



## *Aarabia*, a new Early Devonian vascular plant from Africa (Morocco)

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### Abstract

*Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov. is described from the Early Emsian of Central Morocco. The preserved parts of the aerial system are interpreted as erect shoots bearing branches in a planar-alternate arrangement. Branching is pseudomonopodial in all orders of axes. Distinction is made between short and long branches. Short branches consist of a foreshortened axis dichotomising in two terminal segments recurved abaxially and adaxially towards the axis of previous order. Arrangement of short laterals on main stem is unpredictable. It is typically proximal on long branches. Long branches of all orders are characterised by short internodes proximally, that increase in length distally. Fertile branches display few anisotomous divisions and bear a small number of non-paired elongated sporangia. Associated large spores in the vicinity of the fertile appendages suggest that the plant might have been heterosporous. *Aarabia* is compared to Early Devonian euphyllophytes. A preliminary cladistic analysis places it as sister-group of the Euphyllophytina. © 2001 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

The primary radiation of vascular land plants occurred in the Devonian, a time characterised by major morphological innovations (Chaloner and Sheerin, 1979; Raymond and Metz, 1995; Bateman et al., 1998; Steemans, 1999). Efforts undertaken in the past 10 years for the search of new assemblages outside the European and North American zones have greatly improved the worldwide fossil record of Devonian plants and accounted more accurately for its diversity (Cai and Wang, 1995; Thanh and Cai, 1995; Berry and Edwards, 1996, 1997; Mussa et al.,

1996). Recently, the most spectacular findings concerning Early Devonian fossils came from assemblages from the Posongchong Formation in Southern China. In this formation, some plants display novel combinations of characters previously used to separate suprageneric groups (Hao and Beck, 1991; Li, 1992). Others are unexpectedly complex and show more derived constructional features than contemporaneous taxa found elsewhere (Hao and Beck, 1993; Hao and Gensel, 1995). Similarities in distinctive fertile traits were noted between the south Chinese plants and their contemporaries from Australia (Hao and Gensel, 1998; Raymond et al., 1999). Hao and Gensel accordingly hypothesised that, in the Early Devonian, Australia and South China were part of a separate northeastern gondwanan phytogeographic unit. This zone currently represents the best

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documented part of Gondwana based on plant macroremains. Despite a reasonable record of spores indicating that gondwanan assemblages were, at least, as diverse as their counterparts on other continents (Streele et al., 1990; Steemans, 1999), plant macroremains of Early Devonian age are scarce in the rest of Gondwana (Edwards, 1973, 1989; Raymond et al., 1985, 1999). Moreover, the significance of those identified to date is often limited by uncertain dating and doubtful taxonomic identifications.

The single locality from Africa considered in the most recent contributions on Early Devonian phyto-geography occurs in the Sahara (Raymond et al., 1985, 1999). It yielded poorly preserved remains and was dated by the plants themselves (Lemoigne, 1967). In Morocco, fragmentary remains including *Taeniocrada*-like stems and costulate axes of uncertain affinities were obtained from a locality in the northern part of the country (Fairon-Demaret and Régnault, 1986). They were tentatively given an Early Devonian age based on associated poorly preserved acritarchs and spores. Recent investigations in central Morocco resulted in the discovery of a new locality yielding plant macroremains. These fossils are preserved in a marine sediment and dated as Early Emsian from the associated tentaculites (Gerrienne et al., 1999). The assemblage comprises

10 different taxa of diverse affinities, including representatives of the Lycophytina and Euphyllophytina. The plants referred to as gen. nov. 1 in the preliminary description (Gerrienne et al., 1999) are notably abundant. They comprise the longest preserved specimens, some of which display fertile structures in connection. One specific character emphasised in the first paper was related to an unusual branching type producing so-called 'dichotomous globose structures'. Here we describe this new plant, provide details on its remarkable construction, and discuss its affinities and phylogenetic significance.

## 2. Materials and methods

The new locality is situated 20 km northwest of Azrou and 1 km east of Jbel ben Aarab in central Morocco (Fig. 1A). The fossiliferous area includes several outcrops; the 30 specimens attributed to the new taxon were collected from the southernmost one (Fig. 1B, arrow). Information provided by the few associated identifiable miospores indicate an age comprised between the Early Pragian and the Late Emsian/Early Eifelian. Associated Dacryoconarid tentaculites better constrain the age of the plants to the Early Emsian.

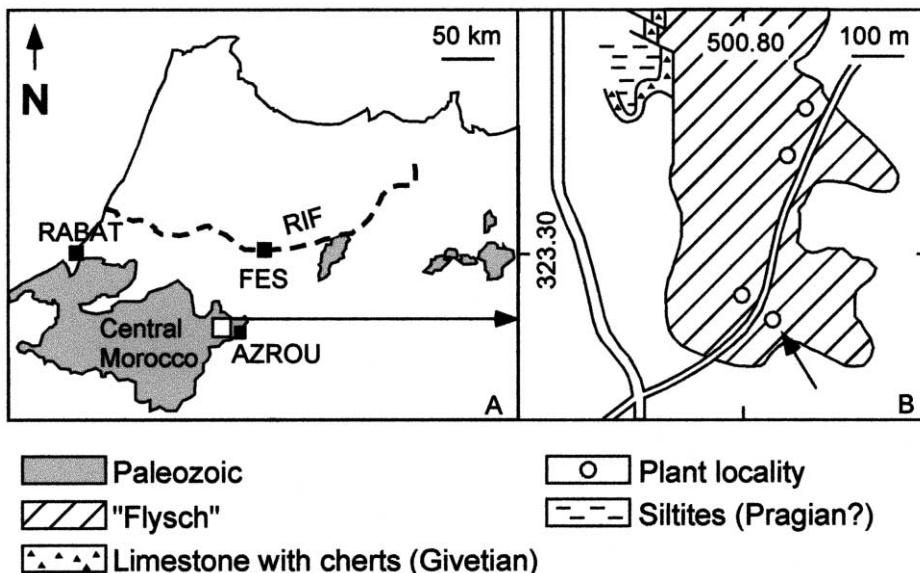


Fig. 1. Location of studied area (A) and fossil localities (B). The arrow points at the type locality.

The plant remains are preserved as devolatilised or decarbonised adpressions (sensu Bateman, 1991) in silty micaceous shales. Degagement was performed by means of steel needles (Fairon-Demaret et al., 1999). Parts and counterparts of specimens were observed using light microscopy and polarised light source. Photographs were made with a Zeiss Tessovar camera. A few specimens were transferred from the matrix (Jones and Rowe, 1999) in order to show epidermal features and patterns of sporangial attachment. Their preservation was insufficient for providing meaningful results. Large isolated spores occurring next to fertile specimens were likewise not well preserved enough for identification.

### 3. Description

Maximum preserved length of specimens is 90 mm. In none are the base or the distal parts of the plant preserved (Fig. 2). Axes are 1.5–4.8 mm wide, naked, and are always incomplete distally. They do not exhibit any conspicuous tapering. Branching is essentially pseudomonopodial. This results in a system of ‘main axes’ and ‘laterals’ which, according to this nomenclature, may comprise up to four orders of axes (Plate I, 1–2; Figs. 2A,B and 3). Three specimens display fertile structures in organic connection (Plate III, 4–5; Fig. 2D,E).

#### 3.1. Branching pattern

Main axes are almost straight and produce  $n + 1$  laterals at 7–25 mm long intervals (Plate I, 1–2; Plate II, 1; Fig. 2A–C). These laterals are produced distichously, according to a planar-alternate arrangement. They depart from the supporting axis at angles ranging 38–55°.  $n + 1$  branches have a proximal diameter about 2/3–3/4 that of the main axis just below branching points.

A few  $n + 1$  laterals are short and morphologically simple (Plate I, 1; Plate II, 1; Fig. 2A,C). They correspond to the ‘dichotomous globose structures’ mentioned in a previous paper (Gerrienne et al., 1999). Their occurrence and arrangement on the main axis are currently unpredictable. They are described in the next section.

Most  $n + 1$  laterals consist of long axes that produce  $n + 2$  lateral branches in two rows (Plate I,

1–2; Plate II, 1; Fig. 2A–C). The 3 or 4 most proximal  $n + 2$  laterals are inserted in a slightly oblique plane relative to that of the preceding axes. On each  $n + 1$  axis, the first borne  $n + 2$  branch is abaxial (Plate I, 3; Plate II, 1–2; Fig. 2A,C). Intervals between consecutive  $n + 2$  laterals are short at base (2.5–5.5 mm) (Plate II, 2); their length increases and may reach 17 mm in the preserved distal parts (Plate II, 4; Plate II, 1; Fig. 2A–C). Spacing of laterals at the apex is unknown.  $n + 2$  laterals borne proximally generally correspond to the ‘dichotomous globose structure’ of Gerrienne et al. (1999) and are inserted at wide angles (Plate I, 5; Plate II, 2; Fig. 2A,C). One specimen, however, produces proximal  $n + 2$  laterals that consist of long axes (Plate I, 2; Fig. 2B). The few preserved bases of  $n + 3$  branches suggest that they are produced according to the same pattern as the  $n + 1$  and  $n + 2$  ones, i.e. in two rows, the most proximal branch occurring in an abaxial position.

#### 3.2. Dichotomous globose structures

In our specimens, the ‘dichotomous globose structures’ correspond to morphologically distinctive laterals of the  $n + 1$  and  $n + 2$  orders. We suspect their occurrence as  $n + 3$  laterals as well. When degaged from the matrix, these structures comprise a short axis (ca. 2 mm long) which divides into two terminal segments, one adaxial, the other abaxial, both recurved towards the supporting axis (Plate I, 5). The plane which comprises the two segments is slightly oblique relative to that of the preceding order of axes (Fig. 4). In some of these structures one segment is longer than the other one or has undergone a second dichotomy (Plate I, 6; Plate II, 3; Fig. 2C).

#### 3.3. Fertile appendages

Information on fertile parts is obtained from three poorly preserved specimens, two of which are illustrated in Plate III, 1, 2; Fig. 2D,E. They are assigned to the same taxon as the vegetative specimens based on the following features: same diameter of axes and comparable branching angles; planar-alternate arrangement of laterals; occurrence of a ‘globose structure’ at base of the best preserved fertile specimen (Plate III, 2; Fig. 2E). These specimens display fertile appendages consisting of reduced lateral branch systems bearing groups of at least three

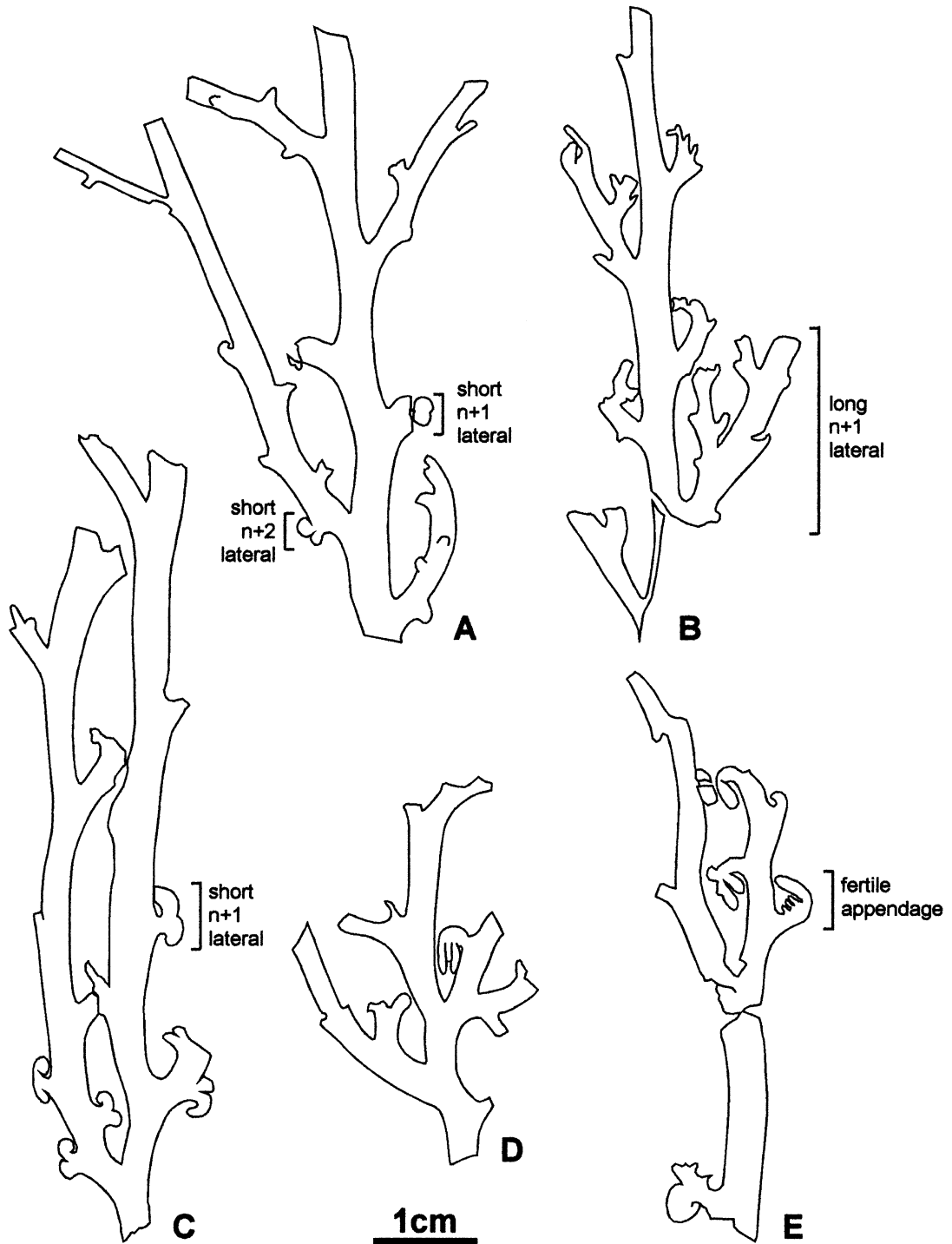


Fig. 2. *Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov. Line drawings of vegetative (A–C) and fertile (D–E) specimens.: A: LPM AZA 137 part and counterpart; B: LPM AZD 205 part; C: LPM AZD 223 part; D: LPM AZ 299; E: LPM AZC 275 part, holotype.

sporangia (Plate III, 4–7). Branching is interpreted as pseudomonopodial. Sporangia are sessile and probably pendulous. They are borne singly, as opposed to the paired arrangement in trimerophyte-type of sporangia. Sporangia are 1.8–4 mm long and 1–1.4 mm wide. They are oblong, either straight or arched. Their distal extremity is blunt or slightly acuminate. No dehiscence line is visible. The single preserved sporangium in the basalmost fertile appendage shown on Plate III, 4 appears larger than those occurring in more distal appendages of the same specimen. This may indicate a distal gradient of maturation of the fertile structures within the plant. The isolated group of sessile sporangia displayed in Plate III, 3 is tentatively assigned to the new plant based on the size, shape and arrangement of the individual sporangia on foreshortened axes.

No spores were preserved inside the sporangia. A number of poorly preserved large spores ranging 175–325  $\mu\text{m}$  (mean: 270  $\mu\text{m}$ ; 22 spores measured) occur isolated in the vicinity of the fertile appendages (Plate III, 4 at arrows–5). Despite the occurrence of a few lycopsid-like axes in the assemblage, the consistent association of megaspores with *Aarabia* suggest that these spores may have been released from the sporangia of the new plant.

#### 4. Taxonomy

Superdivision POLYSPORANGIOMORPHA (Kenrick and Crane, 1997)

Division TRACHEOPHYTA

Plesion *Aarabia* Meyer-Berthaud and Gerrienne *gen. nov.*

*Diagnosis:* Aerial systems of naked axes mostly derived from pseudomonopodial branching; at least four orders of axes. Difference in diameter of axes of successive orders not conspicuous. Main stem almost straight, bearing laterals in distichous, planar arrangement; this pattern reproduced in all orders of elongated laterals in the preserved parts of the plant. Long laterals comprising short internodes proximally, long internodes distally. Short laterals borne principally at base of all orders of long branches; some arranged unevenly on main axis. Short laterals

comprising a foreshortened axis dichotomising into two terminal segments recurved abaxially and adaxially towards the axis of previous order; further elongation or additional division possible in some segments. Fertile appendages consisting of foreshortened lateral branch systems bearing sporangia in clusters, presumably at their distal extremity. Individual sporangium sessile, borne singly, and probably pendulous. Sporangia oblong, either straight or arched, with a blunt or slightly acuminate distal extremity.

*Derivation:* *Aarabia* refers to the locality, close to Jbel ben Aarab.

*Type species:* *Aarabia brevicaulis* Meyer-Berthaud and Gerrienne *sp. nov.*

*Aarabia brevicaulis* Meyer-Berthaud and Gerrienne *sp. nov.*

*Diagnosis:* Small plants at least 9 cm in height, comprising 1.5–5 mm wide axes.  $n + 1$  laterals produced at 7–25 mm long intervals and diverging at 38–55° from main axis. Proximal  $n + 2$  laterals produced on long  $n + 1$  axes at 2.5–5.5 mm long intervals and diverging at 90–100°. Distal  $n + 2$  laterals separated by intervals reaching 15 mm. Short laterals borne on main axis and at base of long laterals; consisting of a 2 mm long axis dividing into 2 short recurved segments. Sporangia 1.8–4 mm long, 1.0–1.4 mm wide.

*Derivation:* *brevicaulis* refers to the occurrence of foreshortened laterals on all orders of axes.

*Holotype:* LPM AZC 275

*Paratypes:* LPM AZC 137, LPM AZG 240, LPM AZD 205, LPM AZD 223, LPM AZC 287, LPM AZ 299

*Locality:* 20 km northwest of Azrou and 1 km east of Jbel ben Aarab in central Morocco.

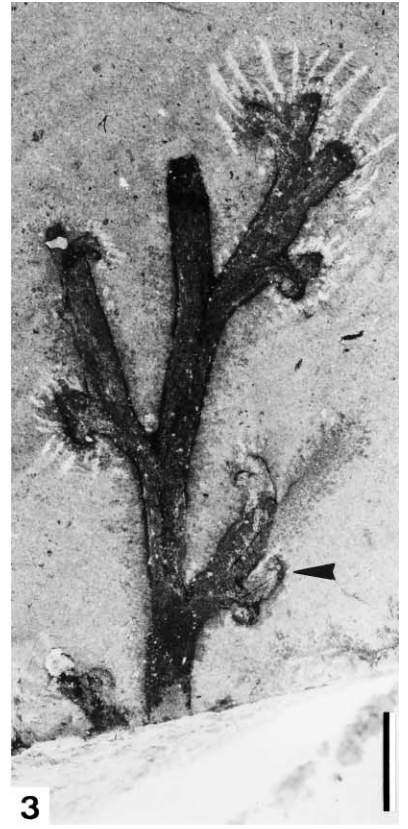
*Age:* Early Emsian

*Repository:* Collections du Laboratoire de Paléobotanique, Université Montpellier II, Montpellier, France.

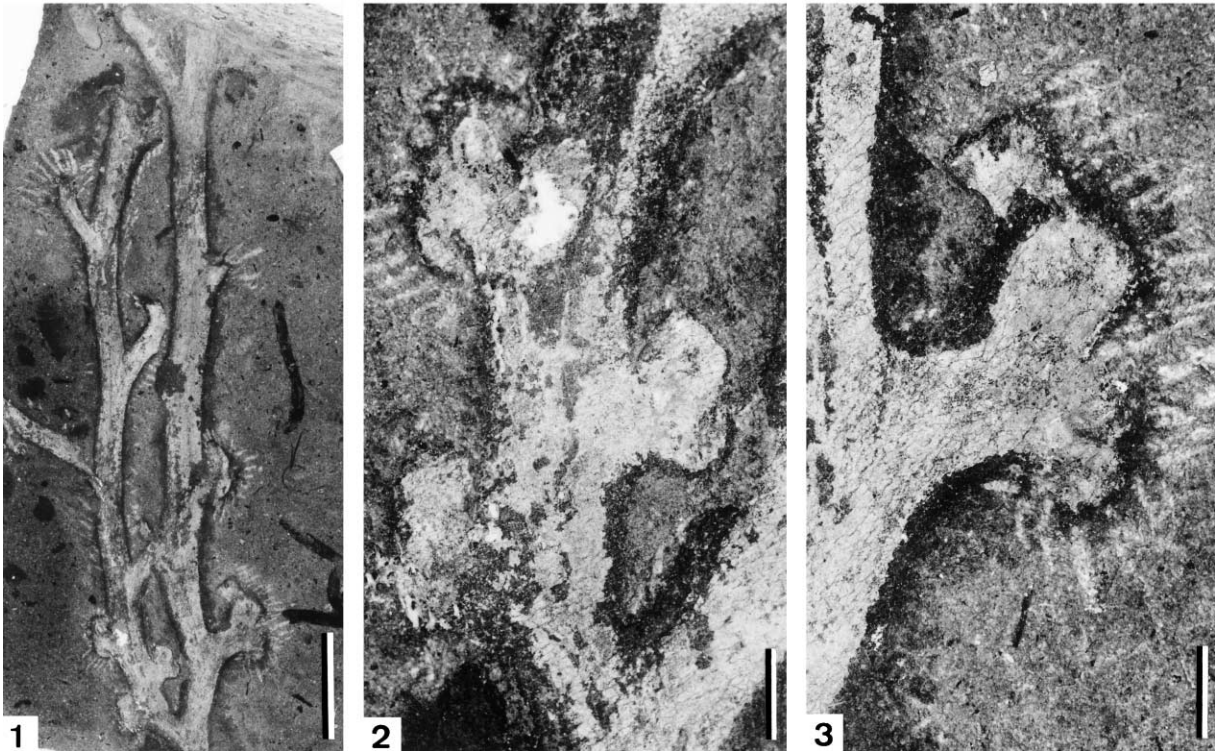
#### 5. Discussion

##### 5.1. Construction and growth habit

There is no available information on the underground system of *Aarabia brevicaulis* or on its



## PLATE II



*Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov.

1. Specimen LPM AZD 223 part. Scale bar = 1 cm. Vegetative shoot showing a long  $n + 1$  lateral on the left side of specimen. See Fig. 2C.
2. Specimen LPM AZD 223 part. Scale bar = 2 mm. Detail of 3  $n + 2$  laterals in proximal position in specimen illustrated in 1.
3. Specimen LPM AZD 223 part. Scale bar = 2 mm. Detail of a short  $n + 1$  lateral on the right side of specimen in 1. Note the elongated, possibly dichotomous, segment in adaxial position.

terminal parts. Fig. 5 is a composite reconstruction based on the best preserved specimens of the sample. It illustrates our interpretation of the sequence of branches produced by a hypothetical

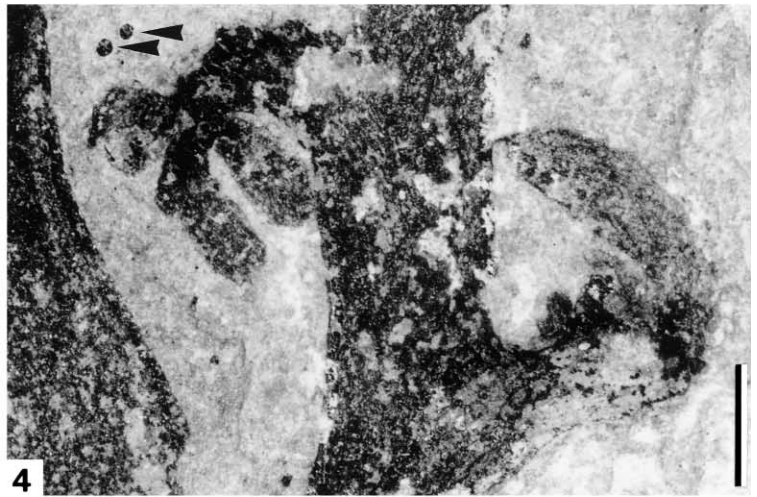
plant. Fig. 4 shows a detail of a short lateral branch or 'dichotomous globose structure'.

Divisions in *Aarabia* produce a branch system of pseudomonopodial type where distinction between

## PLATE I

*Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov.

1. Specimen LPM AZA 137 part. Scale bar = 1 cm. Vegetative shoot consisting of a main axis bearing 6  $n + 1$  laterals. Four are long branches which bear several  $n + 2$  laterals. See Fig. 2A.
2. Specimen LPM AZD 205 part. Scale bar = 5 mm. Vegetative shoot consisting of a main axis bearing 6  $n + 1$  laterals. See Fig. 2B.
3. Specimen LPM AZC 287 part. Scale bar = 1 cm. Vegetative shoot consisting of a main axis bearing 4  $n + 1$  laterals. Note the elongated segment of a short  $n + 2$  lateral at arrow.
4. Specimen LPM AZG 240 part. Scale bar = 5 mm. Portion of vegetative shoot interpreted as a detached  $n + 1$  long branch bearing at least 4  $n + 2$  short laterals.
5. Specimen LPM AZG 240 part. Scale bar = 1 mm. Detail of lower left short lateral of specimen in 4.
6. Specimen LPM AZG 240 part. Scale bar = 1 mm. Detail of upper left short lateral of specimen in 4. Note the longer abaxial segment.





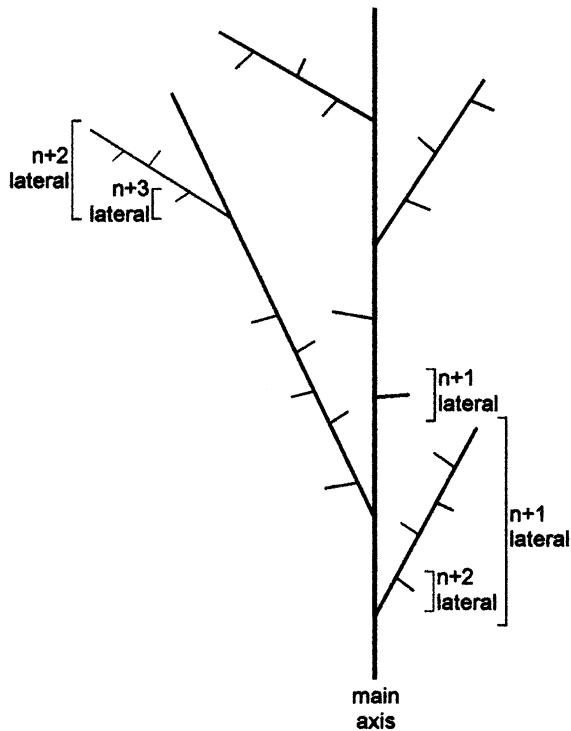


Fig. 3. Sketch of the branching pattern in *Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov., based on specimen LPM AZA 137 part and counterpart. The most completely preserved specimens typically comprise 4 orders of axes, i.e. a main stem and 3 orders of laterals.

‘main axes’ and ‘subordinate branches’ involves principally the orientation of the daughter axes rather than conspicuous differences in their diameter. Based on the sequence of production of the  $n + 1$  and  $n + 2$  laterals on their parent stems, we hypothesise that the plant consists of axes which generally bear closely spaced short laterals proximally. Intervals between branches increase distally, up to an average length

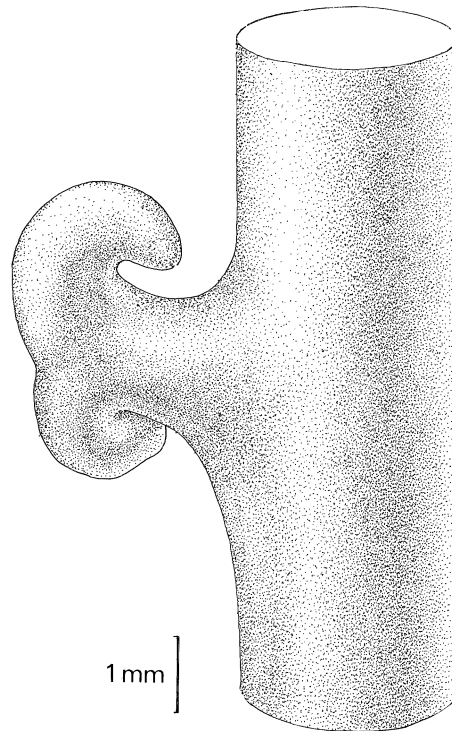


Fig. 4. *Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov. Reconstruction of a short lateral branch.

of 12 mm. Distal laterals consist of long branches in which this pattern is repeated. This morphology suggests that developmental interactions occur between organs, analogous to those involved in monopodial plants and related to apical dominance.

Based on morphological features, we made a distinction between short and long laterals. From a developmental point of view, the question arises whether short laterals correspond to branch systems whose growth is momentarily or definitively stopped.

### PLATE III

*Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et sp. nov.

1. Specimen LPM AZ 299. Scale bar = 1 cm. Fertile shoot showing a group of sporangia borne on a short  $n + 2$  lateral. See Fig. 2(D).
2. Specimen LPM AZC 275 part. Scale bar = 1 cm. Holotype showing 3  $n + 2$  fertile laterals. A typical vegetative short branch is attached in  $n + 1$  position on the bottom left of the main stem. See Fig. 2(E).
3. Specimen LPM AZD 206. Scale bar = 1 mm. Isolated sporangia possibly referable to *Aarabia*.
4. Specimen LPM AZC 275 part. Scale bar = 2 mm. Part of fertile zone of holotype specimen in 2, enlarged. Some dispersed megaspores are visible at arrows.
5. Specimen LPM AZ 299. Scale bar = 2 mm. Fertile zone of specimen in 1, enlarged. Note dispersed megaspores on top right of figure.
6. Specimen LPM AZ 299. Scale bar = 2 mm. Fertile zone of specimen in 1, after transfer.
7. Specimen LPM AZ 299. Scale bar = 1 mm. Enlargement of 6 to show the blunt apex of a sporangium at arrow.

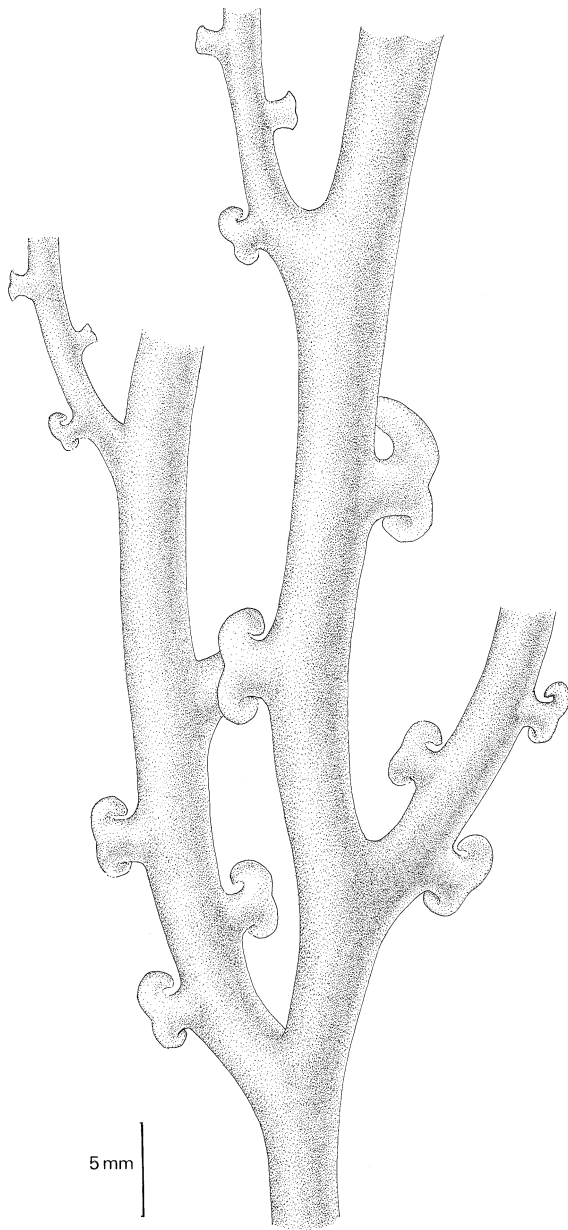


Fig. 5. *Aarabia brevicaulis* Meyer-Berthaud and Gerrienne, gen. et. sp. nov. Hypothetical reconstruction of a portion of vegetative shoot.

In the latter case, the short laterals may be interpreted as appendicular recurved appendages, possibly adapted to perform certain functions. However, short laterals like those figured in  $n + 1$  position in

Fig. 2C suggest that some undergo more extended growth. One segment, at least, may grow longer or divide once more. Moreover, occurrence of a long  $n + 2$  branch in a proximal position in one specimen (Plate I, 2; Fig. 2B) suggests that, under favourable conditions, an extended growth of short laterals may occur and result in branch systems morphologically similar to long branches. In this case, short laterals may represent branch systems that have temporarily ceased to grow. Based on the present evidence, we are unable to determine if the recurvation of the segments in such short laterals is related to circinate vernation. Branching is limited in fertile appendages. We interpret these organs as representing a category of short lateral branch systems that have definitively ceased to grow due to the irreversible differentiation of their apical meristems for reproduction.

The long type of axes either show a slight increase in diameter distally or remain stable. None shows any distal tapering. These Early Devonian plants likely did not produce secondary tissues and the external diameter of axes may faithfully measure their primary body. The preserved parts of *Aarabia brevicaulis*, therefore, represents indeterminate phases of growth where primary bodies enlarge or are stable in size. This suggests that the actual size of the aerial part of *Aarabia* greatly exceeded the 90 mm recorded in the longest preserved specimen.

The planar arrangement of branches in the preserved portions of *Aarabia brevicaulis* is suggestive of a non self-supporting habit, whether scrambling or climbing. In addition, the recurved tips of the short laterals superficially resemble the hook-like appendages of lianas. Despite these features, we think that our specimens represent erect shoots for the two following reasons: (1) branching angles are relatively narrow. They contrast with the wide angles generally recorded in climbers, that optimise the supporting function of the branches; (2) fertile appendages lie in the same plane as the other branches and they are consistently orientated towards their parent axis. This morphology looks counter-adapted for the efficient dissemination of spores in case of a scrambling habit. We favour the hypothesis that the fertile appendages were pendulous and borne on erect axes. This assumption does not preclude a scrambling habit for the proximal portions of *Aarabia*.

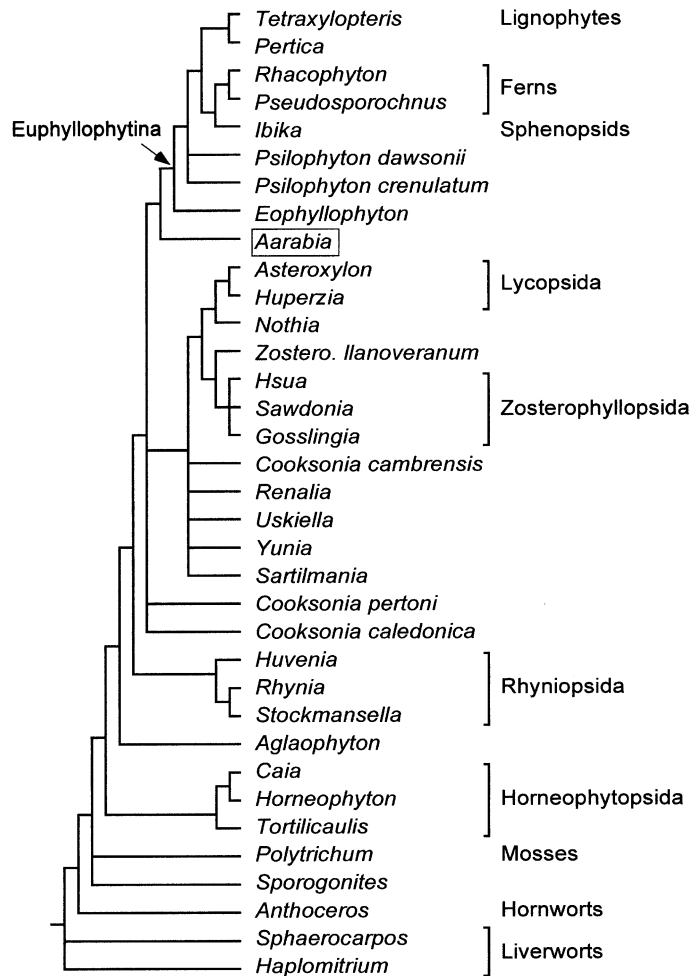


Fig. 6. Cladogram of relationships of *Aarabia* within basal polysporangiophytes. Strict consensus tree from cladistics analysis. Based on Kenrick and Crane's (1997) analysis.

## 5.2. Comparisons

Distinctive features of *Aarabia brevicaulis* include: (1) a pseudomonopodial habit; (2) the production, together with long branches, of short laterals characterised by a small number of divisions. In most cases, these structures display a single dichotomy and terminate in two segments with recurved tips; (3) branches showing increasingly longer internodes and bearing more complex laterals distally; and (4) short fertile branches, showing few anisotomous divisions, and bearing a small number of non-paired elongated sporangia. This set of characters is unknown in

previously described taxa. Plants of Emsian and Early Middle Devonian age which compare more closely to *Aarabia* form a plexus of basal euphyllophytes characterised by a pseudomonopodial habit and the possession of longitudinally elongated sporangia borne terminally on distinctive fertile branch systems. Among them are a number of species assigned to *Psilophyton*. One character of the species *Psilophyton dawsonii* which deserves special attention is the production, along the main-axis, of reduced lateral branches together with elongated ones (Banks et al., 1975). This pattern recalls the arrangement of the short laterals on the main axis of *Aarabia*. But the

consistent arrangement of such short branches at the base of axes of subsequent orders was not observed in *P. dawsonii*. A second feature displayed by *P. dawsonii* and others species of *Psilophyton* is the recurvation of the distalmost vegetative branchlets. The two terminal segments in the short laterals of *Aarabia* are likewise recurved. *Psilophyton* plants, however, clearly differ from the Moroccan specimens. They have a three-dimensional habit and produce lateral branches helically whereas *Aarabia* displays its branches in planar-alternate arrangement. The branching type in *Psilophyton* combines a predominantly pseudomonopodial habit for the main stem with predominantly isotomous divisions in lateral branches; in *Aarabia*, the main stem and all observed subsequent orders of axes, except the short laterals divide pseudomonopodially. Fertile branches in *Psilophyton* divide more than those of *Aarabia* and bear more numerous sporangia. Finally, Sporangia are borne singly in *Aarabia*, but produced in pairs in *Psilophyton* (Hueber and Banks, 1967; Gensel and Andrews, 1984), the two members of a pair being consistently twisted around each other in a sinistral direction (Gerrienne, 1997).

*Pertica varia* (Granoff et al., 1976) displays some lateral vegetative branches that divide pseudomonopodially and, in this way, compare better to *Aarabia*. But all *Pertica* plants exhibit a typical three-dimensional habit (Kasper and Andrews, 1972). They are bigger, and have stouter main axes than *Aarabia*. Their fertile branches produce a larger number of sporangia which, in the species *P. varia*, are paired and twisted. Based on branching type, the monospecific genus *Oocampsa* (Andrews et al., 1975) whose affinities are currently uncertain is closer to *Aarabia* than any other taxon of comparable age. In this genus, all orders of branches including the fertile ones divide pseudomonopodially. But *Oocampsa* include larger and more frequently branched plants than *Aarabia*, in which the main stem is distinctly wider than the lateral branches. The sporangia of *Oocampsa* are larger, more ovoid, slightly twisted and erect.

In a section above we evoked the possibility that *Aarabia* produced megaspores. The oldest recorded heterosporous plant is *Chaleuria cirrosa* from Emsian beds in New Brunswick (Andrews et al., 1974). *Chaleuria* represents another plant where pseudo-

monopodial branching is expressed in all orders of axes except the ultimate ones. *Chaleuria* also possesses distal appendages with recurved tips. Such structures, however, differ from the short laterals of *Aarabia* in that they are not borne on main axes, but exclusively on lateral branches. Moreover, these appendages occur along the whole length of branches and are not restricted to the proximal part. Finally, the arrangement and branching patterns of the fertile branches are unlike those of *Aarabia*.

Table 1

List of characters and character states of *Aarabia* (characters and character coding taken from Kenrick and Crane, 1997, chapter 4)

Character	Character state	
1 Sporophyte independence	unknown	?
2 Well developed sporangiophore	Present	1
3 Sporophyte branching	Present	1
4 Branching type	pseudomonopodial	1
5 Branching pattern	planar-alternate	2
6 Subordinate branching	absent	0
7 Rhynia-type adventitious branching	absent	0
8 Circinate vernation	recurvation	2
9 Multicellular appendages	absent	0
10 Dichotomous pinnulelike appendages	absent	0
11 Conical sporangium emergences	absent	0
12 Stomates	unknown	?
13 Sterome	unknown	?
14 Xylem strand shape	unknown	?
15 Protoxylem	unknown	?
16 Decay-resistance of tracheid cell wall	unknown	?
17 Tracheid thickenings	unknown	?
18 Metaxylem tracheid pitting	unknown	?
19 Simple pitlets in tracheid wall	unknown	?
20 Aligned xylem	unknown	?
21 Xylem rays	unknown	?
22 Sporangiotaxis	unknown	?
23 Sporangium attachment	terminal	0
24 Specialised fertile zone	present	1
25 Specialised sporangium-axis junction	absent	0
26 Sporangium abscission	absent	0
27 Sporangium shape	more or less fusiform	0
28 Sporangium symmetry	radial	0
29 Sporangium dehiscence	unknown	?
30 Thickened sporangium valve rim	unknown	?
31 Sporangium branching	absent	0
32 Columella	unknown	?
33 Elaters and pseudoelaters	unknown	?

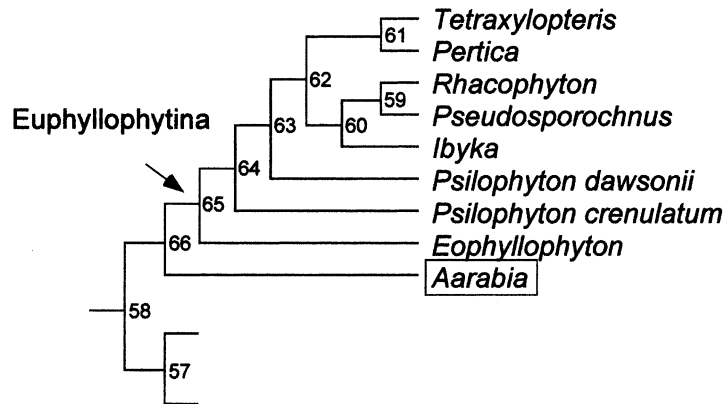


Fig. 7. Cladogram of relationships of *Aarabia* within basal polysporangiophytes. Character state changes on one of the 648 most parsimonious trees (tree no. 30). Based on Kenrick and Crane's (1997) analysis.

### 5.3. Systematics

The affinities of *Aarabia* with other polysporangiophytes were estimated through a cladistic analysis using the framework of Kenrick and Crane for Polysporangiophytes (1997, chapter 4) to which we added our data. The analysis was based on 35 taxa (Kenrick and Crane's 34 taxa + *Aarabia*), with the extant genera *Haplomitrium* and *Sphaerocarpos* designated as outgroups. Coding of the 33 characters and character states of *Aarabia* is reported in Table 1. Character 8 which refers to the occurrence of circinate veneration is coded 2 (= recurvation) in Table 1. In a previous section, we discussed the significance of the short laterals, whether as recurved appendicular organs or as branches that may resume growth and if so, whether they display circinate veneration or not. Because it is ambiguous in *Aarabia* (see Section 5.1 above) we tested the two alternative codings: 0 = no circinate veneration and 1 = circinate veneration present.

Trees were generated using the Branch-and-Bound routine of PAUP (version 3.1.1; Swofford, 1991). The analysis resulted in 648 equally parsimonious trees of 73 steps, with consistency indexes of 0.74. Fig. 6 illustrates the strict consensus tree. A heuristic search provided 643 trees and gave the same topology for the consensus tree. Character changes are mapped on one representative most parsimonious tree (Fig. 7; Table 2). This analysis places *Aarabia* in a sister-group relationship with the euphyllophytes. The clade

Euphyllophytina + *Aarabia* is defined by pseudo-monopodial branching (character 4; Fig. 7, node 58 > node 66; Table 2) and occurrence of specialised fertile zones (character 24; Fig. 7, node 58 > node 66; Table 2). Other possible synapomorphies would include the more or less fusiform shape of the sporangia. *Aarabia* is distinguished from the other euphyllophytes by its planar-alternate branching pattern (character 5: Fig. 7, node 66 > *Aarabia*; Table 2). Tests conducted with the different codings of character 8 did not affect the topology of the tree. Finally, an analysis was performed with one additional character in the matrix, i.e. homosporous/heterosporous and the coding of *Aarabia* as heterosporous. The resulting consensus tree again placed *Aarabia* as the sister-taxon of the euphyllophytes.

These analyses suggest that *Aarabia* is closely related to *Eophyllophyton*, a Pragian genus from Yunnan, China (Hao, 1988; Hao and Beck, 1993).

Table 2  
Significant changes of characters in tree in Fig. 7

	Characters	Changes
4	Branching type	Node 58–node 66, 0–1
5	Branching pattern	Node 58–node 66, 0–1
5	Branching pattern	Node 66– <i>Aarabia</i> , 1–2
8	Circinate veneration	Node 58–node 66, 0–2
9	Multicellular appendages	Node 66–node 65, 0–1
10	Dichotomous pinnulelike appendages	Node 66–node 65, 0–1
24	Specialised fertile zone	Node 58–node 66, 0–1

*Eophyllophyton* is a very distinctive genus characterised by the possession of small laminate leaves, the fertile ones bearing ovoid to spherical sporangia on their adaxial surface. This putative relationship which is based on a few shared synapomorphies, i.e. pseudomonopodial branching and specialised fertile zones, would have a great significance from a phyto-geographical point of view. It would point to the possibility that the Euphyllophytina clade originated in Gondwana. We nevertheless think that this result is biased due to the rarity of Early Devonian fossils outside the palaeocontinent Laurussia on one hand, to the general lack of ‘whole plants’ relevant for phylogenetic studies, on the other hand.

These tentative analyses further suggest that *Aarabia* and *Eophyllophyton* are plesiomorphic within the clade Euphyllophytina + *Aarabia*. This contradicts more intuitive approaches according to which generalised pseudomonopodial branching and perhaps heterospory for *Aarabia*, laminate leaves and sporangial covering for *Eophyllophyton* would be interpreted as rather advanced features compared to those that characterise *Psilophyton* for example.

## 6. Conclusion

*Aarabia* is a new plant from the Early Emsian of Africa of which a reasonable part of the aerial system is reconstructed. Preserved parts display a bidimensional branching type; narrow angles between branches and the orientation of fertile appendages let us interpret them as portions of upright shoots. The closest affinities of *Aarabia* are with the basal euphyllophytes. Branching is distinctively pseudomonopodial and profuse, resulting in shoots comprising up to four orders of axes. A unique character of the plant is the possession of short laterals separated by small internodes in the proximal part of branches, and irregularly distributed elsewhere. They superficially resemble the determinate appendages with recurved tips in *Psilophyton* and *Chaleuria*. An alternative hypothesis is that they represent branches in which growth is temporarily stopped. If confirmed, the capacity for some branches to resume growth after a period or rest is an innovation that might have conferred adaptive advantages to the plant. Compared to the fertile branches of most basal euphyllophytes known

to date, those of *Aarabia* combine a derived, entirely pseudomonopodial type of branching with a reputedly primitive morphology of the sporangia that are straight and borne singly. We evoked the possibility that *Aarabia* represented one of the earliest plants with a heterosporous biology. This new genus is an additional example of the diversity of plants that evolved in the Early Devonian. It suggests that, during this period, diversification in basal euphyllophytes and related plants occurred in parallel, and possibly to the same extent, as the better documented diversification of the zosterophylloids.

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