Acta Palaeontologica Polonica
Vol. 28, No. 1—2 pp. 265—269; pls. 13—14 Warszawa, 1983
Second Symposium on Mesozoic Terrestial Ecosystems, Jadwisin 1981

JOAN WATSON

TWO WEALDEN SPECIES OF *EQUISETUM* FOUND *IN SITU*

WATSON, J.: Two Wealden species of *Equisetum* found *in situ*. Acta Palaeont. Polonica, 28, 1—2, 265—269, 1983.

Equisetum lyellii Mantell is known from *in situ* rhizomes and underground portions of aerial shoots in the Wealden 'soil beds' of Sussex. Aerial parts including probable sporangiophores and dispersed spores are known from fragment partings above the so called 'soil beds' which probably represent an aquatic environment. *E. lyellii* lacks tubers and was probably wintergreen.
Equisetum burchardtii Dunker is known from *in situ* rhizomes and tubers from the Wealden of England and also underground parts of aerial shoots from the German Wealden. It closely resembles living members of the subgenus *Equisetum* and probably died down in autumn.

Key words: *Equisetum*, taxonomy, ecology, Wealden, England.

Joan Watson, Departments of Botany and Geology, University of Manchester, England. *Received: April 1982.*

In 1833 Gideon Mantell first described *Equisetum lyellii* Mantell from the English Wealden. He didn't recognise that the specimens were in growth position and he failed to distinguish between rhizomes and aerial parts. Two of Mantell's specimens survive, one a poorly preserved but clearly recognisable portion of rhizome (the lectotype), the other a portion of aerial shoot. Since Mantell's time *E. lyellii* rhizomes have been found in large numbers in growth position in the numerous soil horizons which occur in the Wealden of Sussex throughout the Hastings Beds (Allen 1975).

Mantell, at the same time, redescribed specimens which had previously been described as *Carpolithus mantellii* Stokes and Webb (1824). He thought they were seeds of palms but they were almost certainly *Equisetum* tubers. I cannot recognise the exact specimens in the collection of the British Museum (Natural History) but there are numerous similar ones. Thin tuberous rhizomes have also been found at several horizons and pl. 13: 3 shows a specimen described by Seward (1894) with the tubers clearly borne on the rhizomes. However *E. lyellii* can also have

rather thin rhizomes and the exact distinction has never been clear. Allen who has worked extensively on Wealden sedimentology (1959, 1975) refers to thick and thin rhizomes and never finds tubers with the fattest ones. The specimen in pl. 13: 3 is strikingly like the living *Equisetum palustre* and in searching for aerial parts it seemed probable that it would be a shoot typical of the subgenus *Equisetum* which, as we shall see, *E. lyellii* is not. Seward suspected in 1894 that these tubers may belong to the species *Equisetum burchardtii* Dunker from the German Wealden but this was not confirmed until recently. Specimens in the Berlin Museum für Naturkunde from the old Dunker collection were found to have *in situ* tubers and thin rhizomes, exactly like the English specimens, as well as aerial shoots, probably underground parts. These are shown in pl. 13: 1, 2. *E. burchardtii* is thus exactly the sort of plant which was envisaged with thin aerial shoots bearing very few leaves per whorl. *Equisetum palustre* usually has 5, *E. burchardtii* probably has 8 or so. Members of the *Equisetum* subgenus die down in winter when the tubers are fully developed. It therefore seems probable that *E. burchardtii* was preserved at an unfavourable time of year when there were no sub-aerial parts. This perhaps gives an indication of seasonal variations in the climate. Harris (1981) envisages a long dry season with a brief but stormy wet season. No microscopic details of *E. burchardtii* are known.

Equisetum lyellii is uncommon in the German flora. The specimen in plate 13 figure 4 is the specimen which was figured by Allen in 1941. Unfortunately this specimen in the Sedgwick Museum now has most of the aerial shoot and the growing end of the rhizome missing. This photo has been prepared from one of Allen's negatives. Abundant material, both rhizomes and underground parts of aerial shoots, has since been collected by Allen, Batten and others. The features of *E. lyellii* are in general: large rhizomes which probably had a large central canal; large numbers of leaves, up to 40 per node; short internodes, in fact shorter than in any living species. The aerial shoots also have a large number of leaves for their size and often show eroded tips of leaves. This probably indicates that they were fully expanded in length and fossilised when mature. All these features are indicative of non-affinity with the subgenus *Equisetum* and are more typical of the subgenus *Hippochaete*. *E. lyellii* was probably wintergreen as are extant *Hippochaete* species. A few petrified specimens found in carbonate nodules confirm that the rhizomes and aerial shoots are indeed hollow with a large central canal. Plate 13 figure 7 is a transverse section of an aerial shoot which also shows clear indication of the vallecular canals. These petrified sections, together with specimens which appear to be internal moulds of the central canal, indicate that the xylem was much more strongly developed in *E. lyellii* than in living *Equisetum* (pl. 13: 8; pl. 14: 1).

The epidermis of the rhizome was figured by Allen and is easy to

obtain although it very rapidly becomes featureless in acid so that no cell outlines can be seen. It is best when naturally oxidised pieces are obtained as in pl. 14: 2. The epidermis is very similar to that in Australian Mesozoic species figured by Gould (1968). Similar cells can be found in living species by desilicifying in HF. Stomata are, of course, absent from the rhizome epidermis.

Aerial shoots from above ground level were totally unknown until Batten collected and gave me pieces from fragment partings above the so called soil beds. These partings are full of debris of what must be the sub-aerial parts of *E. lyellii*. Under paraffin (pl. 14: 4—7) a number of interesting bodies can be seen which help in reconstruction of the plant. Plate 14 figure 4 shows what I take to be an unexpanded shoot with features suggesting the presence of whorls of branches. Further evidence of branches comes from a number of fragments which proved to be narrow cylinders of cuticle, about 1—2 mm across. These can be mounted for the SEM and split open to reveal the characteristic sinuous cells of *E. lyellii*.

Nodal diaphragms are found in nearly all fossil *Equisetum* species though the diaphragms found in the fragment bed (pl. 14: 5) are only about 2 mm in diameter, so probably come from the branches. However I have recently had cause to question the exact nature of so called diaphragms in fossil *Equisetum*. No such structure is known in living species. Some specimens of *Equisetum telmateia* had been kept in a polythene bag for several months for obtaining epidermal preparations. When the shoots were removed and handled they immediately fell apart revealing 'diaphragms' at the nodes as in pl. 14: 8. Drying and shrinkage had caused the stem to shrivel inwards about $^1/_4$ inch below the node whilst the node remained as a firm ring. As can be seen this had the effect of making the vascular bundles appear as spokes radiating from the centre. In the light of this it seems to me not unlikely that at least some of the diaphragms recorded in fossil species are preservational features.

Other circular bodies (pl. 14: 6) with radiating striations are quite different from the diaphragms. They have a definite cuticle covering which the SEM shows to have the usual wavy walled cells (pl. 14: 9). These became my candidates for sporangiophores and indeed macerating them yielded clumps of spores (pl. 14: 10). The spores are fairly featureless and match the probable dispersed spores described from the matrix by Batten (1968). I would certainly expect them to have elaters; perhaps they do not survive oxidative maceration.

The stomata of *E. lyellii* present one of the most interesting features, both in their form and arrangement, which are totally unlike species of the subgenus *Hippochaete*. They are scattered in wide bands (pl. 14: 11) and are strikingly like those of *Equisetum sylvaticum* of the subgenus *Equisetum*, having the outer pair of stomatal cells level with the surface

(pl. 14: 12, 13). In the *Hippochaete* the stomata are in one or two longitudinal rows, sunken below the epidermal surface which is often coarsely sculptured. It may well be that *E. lyellii* represents a third group of species, now extinct, which combined the features of the two living subgenera. There is evidence from preliminary studies that various Jurassic species of *Equisetum* may be similar.

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EXPLANATION OF THE PLATES 13 AND 14

Plate 13

Equisetum burchardtii Dunker

1, 2. Underground parts of aerial shoots showing whorls of leaves. *1* ×1.5 Dunker Catalogue 6; *2* ×3 Dunker Catalogue 57, Museum für Naturkunde, Humboldt Univ., Berlin.

3. Rhizome bearing tubers. ×0.75, B.M. (N.H.) V. 1070.

Equisetum lyellii Mantell

4. Specimen preserved *in situ* showing growing tip of rhizome and aerial shoot. ×0.75. Specimen K2221 in Sedgwick Museum, Cambridge, now incomplete. Photograph prepared from old negative of P. Allen's.
5. Portion of rhizome showing large number of leaves in whorl with pointed tips intact. ×3.75, B.M. (N.H.) V. 710.
6. Portion of aerial shoot showing leaves with eroded tips. ×7.5, B.M. (N.H.) V. 28643.
7. T.S. aerial shoot indicating large central canal and vallecular canals. ×37.5, B.M. (N.H.) V. 44953.
8. T.S. vascular bundles showing more extensive xylem than in living species. Phloem was probably present between the arms of the V-shaped xylem. ×3.75, B.M. (N.H.) V. 44951.

Plate 14

1—7, 9—12; *Equisetum lyellii* Mantell

1. Internal mould of rhizome showing vascular strands along internode and probable leaf-gaps at node. ×3, B.M. (N.H.) V. 51137.
2. Light micrograph of rhizome cuticle showing cells with transverse bars of thickening. ×75.
3. Same in scanning electron microscope. ×190.
4. Probable unexpanded shoot apparently with whorls of branches. ×6.
5. Nodal diaphragms. ×7.5.
6. Sporangiophore head. ×15.
7. Spotted body of type very common in fragment bed; of unknown derivation. ×15.
9. Cells on outer surface of sporangiophore showing sinuous walls. SEM ×375.
10. Spore mass obtained by macerating sporangiophore. ×525.
11. Cuticle of aerial shoot showing stomata distributed in wide band. ×95.
12. Single stoma. SEM ×750.

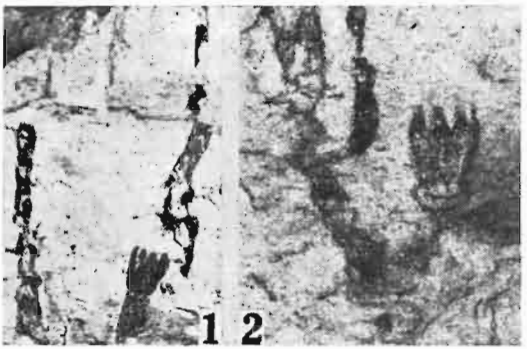
Equisetum telmateia Ehrhart

8. "Nodal diaphragm", see text for details. ×2.25.

Equisetum silvaticum Linné

13. Single stoma. SEM ×750.

All unregistred specimens to be deposited in B.M. (N.H.)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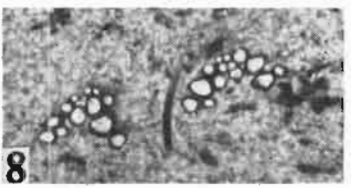
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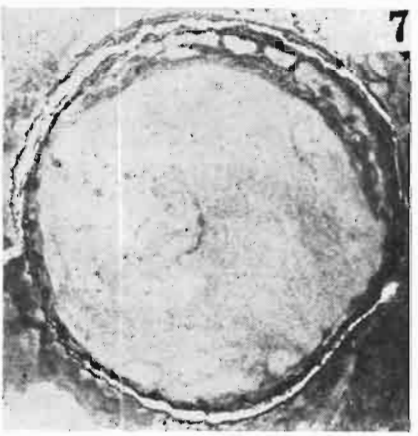
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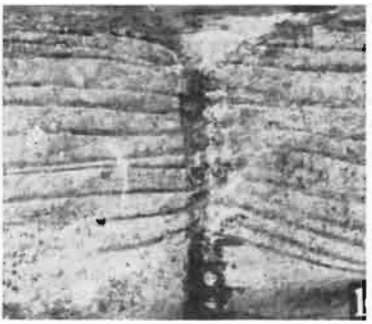
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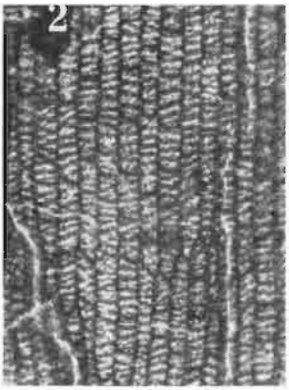
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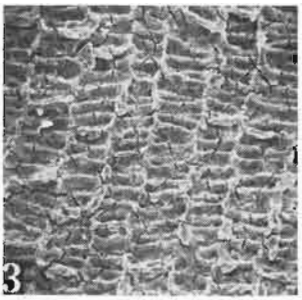
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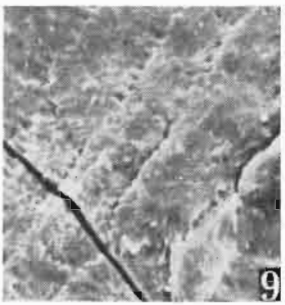
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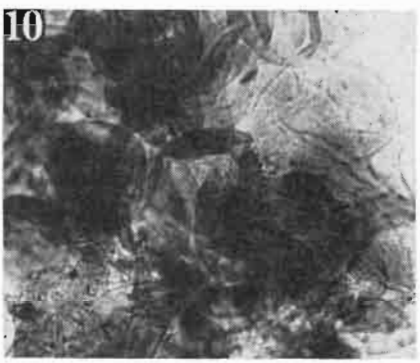
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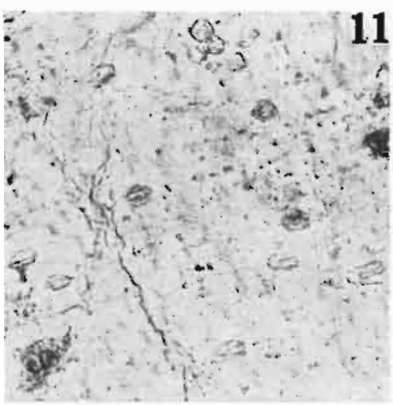
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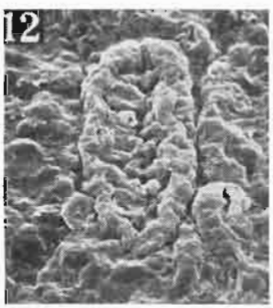
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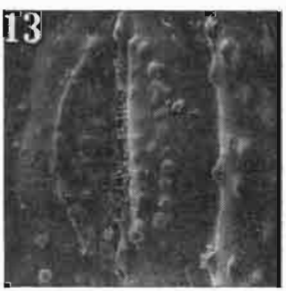
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