Sequoia Couttsiae, Heer, at Hordle, Hants: A Study of the Characters which serve to distinguish Sequoia from Athrotaxis.

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With five Figures in the Text.

IN a note published recently¹ I drew attention to the fact that the Conifer remains of the Lower Headon Beds of Hordle (Hordwell), Hants, which Mr. Starkie Gardner had referred to *Athrotaxis*,² must now be placed in the genus *Sequoia*.

This conclusion was based on the study of leaves, cones, and seeds, the relationship of these organs being proved by the discovery of one cone attached to its twig, and of another still bearing seeds. The material examined was collected from the Hordle 'Leaf-Bed',³ where it is very abundant.

A comparison of the Hordle and Bovey Tracey specimens has shown that, though in error as to the generic name, Mr. Starkie Gardner was right in classing the Bovey and Hordle fossils as the same species, for the two plants are identical in character. Hence the excellent specific description of Heer⁴ renders superfluous further reference to the macroscopic characters, except in regard to certain points not mentioned by him. These will be dealt with as occasion requires in treating of the different plant organs.

To the earlier descriptions of the twigs there is nothing new to add, their condition being such as to render section-cutting unprofitable labour.

Microscopic study of the leaves shows that stomata occur on both

¹ Ann. Bot., vol. xxxv, No. cxxxix, July 1921.

² Starkie Gardner: Monograph of Palaeontographical Soc. The Eocene Flora, vol. ii, 1883-6, p. 90, Pl. X, Figs. 6-9.

³ Bed 10 of Tawney and Keeping: Quart. Journ. Geol. Soc., vol. xxxiv (1883), p. 566. On the Section at Hordwell Cliffs.

⁴ Heer: Phil. Trans. Roy. Soc., Part III, 1862. On the Lignite Formation of Bovey Tracey, Devonshire, p. 33, Plates VIII, IX, X.

surfaces; on the lower they are irregularly scattered from apex to base, but are few in number, or absent, around the margin and along the median dorsal angle. On the upper they are very abundant, occurring more or less unevenly on either side of the median line, both on the decurrent and falcate parts of the leaf, but they are absent from the median line itself and from the thick margin (Fig. 1, *b*). Nevertheless, despite the general differentiation into stomata-bearing and non-stomata-bearing regions, the limiting line between the two is ill-defined and sinuous. Though the general distribution of the stomata can readily be seen, the actual details of cell structure can only be distinguished occasionally. Each stoma is ringed by about four narrow, parallel-sided cells (Fig. 2, *b*), and usually three or more stomata occur in a row placed end to end, while the

FIG. 1. Distribution of stomata on the upper surface of leaves. (a), *Sequoia gigantea*; (b), *S. Coultisiae*; (c), *Athrotaxis laxifolia*; s = stomata. Above dotted line = falcate part of leaf. Below dotted line = decurrent part of leaf. a = attached area.

FIG. 2. Detail of stomata and non-stomata-bearing cuticle. (a), *S. gigantea*; (b), *S. Coultisiae*; (c), *A. laxifolia*; s = stomata.

cells of the interspaces have curved outlines. In areas where stomata are absent the cuticle cells are elongate parallel to the length of the leaf.

A comparison of the fossil with recent *Sequoia* and *Athrotaxis* shows that it is related to the former (compare Fig. 1, *a*, *b*, *c*, and Fig. 2, *a*, *b*, *c*), for in *Athrotaxis* the stomata on the lower surface of the leaf occur only where the decurrent base merges into the falcate portion (compare description of *Sequoia* above), while on the upper surface they are confined to the falcate region, where they occupy a clear-cut, inverted-V-shaped tract shown in Fig. 1, *c*. There is no aligned arrangement; instead, stomata are evenly and thickly scattered over the whole V-shaped area; the cells between them are triangular and are radially arranged (Fig. 2, *c*). The evidence from the leaves is, then, fairly conclusive that the fossil belongs not to *Athrotaxis* but to *Sequoia*.

In Heer's account of the cones of *S. Couttsiae*¹ the following features, which have a generic significance, have been overlooked. The seminiferous scale and bract are almost completely fused to form a single structure—the cone-scale. In each cone-scale there are two regions, the stalk and the escutcheon; in the latter only do traces of the original double structure of the scale remain, but there a small mucro and associated transverse ridge seem to represent the apex of the bract and the line of fusion respectively. This is a character of recent *Sequoias*, though in these the complete ridge is only seen in the basal scales of *S. sempervirens*; in all other scales of both species the mucro is sunk in a groove and the ridge is apparent only at the edge.

The surface of the escutcheon is always ornamented with radial wrinkles. Its form may be quadrilateral, pentagonal, hexagonal, or irregular, and its margin is always clearly defined (Figs. 3, *a, b*, and 4, *a, c*); it is set at a marked angle to the stalk, there is never a gradual passage from one to the other. The stalk occasionally meets the escutcheon symmetrically at its centre and at a right angle; more frequently, it meets it asymmetrically, towards its lower margin and at an obtuse angle; this angle is greatest in the lowest scales, where it may be about 150°. Thus there are two extreme forms of scale—peltate and imbricate—with a variety of intermediate forms.

In the recent *S. sempervirens* both these types are present; the imbricate character is, however, confined to a few basal scales (Fig. 3, *c*). In *S. gigantea* it is completely lost, and only peltate scales remain. Apparently it was the presence in the fossil of imbricate scales which led Mr. S. Gardner to identify it as *Athrotaxis*, for he wrote that an uncrushed specimen 'revealed the fact that the scales of the cone are overlapping or imbricate as in *Athrotaxis*, and not at right angles to the axis as in *Sequoia*'.² As the new evidence from *S. sempervirens* shows that imbricate scales can occur, their presence in the fossil is not sufficient cause for placing it in *Athrotaxis* rather than in *Sequoia* when all other evidence points to the latter genus, as will be shown.

The cone-scales of *Athrotaxis* differ radically from those of the fossils and of the recent *Sequoia*. In *Athrotaxis* bract and seminiferous scale retain their identity to a marked degree. The thin, horny bract projects as a pointed tongue beyond the woody, seminiferous scale; hence the lower side of the cone-scale shows a continuous surface of bract from attachment to apex. There is no differentiation into stalk and escutcheon, and no ornamentation of the exposed surface. The seminiferous scale has a thickened, involute margin (Figs. 3, *d*, and 4, *b, d*).

Further, while *Sequoia* and the fossil agree, *Sequoia* and *Athrotaxis* differ widely in respect of the number and mode of attachment of the seeds

¹ Loc. cit.

² Loc. cit.

on each scale. In the fossil and in *Sequoia* the attachment is at a third of the length of the scale from its distal margin, in *Athrotaxis* the attachment scars are found immediately adjacent to the involute margin (Fig. 4, *b*); and again, in the fossil five and six seeds have been counted on a scale, while recent *Sequoia* scales each bear from five to nine; but in *Athrotaxis* the maximum is five, and the limits of variation are from three to five.

FIG. 3. Cones. (a) and (b), two aspects of a cone of *S. Couttsiae*; (c), *S. sempervirens*; (d), *Athrotaxis laxifolia*. *s*, seeds; *i*, imbricate scales; *o*, seminiferous scale; *b*, bract; *e*, escutcheon; *x*, stalk. All magnified.

Once again, therefore, there is adequate reason for referring the fossil to *Sequoia*.

To the previous descriptions of the seeds of *S. Couttsiae* I would add that considerable variations of size and shape occur; the smallest specimens measured were 2.5 mm. long and 2 mm. broad, the largest 5 mm. long and 2.5 mm. broad. The shape varies from a broad oval to a very narrow one; sometimes the apex is provided with a mucro, and though a curved embryo

is common, straight ones are found too, both in the Bovey and in the Hordle material. The embryo in the fossil is long and narrow, and the wing is thick and horny in texture. The testa is covered with close longitudinal striae whose direction of curvature conforms over the embryo

FIG. 4. Cone-scales. (a), *S. Coulttsiae*, upper surface. (c), Do., lower surface. (b), *Athrotaxis laxifolia*, upper surface. (d), Do., lower surface. *e*, escutcheon; *x*, stalk; *b*, bract; *o*, seminitiferous scale; *h*, attachment of seed. All magnified.

FIG. 5. Seeds. (a), *S. Coulttsiae*; (b), *Athrotaxis selaginoides*. *e*, embryo; *w*, wing.

to the curvature of the embryo, over the wing to the curvature of the wing (Fig. 5, a). In the hollows between the striae pits occur in longitudinal rows; they are most conspicuous in worn specimens. The likeness which the fossils bear to recent *Sequoia* seeds, more especially to *S. sempervirens*, is very striking.

In *Athrotaxis* the seeds, instead of being horny and tough all over

have a membranous, puckered wing, whose surface is formed of large, inflated, oblong or polygonal cells. Only near the margin are their longer axes parallel to the lateral edge of the wing, elsewhere they are inclined obliquely to it; thus they are arranged in lines which sweep transversely across the wing, meeting the edge of the embryo at an angle of about 50° (Fig. 5, *b*).

The work of Mr. and Mrs. Clement Reid has shown that seed character is an admirable generic guide, and in the present instance the seed characters are so distinctive that, had seeds alone been available for study, I should unhesitatingly have assigned the fossil to *Sequoia*; but when, as in this case, evidence from other organs all points in one direction, the case for *Sequoia* appears to be indisputable.

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Chandler, Marjorie Elizabeth Jane. 1922. "Sequoia couttsiae, Heer, at Hordle, Hants: a study of the characters which serve to distinguish Sequoia from Athrotaxis." *Annals of botany* 36, 385–390.

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