A RECONSTRUCTION OF *EQUISETUM COLUMNARE* AND NOTES ON ITS ELATOR BEARING SPORES

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ABSTRACT

The aerial stem of *Equisetum columnare* differs from that of Recent species in being smooth and in possessing separate subepidermal fibres instead of collenchymatous ribs. Its spores, however, have similar elators.

A restoration of the whole plant brings several points of uncertainty to notice, in particular where the cones were borne. It places parts known as separate fragments in particular positions and assigns their functions. This is done in the hope that directed search might demonstrate their nature and position.

INTRODUCTION

E. COLUMNARE is one of the longest known Yorkshire Jurassic plants. Brongniart described it in 1828 but local naturalists had figured it earlier and interpreted it as a reed, (Harris, 1961). Although it is by far the most abundant plant in the Yorkshire Bajocian and I imagine the number of determinable specimens looked at by collectors may amount to millions, we still do not know it in the way a palaeobotanist has the right to know a fossil. Little progress was made from the early days till recent times. We know the cones imperfectly and nothing about how they were borne. On the other hand, we have detached parts which we do not know where to place. But happily *E. columnare* often occurs as the only species and the field evidence of repeated association of the detached parts shows that they belong to it. It is the only species widely preserved in its position of growth. I put forward a reconstruction, starting with what is certain and adding what is less securely known. I then place the separate parts where they possibly fit and finally fabricate the unknown parts. I use the living species for comparison but limit myself to those familiar to me as wild British plants.

The procedure would have suited palaeobotanists a century ago better than today when cautious advance based on critical appraisal of evidence is our ideal. But optimism is surely proper at a jubilee. I think of my first visit to the Institute, just after its foundation followed by the untimely death of its founder and judge that it was virtues warmer than the critical and the cautious that saved it in those dark days.

When I began this essay I thought I knew *E. columnare* rather well and planned a restoration giving the secure main features and then adding the doubtful ones in a tentative fashion. But I soon realized that I was ignorant of much more than I had supposed and the balance of the known and unknown was altered, some of the unknown points being ones which I might have settled by directed work in the field but others would need the finding of an uncommon organ still attached. The restoration became a display of ignorance in an organised and provocative way but its value in clearing my ideas was real. I wished a restoration had been published earlier, one might have been drawn long ago, and certainly since Halle figured stems, rhizomes and roots in 1913. I would have looked critically for evidence supporting what had been guessed, and for this a guess that proved right and one that was wrong have equal value.

I would have searched for the stem apex in beds full of broken bits of aerial parts. I would have measured many internodes and might perhaps have deduced the stature of the stem. I would have searched deliberately for narrow aerial stems and for evidence of branching. I could have learnt the thickness of the wall of the tubular stems by measuring the coaly compression border in horizontally compressed internodes partly filled with matrix. Stems have suffered early oxidative decay in some beds leaving a translucent brown film and these may show more about the internal tissues. The vertical roots are often partly filled with matrix; their study might give the distribution of air spaces and parenchymatous tissue. If my suggestion that the cones grew from buds at the base of old vertical stems is right we might expect to find stems broken off the majority; I never looked. I know too little about the rhizomes; in most localities they are badly preserved, but surely in some places there may be specimens to supplement Halle's observations.

After giving the construction I contribute three fresh descriptive facts. One is a small rosette shaped leaf sheath which for the sake of being positive I place in the reconstruction. The other is the elator-bearing spores. These are like those of a living *Equisetum* as everyone may have supposed but fossil spores are usually prepared in a way that inevitably destroys elators. I used a different method, and at the same time isolated a piece of the surface showing hypodermal fibres, the only strong tissue so far recognnized in the internode.

HABITAT

E. columnare stems are preserved standing erect and in large numbers, e.g. 10-20/m^2 at many levels in the Yorkshire Bajocian delta. I know one such bed that can be traced in a cliff section for nearly 1 km. In 1821, such a bed was recognized and described as erect reeds growing in a swamp. These swamps are the only fraction of the vegetated land surface preserved intact. The delta surface stood just above sea level but though it sank more or less steadily for 100 m, its level was maintained by surface deposits of sediment from floods.

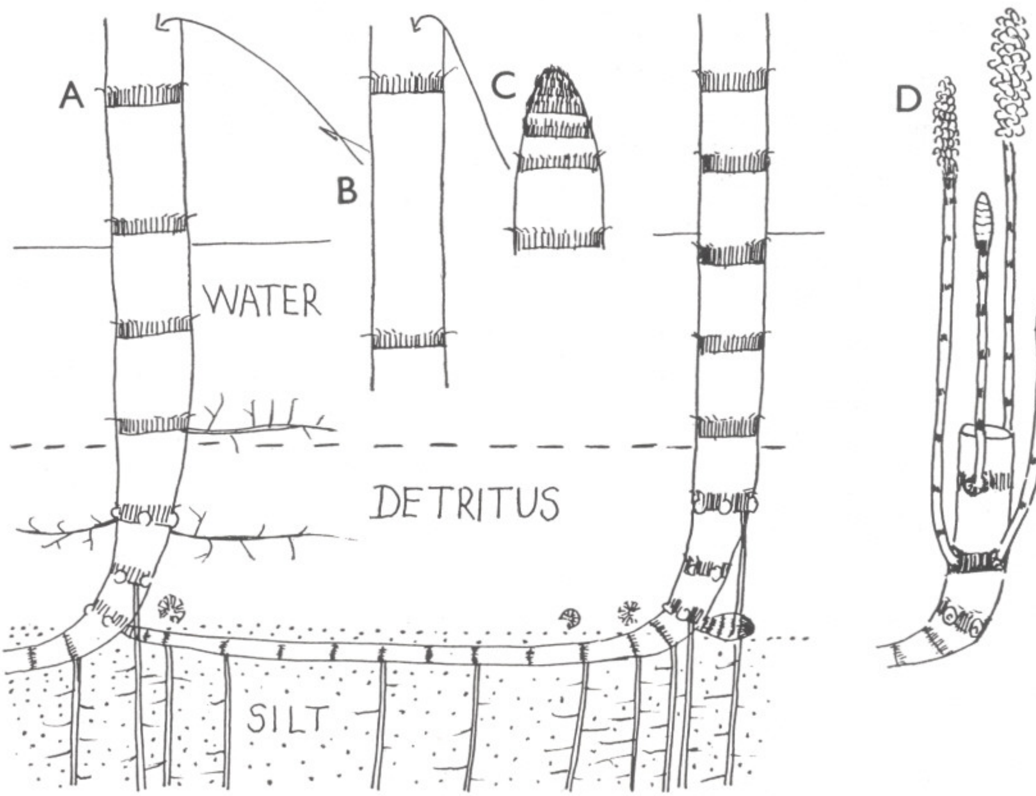
I believe the plants grew in peace in their swamps for a good many years and old aerial stems fell into the water and formed a detritus prevented from complete oxidative decay by lack of oxygen under water. Eventually the swamp was destroyed catastrophically. A flood swept over it dropping sandy silt around the erect stems and then flowing more strongly broke them off. Sand dropped into the open ends and though there were diaphragms they broke under the load and the sand fell to the base of the erect part. It appears that the plants died at once for I have never seen any sign of shoots growing up through the covering silt. Subsequently meandering distributories cut sediments away and deposited rather more and often provided a new swamp occupied by *E. columnare* but this is a fresh formation. The detritus lying around the erect stems is compressed to a few centimetres of coal which maceration shows to be full of cuticles of aerial stems. What remains of the tissue of the erect stems is a thin layer of coal between the stony core and the surrounding matrix

RECONSTRUCTION OF THE PLANT

In a typical bed the erect columnar stems 4-5 cm wide rise to 50 cm where they are cut off, while below they bend into the horizontal and are then lost in a coal. I have rarely tried to study the rhizome but Halle (1913) showed that it is rather slender, hollow (and may be filled with sandstone), it arises from the base of an erect stem and in the end thickens and grows up into another erect stem. Many vertical roots 5 mm thick descend from the nodes of the rhizome and the base of the erect stems. A few spreading and richly branched roots also grow from low nodes of erect stems.

I figured (1961; text-fig. 4 K) what I believe is the apical bud of a rhizome, a very obtuse end covered with narrow, tapering leaves which converge over it to a point. They are unlike ordinary leaves and leaf sheaths and this apex could scarcely have given rise to an ordinary aerial stem. Sheaths of these converging leaves are sometimes found detached, isolated or one inside another.

Most of the features of the erect stems are shown equally by the core and its imprint in the matrix, but it was always the cores that were collected and preserved in museums. The core alone may show the broken diaphragms; it shows the leaf sheaths clearly and these are nearly always broken off at their tops because the free leaves usually turn horizontally and are only seen in the surrounding matrix. Certain old accounts of the stem mistakenly described it upside down; stem cores in



TEXT-FIG. 1 — Restoration of *E. columnare* in a swamp, reduced to about ¼ natural size. **A**, rhizome resting on silt and joined to two upright stem bases. Vertical roots penetrate downwards for 50 cm, lower parts omitted. The vertical stems bear nodal buds and a few spreading roots in the detritus or water. The only solids indicated in the detritus are a few detached rhizome sheaths but most of the material is aerial stem fragments. **B**, aerial stem internode at an unknown level above **A**. **C**, imaginary stem apex. **D**, imaginary broken off stem base bearing cones above the water. They arise from basal rosettes.

museums show nothing about their occurrence and the free leaves which might have helped are broken off. Their vertical preservation was imagined to be due to floating with one end upwards.

In the preserved 50 cm of erect stems the internodes become progressively longer but I failed to look for the level at which stomatal pits first become common. The aerial stem fragments have considerably longer internodes (10-20 cm) and their surface is conspicuously pitted by large stomata.

The nodes bear close fitting sheaths of about 50 united segments separated by grooves broadening above and vanishing just below the node. The rest of the internode is smooth but evenly and densely pitted with stomata. No ribs like those of most recent species are present.

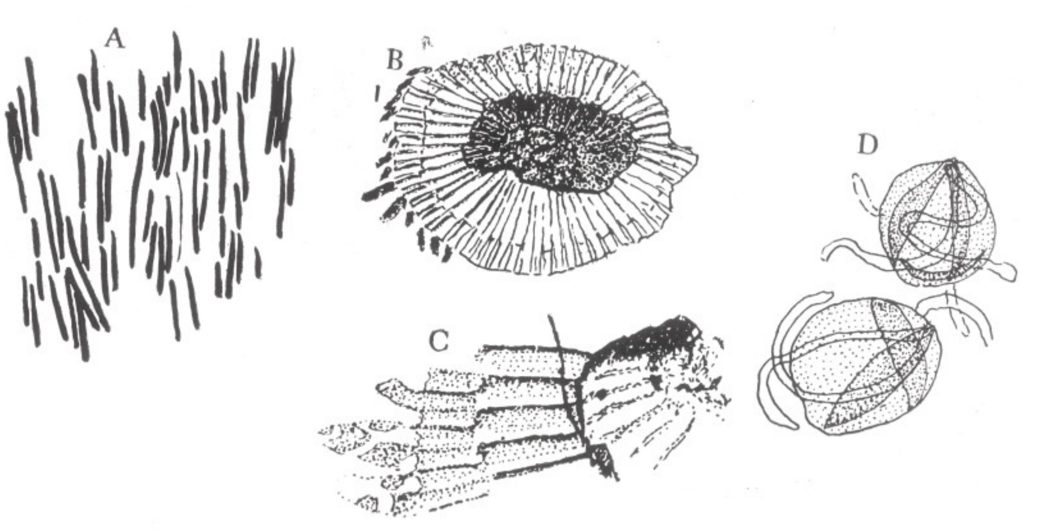
I have very rarely seen any sign of a branch base on an aerial stem node and have no idea what the few I have seen may have borne. This, however, was not a point to which I gave special attention in the field and I have omitted any aerial branch from the reconstruction but it is possible that the cones were borne here. The lower nodes of nearly all erect stems show conspicuous bulges or buds. The buds were noted in the earliest accounts, Seward figured them; I figured them on two stems one with large ones, one small. Such moulds as I have examined merely showed a corresponding hollow with, nothing extending into the rock. However, new rhizomes arose at this level and the bulges may be dormant rhizome buds. Clearly whatever should have happened to them failed once the marsh was overwhelmed with muddy sand.

The buds are at roughly even intervals, 4 or 5 on each node and thus separated by 12-15 leaves and the buds of the next node alternate, the total number being about 12. In my restoration I suggest that while a few of the buds formed rhizomes most remained dormant or else grew out to bear cones.

I think that the tubular *E. columnare* stems were built of rather soft tissue. No specimen, however, preserved shows any sign of bundles of fibres or strands of wood. Some that had undergone oxidative decay have become translucent and consist of the cuticle, traces of the epidermal cells and then a single discontinuous layer of hypodermal fibres (Tex-fig. 2A). The vascular bundles are never seen as coaly strands as they are in *Neocalamites* and *Calamites* (where they are known to represent compressed masses of tracheids). I imagine *E. columnare* had vascular bundles like a living species, where water conduction takes place mainly through the large protoxylem canal ('carinal canal') and not through the few small tracheids. This is demonstrable by putting a cut shoot in dye or simply by cutting a shoot and watching the sap well up from these canals. On compression solid tissue forms a coaly ridge but a mere hole in parenchyma makes no ridge at all and I have demonstrated this by compressing recent *Equisetum* stems. Only at the node there is much metaxylem and at the edges of the nodal diaphragm of *E. columnare* there are little tubercles, twice as many as the leaves, which I am sure represent metaxylem.

CONE — THE LEAST KNOWN PART

All we have is a few Delapidated specimens lying on a rock surface among bits of the aerial shoots. Such cones are mainly known to me from one locality, but similar sporangiophore heads preserved separately have been found in five, all in the presence of *E. columnare* and no other Equisetalean plant. The best of these cones shows an axis about 3 mm wide, sporangiophore stalks 3-4 mm long and robust heads consisting of a slightly hollow central part



TEXT-FIG. 2 — *E. columnare*. **A**, hypodermal fibres underlying naturally cleared epidermis. Many of the fibres are broken and some have probably vanished in preparation × 50. **B**, **C**, 'rosette'; **B**, part; **C**, counterpart, both illuminated from top left. **B**, shows the four zones, coal remains in the centre and a little in the leaves to the left × 4. **C**, coaly imprint stippled to show relief in the centre (to the right) which is the imprint with adherent grains of coal × 10. **D**, two elator bearing spores at edge of a confused mass of spores in transfer of cone × 400.

surrounded by a facetted flange, the whole if flattened being 3 mm wide, but the flange is often bent inwards. Very similar sporangiophores occur in *E. arvense* and form a cone of similar size.

I think these cones are ones which had duly shed their spores and broken off, had then been transported by water to a mud surface where they rotted for some time in the presence of oxygen until all but the more robust parts had vanished and only then had they been buried and preserved.

We do not know the cone-bearing axes at all. However, associated with the cones are some slender axes which might have borne them. I figured two, one 5 mm wide with long internodes, the other 10 mm with short internodes and ending in a bud; perhaps this is a young one not fully grown. It is curious that these stems have relatively robust diaphragms which have rotated into the plane of compression (Harris, 1961; text-fig. 4).

I now (without evidence) suppose that these slender stems grew from the nodal bulges of the erect shoot bases and since no shoot specimen shows anything of the sort I suppose that it grew out at a season after most of the shoots had died off. Also, for the sake of being positive and leaving no known part out of my reconstruction, I place the little rosettes described below as the basal leaf whorls of these fertile shoots, in fact the opened out basal leaf sheath of the buds on the erect stems.

DESCRIPTION OF CERTAIN PARTS

Spores & Elators — No nearly mature cone of *E. columnare* is available but such cones are known in a few Mesozoic species. When macerated they yield round, thinly cutinized spores comparable with those of a living species, but elators are lacking. But we know that Recent *Equisetum* elators are rapidly destroyed by Schulz and ammonia (those of *E. arvense* in a minute) so they would not be likely to survive this treatment in the fossil. In 1971, I tried to find *Equisetum*-like spores in celloidin pulls from the old *E. columnare* cones but failed. I tried again with another specimen, this time making a transfer onto nail varnish (which adheres well to fossil substance) the film being at first supported with resin, then freed and mounted in glycerine jelly.

The rock matrix among the sporangiophore heads showed a large number of round spores which seem to bear fine threads resembling *Equisetum* elators in thickness. Most of the threads are confused but the two spores figured are ones lying apart and show threads fairly clearly. If these are *E. columnare* spores and the threads are elators, I am sure they are incomplete as the parts seen would by no means cover the whole spore surface if wrapped round the spore.

The discovery of elators on the microspores of *Calamocarpon insignis* by Good and Taylor (1974) confirms earlier observations by several authors that certain Carboniferous Calamitean cones probably produced elator-bearing spores and as Good and Taylor point out their occurrence may be widespread in suitably preserved and suitably prepared material. The isolated spores called *Elaterites triferens* Wilson bear three short broad elators whereas the living *Equisetum* has four long narrow ones. *E. columnare* has narrow ones, broken short, as I suppose. I am not sure of their number, but the evidence suggests agreement with the living *Equisetum* rather than with *Elaterites triferens*.

Rosette — The small round organ shown in Text-fig. 2B, C is of a kind met occasionally in layers rich in *E. columnare*. It has not been described previously and the following notes are based on a single specimen collected recently. It was not studied by methods which would have caused damage. The organ, about 1 cm wide, is divided into four concentric zones and one surface which I imagine faced upwards, is slightly concave. I call the convex surface which retains most of the coaly substance, the 'part', the concave one the counterpart.

Zone 1, a central disc 0·2 mm wide of coal has an uneven upward facing surface. The coal is 0·2 mm thick and it includes thin films of matrix; the opposite surface has not been seen. There is no suggestion of epidermal cells on the exposed surface and I imagine it represents broken and partly rotted stem tissue.

Zone 2, 2·5 mm wide is marked by radiating ribs. On the upward facing surface the top of each rib is angular but the broad valleys between are gently rounded. Both show somewhat elongated cells which may be epidermal. On the downward surface (imperfectly seen in the imprint of its inner part only) there are also ridges which may correspond but are less well marked and their surface seems rough so that crumbs of coal adhere to the matrix. This zone is the main region of concavity of the counterpart.

Zone 3, nearly 2 mm wide, begins when the valleys of zone 2 and and new radiating ridges appear opposite their middles. The ridges of zone 2 continue but are lower and no longer angular and less marked than the new ones. Surface cells are well marked.

Zone 4 consists of free leaves possibly 2 mm long but most are missing or represented by their basal parts only. The ridges of zone 2 seem to point to the middles of the leaves, but the leaves themselves which are of very thin substance show no midrib. Similar cells are visible on both surfaces. Though there was no opportunity to measure the thickness of the coal, it seems that it becomes progressively thinner towards the outside.

This small organ is attributed to *E. columnare* because it is associated with it and with no other Equisetalean plant but there is no resemblance between its parts and the ordinary leaf sheath and leaves of the upright stems. I have placed it in the reconstruction on the main stem bases and imagine that it formed the coverring of the large basal buds. When these grew out, either to form a new rhizome, or perhaps to form slender cone-bearing shoots, the protective scales spread widely. Later after these shoots had died and rotted, and then the upright stems rotted, the relatively robust rosette was isolated. Such a suggestion could only be proved by the finding of attached specimens, but some advance might be made if several rosettes were available for study in transfers or the preparation of cuticles

Hypodermal fibres of the Stem Internode—These fibres were found unintentionally when the nail-varnish transfer of the cone was made. It happened to include a piece of internode surface. It is a brown film consisting mainly of the cuticle, but showing also indistinct outlines of epidermal cells, probable stomata and small ornamentations which might be related in silica nodules. These parts are all obscure in this specimen and have not been represented, but what are very clear are black almost parallel rods forming an incomplete layer. Many of these are broken, in preservation or preparation but some with rounded ends are probably perfect.

The rods are taken to be thick-walled hypodermal cells; rather similar ones have been noticed in another Yorkshire *Equisetum* (but not yet published), but I do not know of anything precisely similar in a living species. In the living kinds thick-walled cells do occur near the surface but they form bundles and form the ribs on the internode (Brown, 1976). *E. columnare* with no ribs has evenly dispersed thick-walled cells.

This find indicates the need for further work on specimens naturally cleared by oxidative decay. It is known (but again not published) that such translucent *Equisetum* membranes vary in what they show clearly, sometimes it is the cuticle ornamentation, sometimes epidermal cell walls and perhaps the lignified thickenings of the stomata, sometimes the hypodermal thick-walled cells.

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