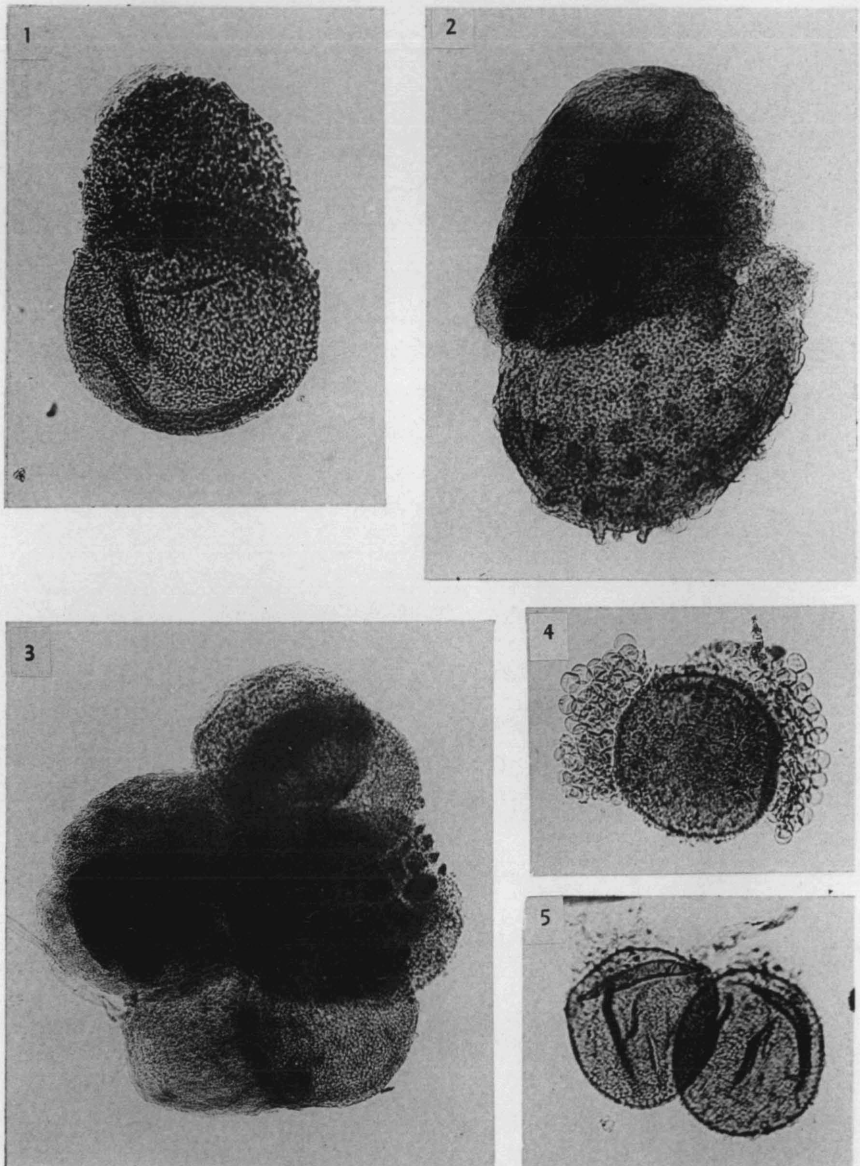


PLATE II



EXPLANATION OF PLATE II

Azolla primaeva (Penhallow) Arnold, comb. nov.

FIG. 1. Megaspore apparatus with unornamented perispore. × 130.

FIG. 2. Megaspore apparatus with papillate perisporic layer. × 130.

FIG. 3. Cluster of massulae and megaspore apparatuses. × 75.

FIG. 4. Isolated megaspore free of its perisporic layer and surrounded by microspores. × 130.

FIG. 5. Two free megaspores. × 130.