AN OPPOSITE-LEAVED CONIFER FROM THE JURASSIC OF ISRAEL

by W. G. CHALONER and J. LORCH

ABSTRACT. *Cupressinocladus ramonensis* sp. nov., a species of Jurassic conifer based on compressions of leafy shoots, is described, and the genus *Cupressinocladus* Seward emended. The material is from the Makhtesh Ramon (Wadi Raman) in southern Israel. The leaves are small, closely appressed, and are decussate in arrangement, suggesting comparison with the living Cupressaceae. Faunal evidence shows that *C. ramanensis* sp. nov. is not younger than Middle Jurassic and that it is probably of Lower Jurassic age. No well-founded record of the Cupressaceae has been previously known earlier than the Cretaceous.

THE conifer described in this paper, *Cupressinocladus ramonensis* sp. nov., occurs in the form of compressions of small leafy shoots in a Jurassic black shale from the Makhtesh Ramon (Wadi Raman) in southern Israel. The material was collected from an exploratory tunnel dug in the Makhtesh with a view to exploiting the 'flint clay' (Würzburger 1958) in which the shale band occurred. A number of species of conifers were represented by fragments of leafy shoots and cones exposed on the bedding planes. One of us (J. L.) is preparing an account of these for publication elsewhere. The shoots dealt with here are of interest in having decussate leaves, and in being in their general character similar to those of living Cupressaceae. The age of the material, which is not younger than Middle Jurassic, is considered in more detail below.

A few fragments of *C. ramonensis* sp. nov. were seen exposed on the bedding planes of the rock, but much more material was obtained by bulk maceration of the matrix. Some breakdown of the shale was effected simply by soaking in water and subsequent drying, repeated a number of times. More complete breakdown was obtained by soaking pieces of shale in concentrated nitric acid for several days, washing off the acid, and soaking in dilute ammonia solution. Sieving of the residue produced several shoots comprising a few internodes which had cohered throughout the treatment. Others had separated into pairs or even single leaves. Some of these shoot fragments have been figured as opaque objects (Pl. 36, figs. 4 and 5) while others were further macerated in Schulze's solution (nitric acid and potassium chlorate), washed in distilled water, and mounted in glycerine jelly (Pl. 36, fig. 3). Individual leaves could be separated from shoots macerated in this way, and the upper and lower cuticles pulled apart and examined individually (Pl. 36, fig. 2).

The conifer shoots described here are assigned to the form-genus *Cupressinocladus* Seward. An emended diagnosis of the genus is given here, and the reasons for doing this are considered in the discussion below.

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SYSTEMATIC DESCRIPTION

CUPRESSINOCLADUS Seward 1919 emend.

Cupressinocladus Seward 1919, pp. 303–4.

Emended diagnosis. Conifer twigs with decussate leaf arrangement. Leaves small, decurrent, the free part not exceeding the length of the decurrent part.

Type species. C. salicornoides (Unger) Seward 1919, p. 307. Although Seward does not specifically cite this as the type species, it is the first species for which he uses the generic name *Cupressinocladus*, and it has accordingly been acknowledged by Andrews (1955) as the type species. Unger's figure (reproduced in Seward) leaves open the possibility that the leaves in this species were borne in groups of more than two—possibly in fours. Further, the cuticle of Unger's material is not known. However, we have had access to the holotype of Seward's own species, *C. valdensis* (see p. 240 below). This emendation of *Cupressinocladus* is meant rather as a more precise statement of what was intended by Seward than as a reinterpretation based on the type species.

Cupressinocladus ramonensis sp. nov.

Plate 36, figs. 1–8

Diagnosis. Branchlets without dorsiventral differentiation. Leaves decussate, regularly spaced. Leaf base decurrent, rectangular, in contact with the opposite leaf base. Distal part of the leaf free, one-quarter of the length of the decurrent part in larger shoots, but in smaller shoots, up to the full length of the decurrent part; triangular, concavo-convex. Junction of the small adaxial leaf surface with the remainder of the leaf marked with a narrow scarious margin. Stomata of the adaxial surface forming a few rows confined to the marginal zones, leaving the central part of this surface free of stomata. Abaxial surface with stomata rather widely separated in eight to fifteen regularly spaced longitudinal rows. Stomata monocyclic, or incompletely amphicyclic, with four to six (typically five) subsidiary cells, the walls of which are about as thick as the walls of the remaining epidermal cells. Majority of epidermal cells bearing a single cuticular papilla; each subsidiary cell bearing a broad rounded papilla extending over the stomatal aperture. Guard cells not seen, presumably lying originally below the level of the subsidiary cells and overlapped by them.

Syntypes. Specimens number V 36332 and V 36334, British Museum (Natural History); Plate 36, figs. 3 and 4.

Occurrence. From the plant bed in the 'Marly Cuesta' of the Lower Jurassic (Nevo 1954) from the exploratory tunnel of the Israel Mining Company at lat. 30° 37′ 15″ N., long. 34° 54′ 50″ E. (Survey of Israel Grid ref. 1417500350); Makhtesh Ramon, Israel.

Description. Only short leaf-bearing branchlets 2–4 mm. wide have been found. The free part of the leaf is about equal in length to the decurrent part in some leaves (cf. Pl. 36, fig. 4) but may be only a quarter that length in others (cf. Pl. 36, fig. 3). The free part of the leaf is concavo-convex (Pl. 36, figs. 1, 3), more or less appressed to the branch, with a pointed tip of which the margins subtend an angle of about 60°. The small adaxial surface has stomata confined to two to three lateral rows which converge

towards the apex, leaving a central zone of about one-half the total width free of stomata (Pl. 36, fig. 2). Apart from the stomata and subsidiary cells the epidermis is composed of rectangular cells each bearing a papilla with its apex turned so as to lie at the distal end of the cell. Towards the edge of the leaf the epidermal cells become narrower and more heavily cutinized, merging into a scarious margin consisting of one layer of cells elongated perpendicular to the edge of the leaf. The abaxial surface is in contact at its margin with the corresponding margin of the opposite leaf (Pl. 36, fig. 3). The stomata, in eight to fifteen longitudinal rows, are rather sparse in the proximal part of the leaf. Higher up the leaf they are rather uniformly arranged in longitudinal rows which are separated by four to six rows of normal epidermal cells. Two to four epidermal cells lie between the subsidiary cells of neighbouring stomata of the same row. Only very few stomata within a row are ever seen with their subsidiary cells in contact. The stomatal apparatus, including the four to six subsidiary cells, is 45–50 μ across. The subsidiary cells are all of similar shape, with radial and tangential walls about as thick as, or slightly thinner than, those of typical epidermal cells. Some of the epidermal cells in contact with the subsidiary cells have one or two of their walls continuous with the radial walls of the subsidiary cells, and the stomata may therefore be regarded as being incompletely amphicyclic (Pl. 36, figs. 6–8). The inner tangential wall of each subsidiary cell bears a broad hemispherical papilla. The development of this papilla is such that in the flattened cuticle the papillae sometimes seem to fill the whole stomatal aperture (Pl. 36, fig. 7). The almost circular shape of the stomata and the absence of the guard cells make it difficult to determine the orientation of the stomatal apertures. The general impression given is that the orientation is more or less random.

SOURCE AND AGE OF MATERIAL

The plant bed containing *Cupressinocladus ramonensis* is exposed in an exploratory tunnel in the Makhtesh Ramon (see p. 236 above for the exact location). A map showing the position of the Makhtesh is given in Hudson 1958, p. 417. Shaw (1947, pp. 20–21) gives the complete Jurassic sequence in the Makhtesh. In his account the bed containing the plant remains is that shown as the 18-metre layer extending from 40·2–58·2 metres

EXPLANATION OF PLATE 36

Figs. 4 and 5 have been photographed by reflected light and the remainder by transmitted light.

Figs. 1–8. *Cupressinocladus ramonensis* sp. nov. from the Jurassic of Makhtesh Ramon, Israel. 1, Cuticle of a whole leaf, ×30. In the upper part the cuticles of both adaxial and abaxial surfaces are superimposed, and at the left side the abaxial cuticle is folded over. Several longitudinal rows of stomata are recognizable over most of the length of the leaf. The scarious margin can be seen along much of the right-hand edge (V.36333). 2, Cuticle of the adaxial (upper) leaf surface, showing central band of papillate cells free of stomata, and the several marginal stomatal rows, ×80 (V.36331). 3, Cuticle preparation of a whole leafy shoot showing the decussate decurrent leaves, ×10 (V.36334). 4, 5, Leafy shoots, after removal from the matrix, showing decussate leaf arrangement and variation in leaf shape, ×10. 6, Part of the cuticle of the abaxial leaf surface from the decurrent part of the leaf, showing rectangular epidermal cell outlines, low rounded papillae, and two stomata, ×300 (V.36336). 7, 8, Two stomata from the vicinity of the last preparation; the guard cells are missing, only the subsidiary cells indicating the positions of the stomata. Papillae overarch the stomatal aperture, almost obliterating it in fig. 7; ×600 (V.36336).

(The numbers in brackets are slide numbers in the Palaeontology collection of the British Museum, Natural History, London.)

from the base of the 458 metres assigned to the Jurassic. Nevo (1954) places the bed (which is included in his 'Marly Cuesta') even closer to the base of the Jurassic, within the 'Lower Marine Jurassic (Lias)'.

Palaeontological evidence for the dating of the plant bed is as follows. Shaw (1947) records '*Terebratula subsella* and *Rhynchonella moravica*' from 350 metres above the plant bed horizon. According to Dr. R. G. S. Hudson (verbal communication Oct. 1958) this latter species, when recorded from this area, can be regarded as representing *Somalirhynchia jordanica* (Noetling), and in association with *T. subsella* this indicates an Oxfordian (s.l.) age. This means that the plant bed is certainly older than Upper Jurassic. Mr. Lehrman (Geological Institute of Israel, verbal communication Dec. 1958) states that 32 metres below the plant bed there is a limestone band containing *Myophoria* sp., indicating an Upper Triassic age; and that 20 metres above the plant bed the occurrence of *Nerinella* indicates a Lower Jurassic age. This would mean that the plant bed is not younger than Lower Jurassic, nor older than Upper Triassic.

DISCUSSION

Generic assignment. The genus *Cupressinocladus* was made by Seward (1919, p. 303) for 'vegetative shoots agreeing in habit of branching and in the predominance of a decussate arrangement of appressed leaves with recent Cupressineae such as *Cupressus*, *Thuya*, *Libocedrus*, and similar types. When cones are present which throw any light on generic affinity some other term should be adopted.' Seward leaves open the rather critical question of just what constitutes predominance in this context. In the past there has been some confusion as to whether some small-leaved *Cupressus*-like leafy shoots had a truly spiral or decussate leaf arrangement. Kendall (1949) has pointed out that several of Sternberg's *Thuites* species had in fact spirally arranged leaves of the *Brachyphyllum* type. We have given an emended diagnosis of *Cupressinocladus* to restrict it to forms showing an exclusively opposite leaf arrangement. Seward gave no formal diagnosis, but the type species that he uses (*C. salicornoides*) and his own species (*C. valdensis*) are in accord with this emendation. Defined in this way, *Cupressinocladus* becomes a form genus comparable with the spiral-leaved genera *Brachyphyllum* and *Pagiophyllum*, but having decussate, *Cupressus*-like leaves. *Cupressinocladus* may consequently include forms other than Cupressaceae; decussate leaves are not restricted to this one family in the conifers, but occur also in the Podocarpaceae and Taxodiaceae. Within this latter family, the leaf arrangement of *Metasequoia* combined with the leaf shape of *Sequoiadendron* would give the essential characters of *Cupressinocladus*. However, when cuticle characters are also available, as with our material, more certain evidence of affinity is available.

Several genera, having priority in date of publication over *Cupressinocladus*, have been based on leafy conifer shoots with minute decussate (or supposedly decussate) leaves. A few are based on fertile material, but the cuticle characters of the majority are unknown. Of these genera, the two following warrant close comparison with *Cupressinocladus*:

1, *Frenelopsis* Schenck 1869. This genus was based on *Thuites hoheneggeri* Ettingshausen (1852), from the Lower Cretaceous of Austria; this consisted of leafy conifer shoots with very reduced, whorled leaves. According to Seward (1919, p. 343) the leaves

were borne sometimes in twos, sometimes in whorls of four, although Schenck (1869) in his diagnosis mentions only pairs of decussate leaves. Zeiller's (1882) re-examination of this species makes it clear that the leaves were borne in fours, and that the leaves of each whorl are partially fused along their margins. Florin (1955) considers that on their vegetative structure alone (wood attributed to this genus, and its cuticle) *Frenelopsis* is of Cupressaceous affinity. While this gives *Frenelopsis* a claim to being one of the earliest known Cupressaceae, the arrangement of its leaves in fours is a clear distinction from the Israeli material described here.

2, *Widdringtonites* Endlicher 1847. Endlicher founded this genus on a number of previously described specimens, including *Thuites gramineus* Sternberg and *Juniperites baccifera* Unger 1843. The inclusion of the latter species is particularly significant as Unger's material of *J. baccifera* was fertile. Unger describes the 'fruit' as being of about the same size as those of *Juniperites communis*. Endlicher describes the leaves of *Widdringtonites* as spiral in arrangement, although Unger's figures of *Juniperites baccifera* (loc. cit., pl. 21, figs. 1–3) suggest a decussate arrangement, and Berry's fertile material of *Widdringtonites* from Alabama (Berry 1912) is also clearly decussate. Regardless of leaf arrangement, *Widdringtonites* is based on material with well-characterized cones, and should accordingly be reserved for specimens with the same type of fructification, or for specimens with cuticle characters giving strong evidence of affinity with such material.

Saporta (1894) described and figured some apparently decussate shoots from the Upper Jurassic of Portugal under the name *Widdringtonites*. Some of Saporta's figures superficially resemble the Israeli material described here. Teixeira (1948) has since reassigned this material of Saporta's (which the latter author had placed in *Palaeocyparis*, *Brachyphyllum*, *Thuites*, and *Widdringtonites*) to a single species, *Cyparissidium micromerum*. The type of this genus (*Cyparissidium gracile* Heer) has a spiral arrangement of the leaves and cone scales, and Teixeira also describes cones with spirally arranged scales in his Portuguese material. From this work of Teixeira it is evident that the decussate leaf arrangement suggested by some of Saporta's figures may be misleading and that further comparison between our Israeli material and the Portuguese based solely on Saporta's figures would be unwise.

Comparison with Cupressinocladus valdensis *Seward*. *Cupressinocladus valdensis* Seward is based on a single specimen of a leafy conifer shoot from the British Wealden (Seward 1895, p. 209, pl. 20, fig. 6). This is still the only specimen of the species known to us. Originally described as *Thuites valdensis* Seward 1895, the species was transferred to *Cupressinocladus* by Seward (1919) when he erected that genus. Examination of the holotype (British Museum, Natural History No. V 2139) shows that the leaves are small, appressed, have strongly decurrent bases, and are undoubtedly decussate in arrangement. In its general superficial appearance it is quite similar to some specimens of the Israeli *Cupressinocladus ramonensis*.

The carbonaceous matter of Seward's holotype was fractured by shrinkage into minute fragments. Such a leaf fragment was removed from the base of the specimen, and a cuticle preparation was made. This sufficed to show that its cuticle is distinct from that of *C. ramonensis*. Beyond this, we make no attempt to redescribe Seward's species here, nor to give a full account of its cuticle characters.

Our cuticle preparation of *C. valdensis* Seward consisted of a fragment about 1 mm. square, apparently from the decurrant base of a leaf; only a single cuticle was present and this was regarded as being that of the abaxial leaf surface. The cuticle was very much thicker and more opaque than that of the Israeli species, after similar maceration. We regard this as an original feature, and not an effect of different states of preservation. Forty stomata were counted on the fragment, arranged in rather clearly defined rows much as in *C. ramonensis*. At the contact between their subsidiary cells and the surrounding epidermal cells, a ridge of cuticle is developed, giving a dark rim encircling each of the stomata. The epidermal cells between the stomatal rows are rounded-rectangular, generally rather elongated in the longitudinal direction and lack papillae. The cuticle of *C. valdensis* therefore differs from that of *C. ramonensis* in its much greater thickness, the lack of papillae on the epidermal cells, and the markedly sunken stomata within an encircling cuticular ridge.

The affinity of Cupressinocladus ramonensis *sp. nov.* Only vegetative material of *C. ramonensis* is known at present, so that its attribution to a family of living conifers must be qualified to this extent. The only family of living conifers having opposite scale-like leaves with decurrent bases (as in *C. ramonensis*) is the Cupressaceae, and, so far as we know, no leafy shoots of this type ever occurred in any other family. The same general type of leaf arrangement and shape occurs in the Cupressaceae in the genera *Widdringtonia*, *Thuja*, *Thujopsis*, *Libocedrus*, *Cupressus*, and *Chamaecyparis*. Stomata occur in more or less clearly defined rows on both leaf surfaces in these genera as in *Cupressinocladus ramonensis*; however, our fossil differs from all of them in having the stomata on the lower (abaxial) leaf surface arranged in a series of longitudinal rows extending across the whole width of the leaf, instead of being restricted to two marginal stomatal bands (cf. Florin 1931). In their structure the stomata themselves are similar to those of several living Cupressaceae (*Thuja*, *Cupressus*) in being monocyclic or incompletely amphicyclic, with four to six subsidiary cells which are papillate. However, in our fossil the papillae overarch the stomatal aperture more than in those living Cupressaceae (e.g. *Libocedrus*) which have similar, distinct proximal papillae on the subsidiary cells. Papillate epidermal cells (similar to those of *C. ramonensis*) are widespread in the Cupressaceae. On the basis of this comparison it can be said that while *Cupressinocladus ramonensis* agrees with the Cupressaceae more closely than with any other family of conifers, it does not agree with any one living genus in all the features considered.

Hitherto there has been no bona fide record of the Cupressaceae earlier than the Cretaceous (cf. Arnold 1948). Florin (1958) in his recent work on Mesozoic taxads and conifers states (p. 383) that 'there are no indisputable members of the . . . Cupressaceae in northern Lower and Middle Jurassic floras'. The fossil described here appears to extend the record of this family back to at least the Middle Jurassic.

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J. LORCH
Botany Department,
The Hebrew University,
Jerusalem, Israel.
W. G. CHALONER
Botany Department,
University College,
London W.C. 1

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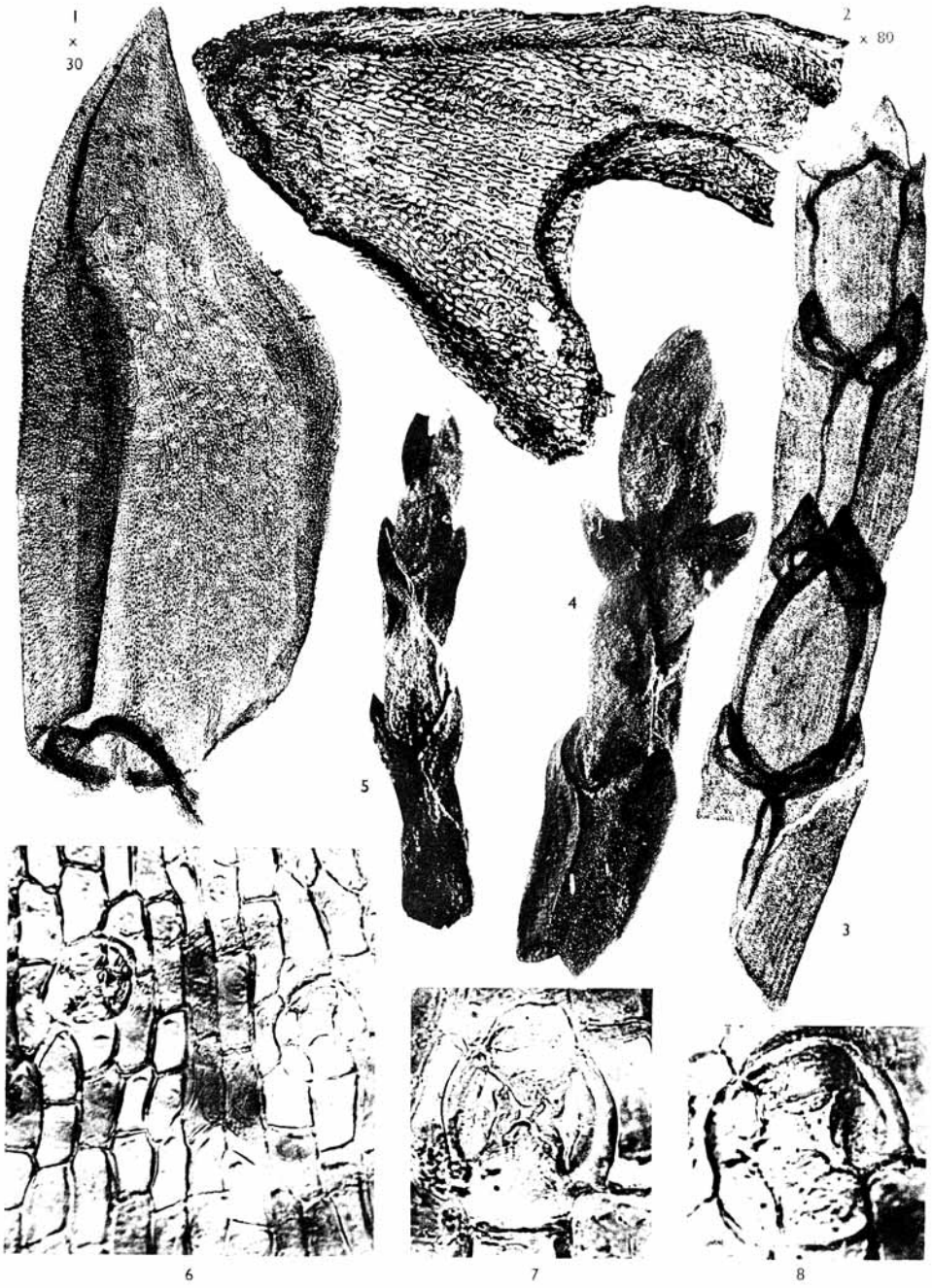

CHALONER and LORCH, *Cupressinocladus ramanensis* sp. nov.