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ORIGINAL ARTICLES.

I.—PLANT CUTICLES FROM THE COAL-MEASURES OF BRITAIN.

By LUCY WILLS.

(PLATES XXX AND XXXI.)

I. INTRODUCTION.

OUR knowledge of the structure of the cuticle of Coal-measure plants is very meagre in comparison with the amount of information recently published as to the cuticular characters of Mesozoic genera. So far as I know, no detailed descriptions have been published of the cuticles of British Palæozoic plants. Professor Zeiller<sup>1</sup> has described a few cuticles of French Carboniferous plants, and Dr. Huth<sup>2</sup> recently gave an account of the cuticle of *Mariopteris muricata*, but very little has so far been attempted in this branch of research. The present preliminary account deals with material obtained by Mr. L. J. Wills from the Middle Coal-measures of the Denbighshire Coal-field near Chirk and from the Old Hill Marls (Etruria Marls?) in the Upper Coal-measures of South Staffordshire. The cuticles are preserved as brown films in clayey shales, approaching fireclays in composition, none having yet been found in carbonaceous or sandy shales. It is hoped that this note will incite collectors to search for further specimens in this state of preservation.

The chief interest of the discovery of actual plant cuticles is that they afford a new weapon with which to attack the palæobotanical problems of the Coal-measures. The fact that different parts of the plant are preserved in this way may lead, on further investigation, to a correlation of these parts and to the identification of detached fragments. I have been unable in the time available to examine in any detail the spores and seeds collected, but I have made preparations of both macrospores and microspores from the cones of different species of *Lepidostrobus* and of platyspermic seeds of the *Cordaites* type and others of unknown affinity. I hope in the future to investigate these more fully.

The following account records briefly the results obtained from an examination of the leaf cuticles of several different species.

2. METHOD OF PREPARATION.

The methods of preparation employed are those which have yielded much valuable information as to the cuticular structure in many Mesozoic forms.<sup>3</sup> The cuticles were soaked off the shale, treated with

<sup>1</sup> R. Zeiller, *Houille et Perm d'Autun et d'Épinac*, p. 115.

<sup>2</sup> W. Huth, *Palæobot. Zeitsch.*, Bd. i, pp. 7-14, 1912.

<sup>3</sup> For details of this method see A. G. Nathorst, *Palæobot. Zeitsch.*, Bd. i, p. 26, 1912, and H. H. Thomas and N. Bancroft, *Trans. Linn. Soc.*, vol. viii, pt. v, p. 157.

Schülze's macerating fluid, and then washed in ammonia. The bleached cuticle alone remains after this treatment. The two surfaces of the leaf when present were separated by careful teasing with needles. The preparations were stained with either Bismarck brown or diamant fuschin.

### 3. DESCRIPTION.

#### *Neuropteris heterophylla*, Brongn.

Localities: Preesgwyn and near Cefn. Horizon: Middle Coal-measures.

The general form and venation of the leaflets are indicated in Pl. XXX, Fig. 1. Under the microscope the leaflets show two distinct types of cuticular structure; both types possess the following common features. The cells of both the upper and lower epidermis are roughly polygonal in outline, except over the vein-courses, where they are rectangular and elongated in the direction of the venation. The cell-walls are of a normal thickness and straight. On one surface the stomata are fairly numerous, approximately sixty-eight to the square millimetre, while on the other there are only a few scattered ones. On both surfaces they are restricted to the areas between the vein-courses.

The stomata (Pl. XXX, Figs. 2, 3, 4, 5, S) are irregularly arranged. Each individual one (Text-fig. 1) is nearly spherical in shape. The guard-cells are slightly sunk, lightly cuticularized, and sometimes imperfectly preserved. The cells surrounding the stomatal cavity, generally five or six in number, are similar to the other epidermal cells, but take a deeper stain; where they abut on to the stomatal cavity they form a solid ring of thickening (Pl. XXX, Fig. 4).

The distinguishing feature between the two types is the presence of small papillate hairs on one surface of the leaf in type  $\beta$  and their absence in type  $\alpha$ . As there are corresponding types of *Cyclopteris* leaflets (*Cyclopteris* is a name given to one type of *Neuropteris* foliage), it would seem possible that two distinct species of *Neuropteris* are here represented. Further, in a few specimens of type  $\alpha$  a marginal zone of water-stomata occurs (Pl. XXX, Fig. 2, W). This is of interest, as the same structure is found in the corresponding *Cyclopteris* type (Pl. XXXI, Fig. 7) and in some modern forms.<sup>1</sup> These stomata are similar in structure to the ordinary air-stomata but larger, more circular in outline, and with a less prominent ring of thickening round the stomatal cavity (Pl. XXX, Fig. 2; Pl. XXXI, Fig. 7). Certain of these stomata have a thin walled tissue in the stomatal cavity in place of the normal two guard-cells.

In addition to the two types described two specimens show glandular patches on certain cells of the single surface preserved (Pl. XXX, Fig. 5). These glandular cells, like the hairs in type  $\beta$ , are irregularly scattered over the whole leaf surface. No water-stomata have been observed in this type.

Leaflets of a *Neuropteris* have been collected from the Old Hill Marls, but have not yet been identified.

<sup>1</sup> G. Haberlaudt, *Physiologische Pflanzenanatomie*, 1909, p. 449.

*Cyclopteris* sp.

Locality: Preesgwyn. Horizon: Middle Coal-measures.

Specimens examined show two types of epidermal structure similar to those described for *Neuropteris heterophylla*.

The form and venation of the leaflet is shown in Text-fig. 2. In several specimens both surfaces of the leaf were preserved and were separated; Pl. XXXI, Figs. 6, 7, represent the two surfaces of one fragment. The form and arrangement of the cells and stomata are illustrated on Pl. XXXI, Figs. 6, 7, and Text-fig. 3. Their close similarity to type *a* of *Neuropteris heterophylla* can be clearly seen by comparing these figures with Pl. XXX, Figs. 2, 5, and Text-fig. 1.

## STOMATA AND GUARD-CELLS.

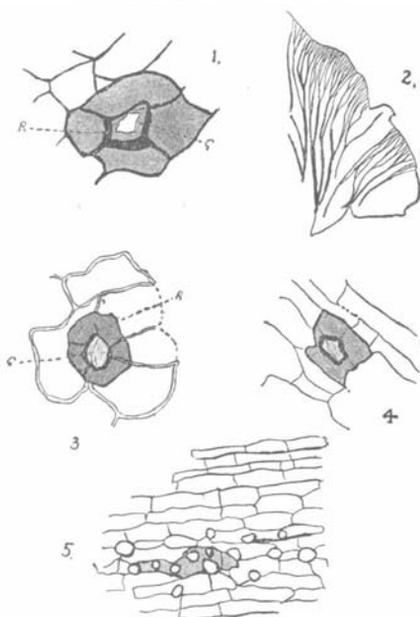


FIG. 1. *Neuropteris heterophylla*. R, ring of thickening; G, guard-cells.  
 ,, 2. Half of a *Cyclopteris* leaflet.  
 ,, 3. *Cyclopteris* sp. R, ring of thickening; G, guard-cells.  
 ,, 4. *Cordaites* sp.  
 ,, 5. *Cordaites* sp.

Water-stomata similar to those already described form a continuous band round the edge of that leaf surface which carries the numerous stomata.

Type  $\beta$ . The specimens classed under this heading are similar to those of type *a* in form, but are frequently not lobed. The one surface is slightly hairy and imperfectly preserved; the other shows cells of a normal structure and a few scattered stomata. Water-stomata have not been observed.

*Alethopteris* sp.

Locality: Preesgwyn. Horizon: Middle Coal-measures.

Both surfaces are preserved, but could not be separated. As in the two species already described the cells over the vein-courses are rectangular and elongated in the direction of the veins, those in the intervening areas polygonal.

The stomata can only be observed on one surface; they are fairly numerous, approximately eighteen to the square millimetre, and arranged in rows parallel to and between the vein-courses as shown on Pl. XXXI, Fig. 9. In structure the stomata are of the same type as in *Neuropteris heterophylla*. The guard-cells can be clearly seen in the stomatal cavity. The whole structure is similar to that described by Professor Zeiller for *Alethopteris grandini*, except that in the present case the guard-cells are also preserved. They are illustrated on Plate XXXI, Fig. 10.

*Pecopteris* sp.

Locality: Preesgwyn. Horizon: Middle Coal-measures.

Only one epidermal surface is preserved in this species. The cells are polygonal except over the vein-courses, where they are rectangular and elongated in the direction of the veins. No stomata have been observed in the specimens examined.

*Cordaites* sp.

Locality: Preesgwyn. Horizon: Middle Coal-measures. Locality: Old Hill, S. Staffs. Horizon: Upper Coal-measures.

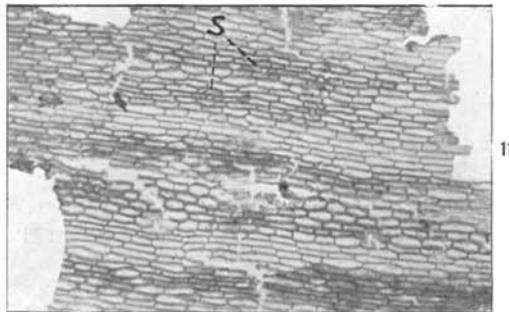
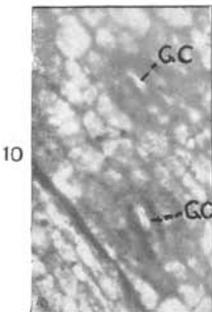
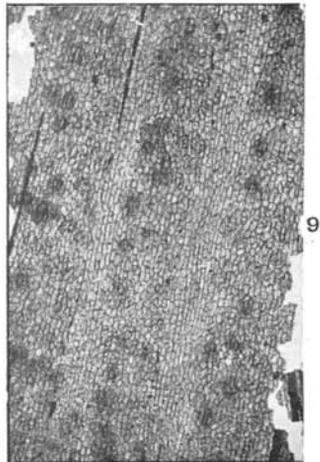
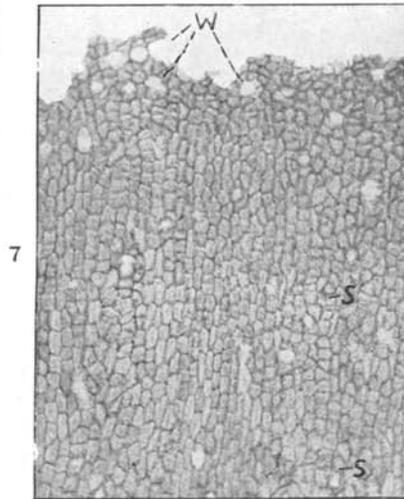
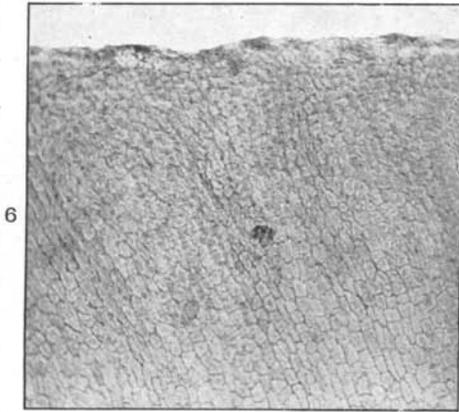
Preparations from several species have been made, all of which show the same cuticular structure. The two surfaces are preserved, but the one epidermis does not make good microscopic preparations; it shows, however, thin-walled cells and rows of stomata between the vein-courses. The other surface is well preserved. The cells are thick-walled, rectangular, and elongated in the direction of the vein-courses; those immediately above these being narrower and longer than those in the intervening areas (see Pl. XXXI, Fig. 11). There are a few stomata on this surface; they are oval in shape and arranged in rows parallel to the venation. The stomata are smaller than in the forms described above, and are frequently surrounded by four cells which form a ring of thickening round the cavity (Text-fig. 4). The guard-cells are lightly cuticularized and frequently imperfectly preserved. Circular structures of unknown significance occur at irregular intervals on the well-preserved surface (Text-fig. 5).

*Thalloid growth.*

Locality: Old Hill. Horizon: Upper Coal-measures.

A thalloid growth of uncertain affinity covers certain layers in the Old Hill Marls. A typical piece is figured on Pl. XXXI, Fig. 8. At first sight it appears to be formed of cutin, but since it dissolves in Schülze macerating solution it must be of a different chemical composition.

The fragments found measure as much as 10 mm. in length and average 1.5 mm. in breadth. They branch dichotomously and repeatedly. This fact, together with the lack of differentiation of



O. T. Elliott & W. Tams phot.

Plant-cuticles from British Coal-measures.

the tissue and the presence of spore-tetrads embedded in the thallus, points to the possibility of its being a primitive type of Bryophyte. Should further study support this view, these specimens will be of great interest as being the first Bryophytes recorded from the Palæozoic rocks.

#### 4. CONCLUSIONS.

1. *Morphological*.—The chief interest in a study of the structure of a leaf cuticle centres round the stomata. In the specimens described above one type of stoma is common to all the species. The type is simple. A girdle of subsidiary cells surrounds the stomatal cavity, forming a ring of thickening where they abut on to it. The two guard-cells are slightly sunk in the stomatal cavity. The prevalence of this simple uniform type of stoma is of interest, since the cuticles examined by Professor Zeiller and Dr. Huth respectively showed distinct differences of stomatal structures, and in the case of *Alethopteris* the structure observed was interpreted differently by the two observers. Professor Zeiller<sup>1</sup> concluded that the guard-cells, which were missing in his specimen, were originally present but had not been preserved. Dr. Huth,<sup>2</sup> however, maintains that in all probability the guard-cells were never present, and that stomata were of an aquatic type similar to those in *Mariopteris muricata*. The description of the stomata of *Alethopteris* given above entirely bears out Zeiller's contention, but it is hoped that a further study will throw more light on this structural point.

2. *Ecological*.—The discovery of cuticular remains in the Coal-measures is of importance ecologically, since the epidermal features of a plant, especially the arrangement, structure, and number of the stomata, are intimately related to climate and habitat. Yet results based on the cursory examination of a few species can be of little value, and I do not propose to do more than make a few tentative suggestions. Dr. Huth has already suggested that the aquatic type of stoma found in *Mariopteris muricata* indicates an extremely humid atmosphere. The different types of cuticular structure found in *Neuropteris heterophylla* and *Cyclopteris* would seem to lend support to this view, for such authorities as Warming<sup>3</sup> and Haberlandt<sup>4</sup> cite water-pores, glandular patches, and hairs on the epidermis as characteristics of plants living under humid conditions. If we assume that these structures functioned as hydathodes it is probable that the hairs and glandular patches occurred on the lower surface of the leaf and the water-stomata on the upper. If this be so, the stomata are more numerous on the upper surface, a feature which is consistent with the view that the plants were hygrophytic. Yet the number of stomata is less than might have been expected under such circumstances.

3. *Phylogenetic*.—It is possible that the structure of the stomata may eventually prove of use in tracing the phylogeny of modern forms. Suggestive in this respect is the similarity between the

<sup>1</sup> R. Zeiller, op. cit.

<sup>2</sup> W. Huth, op. cit.

<sup>3</sup> E. Warming, *Ecology of Plants*, English trans., 1909, p. 101.

<sup>4</sup> G. Haberlandt, op. cit., pp. 445, 451.

stomata in these Palæozoic types and those of certain Cycads described by Messrs. Thomas and Bancroft.<sup>1</sup>

In conclusion I would like to express my gratitude to Professor A. C. Seward for many valuable suggestions and criticisms, and to Mr. Hamshaw Thomas, of Downing College, Cambridge, who gave me numerous useful hints on the methods of preparing and mounting the cuticles. I wish also to thank my brother, Mr. L. J. Wills, for very kindly placing the material at my service and for his encouragement during this research.

## EXPLANATION OF PLATES.

## PLATE XXX.

- FIG. 1. *Neuropteris heterophylla*, Brongn. Leaflet. × about 4.  
 " 2. " " Stomata *S*, water-stomata *W*. × 50.  
 " 3. " " Group of stomata. × 50.  
 " 4. " " Stomata. × about 167.  
 " 5. " " Glandular patches *G*, stomata *S*. × 50.

## PLATE XXXI.

- FIGS. 6, 7. *Cyclopteris* sp. Type *a*. Two surfaces of same leaflet. Stomata *S*, water-stomata *W*. × 50.  
 FIG. 8. The cuticle of a dichotomously branched thalloid structure. × 17.  
 " 9. *Alethopteris* sp., showing rows of stomata. × about 24.  
 " 10. *Alethopteris* sp., stomata, guard-cells *G.C.* × about 167.  
 " 11. *Cordaites* sp., stomata *S*. × 50.

The Text-figures are all camera-lucida drawings of the actual specimens.

## II.—A NEW TRILOBITE FROM THE MILLSTONE GRIT OF NORTH YORKSHIRE.

By W. B. R. KING, B.A., F.G.S.

## (PLATE XXXII.)

THE highest beds of the Carboniferous rocks of Wensleydale are found on the summit of Great Shunner Fell, which is situated on the watershed between Wensleydale and Swaledale, and forms the high ground to the west of the Buttertub Pass on the road between Hawes and Muker.

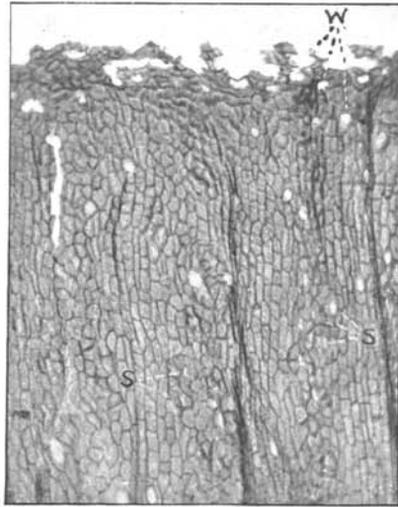
At a point 650 yards south-west of the Currack of Great Shunner Fell, called Shunner Fell Well on the 6 in. to a mile ordnance map (Yorkshire, Sheet L), a thin band of limestone and calcareous shale is seen forming a conspicuous feature. A detailed section of the beds exposed at this locality shows about 12 feet of calcareous beds. The limestone in question is described in the Geological Survey memoir on *The Geology of the Country around Mallerstang, etc.*, where the following description of the Millstone Grit of that area is given "The overlying bed is a very thick shale, which forms the greater part of Shunner Fell. In it there are two thin bands of fossiliferous limestone, which are to be seen near Shunner Fell Well on the west side of the hill. In one of these Mr. Goodchild found a trilobite. A tiny outlier of grit forms the extreme top of Great Shunner Fell."<sup>2</sup>

<sup>1</sup> H. H. Thomas and N. Bancroft, op. cit., pp. 155–204.

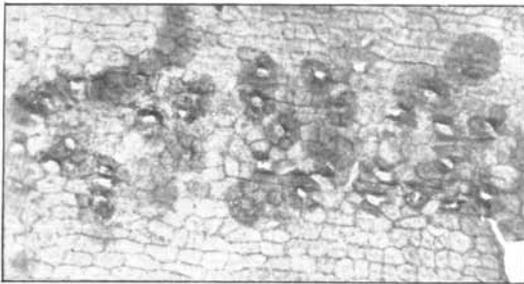
<sup>2</sup> *The Geology of the Country around Mallerstang, etc.* (Mem. Geol. Surv.), 1891, p. 145.



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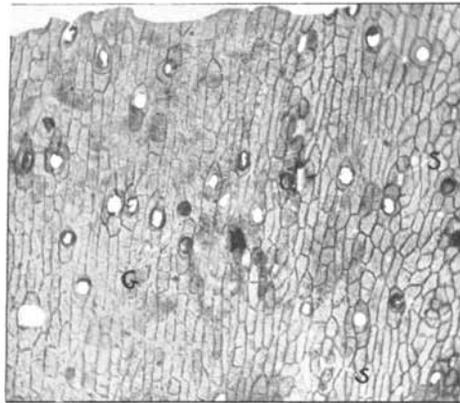
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*O. T. Elliott & W. Tans phot.*

Plant-cuticles from British Coal-measures.