

A new conifer species from the Wealden beds of Féron–Glageon, France

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Synopsis

Cuticle studies of various Lower Cretaceous conifers revealed a plant with several unusual features, here described as *Brachyphyllum carpentieri* n. sp., known only from the Wealden beds of Féron–Glageon (Nord), France. Whilst resembling a typical *Brachyphyllum* Lindley & Hutton ex Brongniart species in gross morphology, the combination of lobed leaf margin, abaxial glands, minute hypodermal cells and a complex form of stomatal apparatus distinguish it from any other known conifer, fossil or extant. Silicified wood from the same locality has been described by Lemoigne & Demarcq (1967) and may belong to the same plant.

Introduction

During the recent revision of some Lower Cretaceous conifer species several hand specimens in the foreign Cretaceous collection at the British Museum (Natural History) were re-examined. More precisely the revision of a supposedly widespread conifer *Sphenolepis kurriana* (Dunker) Schenk (Fisher 1981) led to the examination of French material previously thought to belong to this species (Carpentier 1927, 1939). These French specimens from Féron–Glageon were given to the Museum by A. Carpentier in exchange for English Wealden specimens. Hand specimens of the French material bear a close resemblance to known German specimens of *Sphenolepis kurriana* (Dunker) Schenk. Several cuticle preparations were made using Schulze's solution for maceration. When examined microscopically it was immediately apparent that this conifer displays several unique features which clearly distinguish it from the other revised conifer species. The combination of a lobed leaf margin with glands opening into the notches between the lobes and a complex stomatal apparatus, coupled with extensive minute hypodermal cells which completely obscure the epidermis, could lead one to question whether the cuticle is indeed coniferous. However, the leaf shape, phyllotaxy and pattern of stomatal distribution could hardly be more typical of many *Brachyphyllum* species. It is interesting to note that Lemoigne & Demarcq (1967) raised a similar question concerning silicified wood described from the same locality. Evidence of association led them to suggest that the wood and the leafy shoots belonged to the same conifer although the wood had some characteristics which were not typically gymnospermous.

Systematic description

Order CONIFERALES

Form-genus *BRACHYPHYLLUM* Lindley & Hutton ex Brongniart

Brachyphyllum carpentieri sp. nov.

Figs 1–10

1927 *Sphenolepidium kurrianum* (Dunker); Carpentier: 71; pl. 19, figs 1–7.

1939 *Sphenolepidium kurrianum* (Dunker); Carpentier: 157; pl. 1, figs 1–11.

DIAGNOSIS. Small shoots up to 3 mm wide. Leaves scale-like, tips free, arising from the centre of a rhomboidal leaf base cushion; leaf and basal cushion combined up to 3 mm long × 2 mm wide.

Free part of leaf up to one-third total length. Leaf margins converging at up to 55° towards bluntly pointed apex; margins microscopically lobed with glands present in notches between lobes.

(Adaxial cuticle imperfectly known). Abaxial cuticle up to $7\text{ }\mu\text{m}$ thick. Stomata occurring in two broad bands on leaf and basal cushion, concentrated on cushion, avoiding mid-line. Stomatal apparatus circular, guard cells deeply sunken below a ring of papillate, subsidiary cells; up to 6 papillae around rim of circular stomatal pit. Diameter of stomatal apparatus $28\text{--}44\text{ }\mu\text{m}$ ($n = 32$); stomatal orientation irregular. Ordinary epidermal cells rectangular or spindle-shaped, some bearing small papillae. Hypodermal cells small, oval to circular, strongly cutinized, randomly arranged in main part of leaf, diverging in lobes; $4\text{--}8\text{ }\mu\text{m}$ long \times $3\text{--}5\text{ }\mu\text{m}$ wide ($n = 100$) with straight, unpitted anticlinal walls up to $1.5\text{ }\mu\text{m}$ wide.

HOLOTYPE. V.17064, British Museum (Natural History).

TYPE LOCALITY AND HORIZON. Féron–Glageon (Nord), France. Barremian.

MATERIAL. This species is common in the Wealden beds of Féron–Glageon, the precise locality of which was poorly understood until Lemoigne & Demarcq (1967) published the following details. The beds are near the Hirson–Avesnes railway line; 1 km west of Couplevoie (parish of Glageon) and barely 100 m from the boundary of the parish of Féron.

NAME. The species is named after Alfred Carpentier.

Description

The description is based on the holotype, V.17064, from the foreign Cretaceous collection in the British Museum (Natural History), Fig. 1, together with information from the work of

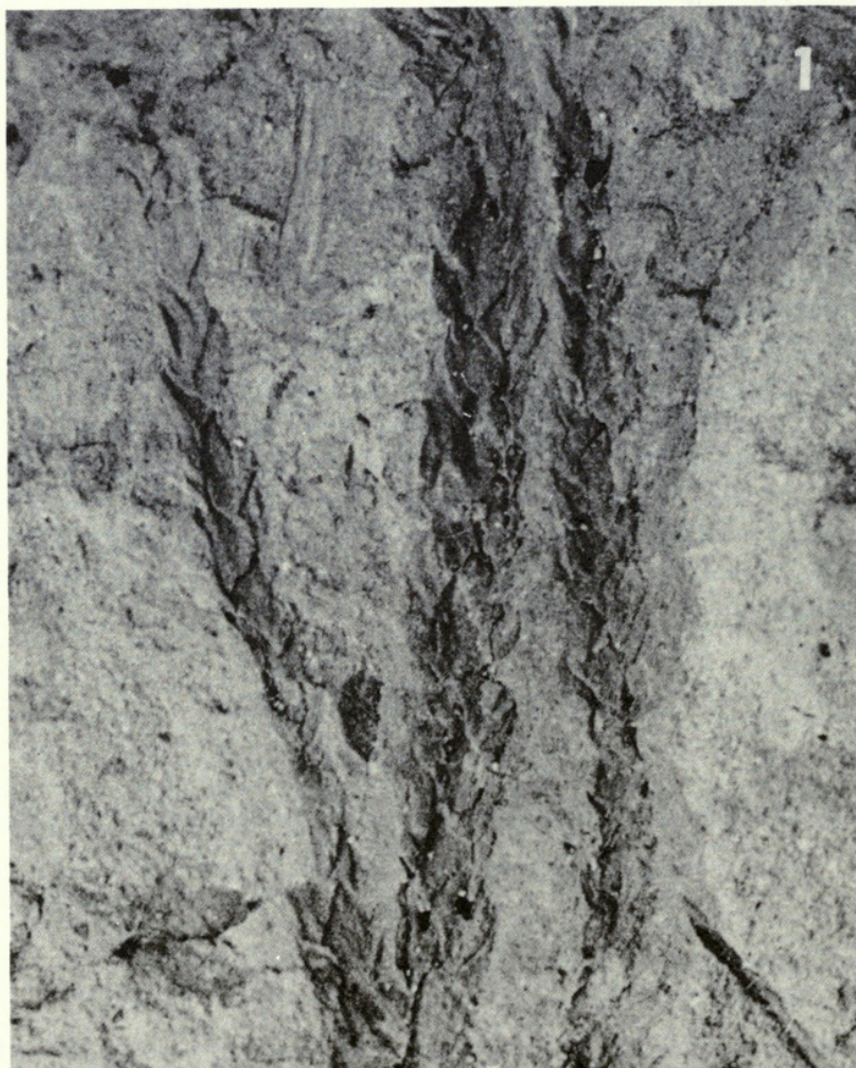
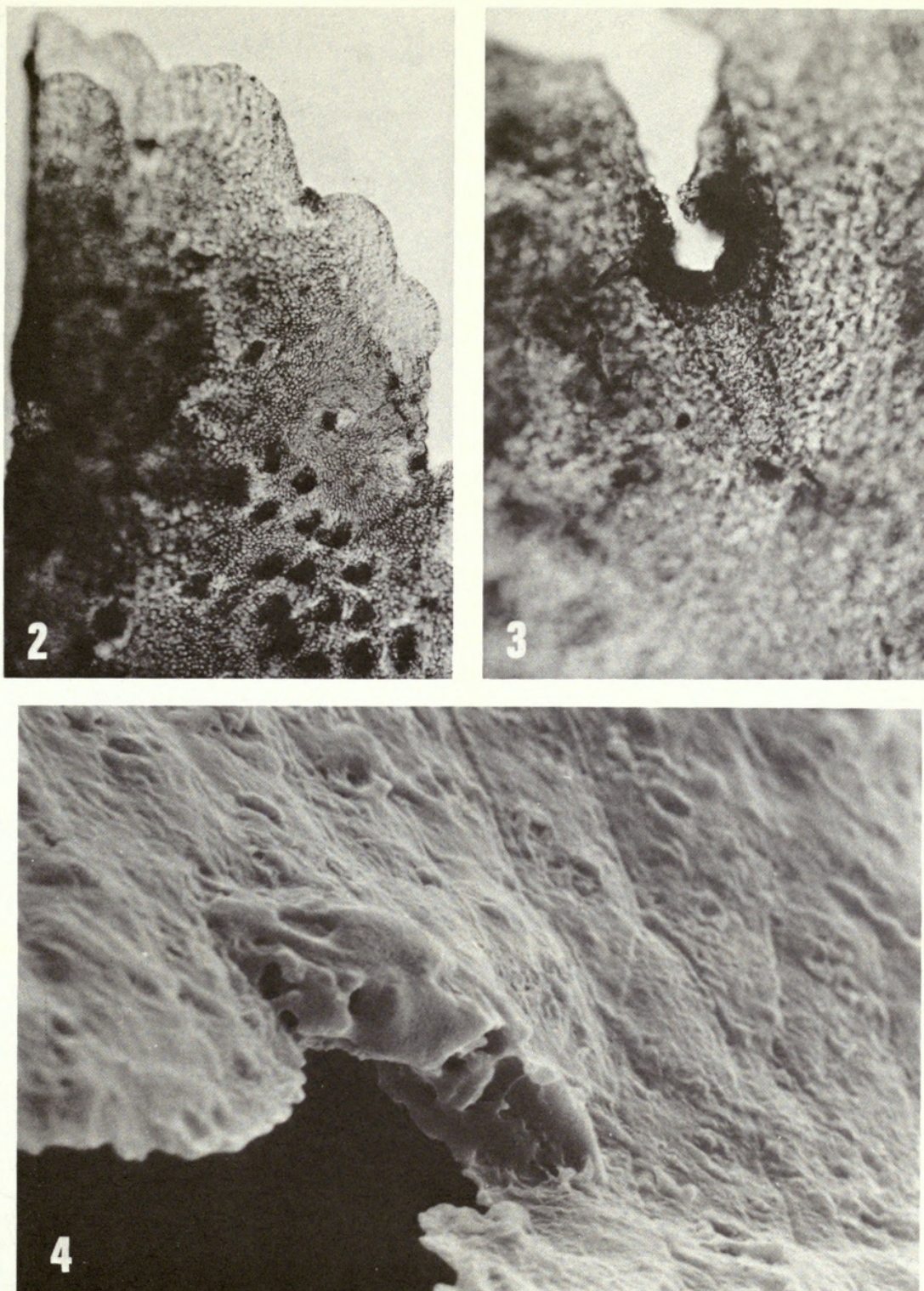
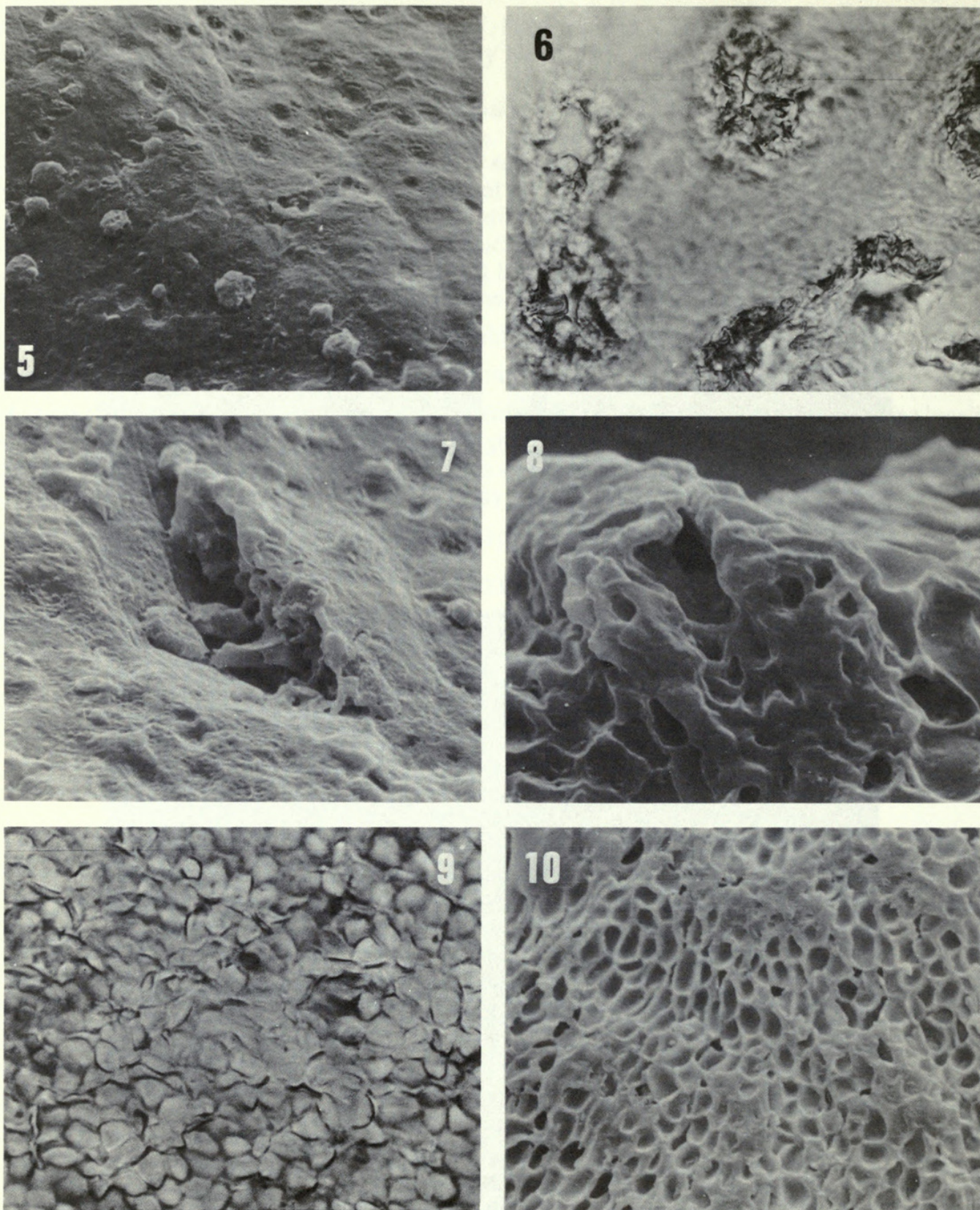


Fig. 1 *Brachyphyllum carpentieri* n. sp. Holotype, $\times 4$. V.17064, BM(NH).



Figs 2–4 *Brachyphyllum carpentieri* n. sp. Fig. 2, single leaf showing lobed margin; apex top left, patch of stomata bottom right, with unusual pattern of hypodermal cells between; $\times 100$. Fig. 3, margin of leaf showing portions of two lobes with gland in notch between; $\times 175$. Fig. 4, SEM view of portions of two marginal lobes in foreground with gland in notch between. Spindle-shaped epidermal cells with pitted walls show clearly on the right; $\times 700$. All preparations from holotype, V.17064.

Carpentier (1927, 1939). Three of Carpentier's figures (1939: pl. 1, figs 1–3) agree with the cuticle obtained from the holotype in every detail. The remaining figures show the epidermal cells and subsidiary cells of the stomata; such detail has not been seen in cuticle preparations of the holotype. The small amount of cuticle remaining on V.17064 is thick and easy to prepare but most of the preparations are from the abaxial surface. Only a small part of the adaxial surface was seen, thus the stomatal distribution on the adaxial surface is still unknown.



Figs 5–10 *Brachyphyllum carpentieri* n. sp. Fig. 5, SEM view of outer surface showing papillae, pits and faint outlines of epidermal cells; $\times 700$. Fig. 6, group of stomata showing subsidiary cell papillae around stomatal pits; $\times 400$. Fig. 7, SEM view of outer surface showing probable stomatal pit; pits and papillae were as ill-defined as this in all SEM preparations. Epidermal cells just discernible; $\times 1000$. Fig. 8, SEM view of inner surface of cuticle showing a stoma closely invested with highly cutinized hypodermal cells. Guard cells missing; $\times 2000$. Fig. 9, hypodermal cells seen by light microscope; $\times 700$. Fig. 10, hypodermal cells by SEM; $\times 700$. All preparations from holotype, V.17064.

The epidermal details of the abaxial surface, though clearly seen in several of Carpentier's figures, are extremely difficult to distinguish in the preparations from the holotype because they are totally obscured by the tiny, thickly cutinized hypodermal cells. Under the light microscope ordinary epidermal cells are impossible to detect, but when the outside surface of the cuticle is viewed by scanning electron microscopy (SEM) the outlines of these cells are discernible (Figs 4, 5). They are long and rectangular or spindle-shaped, resembling those figured by Carpentier (1939: pl. 1, figs 4, 5). In these preparations of Carpentier, showing the epidermal cells clearly, there is no sign of hypodermal cells. Some epidermal cells bear papillae, often several per cell, but we can detect no pattern to the distribution of papillate cells. Many cells have pores or pits in the outer periclinal walls (Fig. 5), a feature exhibited by another Wealden conifer species (*Brachyphyllum obesum* Heer), which is to be redescribed in detail elsewhere.

In the greater part of the leaf and cushion the hypodermal cells are arranged in long arcs which radiate from the centre, swirl around the stomata and then diverge in the marginal lobes (Fig. 2). When the inside surface of the cuticle is viewed by SEM the nature of these hypodermal cells is fairly clear (Fig. 10). They are quite thickly cutinized, unpitted and very small, certainly the smallest of any conifer known to us.

The details of the stomatal apparatus are still imperfectly understood. Carpentier's figures (1939: pl. 1, figs 4, 6, 9, 10) show the stomatal apparatus to have 4–6 subsidiary cells with occasional encircling cells present. In V.17064 the hypodermal cells completely obscure the subsidiary cells (Fig. 6). Individual subsidiary cells have not been observed but using the light microscope up to six papillae have been seen around the stomatal pit. The stomata in Fig. 6 show those papillae quite clearly, yet by SEM the pits and papillae all appear ill-defined, as in Fig. 7. The guard cells are quite deeply sunken and have only been seen as rather eroded remnants.

The multicellular glands deeply embedded in the leaf tissue are another unusual feature. They frequently occur below many of the notches separating the marginal lobes and several are apparent in other parts of the leaf surface. The glands appear conical in shape with the widest part of the cone opening into the notches (Figs 3, 4).

Discussion

The shoots of this species closely resemble those of *Sphenolepis kurriana* (Dunker) Schenk in gross morphology and the original attribution by Carpentier is quite understandable. The cuticle however is unique, bearing no resemblance to *S. kurriana* or to any other conifer, fossil or extant, that we have seen. A similar lobed leaf margin has been seen in one other conifer, from the Lower Cretaceous of China, but the cuticles of the two species differ considerably (Zhou Zhiyan, personal communication).

The presence of glands on the abaxial surface, whilst not unknown in conifers, is certainly not common. Many extant members of the Cupressaceae have prominent resin glands but of the species we have studied none bear any resemblance to *Brachyphyllum carpentieri*, where the glands open into the notches of the leaf and involve a complex organization of the epidermal cells.

Wood described by Lemoigne & Demarcq (1967) as *Dadoxylon arduennense* may belong to the same plant as *Brachyphyllum carpentieri*. The silicified wood indicates a tall arborescent plant which was at least 20 cm in diameter at the base of the trunk. The wood is of a type limited to the Jurassic–Cretaceous. It is characterized by septate tracheids which are unknown in modern gymnosperms. The nature of these septa is unclear and indeed it is difficult to conceive what function they may have had in the water transport system. Lemoigne & Demarcq stress that they cannot confirm that the wood is coniferous and comment that the affinity of the wood may be closer to that of the Caytoniales, which are also represented at Féron–Glageon.

If, however, *D. arduennense* should prove to be coniferous it seems probable that the unique structure of the wood combined with the unusual cuticle characters of *B. carpentieri* imply a specific adaptation to particular environmental conditions.

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