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To cite this article: Elliott Capel, Cyrille Prestianni & Borja Cascales-Miñana (2022) Revisiting the Rebreuve plant assemblage from the Lower Devonian of Artois, northern France, Botany Letters, 169:4, 540-556, DOI: [10.1080/23818107.2022.2101516](https://doi.org/10.1080/23818107.2022.2101516)

To link to this article: <https://doi.org/10.1080/23818107.2022.2101516>



Published online: 01 Aug 2022.



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## Revisiting the Rebreuve plant assemblage from the Lower Devonian of Artois, northern France

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### ABSTRACT

French Lower Devonian floras are rare, especially compared to certain other Western European countries. In this study, we reassess an assemblage collected in the 1930s in the Rebreuve quarry (Pas-de-Calais, northern France). We describe new features in several taxa and update taxonomic names from original descriptions. For instance, re-examination of vegetative remains previously described as *Psilophyton princeps*, led to the discovery of fertile structures allowing us to refer these specimens to *Sawdonia*. In total, this flora consists of 10 taxa, including up to four different *Psilophyton* species, such as *P. parvulum*. Other taxa include *Danziella artesianiana*, *Drepanophycus* cf. *spinaeformis*, *Sporogonites exuberans* and some specimens of *Taenioocrada* and *Sciadophyton*, revealing a diverse Lower Devonian plant assemblage. The Rebreuve assemblage represents a typical Emsian flora from Laurussia and bears striking resemblance with coeval Belgian assemblages. Previous palynological investigations, in addition to the similarities with well-dated Belgian floras, suggest an early Emsian age for this assemblage. The paleogeographical implications of findings are discussed.

### ARTICLE HISTORY

Received 31 March 2022  
Accepted 8 July 2022

### KEYWORDS

Lower Devonian; France;  
plant fossils; Rebreuve;  
*Sawdonia*; *Psilophyton*;  
*Drepanophycus*

### Introduction

Western Europe has historically been a major source of Lower Devonian plant fossils (see e.g. Gerrienne 1983, 1993; Schweitzer 1983; Edwards and Richardson 2004; Morris and Edwards 2014; Gossmann et al. 2021). Lower Devonian outcrops in northern France (Artois region) are far less extensive, compared to the nearby Belgian Ardennes and German Rhenish region. Plant fossils have only been recovered from a handful of localities (Bertrand 1913; Corsin 1933; Degouy 1973; Leclercq 1975). Lower Devonian plants were first discovered in the Artois region by Gosselet and Dollé (1910) at a quarry in Matringhem (Figure 1a–b). Plant fossils were subsequently reported by Corsin (1933) at a quarry in Rebreuve (Figure 1c), 30 km ESE of Matringhem. However, this short note only included a brief account of the findings. The Rebreuve assemblage was then formally described by Danzé-Corsin (1956b), revealing a richer assemblage than previously thought. Twelve taxa were identified, including two new species: *Zosterophyllum artesianum* and *Yarravia minor*. More recently, reinvestigation of *Z. artesianum* was undertaken by Edwards (2006) leading to the erection of a new genus for this plant: *Danziella artesianiana*, classed as an *incertae sedis* taxon with zosterophyll affinities. Edwards (2006) emphasized, as well as other authors (e.g. Hao and Gensel 1995; Hao and Xue 2013; Gess and Prestianni 2021;

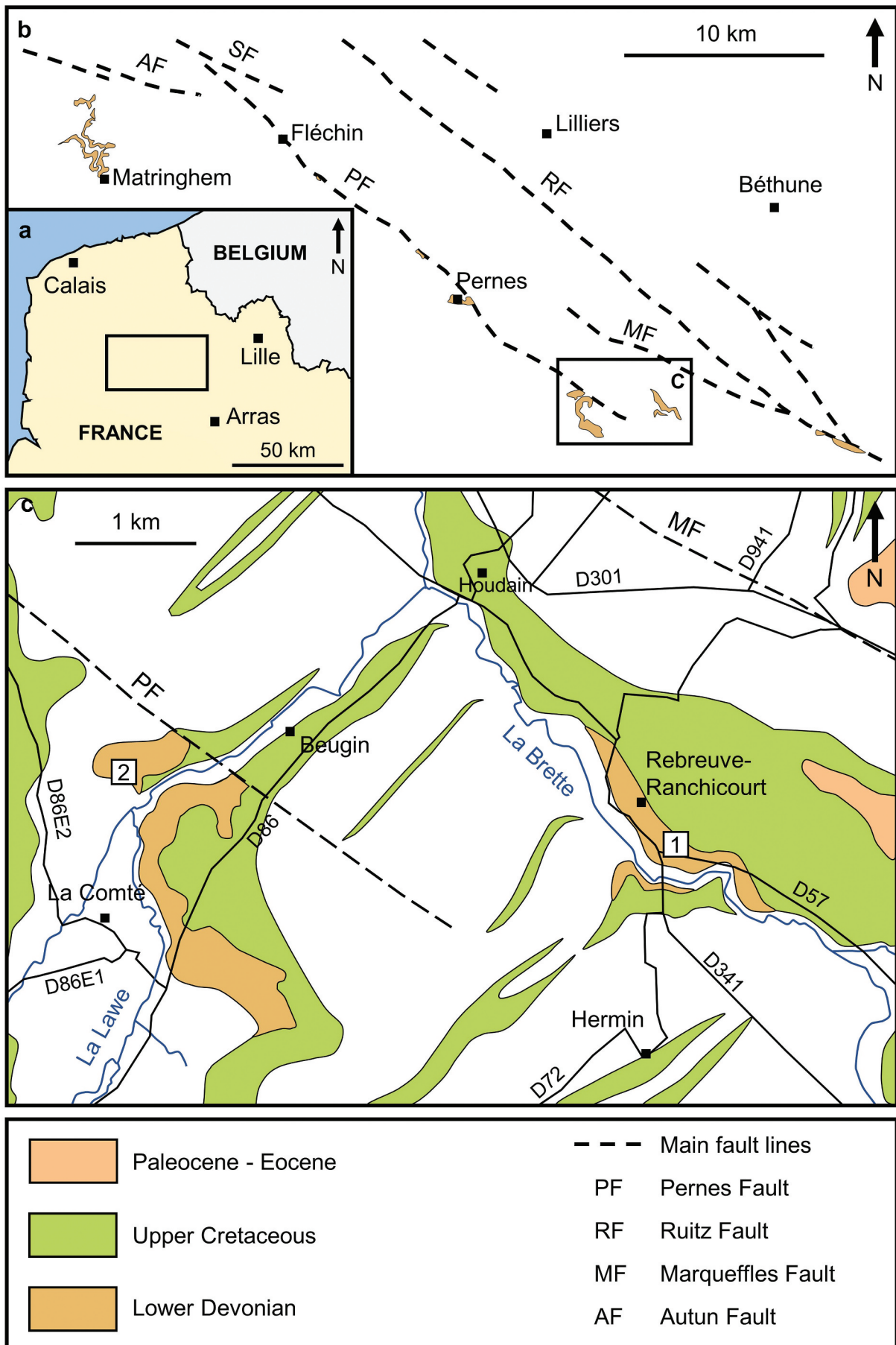
McSweeney et al. 2021), the necessity of reinvestigating the entire fossil content of this assemblage, as several taxa appeared dubiously identified.

Furthermore, the age of these localities in the Artois region is still not properly constrained. They were originally dated as Taunusien (~Pragian), mainly based on a correlation with other localities possessing a similar floral composition. However, this age is questionable. Further studies indicate younger ages using spore and ostracoderm biostratigraphy (Degouy 1973; Leclercq 1975; Blicek and Janvier 1989), leading Edwards (2006) to conservatively refer to these localities as Pragian–Emsian.

The aim of this paper is to provide a taxonomic revision of the Rebreuve assemblage described by Danzé-Corsin (1956b), based on specimens collected by Corsin (1933), housed within the paleontological collections of the University of Lille (France). The age of the flora is also reexamined using previous palynological studies and lithostratigraphic correlations. Finally, the composition of this flora and its paleophytogeographic implications are discussed.

### Geological setting and stratigraphy

Rebreuve is situated in the Artois region of the Pas-de-Calais department, France (Figure 1a–b). In this area, the Devonian basement is unconformably overlain by



**Figure 1.** Geography of the study area. a. Map of northern France showing the location of the study area. b. Map of the studied area highlighting the main fault lines and Devonian outcrops (Redrawn from Minguely et al. 2010). c. Geological map of Rebreuve-La Comté-Beugin redrawn based on scanned maps of northern France at 1/50,000 scale (<https://infoterre.brgm.fr/>), also including the location of plant fossil localities: 1. Rebreuve quarry, 2. Bois d'Épenin quarry.

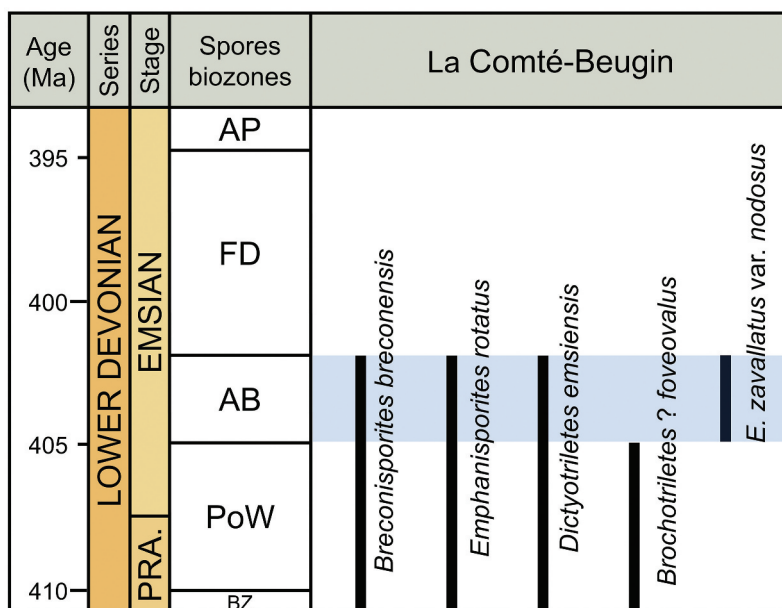
Cretaceous/Paleogene sediments. During the Cenozoic, Devonian sediments were uplifted because of structural inversion of Paleozoic normal faults, caused by the reactivation of the Midi thrust (Delattre 1969; Minguely et al. 2010). It is along this series of faults, generally oriented NW-SE, that Devonian rocks locally outcrop (Figure 1b). However, Devonian rocks are also exposed due to erosion caused by several rivers in the immediate vicinity of the faults (Figure 1c).

The Devonian outcrops in Rebreuve are situated in the Brette River valley between the Pernes and Marqueffles fault lines (Figure 1b–c). No natural exposure occurs in this area, and stratigraphy of the layers could only be characterized based on the outcrops unveiled by active quarrying operations (Loc. 1, Figure 1c). The Grès de Rebreuve Formation consists of white sandstones intermittently separated by red schists and mudstones (Delattre 1969). Plants were found at various levels within the sandstones in either white, grey or orange mudstone lenses, each more or less micaceous and sandy (Corsin 1933; Danzé-Corsin 1956b; Edwards 2006). Most of these lenses were sterile and only a few yielded plant remains (Corsin 1933). Unfortunately, the quarry is no longer active, and has since been flooded, making the outcrops inaccessible for additional sampling. Corsin (1933) and Danzé-Corsin (1956b) argued that the plant remains had not been transported over long distances (autochthonous or parautochthonous assemblage), as some specimens are well-preserved and sometimes nearly complete (e.g. *Danziella artesianana*). Nevertheless,

Delattre (1969) interpreted the facies as coastal or lagoonal, similar to the other Lower Devonian outcrops of the region.

The La Comté-Beugin massif represents the closest Devonian outcrops to Rebreuve, occurring along the Pernes fault line, and further south along the Lawe river banks about 3 km west of Rebreuve (Loc. 2, Figure 1b–c). In this area, spores were found in grey to green fine-grained shales, in the Bois d'Épenin quarry (Degouy 1973; Loc. 2, Figure 1c), associated with “*Psilophyton*” fragments, without any further description nor illustrations of the macroflora. These specimens could not be located within the collections of the University of Lille. Spores were identified by M. Strel (Liège) in Degouy (1973) and the locality was originally dated as late Pragian. However, our taxonomic revision of the assemblage instead suggests an early Emsian age (Figure 2). Contrary to the La Comté-Beugin and Matringhem areas, a detailed study of the Rebreuve Devonian outcrops has not been undertaken, and no previous attempts have been made to date these rocks. Our own attempts to recover palynomorphs were all unsuccessful.

The Devonian basement being covered by Cretaceous sediments, the dip and direction of Devonian sediment layers around Rebreuve are mostly unknown and quite complex near this fault system. It is therefore difficult to directly extrapolate an age for the Rebreuve assemblage based on La Comté-Beugin outcrops. Nevertheless, the “Grès de Rebreuve” Formation has been interpreted to be an analog to the other sandstone formations of the region, based



**Figure 2.** Stratigraphic ranges of several key spore taxa described in La Comté-Beugin. Blue boxes represent the assigned temporal interval of each locality. Absolute ages according to the International Chronostratigraphic Chart (v2020/12). Miospore biozones according to Steemans (1989) adapted from the Geological Time Scale (Gradstein et al. 2020): BZ, *breconensis*–*zavallatus*; PoW, *polygonalis*–*wetteldorfensis*; AB, *annulatus*–*bellatulus*; FD, *foveolatus*–*dubia*; AP, *apiculatus*–*proteus*. Abbreviations: PRA., Pragian.

on their similar lithofacies (Delattre 1969; Blicke et al. 1988). Since an (early) Emsian age has been recovered both in La Comté-Beugin (Figure 2) and Matringhem-Vincly (Leclercq 1975) using spore biostratigraphy, a similar age can be assumed in Rebreuve. Without any biostratigraphic tools to directly date Rebreuve rocks, this age remains equivocal, but the association of plants described in this paper seems to corroborate this estimation (see discussion).

## Materials and methods

The Rebreuve assemblage consists of about 100 specimens collected by P. Corsin and P. Bertrand in 1933 during a thorough sampling in the Rebreuve quarry (Loc. 1, Figure 1c). Fossils are preserved as adpressions and impressions. Unfortunately, a few specimens illustrated in Danzé-Corsin (1956b) could not be reinvestigated as they could not be located within the collections. Although P. Danzé-Corsin already undertook some *dégagement* on certain specimens, additional *dégagement* was performed using triangular steel needles to reveal further details (Fairon-Demaret et al. 1999). Macrophotography was achieved using a CANON EOS 700D and a macro lens. Studied plant fossils are housed in the paleontological collections of the University of Lille, France.

## Plant descriptions

### *Incertae sedis* Bryophyta

#### 1. *Sporogonites exuberans*

1956b *Sporogonites exuberans* Halle, Danzé-Corsin, pl. III, figs. 9–9a.

**Material.** This plant is represented by a single specimen (part and counterpart) numbered USTL 3709A and USTL 3709B (Figure 3a).

**Description.** This specimen consists of an undivided slender axis bearing a single terminal sporangium (Figure 3a). The stem is 8 mm long and its maximum width reaches 0.25 mm. The stem is not connected to any other structure and appears truncated at its base. The shape of the sporangium is ellipsoidal with an acutely pointed apex and is 4.5 mm long, and 1.7 mm wide at its maximum. The distal part of the stem progressively widens. The lower half of the sporangium is marked by at least four longitudinal ridges alternating with grooves. The base of the sporangium is 2.4 mm long and separated from the 1.8 mm long apical area by a 0.3 mm median ridge.

**Interpretation.** Elongated sporangia borne terminally on a slender and smooth undivided axis are singular to the genus *Sporogonites*, firstly described by Halle (1916) based on specimens from Røragen, Norway. The type species *S. exuberans* discovered in Norway was subsequently found in the Pragian and Emsian of Wales (Croft and Lang 1942) and Belgium (Lang 1937; Stockmans 1940; Andrews 1958; Gerrienne 1993). Other species include *S. chapmanii* from Australia (Lang and Cookson 1930) and *S. yunnanense* from China (Hsü 1966). However, *Sporogonites* was subsequently discovered in older (late Silurian–Lochkovian) strata in Brazil (Gerrienne et al. 2001; Gonez 2012), Vietnam (Gonez 2012) and South Africa (Gess and Prestianni 2021).

A wide array of sporangial morphologies was documented among all currently recognized species (Bharadwaj 1981). One of the most distinctive features of this Rebreuve specimen is the sporangium's acutely pointed apex (Figure 3a), whereas most species possess a rounded to bluntly pointed apex. This feature is uniquely known to occur in one early Emsian locality from Belgium, in the Carrière du Bois de Bescaille in Estinnes-au-Mont (Stockmans 1940). The distinct nature of these specimens already led Lang (1937) to refer to them as *S. exuberans* f. *belgica*. Stockmans (1940) illustrated a few of these specimens (Planche IV, figures 6, 8), without distinguishing them from other *S. exuberans* occurrences in Belgium. However, Bharadwaj (1981) went further than Lang (1937) and created a new species (*S. belgica*) to accommodate them, characterized by “oval capsules with acutely conical tips and the apical and basal part separated by a median, wide band”. This emendation of the genus and species was subsequently ignored in the literature. Gerrienne (1993) in his inventory of Belgian Early Devonian plants still classed all Belgian specimens as belonging to *S. exuberans*. We thereby refer to this specimen as *S. exuberans*, whilst acknowledging its distinctiveness from the type specimens from Norway. Reinvestigation of the genus would be required to further discriminate if it is a distinct species or whether the morphotype falls within the range of intraspecific variability of *S. exuberans*.

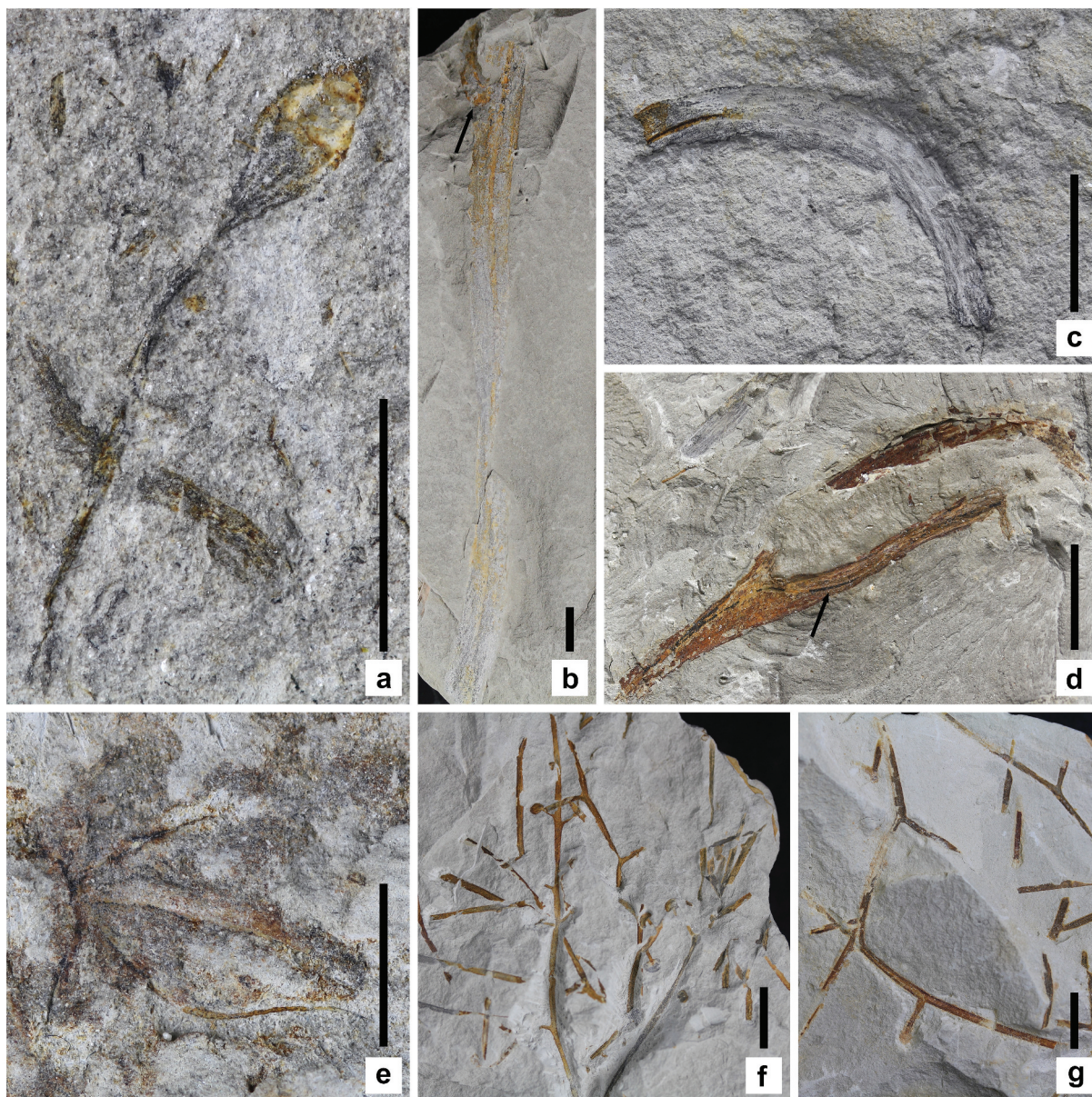
### Rhyniopsida

#### 2. *Taeniocrada* sp.

1933 *Taeniocrada* sp. White, Corsin

1933 *Taeniocrada decheniana* Kräusel and Weyland, Corsin

1956b *Taeniocrada decheniana* Kräusel and Weyland, Danzé-Corsin, pl. II, figs. 7–8.



**Figure 3.** Plant fossils from the Rebreuve assemblage, France (l). a, *Sporogonites exuberans*, axis bearing a single terminal sporangium, USTL3709B. b, *Taeniocrada* sp., general view of specimen USTL 3643; note the location of an anisotomous dichotomy at arrow. c, *Taeniocrada* sp., axis showing a central vascular strand and vascular strand trace, USTL3674B. d, *Taeniocrada* sp., specimen displaying an isotomous dichotomy; note the meandering vascular strand at arrow, USTL 3818. e, *Sciadophyton* sp., general view of specimen USTL 3686. f, *Danziella artesiana*, general view of lectotype showing axes bearing sporangia on short stalks, USTL 3595A. g, *Danziella artesiana*, specimen showing sterile axes, isotomously branched at a wide angle, USTL 3610A. Scale bars: a, e = 5 mm; b–d, f–g = 10 mm.

**Material.** Several fragments are found scattered in numerous samples. Description is here based on best preserved specimens: USTL 3643 (Figure 3b), USTL 3669, USTL 3674B (Figure 3c), USTL 3699A and USTL 3818 (Figure 3d).

**Description.** This plant consists of smooth naked axes measuring between 2.5 and 11.6 mm wide. The longest axis measured is 14.8 cm long (Figure 3b). A conspicuous vascular strand or vascular strand impression, less than 1.2 mm wide, can be observed on all specimens (Figure 3b–d). The width of the vascular strand is more or less proportional to the width of the stem. This

vascular strand is usually found at the center of the axis (Figure 3c) but it can also be seen meandering on several specimens (Figure 3d at arrow). Branching is rare, although anisotomous (Figure 3b at arrow) and isotomous (Figure 3d) branching are recorded on separate specimens. No fertile axes were identified.

**Interpretation.** Naked axes showing a meandering vascular strand are typical of *Stockmansella langii* (basionym *Taeniocrada langii*) bearing lateral sporangia, and the fossil-genus *Taeniocrada* formerly solely based on sterile axes (Fairon-Demaret 1985, 1986). *Taeniocrada*-like axes are commonly found in Lower

Devonian strata (e.g. Kräusel and Weyland 1930; Stockmans 1940; Kennedy et al. 2012; Cascales-Miñana et al. 2015). Among well-defined Lower Devonian *Taenioocrada* species, *T. decheniana* is characterized by very frequent bifurcations and circinate tips. *T. dubia* is on the other hand exhibits small oblong punctae on the surface of axes. None of those features are recorded in the Rebreuve specimens. Vegetative axes herein described bear the most resemblance with those of *S. langii* and other vegetative axes defined as *Taenioocrada* sp. in Stockmans (1940, pl. VI, fig. 1b, pl. X, fig. 5). However, the lack of fertile structures precludes assignation of these specimens to either *Stockmansella* or any other species of *Taenioocrada* where fertile remains have been found (Taylor 1986). In addition, the lack of preserved anatomy of water-conducting cells is problematic as such axes may belong to a zosterophyll or a rhyniophyte. Considering all of this, we leave those specimens as *Taenioocrada* sp.

### Gametophyte *Incertae sedis*

#### 3. *Sciadophyton* sp.

1956b *Sciadophyton* cf. *laxum* (Dawson) Steinmann, Danzé-Corsin, pl. II, figs. 10–10a.

**Material.** Several poorly preserved specimens can be observed along a single bedding plane on one sample numbered USTL 3686. The best-preserved specimen is illustrated and provides a basis for description (Figure 3e).

**Description.** Four slender axes departing radially from an elongated center 2 mm in length and 0.5 mm wide. Axes between 3.2 and 10 mm long with a maximum width of 0.3 mm. The specimen is incompletely preserved so the actual number of axes radiating from the center is unknown.

**Interpretation.** Axes expanding radially from a center in a rosette-like configuration is characteristic of the genus *Sciadophyton* (Remy et al. 1980a, 1980b, 1992, 1993). This taxon is often found in other European Lower Devonian localities (i.e. Stockmans 1940; Croft and Lang 1942; Remy et al. 1992). Similar structures have already been interpreted as gametophytes of different taxa in different lineages such as *Zosterophyllum rhenanum*, *Stockmansella langii* (Schweitzer 1983) or *Huvenia kluei* (Hass and Remy 1991). Due to the specimen's incompleteness and until the affinities of *Sciadophyton* are clarified, it is wiser to refer to this specimen as *Sciadophyton* sp.

### Lycophytes – Zosterophyllopsida

#### 4. *Danziella artesiana*

See Edwards (2006) for complete description and discussion of these specimens.

**Material.** About 20 specimens have been identified in the collections. The lectotype numbered USTL 3595A (Figure 3f), as well as sterile axes USTL 3610A, Figure 3g), are here illustrated.

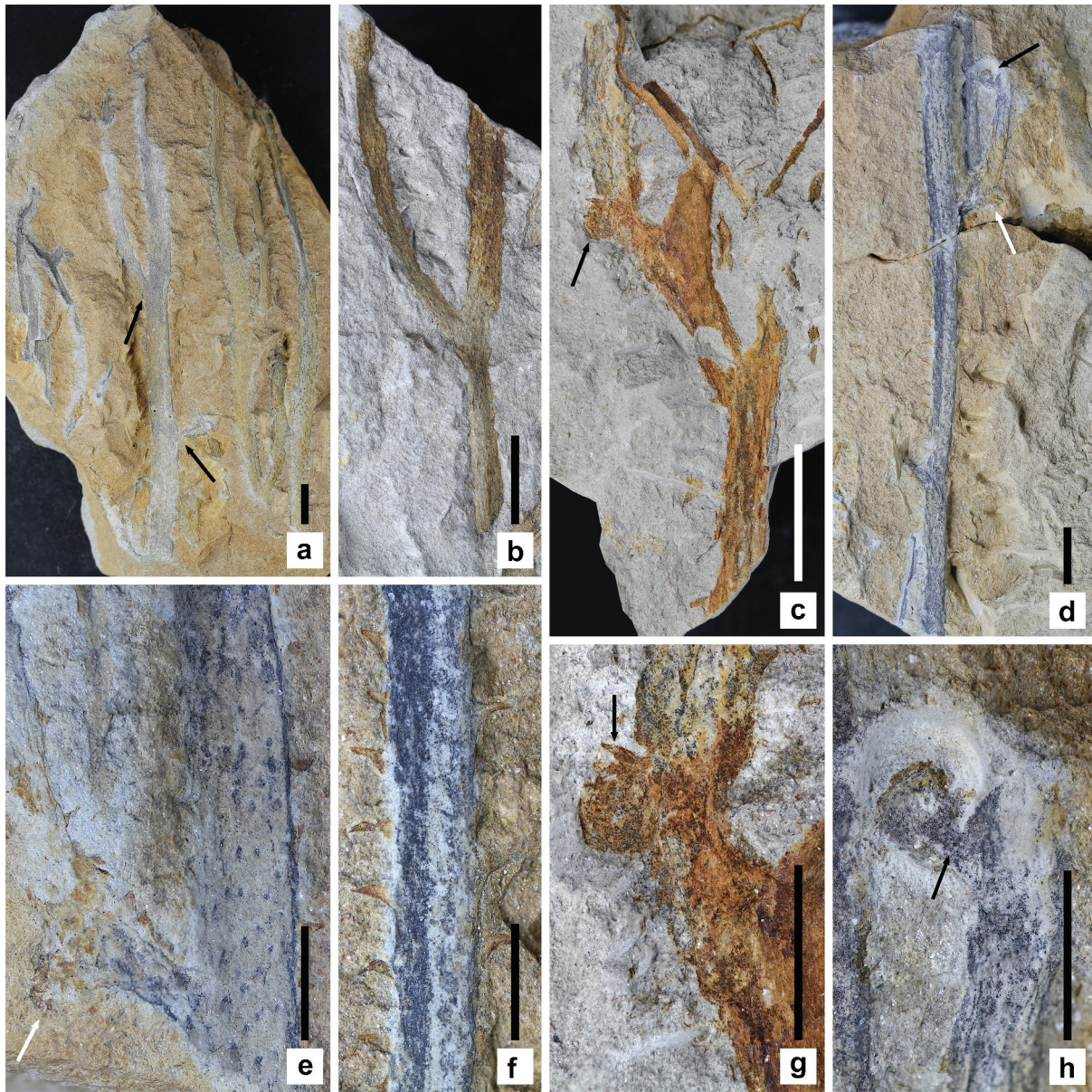
**Description and interpretation.** This plant consists of smooth leafless axes with bivalved sporangia borne laterally on long straight stalks (Figure 3f–g). It was originally described as a new species (*Zosterophyllum artesianum*) in Danzé-Corsin (1956b). However, Edwards (2006) excluded this taxon from *Zosterophyllum* due to its lack of compact spike and the fact that sporangia in *Zosterophyllum* are upright and inserted on short stalks. Its placement within the zosterophyll clade remains equivocal due to its simplicity in organization and lack of preserved anatomy. Nevertheless, Edwards (2006) hypothesized that *Danziella* may be a representative of a stem-lineage of the Zosterophyllopsida.

**Remarks.** Edwards (2006) described this new taxon as coming from the Rebreuve locality although she also illustrated two specimens reportedly coming from Matringhem. However, Danzé-Corsin (1956a) did not mention or illustrate any specimens, whether fertile or sterile, similar to *Danziella* in Matringhem, indicating that they were not originally recorded there. Upon reinspection, it is clear that all specimens of *Danziella* come from Rebreuve as they are preserved in a finer-grained lighter color matrix characteristic of other samples from Rebreuve. This mistake stems from a mixing of specimens over the years in the collections. *D. artesiana* should therefore be excluded from the Matringhem assemblage.

#### 5. *Sawdonia* sp.

1933 *Psilophyton princeps* Dawson, Corsin.  
1956b *Psilophyton princeps* Dawson, Danzé-Corsin, pl. II, figs. 1–3.

**Material.** 14 specimens were identified in the collections. Description is based on specimen numbered USTL 3547, USTL 3638A, USTL 3639, USTL 3649 (Figure 4a), USTL 3645 (Figure 4b), USTL 3631 (Figure 4c, g), USTL 3644–1 (Figure 4d, f), USTL 3644–2 (Figure 4d, h), USTL 3548 (Figure 4e) and USTL 3650A.

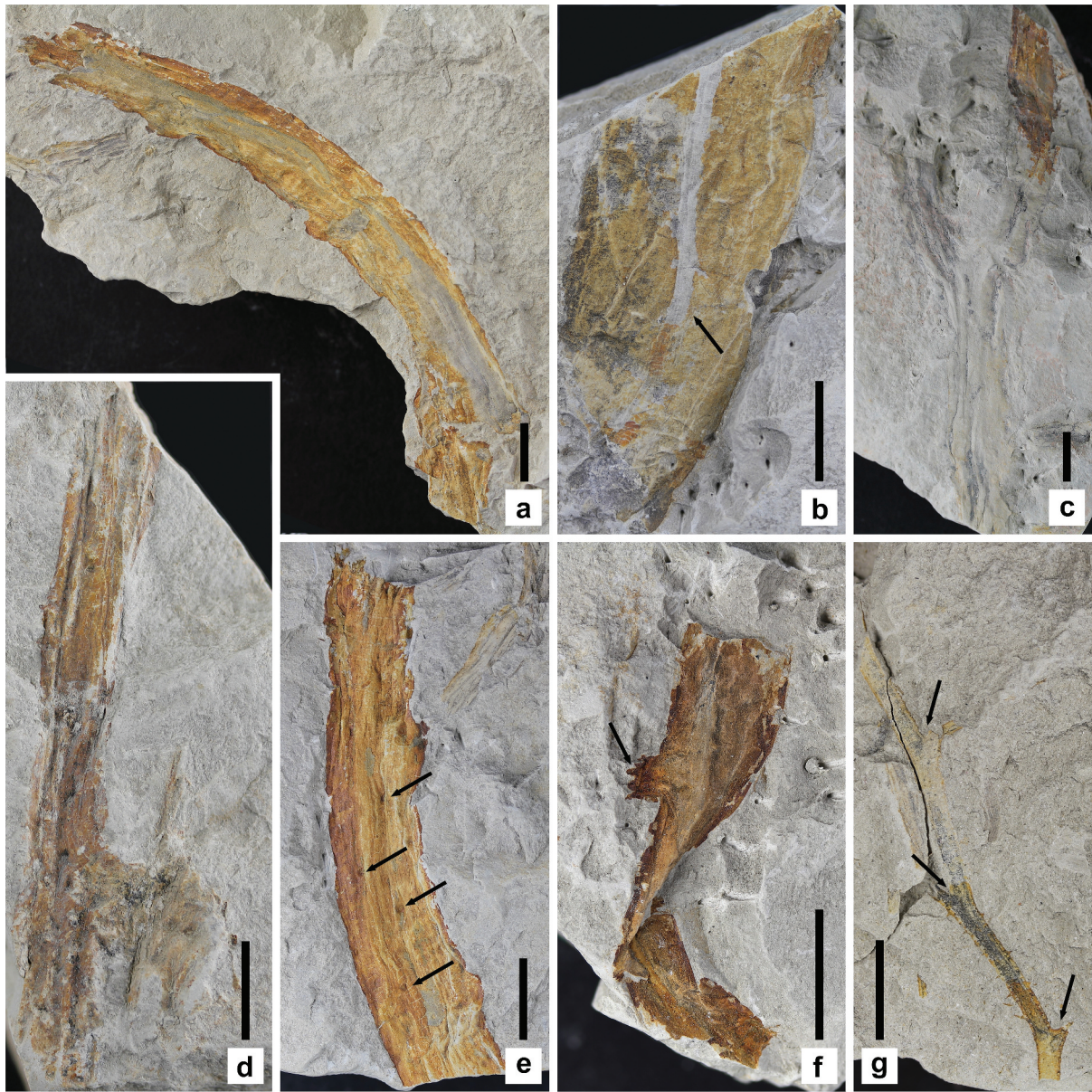


**Figure 4.** *Sawdonia* sp. from the Rebreuve assemblage, France. a, Vegetative axes with anisotomous type of branching; note two successive dichotomies at arrows, USTL 3649. b, Anisotomously branching sterile axis, USTL 3645. c, General view of a fertile specimen displaying two consecutive isotomous dichotomies; note the position of sporangium-like structure at arrow, USTL 3631. d, General view of a fertile specimen displaying a pseudomonopodial type of branching; white arrow points to the location of a subaxillary bud; black arrow shows the location of sporangium-like structure, USTL 3644–1 and USTL 3644–2. e, Counterpart of specimen illustrated in Figure 4d showing the helical arrangement of spine scars; arrow show the counterpart of the subaxillary bud, USTL 3548. f, Detailed view of specimen illustrated in Figure 4d displaying diversity of spine morphologies encountered on a single axis, USTL 3644–1. g, Detailed view of specimen illustrated in Figure 4c with sporangium-like structure seen in adaxial view. Arrow shows the location of spines on the abaxial valve, USTL 3631. h, Detailed view of specimen illustrated in Figure 4d with sporangium-like structure seen in abaxial view. Arrow shows the stalk connecting the axis with sporangium, USTL 3644–2. Scale bars: a–d = 10 mm; d–h = 5 mm.

**Description.** Spiny axes up to 12 cm long on largest samples (Figure 4a). Axes diameter between 2.2 – (4) – 7.4 mm ( $n = 20$ ). Branching is planar and mostly anisotomous (Figure 4a–b), although isotomous (Figure 4c) and pseudomonopodial (Figure 4d) branching also occurs. Shortly after its divergence from the main axis, the lateral branch recurves upward, growing in parallel to the main axis. Interval between two dichotomies varies from 1.2 to 3.5 cm (Figure 4a at arrow, Figure 4c–d), although most

specimens do not show more than one branch departing from the main axis. One subaxillary bud close to the branching point (3.4 mm wide, 2.7 mm high) is also observed (Figure 4d–e at white arrows). All axes are covered with spines and/or spine scars. Spine scars form oval to circular depressions in the matrix (Figure 4e). Spines are locally helically arranged on the stem surface and up to 5 spine scars are observed in each gyre (spines on the visible side of axis) suggesting at least 10 spines per helix (Figure 4e). Up to four

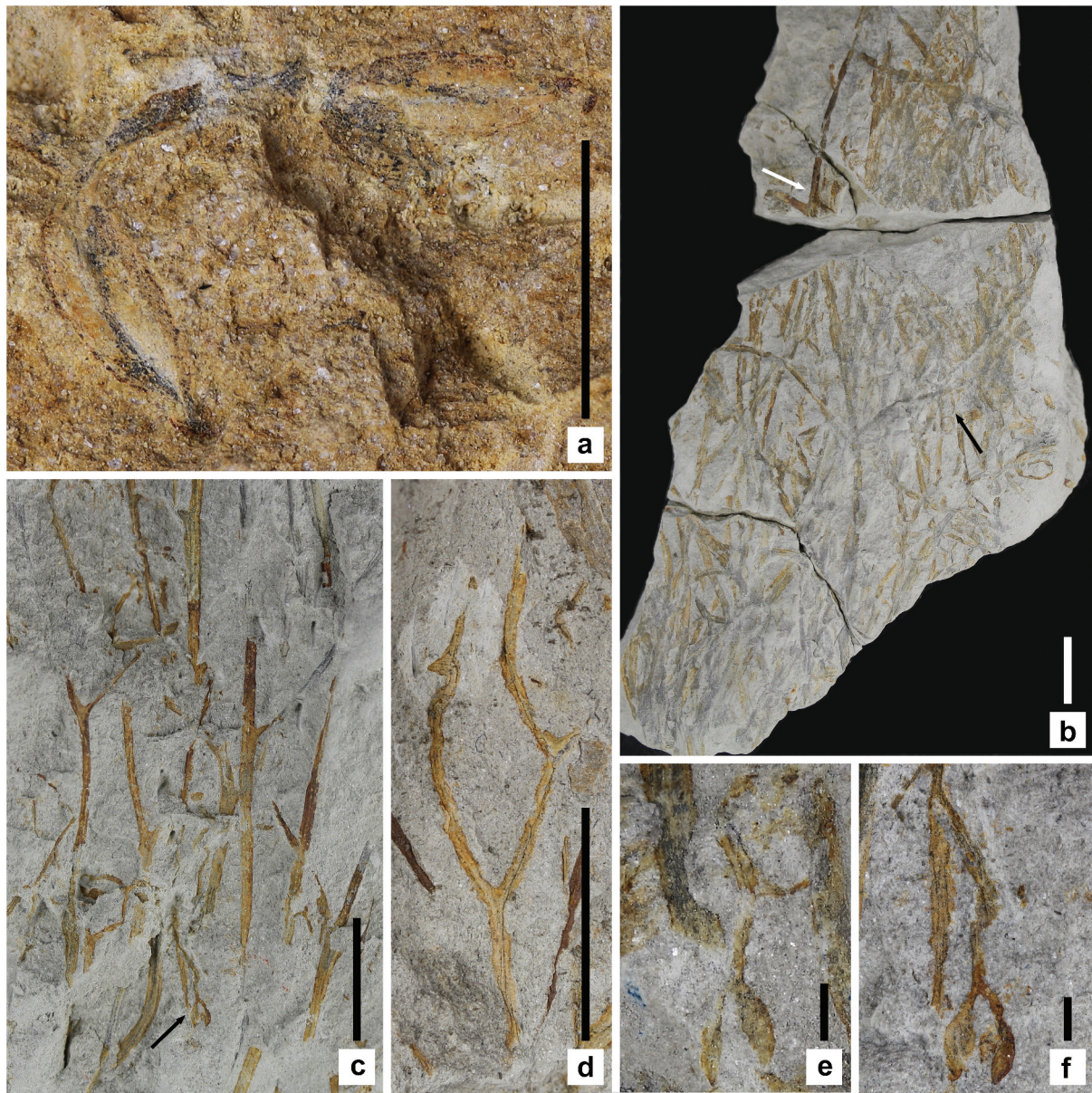




**Figure 5.** Plant fossils from the Rebreuve assemblage, France (II). a, *Drepanophycus* cf. *spinaeformis*, general view of a large vegetative specimen, USTL 3625. b, *Drepanophycus* cf. *spinaeformis*, specimen showing the trace of a vascular strand in the center of the axis, USTL 3619. c, *Drepanophycus* cf. *spinaeformis*, impression of an axis dividing isotomously, USTL 3626A. d, *Drepanophycus* cf. *spinaeformis*, specimen displaying H-type of branching, USTL 3620. e, *Drepanophycus* cf. *spinaeformis*, well-preserved vegetative axis bearing round to oval depressions interpreted as leaf scars at arrows, USTL 3621. f, *Drepanophycus* cf. *spinaeformis*, specimen bearing one lateral bud showing several small microphylls at arrow, USTL 3527B. g, "*Psilophyton*" *burnotense*, spiny axis showing three successive anisotomous dichotomies at arrows; USTL 3685. Scale bars = 10 mm.

parallel helices are shown (Figure 4e). Each helix is inclined at a 35–50° angle. Vertical distance between each helix is around 1 mm. Spine scars are separated from each other by a distance of 0.20 to 0.65 mm. Spines have a stout appearance and a deltoid shape, with a triangular base, sometime slightly decurrent, tapering into an acute or apiculate tip (Figure 4f). The tip may sometime be abaxially recurved (Figure 4f). Spines are 0.5 – (1.2) – 2.2 mm wide at base ( $n = 30$ ) and are between 0.5 – (1.2) – 1.9 mm long ( $n = 30$ ).

Two sporangia-like structures were identified on two separate potential fertile axes (Figure 4c–d at black arrows). They are borne laterally on stalks on either side of the fertile axis (Figure 4g–h). Sporangia-like structures are rounded to oval and are 2.4–3 mm long and 2.1–2.5 mm wide. Spines are visible on the upper margin (Figure 4g at arrow) and are smaller than spines on axes (0.3–0.7 mm). In both cases, sporangia-like structures are folded around the axis and bent downward into the matrix hindering the possibility to potentially simultaneously observe both

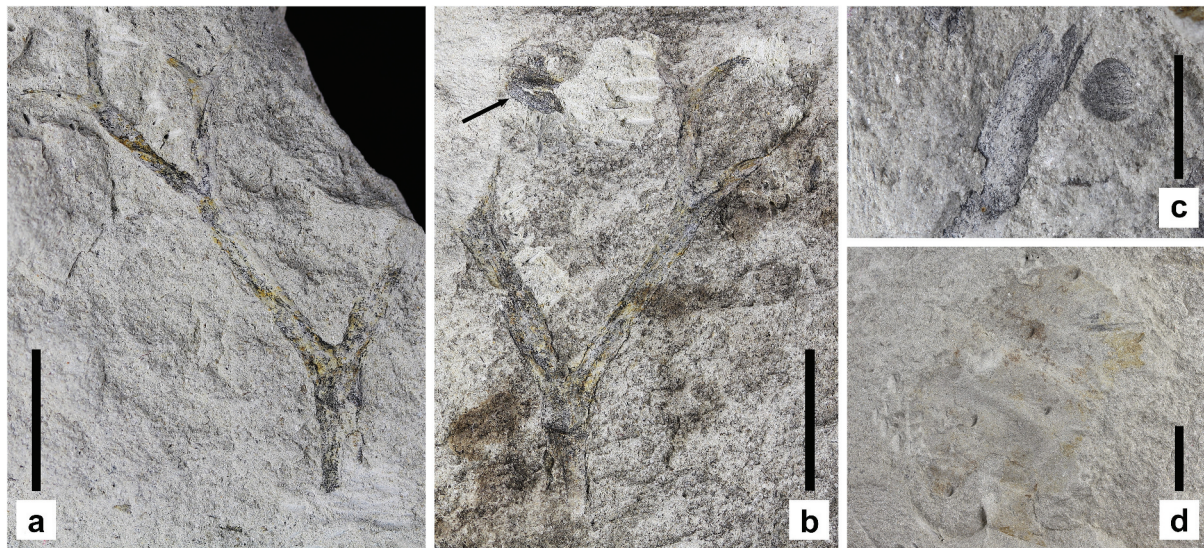


**Figure 6.** Plant fossils from the Rebreuve assemblage, France (III). a, cf. *Psilophyton forbesii*, general view of specimen USTL 3706 bearing two pairs of fusiform sporangia connected by a short stalk. b, General view of axes of *Psilophyton parvulum* and *Danziella artesiana*. Arrow points to the location of a fertile axis of *P. parvulum* shown in Figure 6e. White arrow shows the location of an identifiable *Danziella* axis; USTL 3609–1 and USTL 3609–2. c, *Psilophyton parvulum*, general view of various vegetative striated axes displaying pseudomonopodial and anisotomous branching. Black arrow indicates location of a fertile axis shown in Figure 6f; USTL 3616–1. d, *Psilophyton parvulum* vegetative striated axis displaying two successive isotomous dichotomies, USTL 3814. e, *Psilophyton parvulum*, detailed view of truncated fertile axis bearing terminally a pair of sporangia, USTL 3609–1 and 3609–2. f, *Psilophyton parvulum*, detailed view of truncated fertile axis bearing terminally two pairs of twisted sporangia; USTL 3616–1. Scale bars: a = 5 mm; b–d = 10 mm; e–f = 1 mm.

valves. One specimen shows sporangium-like structure in abaxial view, with a distinct structure interpreted as a stalk, curved upward at a 50° angle (Figure 4h at arrow). The stalk is 2.6 mm long and 0.8 mm wide (Figure 4h). On the other specimen (Figure 4g), the sporangium-like structure is seen in adaxial view but only the abaxial valve can be recognized, probably covering the smaller adaxial valve.

**Interpretation.** Danzé-Corsin (1956b) assigned these vegetative specimens to *Psilophyton princeps* Dawson based on Halle (1916)'s definition of what was

originally described as *Psilophyton princeps* var. *ornatum* in Dawson (1871), now called *Sawdonia ornata* (Hueber 1971). The *dégagement* of two likely sporangia contributes to a better comprehension of this plant. These sporangia-like structures lack an ostensible dehiscence margin and could also be easily mistaken for a bud (Gensel and Berry 2016). Nevertheless, certain features such as dehiscence margin, stalk and spines on sporangium are often poorly preserved (Gensel and Berry 2016, figs. 3–4). In addition, the amount of remaining organic matter preserved here probably prevents simultaneous observation of all



**Figure 7.** Plant fossils from the Rebreuve assemblage, France (IV). a, cf. *Psilophyton* sp., vegetative axis displaying three successive isotomous dichotomies terminating in tapering recurved ultimate appendages, USTL 3670. b, cf. *Psilophyton* sp., counterpart of specimen USTL 3670 shown in Figure 7a; isolated pair of sporangia at arrow, USTL 3742. c, *Psilophyton*-like stem initially described as *Yarravia minor* n. sp. in Danzé-Corsin (1956b); USTL 3829. d, Unknown structure interpreted as *Cyclostigma* sp. in Danzé-Corsin (1956b), USTL 3670. Scale bars: a–b, d = 10 mm; c = 5 mm.

features (Figure 4h–g). Certain features indicate that these structures are more likely sporangia than buds: (1) buds tend to be larger than sporangia e.g. the subaxillary bud in Figure 4d–e, (2) buds grow in the same plane as the subtending axis unlike sporangia which are often found folded around the axis (Gensel and Berry 2016, figs. 9d–f), a characteristic clearly seen in Figure 4h, (3) spines on buds (Figure 4d–e) are not as developed as on structures interpreted as sporangia (Figure 4g), and (4) a well-defined stalk can be observed in Figure 4g. The lack of dehiscence margin may also be explained by the structures representing immature sporangia (Gensel and Berry 2016).

Axes with lateral sporangia both bearing emergences are characteristic of several Lower Devonian taxa with zosterophyll affinities such as *Faironella* (Gerrienne 1996a), *Odonax* and *Sawdonia* (see Jensen and Gensel 2013, table 1). *Odonax* differs from our specimens by having small scaly denticulate emergences and compact bilateral strobili of sporangia

(Gerrienne 1996b). *Faironella* is distinct from our specimens by possessing, among other features (see Gerrienne 1996a), mostly dichotomous and K-branching with oval sporangia and cuneiform in its adaxial part. Here, the branching pattern, emergences morphology, the presence of rounded lateral sporangia bearing spines on the abaxial valve, subtended by a short stalk, can allow us to confidently compare this taxon to *Sawdonia*. The diagnosis of this taxon was recently emended by Gensel and Berry (2016) and subsequently by Berry and Gensel (2019) mainly linked to the fact that sporangia consisted of unequal valves whereas they were previously thought to be equal. We cannot clearly see both valves on our specimens but the fact that the abaxial valve is the only visible one indicates that valves are indeed unequal.

Rebreuve specimens, when compared with other species of *Sawdonia* share common features of currently both well-defined species from the Lower Devonian (Gensel and Berry 2016; Berry and Gensel

**Table 1.** List of Rebreuve plant fossil taxa.

Danzé-Corsin (1956b)	This study
<i>Sporogonites exuberans</i>	<i>Sporogonites exuberans</i>
<i>Taeniochrada decheniana</i>	<i>Taeniochrada</i> sp.
<i>Sciadophyton</i> cf. <i>laxum</i>	<i>Sciadophyton</i> sp.
<i>Zosterophyllum artesianum</i>	<i>Danziella artesianiana</i>
<i>Psilophyton princeps</i>	<i>Sawdonia</i> sp.
<i>Drepanophycus spinaeformis</i>	<i>Drepanophycus</i> cf. <i>spinaeformis</i>
<i>Psilophyton</i> sp.	" <i>Psilophyton</i> " <i>burnotense</i>
<i>Dawsonites arcuatus</i>	cf. <i>Psilophyton forbesii</i>
<i>Hostinella</i> sp.	<i>Psilophyton parvulum</i>
<i>Dawsonites</i> cf. <i>minor</i>	
-	cf. <i>Psilophyton</i> sp.
<i>Yarravia minor</i>	-
<i>Cyclostigma</i> sp.	-

2019, table 1). On the other hand, the late Middle Devonian species *S. hipbotheca*, differs more markedly in terms of branching, emergence type and sporangial morphology (Berry and Gensel 2019). Spines on our specimens resembles more those of *S. deblondii*, despite their stouter appearance. Helical arrangement of spines has not been previously documented in *Sawdonia*, but reexamination of transfers of *S. ornata* from the type locality confirmed this feature to locally occur in this species. Branching is more prevalent here than in *S. deblondii*, but branching pattern has characteristics of both species: *S. deblondii* (iso- to anisodichotomous and K-branching) and *S. ornata* (pseudomonopodial). In terms of sporangial morphology and size, the sporangia of Rebreuve specimens are more reminiscent of *S. ornata* than *S. deblondii*. The only exception is that the stalk in Rebreuve specimens is longer than in *S. ornata* and occurring within the size range of *S. deblondii*. The Rebreuve specimens do not fit exactly in either species and therefore might potentially represent a new species. Without further information on valve morphology and sporangium arrangement on axis, we refer to these specimens as *Sawdonia* sp.

## Lycophytes – Lycopsidea

### 6. *Drepanophycus* cf. *spinaeformis*

1933 *Arthrostigma gracile* Dawson (= *Drepanophycus* Göppert), Corsin

1956b *Drepanophycus spinaeformis* Göppert, Danzé-Corsin, pl. II, figs. 5–6

**Material.** About 15 specimens are recognized in the assemblage. Description is based on specimens numbered USTL 3625 (Figure 5a), USTL 3619 (Figure 5b), USTL 3626A (Figure 5c), USTL 3620 (Figure 5d), USTL 3621 (Figure 5e) and USTL 3527B (Figure 5f).

**Description.** This plant consists of fragmented vegetative axes measuring up to 15 cm long (Figure 5a). Axes range from 0.7 to 2.2 cm in width. The largest specimen clearly shows the trace of a central vascular strand reaching 2.3 mm in diameter (Figure 5b at arrow). Isotomous branching is observed, dividing at a wide angle (Figure 5c). Each lateral then recurves and grows in parallel to each other in the same direction as the parent axis (Figure 5c). One specimen displays H-type branching, the daughter axis growing in the same plane and parallel to the parent axis (Figure 5d). Specimens have a smooth irregular surface with a ribboned-like aspect. Microphylls are not preserved. However, leaf bases are noticeable on the axes surface, appearing as small round to oval depressions (Figure 5e at arrows). The distance between leaf bases ranges from 6.2 to 9.6 mm. No discernable

arrangement of microphylls can be distinguished on stems. One lateral bud bearing six visible microphylls less than 1 mm long is observed (Figure 5f at arrow). No fertile axes were found.

**Interpretation.** Danzé-Corsin (1956b) correctly assigned this plant to *Drepanophycus spinaeformis* based on the singular morphology, size and aspect of *Drepanophycus* vegetative axes described in Kräusel and Weyland (1930) and Stockmans (1940). *Drepanophycus* is a widespread cosmopolitan taxon most commonly found in Emsian strata albeit not exclusively (see e.g. Banks and Grierson 1968). Here, we report previously undescribed features that further corroborate the assignation of these specimens to *D. spinaeformis*. Firstly, the occurrence of H-branching patterns (Figure 5c) is also well documented in *D. spinaeformis* (Croft and Lang 1942; Banks and Grierson 1968; Rayner 1984). Lateral buds are also a known feature to occur in *D. spinaeformis* and the specimen from Rebreuve (Figure 5f) bears strong similarities with buds from specimens from the type locality (Li et al. 2000, figs. 22–23). *D. qujingensis* differs from our specimens by the absence of K- and H-branching (Li and Edwards 1995), whilst they differ from *Sengelia radicans* (another Drepanophycal) by not exclusively possessing the K-branching pattern (Matsunaga and Tomescu 2017). *D. gaspianus* is characterized by a pronounced rhomboidal pattern on axes representing the zone of attachment of leaves, a feature not found on our specimens (Fairon-Demaret 1977). The absence of preserved microphylls and fertile parts precludes a firm assignation of these specimens to *D. spinaeformis*. These features are known to be better preserved (or even uniquely found) on aerial stems rather than on rhizomes. We therefore interpret the Rebreuve specimens as perhaps rhizomes of *D. spinaeformis* considering their smooth surface bearing leaf bases (Figure 5e), similar to rhizomes from the type locality (Li et al. 2000).

## Euphylllophytina

### 7. “*Psilophyton*” *burnotense*

1956b *Psilophyton* sp. Dawson, Danzé-Corsin, pl. II, fig. 4.

**Material.** A single specimen was identified in the collections USTL 3685 (Figure 5g).

**Description.** Truncated spiny axis. Main axis 2 mm wide and 5.2 cm long. Three successive anisotomous dichotomies, distant from each other by 1.7–1.8 cm, are observed (Figure 5g at arrows). Distichous arrangement of branches occurring alternately on

either side of the main axis. Lateral axes narrower than main axis (1 mm wide). One lateral after first dichotomy tapers rapidly giving the impression of an aborted branch (Figure 5g at arrow). Spines slender, less than 1 mm long and less than 0.5 mm wide at their base. Spines are triangular at base then subulate. A thickened margin is noticeable on all the length of the main axis and laterals. No fertile parts were found in connection to the sterile axis.

**Interpretation.** Danzé-Corsin (1956b) recognized this specimen as different from *Psilophyton princeps* (*Sawdonia* sp. in this study), acknowledging similarities with *Psilophyton goldschmidtii*, without formally designating it as belonging to this species. This specimen could be assignable to the form-genus *Psilophytites*, which circumscribes vegetative axes bearing undivided spines (Høeg 1952). Nevertheless, the presence of a thickened margin allows us to compare this axis with other taxa that possesses this feature. Currently, anisodichotomously branched vegetative axes bearing slender pointed emergences and presenting a thickened margin is characteristic of either *Psilophyton burnotense* (syn. *P. goldschmidtii*), a basal euphyllophyte, or *Margophyton goldschmidtii*, a zosterophyll (Gerrienne 1991). The history of these taxa is rather complex (see Schweitzer 1989 for details). Such axes were first described in Belgium under the name *Lepidodendron burnotense* in Gilkinet (1875). Other vegetative specimens with similar morphology were subsequently found in Røragen, Norway for which Halle (1916) created the species *Psilophyton goldschmidtii*. This name was later reutilized by Stockmans (1940) for describing his Belgian specimens, likewise uniquely vegetative. Nevertheless, the epithet *burnotense* in Gilkinet (1875) had priority, so newly found German specimens were consequently named *Psilophyton burnotense* (Kräusel and Weyland 1948).

However, the discovery of identical axes to *P. burnotense* in the Emsian of Siberia bearing lateral sporangia, thereby indicating zosterophyll affinities, blurred our understanding of this taxon (Zakharova 1981). Zakharova (1981) synonymized European specimens of *P. goldschmidtii*, *P. burnotense* and the Siberian specimens under a new combination: *Margophyton goldschmidtii*. Nevertheless, Schweitzer (1989) demonstrated that European specimens of *Psilophyton burnotense* did possess terminal sporangia, therefore belonging to a distinct lineage to *Margophyton*. The Rebreuve specimen is identical to the *P. goldschmidtii* described in Stockmans (1940). Specimens found in Belgium were later conservatively renamed "*Psilophyton*" *burnotense* by Gerrienne (1983, 1993). In Gerrienne (1993)'s opinion, the lack of fertile structures in Belgian specimens could not lead to the definitive assignation to *Psilophyton*, as

these axes could equally belong to *Margophyton*. We follow the same approach here by being conservative regarding its assignation to *Psilophyton*.

#### 8. cf. *Psilophyton forbesii*

1956b *Dawsonites arcuatus* Halle, Danzé-Corsin, pl. III, figs. 7–7a.

**Material.** Only one specimen was recovered (part and counterpart) numbered USTL 3705 and USTL 3706 (Figure 6a). It consists of a faint impression with very little original organic matter preserved. Figure 6

**Description.** It consists of two pairs of fusiform sporangia subtended by short stalks measuring 4.8 mm long in total, and 0.6 mm in width (Figure 6a). Since no axes were found connected to the stalks, the length of each individual stalk is unknown. Stalk and sporangia surface devoid of emergences. The two pairs of sporangia are pendant and a sinistral torsion of the sporangia pair can be distinguished. Each individual sporangium is 4.1 mm long and between 0.5 and 1 mm wide. No dehiscence line could be detected on any of the sporangia.

**Interpretation.** Pairs of fusiform sporangia twisted around each other are characteristic of several basal euphyllophyte taxa such as *Psilophyton*, *Pertica* and *Trimerophyton* (Gerrienne 1997, table 2). However, pairs of sporangia in *Pertica* and *Trimerophyton* are erect and not pendulous, like our specimen (Figure 6a). This specimen was originally described as *Dawsonites arcuatus* in Danzé-Corsin (1956b). *Dawsonites* is a genus intended to circumscribe fertile axes resembling to those of *Psilophyton* or other basal euphyllophytes that are not connected or associated with sterile axes. *Dawsonites arcuatus* has since been renamed *Psilophyton arcuatum* for German material by Schweitzer (1980) and later for Norwegian specimens (Schweitzer and Heumann 1993) because there was enough material to assign it to *Psilophyton*. This taxon was subsequently synonymized by Gerrienne (1997) with *P. forbesii* that likewise occurs in the USA (Andrews et al. 1968), Canada (Gensel 1979) and Belgium (Gerrienne 1997). Among all *Psilophyton* species currently described, sporangia correspond the most in terms of size and shape with *P. forbesii* and especially with the ones described in Gerrienne (1997) that are slightly thinner than other occurrences. However, the lack of associated fertile or sterile axes does not allow us to categorically assign this specimen to *Psilophyton* despite the obvious similarities with *P. forbesii*.

### 9. *Psilophyton parvulum*

1956b *Hostimella* sp. Barrande, Danzé-Corsin, pl. II, fig. 9.

1956b *Dawsonites* cf. *minor* Stockmans, Danzé-Corsin, pl. II, fig. 9.

1956b *Dawsonites* cf. *minor* Stockmans, Danzé-Corsin, pl. III, figs. 5–6.

**Material.** Many fragments were found isolated in several samples or found in dense tufts, mixed with axes belonging to *Danziella artesiana* (Figure 6b). The description is based on USTL 3609-1-2 (Figure 6b, e), USTL 3616-1 (Figure 6c, f) and USTL 3814 (Figure 6d).

**Description.** Fragmented sterile and fertile axes up to 3.5 cm long (Figure 6b–c). Axes are less than 1.4 mm wide and the surface is striated longitudinally. Branching may be pseudomonopodial, anisotomous (Figure 6c) or isotomous (Figure 6d). Pairs of fusiform sporangia were found attached to fertile axes morphologically similar to vegetative axes in two samples (Figure 6b–c at black arrows), and are therefore inferred as belonging to the same plant. Pairs are subtended by short stalks (0.2 mm wide) resulting from an isotomous dichotomy (Figure 6e–f). Sporangia measure between 1.3 and 1.5 mm long and between 0.3 and 0.5 mm wide. Sporangia are erect (borne in the continuation of the direction of the axis) and twisted in a sinistral direction. No dehiscence line is observed on specimens. The tips of the sporangia can be acute (Figure 6e) or blunt (Figure 6f).

**Interpretation.** Dichotomous axes bearing distally pairs of fusiform sporangia twisted around each other, also points to the genus *Psilophyton* (Gerrienne 1997). *Psilophyton* species with surface of axes devoid of emergences and striated, is characteristic of both *P. forbesii* and *P. parvulum* (Gerrienne 1995, fig. 2). The main differences between the two species is the size: *P. parvulum* being much smaller in terms of axes diameter and sporangia than *P. forbesii*. *P. dapsile* is also one of the smallest species of *Psilophyton* but it differs from our specimens by only possessing an isotomous branching pattern, and additionally, the size-range of its sporangia does not overlap with our specimens (Kasper et al. 1974; Gerrienne 1995, fig. 2). The specimens herein described conform in all aspects with *P. parvulum* (branching pattern, sterile and fertile axes size and morphology) and can therefore confidently be identified as this taxon. Danzé-Corsin (1956b) originally described this species as two separate taxa albeit highly suspecting the connection between the *Hostimella* sp. axes (now sterile axes of *P. parvulum*) and *Dawsonites* cf. *minor* (now fertile axes of *P. parvulum*). Careful reexamination of the material clearly showed the similarity of fertile and

sterile axes and allows us to consider them as belonging to the same entity. Axes of *Danziella artesiana* and *P. parvulum* are of equivalent size and can be easily confused, especially when found mixed in dense mats (Figure 6b). Nevertheless, axes of *Danziella* can be distinguished with their wider dichotomizing angle and their unstriated smoother axes surface (Figure 3f–g). Here, a specimen (Figure 6b) interpreted as presumed sterile axes of *D. artesiana* in Edwards (2006, pl. III, fig. 1), is actually mostly constituted of axes of *P. parvulum*.

10. cf. *Psilophyton* sp.

**Material.** One specimen is recorded with both part USTL 3670 (Figure 7a) and counterpart USTL 3742 (Figure 7b) preserved.

**Description.** Isotomously dichotomizing naked axis (Figure 7a–b). Intervals between dichotomies shorten distally as well as width of branches. The main axis is 3.1 mm wide, first-order branches are 1.9–2 mm wide and second-order branches 1.5–1.7 mm wide. Ultimate branchlets slightly taper, recurve, before ending in an acute tip. Ultimate vegetative branchlets are 4 mm long and are 0.6–0.7 mm wide at their base. One pair of sporangia has been uncovered (Figure 7b, at arrow), although it is not directly connected to the vegetative specimen. The only entirely visible sporangium is 3.9 mm long and 1 mm wide. Sporangia are elongated and slightly fusiform, ending in a blunt tip.

**Interpretation.** This specimen was not described nor figured in Danzé-Corsin (1956b). Tapering isotomously dividing sterile axes ending in slightly recurved terminal branchlets is typical of several basal euphyllophyte taxa such as *Psilophyton* and *Pertica* (Kasper and Andrews 1972; Gensel 1979). This type of axis is different from *Psilophyton parvulum* (Figure 6b–f) present in this assemblage by its apparent smooth surface and larger size. *P. krauseli* and *P. dapsile* do not correspond with this vegetative specimen given that their axes diameter is smaller than 3 mm (Obrhel 1959; Kasper et al. 1974; Andrews et al. 1977). *P. microspinatum* and *P. charientos* have emergences and ultimate branchlets divide at a wider angle (Kasper et al. 1974; Gensel 1979). This specimen also presents similarities with *P. szaferi*, but lacks enations, a typical trait of this species (Zdebska 1986). *Pertica* is a closely related taxon, which also bears similar axes ending in recurved ultimate branchlets (Kasper and Andrews 1972, fig. 6–7), so an assignation of the vegetative specimen to *Psilophyton* cannot be asserted with confidence.

On the other hand, sporangia uncovered present striking similarities in size and shape to sporangia described as cf. *P. forbesii* in the assemblage

(Figure 6a). Nevertheless, there is no unequivocal connection between the axis and sporangia, and axes of *P. forbesii* are usually clearly striated although distal branches may apparently sometimes lack this feature (Gerrienne 1997 and references therein). Sporangia of *Pertica* occur as dense clusters and are elliptical, not fusiform, which, if we believe there is connection, precludes an assignation to *Pertica*. Without a direct connection with sporangia and the lack of distinctive features on the vegetative specimen, we refer to this specimen as a possible *Psilophyton*.

### Excluded taxa from the Rebreuve assemblage

*Yarravia* is a genus of probably either rhyniophyte or trimerophyte affinities of the late Silurian and early Devonian of Australia, China and South Africa (McSweeney et al. 2021; Gess and Prestianni 2021). Danzé-Corsin (1956b, pl. III, fig. 10–10a) created a new species based on a single specimen from Rebreuve. She described it as a spherical synangium subtended by a short stalk on a smooth axis, with perhaps 4 or 5 sporangia united at their base but separated in their most distal parts. P. Danzé-Corsin compared this specimen with *Y. subsfaerica* and *Y. oblonga* but distinguished it by its much smaller size, hence calling this plant *Y. minor*. However, *Yarravia*'s fructifications are borne terminally (McSweeney et al. 2021). This plant's apparent "fructification" is borne laterally, even though contrary to Danzé-Corsin (1956b)'s observations, a stalk connecting sporangia and stem is not visible here (Figure 7c). Upon reexamination, this specimen appears to represent a folded *Psilophyton*-like stem and should therefore be excluded from *Yarravia*.

Danzé-Corsin (1956b, pl. II, fig. 11–11a) also described one specimen consisting of a 4 cm wide and 2 cm long smooth impression, with several oval-shaped holes in the matrix, separated from each other by 10–15 mm (Figure 7d). She interpreted these marks as leafscars and compared this fossil to the aspect of a *Cyclostigma* bark impression (Chaloner 1968; Doweld 2017). In addition to the fact that *Cyclostigma* is an exclusively Late Devonian-early Carboniferous lycopod tree, this specimen simply does not conform to the diagnosis of *Cyclostigma* (Chaloner 1968), and the nature of this fossil remains enigmatic.

### Discussion

The Rebreuve assemblage represents a moderately well-preserved, and taxonomically diverse Lower Devonian flora. Taxonomic description of numerous early Devonian plants since the 1950s made possible a better understanding of the plants recorded in this assemblage. Table 1 lists the original taxonomic composition of the flora recorded by Danzé-Corsin (1956b) and our revised

list based on this study. This reinvestigation led to the discovery of likely fertile remains of *Sawdonia* not originally described in Danzé-Corsin (1956b). This discovery is a key finding as the diagnosis of *Sawdonia* has recently been emended (Gensel and Berry 2016; Berry and Gensel 2019). It resulted in many formerly described *Sawdonia* species being excluded from the genus due to inconsistencies with the diagnosis in terms of sporangial morphology or emergence type (Gensel and Berry 2016). The Rebreuve assemblage therefore represents a new occurrence of *Sawdonia* (Berry and Gensel 2019, table 1), the second known occurrence of *Psilophyton parvulum* (Gerrienne 1995) and the single known record of *Danziella artesiana* (Edwards 2006). All major taxonomic groups present in the Lower Devonian are represented here (Bryophyta, Rhyniopsida, Zosterophylloids, Lycopsidea and Euphyllophytina). Zosterophylls (*Danziella artesiana* and *Sawdonia* sp.) are the most abundant components representing a little less than 50% of the entire fossil flora. Basal euphyllophytes are less common but are fairly diverse with potentially up to four different species of *Psilophyton* featured in the flora (Table 1).

The association of plants found in Rebreuve is common in Emsian Western European and North American assemblages, see e.g. Germany (Schweitzer 1983), Scotland (Rayner 1983, 1984), Norway (Halle 1916; Schweitzer and Heumann 1993) and Eastern Canada (Kennedy et al. 2012; Gensel and Berry 2016). More specifically, this flora bears a striking resemblance to Belgian assemblages and especially those found in the early Emsian (AB biozone of Steemans 1989) Grès de Wépion Formation such as Marchin or Thuin (Gerrienne 1993 and references therein). The age of these Belgian localities is similar to the age found in La Comté-Beugin (Figure 2) and an early Emsian age for Rebreuve plants can be reliably inferred. This assemblage therefore probably represents the second oldest French flora (Strullu-Derrien et al. 2010). Other French early Devonian floras are rare and exclusively found (other than in the Artois region), in the Armorican massif (Ducassou et al. 2009; Strullu-Derrien et al. 2010; Gerrienne et al. 2011). The preservation state of most Armorican plants makes comparison with this flora rather difficult. Nevertheless, Lower Devonian Armorican assemblages do not share any common taxa with Rebreuve other than the cosmopolitan taxon *Psilophyton*. The similarities between Rebreuve and other Western European and North American Emsian floras is compatible with the reconstructed position of Lower Devonian paleocontinents, being all located on Laurussia, whereas Armorica was located on the peri-Gondwanan margin (Scotese 2014).

Recent attempts to quantify early land plant diversity through time (e.g. Capel et al. 2021, 2022) requires reliably identified and well-dated plant fossil

occurrences. It is also essential for reconstructing accurate paleophytogeographical relationships (Raymond et al. 1985, 2006; Wellman et al. 2013). For instance, in this case, the exclusion of *Yarravia* from the assemblage has profound consequences for Lower Devonian paleophytogeography, as this taxon is otherwise uniquely found in Gondwanan assemblages (McSweeney et al. 2021). Synthetic works that compile and revise already described plant fossils collected over the past century are critically important (e.g. Gerrienne 1993; Edwards and Richardson 2004) and this study contributes toward this objective. Considering this, in addition to the Rebreuve assemblage, the Matringhem flora (Danzé-Corsin 1956a), located 30 km west of Rebreuve is also in need of revision and will be redescribed in a future study.

## Acknowledgments

The authors thank Sylvie Régner (University of Lille) for preparation of palynological samples and microscopic slides. The authors also thank Jessie Cuvelier (University of Lille) for technical assistance. C.P. is hired under a Belspo FED-tWIN project from the Belgian Federal Government (Prf-2019(R)-017\_PaleoGreen). This manuscript greatly benefited from comments of two anonymous reviewers.

## Author contributions

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Contribution: revision of the manuscript and funding acquisition

## Data availability statement

The data that support the findings of this study are available from the corresponding author (E.C.), upon request.

## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Funding

This research was funded by EARTHGREEN project (ANR-20-CE01-0002-01; Agence Nationale de la Recherche

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