THE STEM OF CAYTONIA

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ABSTRACT

The stem described is a compression with a well preserved cuticle. The stem is woody especially below and has three zones with crowded leaf scars. The apical bud ceased to grow and two laterals grew out giving forked branching. Bud scales (some still attached) occur at the branch bases. The leaf scars are unusually raised and have minute axillary buds. The shoot is thicker (6-8 mm.) than in most temperate trees or shrubs of today. It is suggested that the specimen is more likely to have come from a tall tree than from a shrub. Identification of the specimen was based on the scale leaves. Age: Middle Jurassic, Bajocian; Yorkshire, England.

INTRODUCTION

As we know them to-day the Caytoniales consists just of an isolated plant genus, but it has numerous species and these range from Upper Trias to Middle Cretaceous and occur widely in the N. Hemisphere. The whole plant is a hypothesis based on a number of separate organs which are linked by evidence and arguments which many find convincing. But it is a hypothesis and as such has no formal scientific name, and here I will call it, as I have done earlier, "The Caytonia Plant".

We know its separate organs as well preserved compressions which provide good external cuticles and some internal ones but apart from certain hard cells we know almost nothing of their anatomy. The organs were described at various times, the leaf by Brongniart in 1825 and given its distinctive generic name *Sagenopteris* by Presl in 1838. It was, as usual, classified as seemed reasonable and was long regarded as an ally of *Marsilia*. The microsporophyll was vaguely known to Phillips in 1829 and figured well by Seward in 1900 but regarded as the male cone of *Ginkgo digitata*. The little budscale was first recognised by Halle in 1910 and rightly attributed by him to the same plant as *Sagenopteris*. The fruits, megasporophyll and seed were first recognised by Thomas and published in a series of papers culminating in 1925. (A second species was by Thomas placed in another genus, *Gristhorpia*, but this was later included in *Caytonia*). It was Thomas who gave reasons for assembling the leaf, the megasporophyll and the microsporophyll as belonging to one plant and all his essential conclusions still stand; later work has made only slight modifications and supplied impressive confirmatory support.

DESCRIPTION

As Thomas left it, the stem was unknown, apart from a fragment which he thought was attached to a megasporophyll, but which I find unconvincing. It is discussed below.

The first glimpse of the vegetative twig was a small piece I described in 1940 (and re-figured in 1964). A larger and much better specimen was found by Miss van Cittert in 1964, and is the subject of the present paper. I will not consider the evidence on which the Caytonia plant was assembled (it has been summarised in Harris, 1964) but only the reasons for holding that the present stem belongs to the Caytonia plant.

The evidence is firstly association, and this applies equally for the earlier described stem fragment and the present one. The stems are found in beds where *Sagenopteris* leaves are locally frequent and other organs of the plant occur also but more seldom. Such association in beds with rich floras merely offers a possibility, it demonstrates that the stems were growing at the same time and in about the same place (along with other plants) ; but with a rare fossil such as these stems association does a little more.

The main evidence depends on some characteristic little scale leaves still attached to these two stems. HALLE in 1910 recognised a series of diminutive foliage leaves along with normal ones in the Swedish Rhaetic and then he recognised much smaller organs with only a minute lamina and finally little ovate bud scales with no lamina at all. The last are quite unlike *Sagenopteris* leaves but the whole series is convincing. Harris recognised a similar series of diminutive and scale leaves in the Lower Liassic of E. Greenland, and again later for two species in the Inferior Oolite of Yorkshire. The identification has been generally accepted and is fully supported by the agreement of the trichomes on the bud scales with those of the leaves.

In general, these bud scales along with foliage leaves and mega-and microsporophylls are abscissed and preserved separately, even if in close association. But fortunately both of these stems retain a number.

The specimen described by HARRIS (1940 and 1964) is a small twig fragment only, 2 cm. long and 2 mm. thick. It has at its base stumps of two broken lateral shoots and around the bases of these three shoots there are still several scale leaves of the simple, ovate shape and others with a tiny and undivided apical lamina. A little above is a transitional organ with a broad and scale-like base surmounted by four minute *Sagenopteris* leaflets. This however is partly detached and possibly does not belong here but it looks as though it was merely displaced in preservation. Still higher is a leaf scar with a clearly marked C-shaped vascular print. This leaf scar is raised above the general surface and from its edges two ridges run down the stem. It was already known that a *Sagenopteris* petiole has a single fibro-vascular strand of about this size. This specimen, from the Gristhorpe Bed, is associated with many *S. phillipsi* leaves and I feel sure it belongs to that species rather than to *S. colpodes*, the other *Sagenopteris* species of the Gristhorpe Bed

This specimen, because it is such a small fragment, gives only a little information but still it was useful. It shows that the plant had woody twigs and was quite unlike *Marsilia* in its stem.

The new specimen, from Roseberry Topping, was collected in 1964 by Miss van Cittert, with me (just after the account of the Caytoniales had been completed for publication). It is well preserved in a soft sandy shale without other fossils on its bedding plane. At Roseberry Topping a single species of *Sagenopteris* is common, it has been called "*S. colpodes* large form". This is probably distinct from Gristhorpe *S.colpodes* but the specific distinction is less than satisfactory. Part and counterpart were preserved.

The stem branches at its base (where the downward continuation was broken in collecting and never found). Both halves seem to fork again, the right hand one clearly but the left obscurely, for one half lies over the other. At the levels of branching, rather flat scars are numerous and these I attribute to scale leaves and at one stem forking several of these scale leaves are still attached. Between the levels where the stem forks, scars are more widely spaced and these are roughly semicircular and attributed to foliage leaves. One lateral organ is still attached and I think this must be a leaf petiole and not a sporophyll since it extends for 1.5 cm. without any sign of lateral organs.

The Gristhorpe specimen appeared to be monopodial with two lateral branches. The present specimen may also be primarily monopodial for some sort of stump is seen at the basal forking between the two side branches. There are no recognisable details in this stump to suggest a possible reproductive shoot.

The leaf scars on the stem surface are about 2 mm. wide. On the coaly stem surface of the counterpart most of them were damaged when the rock was cleaved because they stick upwards, but on the part which is largely an imprint in the matrix they form little pits filled with coal. The coal was carefully dug out with a sharp needle to give a clean imprint. The leaf scar was evidently raised on a cushion projecting considerably above the stem surface, but compression of both the stem and matrix has doubtless lowered the leaf cushion relief. At the sides of the compressed stem the leaf cushions project nearly 2 mm. and are so unusual that their nature was not at first recognised. In life this stem must have felt remarkably rough. The leaf scars are clearly on all sides of the stem and no doubt form a phyllotactic spiral. This could not be determined but the few seen most clearly suggested a 2/5 divergence as likely.

One of the best scars (Text-fig. 1C) after excavation showed as a deep pit on the matrix. The deepest part of this pit is a curved print, imagined to be the xylem and below this are two very slight ridges which might represent the position of phloem and of fibres. Finally there is the bottom of the leaf scar, where no doubt the epidermis and cuticle were broken. This particular leaf scar shows no convincing axillary bud, but it has two marginal decurrent sides which are high enough to form coal filled furrows in the mould. Another scar in surface view showed no vascular print after excavation but just above it is a small print which was taken to be a dormant axillary bud (Text-fig. 1E).

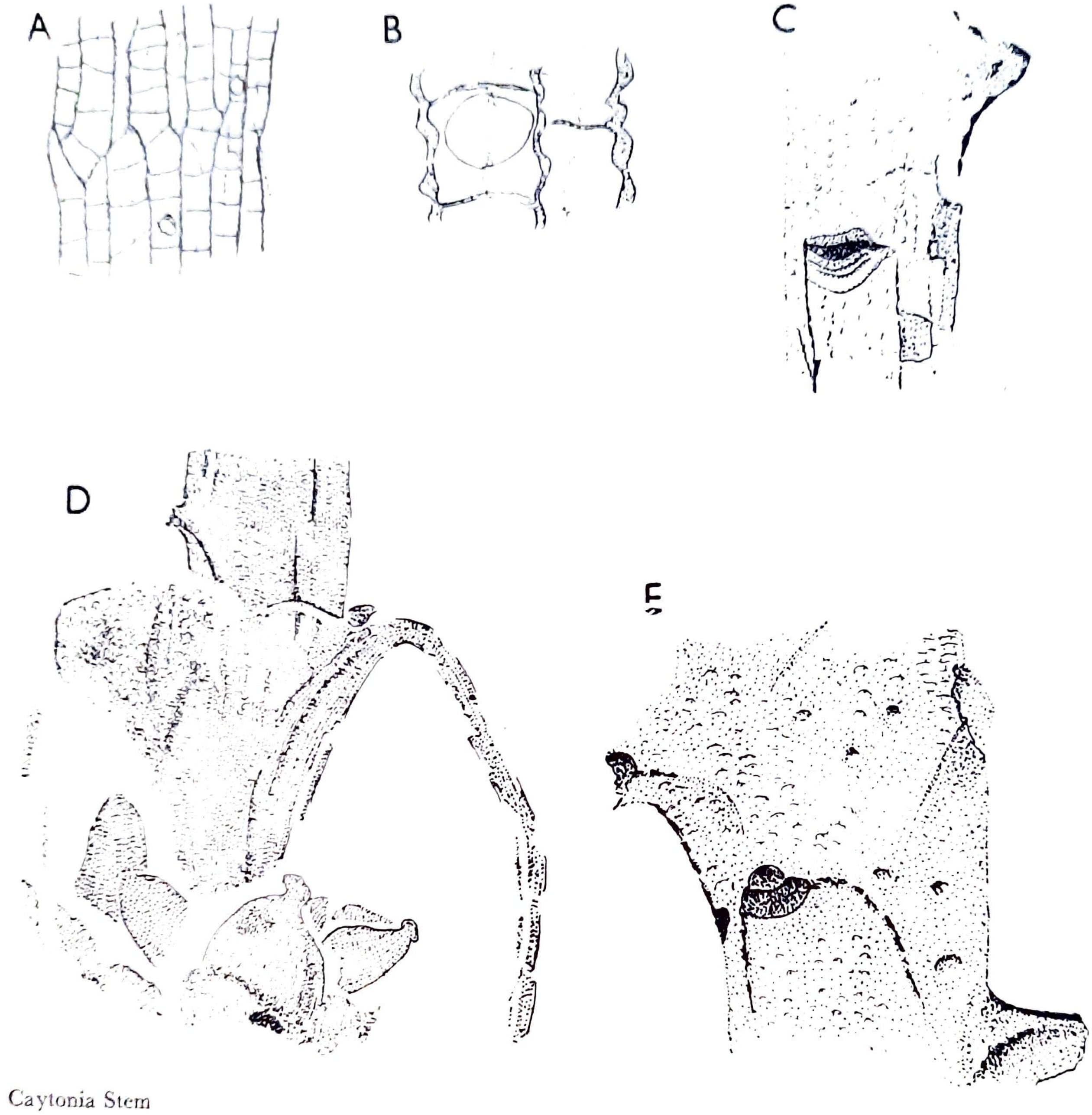
Details are seldom seen satisfactorily in the laterally compressed cushions along the sides of the stem, but the decurrent ridges from the sides of the leaf scar can be seen. One shows what may be an axillary bud.

The surface of the stem is mostly smooth, apart from slight bulges and puckers which I suppose were caused in compression. There are, however, a few pimple-like bulges up to 0.5 mm. wide which look like lenticels but there is no confirmatory evidence for this interpretation.

The bud scales of this specimen were not removed for maceration though some of those of the Gristhorpe specimen were so examined. They proved typical and I have no doubt that the bud scales of the present specimen would have been similar.

Coaly fragments of the stem which flaked off when the specimen was cleaned were macerated. The substance is thick in the lower part and was very crumbly but the upper part which is less substantial gave good pieces, one over 10 mm. long. Maceration was at first done very gently in the hope that tracheids might reveal their thickenings, but the only internal cells seen were narrow and fibre-like. Maceration was then completed to yield cuticles and those proved thick, tough and resistant to oxidation. Their thickness is 10μ or rather more in compression folds. For the most part the cuticle merely shows small, uniform, nearly square cells forming longitudinal files of 20 or more. The anticlinal cell walls are prominent and well marked, the longitudinal ones being specially prominent and having nodular extensions on to the surface. The surface wall is flat. A few epidermal cells show a ring representing the base of a small trichome, the free part was not seen. No satisfactorily clear stoma was recognised but a very few possible ones were seen consisting of a cell or perhaps a pair of guard cells overhung by about six neighbouring cells. On the raised leaf cushion the cuticle is only slightly different, the cells being slightly larger and of a less regular shape and the cell files are shorter.

It may be noted that though the upper epidermis of the associated leaf is very delicate



Caytonia Stem

A. Stem cuticle. The epidermal cell walls are shown by continuous lines, the faint hypodermal cells by dotted lines. Two trichome bases are seen. X 200.
B. Epidermal and hypodermal cell walls and trichome base. X 500.
C. Drawing of about 1 cm. of stem (seen as imprint in matrix) showing a leaf scar on surface and another projecting on right. Part, X 5.
D. About 1 cm. of stem showing four scale leaves below and a bent back petiole above. The nature of some of the coaly streaks is unknown. Counterpart, X 5.
E. About 1 cm. of stem showing (as imprint on matrix) a leaf scar and axillary bud imprint on matrix and some small lumps, perhaps lenticels. Three leaf base cushions project at the sides. Counterpart, X 5. The portions of stem shown in C, D, E, are to be seen also in the photographs but are slightly different because of further cleaning.

and the cells look different, on the associated fruit, *Caytonia kendalli* where the cuticle is thick, the cells are a good deal like those of the stem surface.

A specimen which THOMAS (1925, pl. 12, fig. 16) regarded as a stem fragment of the Caytonia plant must be discussed. This is a short piece of axis at the base of a Caytonia megasporophyll and figured by him. pl. 12, fig. 16. The megasporophyll is at a suitable angle but the figure shows a faint line across its base. The axis is smooth and we have no microscopic details. I think this megasporophyll may be a loose one with its base accidentally lying over some sort of stem but one to which it was never attached. This cannot be settled. The specimen was unfortunately never deposited at the British Museum and is now lost.

The Caytonia stem from the Gristhorpe Bed is from the Gristhorpe Series of the Middle Deltaic, and this bed gave all the Caytonialean material described by Thomas. Its age is Bajocian. This locality is remarkable for its very fine grained sediment and for the astonishingly close association of reproductive organs with their appropriate leaves, the flora changing when the bed is followed horizontally for a few metres. Thomas described the flora as autocthonous but that term should be reserved strictly for plants preserved in the position of growth, *Equisetum* stems rooted in mud and liverworts growing on a mud surface. He meant, however, that the plants grew beside a lagoon and dropped their organs into the still water, and I think something like that may be correct.

The Roseberry Topping plant bed is from the base of the Lower Deltaic and occupies a considerable river channel which cut into the top of the Lias (Whitbian stage). Its age must be between this and Bajocian. The plants were mostly carried some distance by water and moreover the channel was frequently invaded by sea water bringing in marine microfossils; it may have been a channel in a tidal delta. Most of the plants were however purely terrestrial in origin and at many levels rooted stem bases of *Equisetum columnare* are to be found. These are not obvious in the Gristhorpe bed though *Equisetum* stem fragments are met.

DISCUSSION

As mentioned, I think the Gristhorpe Bed specimen belonged to *Sagenopteris phillipsi* and its suite of organs, the Roseberry Topping one to "*Sagenopteris colpodes* large form" and its suite of other organs. The difference between the two stems is very slight—except that the Roseberry Topping one is much larger, 6-8 mm. thick instead of 2-3 mm

The Gristhorpe one has smaller leaf scars, about 1 mm. wide, and the Roseberry Topping one about 2 mm. At Gristhorpe there are plenty of *Sagenopteris phillipsi* leaves with petiole bases only, 1 mm. wide, but larger leaves almost certainly have wider bases than this, and again at Roseberry Topping, though a number of the "*Sagenopteris colpodes* large form" are not very large and would no doubt fit on to a 2 mm. base, others with very large leaflets, up to 15 cm. × 6 cm. would presumably have larger bases and larger scars on the stem. Thus both specimens may have been by no means large ones of their kind.

The specimen described here was evidently a woody stem, more densely woody below, and with well marked zones of slow growth, producing crowded scale leaves, and of quicker growth with foliage leaves. If the zones of bud scales represent a Winter's rest then the annual extension was not very great. Such alternating zones are normal in trees and shrubs of temperate and cold flora and occur also in warm regions where there is a severe dry season. I strongly suspect that the Yorkshire Middle Jurassic flora lived in a temperate and rather moist climate, one where ferns were abundant and where any cold season was only severe enough to favour protected resting buds on some of the plants. Protected buds were produced by *Ginkgo* and presumably by the Caytonia plant but not apparently by many others such as the common Bennettitalians or by many conifers such as species of *Brachyphyllum* and *Pagiophyllum*. The Caytonia plant was already known as one in which the organs are found separately abscissed—a normal feature of trees and shrubs, but exceptional in herbs. This is confirmed by what we know of the stems. The thick cuticle of the stem is another thing characteristic of woody stems.

The Roseberry Topping specimen has an unusually thick stem for a woody plant, between leaf bases it is 6 mm. or, in places, up to 8 mm. while from leaf scar to leaf scar it is up to 11 mm. wide. This is thicker than the leafy twig of any British tree or shrub. Some trees of the Temperate zone have twigs of this width (eg. *Aesculus, Juglans*) but very few shrubs indeed. As examples of thick stemmed shrubs I mention *Fatsia japonica* (*Aralia sieboldii*) and *Paeonia lutea*, both from E. Asia, and these shrubs when grown in England are so unusual as to be considered grotesque. In Tropical floras thick stemmed trees and shrubs may be more common, indeed Corner has written frequently of tropical pachycaul trees and shurbs, plants many of which have considerably thicker stems than the present specimen.

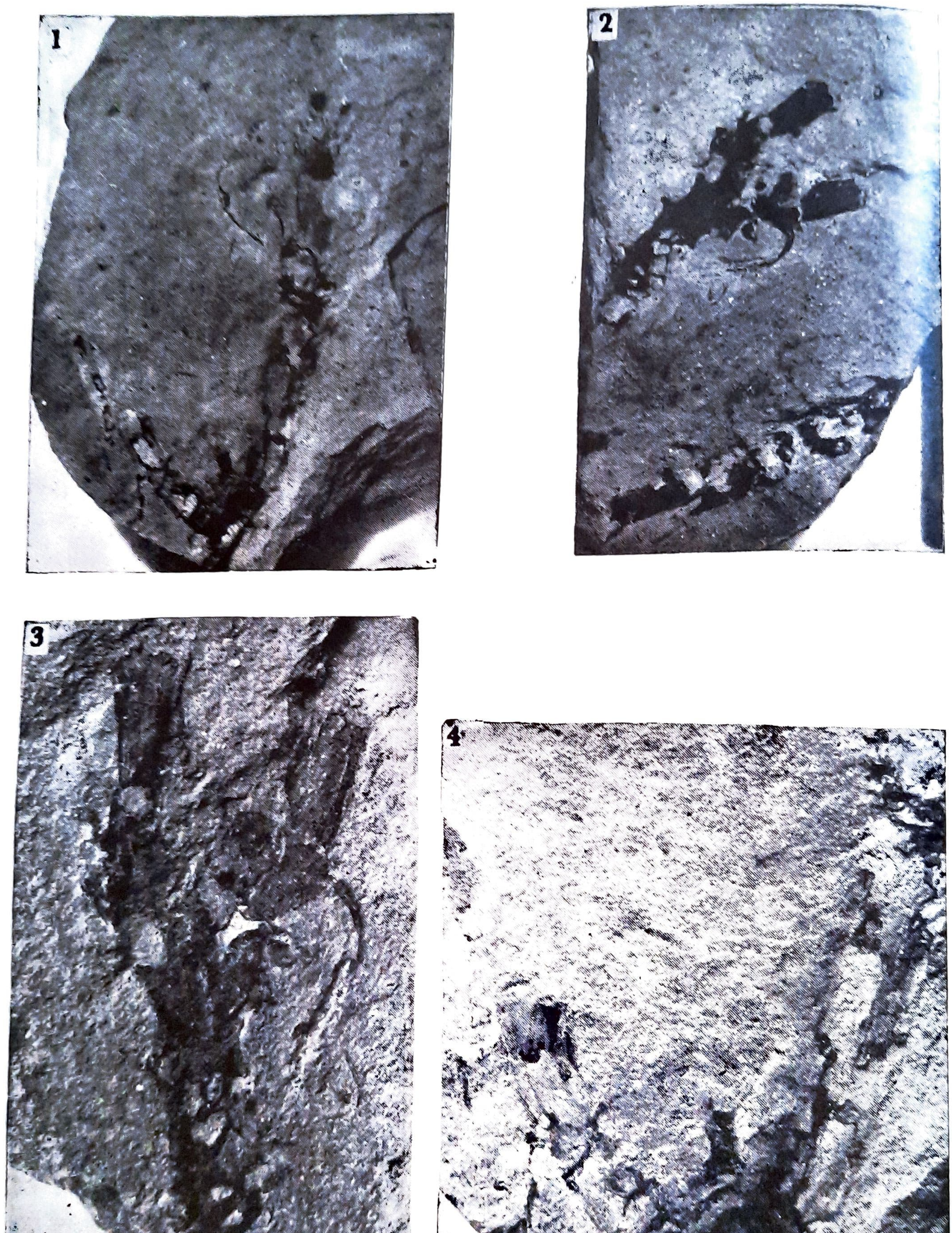
I feel sure the Caytonia plant was woody and I suggest, though less confidently, that it was a tree rather than a shrub. There is no direct evidence but I argue from the manner of occurrence of the fossils, their ecology as it may be termed. It is always perilous to reconstruct ancient ecology and and then to use it as evidence as the basis for further argument, but I do this.

In the Middle Jurassic, N. Yorkshire formed part of a great delta of a river flowing from the N. and E. and facing the sea to the S. and W. This delta sank 200 metres during its existence as a delta, and while most of it was probably land at a low elevation it was crossed by numerous river distributaries and included lagoons and swamps. Periodically it sank faster than the surface was being built up and the sea invaded for a time (these marine incursions divide the deltaic rocks into four). Plant beds are of three chief types. The commonest represent marshes, probably covered with shallow water in which *Equistum columnare* grew to the exclusion of other species. Its rhizomes bear roots penetrating vertically for about a metre and also some richly branched horizontal roots and then erect unbranched stems up to 5 cm. thick and no doubt of considerable height. These often accumulate in a broken state and with the rhizomes form a little coal seam. Less often their basal metre or so is preserved erect and filled with sand. Most commonly indeed some erosion has occurred, removing the rhizomes and just leaving truncated roots.

The next commonest kind of plant bed, and one we are not concerned with here, is a bedded deposit of sand probably laid down in a lake and scattered with water-worn fragments of fusain (charcoal washed from a forest fire) often with some unburnt wood preserved as bituminous coal. Then there are the beds where leaves and other bits of plants have been deposited under water, along with sand or mud and these include the rich plant beds with fine large specimens which must have been deposited near where the plants grew and also beds of waterworn plant fragments that may have been transported long distances. Such beds were formed in river channels which were becoming silted up or in broad lagoons where the sediment is very fine grained. Very commonly broken bits of *Equisetum* stems are found in these lagoon beds and I imagine that while the water was too deep for these reeds to grow in the plant bed itself, they formed a marginal fringe in the shallow waters. These different kinds of bed are not always sharply distinguished.

The Gristhorpe Bed is of the lagoon type and though *Equisetum* fragments are frequent the rooted plants are absent from the rich layers. It is here that reproductive organs are characteristically associated with the leaves of the same species and also the flora changes greatly when the bed is formed a few metres laterally. Thus at different points *Sagenopteris phillipsi* is abundant and its reproductive organs (and the stem) are met, and at another point *S. colpodes* and its organs; but over much of the bed neither is common.

I suggest we have a deep lagon of almost still water to which some small river supplied a very fine silt. There would be a tall reed swamp of *E. columnare* along the shore, and then on dry land a mixed vegetation of ferns, perhaps shrubs, and tall trees, considerably taller than the reeds. Leaves and also reproductive organs of a tree would blow into the water, to be preserved together, but organs of shrubs shorter than the reeds would only reach the water in smaller numbers and probably much mixed with other species.



Harris—Plate 1

We know that trees, producing great logs up to 1 m. thick grew in the delta. Such logs have not been described because no-one has seen how to identify them with a leaf species or indeed to display any satisfactory botanical structure in their wood which has been compressed to a thin coal. (Petrifactions are rare in the Deltaic rocks).

An unusual feature of the Caytonia plant stem (whether tree or shrub) is its very prominent cushions under the leafscars, 2 mm. high in the Roseberry specimen but less in the smaller Gristhorpe one. Few modern plants known to me have such cushions. Most trees and shrubs have either flat leaf scars, or one margin, usually the lower, is strongly raised making a tilted scar. *Morus* has the whole leaf scar raised on a sort of cushion nearly 1 mm. high and *Picea* is well known for its sharp little peg-like cushions which seldom exceed 1 mm. in length, though since they are slender they are longer in proportion than those of the Caytonia stem. I know nothing of the biology of raised leaf cushions but those of this stem are so unusual that they may prove of use to the palaeobotanist—they could help identify another stem, perhaps one giving further information.

The stem described here does somewhat fill a gap in our knowledge of the Caytonia plant, but as far as I can see it does nothing to settle its affinities. Anyone who is already convinced that Caytonia is allied to the Angiosperms will be encouraged by the marked resemblance of its stem to that of the Horse Chestnut, *Aesculus*. But I refuse to accept "affinity" as having any meaning until I can explain every single organ of the one plant in terms of the corresponding organ of the other. Emphatically this is not yet so, but of course further discoveries may make it possible. The stem of the Caytonia plant (as far as we know it) gives no difficulty in comparison with that of some Dicotyledon tree, the leaf seems not too difficult; but the megasporophyll, fruit and seed, the microsporophyll, anther and pollen are extraordinarily different.

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EXPLANATION OF PLATE 1

Caytonia Stem

1. Roseberry Topping specimen, part, photographed under oil. ×1.
2. Counterpart with more coaly matter, also under oil.
3. Upper region of counterpart showing reflexed petiole also bud scales, dry. ×2.
4. Base of shoot shown in Fig. 1, dry. ×2.
   A small possible continuation of the main stem is seen between the two branches.