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Author(s): Imogen Poole and Christopher N. Page

Source: *New Phytologist*, Vol. 148, No. 1 (Oct., 2000), pp. 117-125

Published by: Blackwell Publishing on behalf of the New Phytologist Trust

Stable URL: <http://www.jstor.org/stable/2588907>

Accessed: 26/11/2008 06:04

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# A fossil fern indicator of epiphytism in a Tertiary flora

IMOGEN POOLE<sup>1\*</sup> AND CHRISTOPHER N. PAGE<sup>2</sup>

<sup>1</sup>*Geochemistry, Earth Sciences, Utrecht University, PO Box 80021, 3508 TA Utrecht, The Netherlands*

<sup>2</sup>*Cornwall Geological Museum, Alverton Street, Penzance, Cornwall TR18 2QR, UK*

*Received 29 November 1999; accepted 22 May 2000*

## SUMMARY

The first known indicator of probable fern epiphytism in the Tertiary fossil record is documented from the Eocene London Clay of southeast England. This pyritised fern rachis exhibits major deviation from the basic form of petiolar vascular trace morphology shown by the other London Clay fossil ferns and is here attributed to the Polypodiaceae. This represents the first known occurrence of this family in the London Clay macroflora, and brings the total of distinct fern rachis types from the Lower Tertiary of southeast England to six. The significance of this find is interpreted in relation to its probable origins from a tropical rainforest palaeoflora in which it is proposed that this specimen represents the first occurrence of an epiphytic component.

Key words: palaeobotany, rachis, stipe, Eocene, London Clay, Polypodiaceae, epiphyte.

## INTRODUCTION

The flora of the British Tertiary is already known to be relatively rich in its fern diversity. On the basis of either vegetative or reproductive organs, including spores, rhizome or leaf remains these have been assigned to one of eight families which include the Osmundaceae (Chandler, 1957), Schizaeaceae (Chandler, 1955), Gleicheniaceae (Chandler, 1963), Cyatheaceae (Chandler, 1964), Hymenophyllaceae (Chandler, 1964), Salviniaceae (Chandler, 1961; Collinson, 1980), Adiantaceae (Collinson, 1978) and Polypodiaceae (Collinson, 1978). A list of fern genera known from elsewhere in the Eocene is given in an overview by Collinson (1996). Of the fern families listed for the British Tertiary, only three are represented in the extant British flora (Page, 1997), namely the Osmundaceae, Polypodiaceae and Adiantaceae (although the family Azollaceae, of the order Salviniales, has become naturalized in Britain). Thus, a great diversity of fern life-forms is present in the fossil record ranging in size from small filmy ferns to large tree ferns, and in habitat from probable lithophytes to floating aquatics (Page, 1979a).

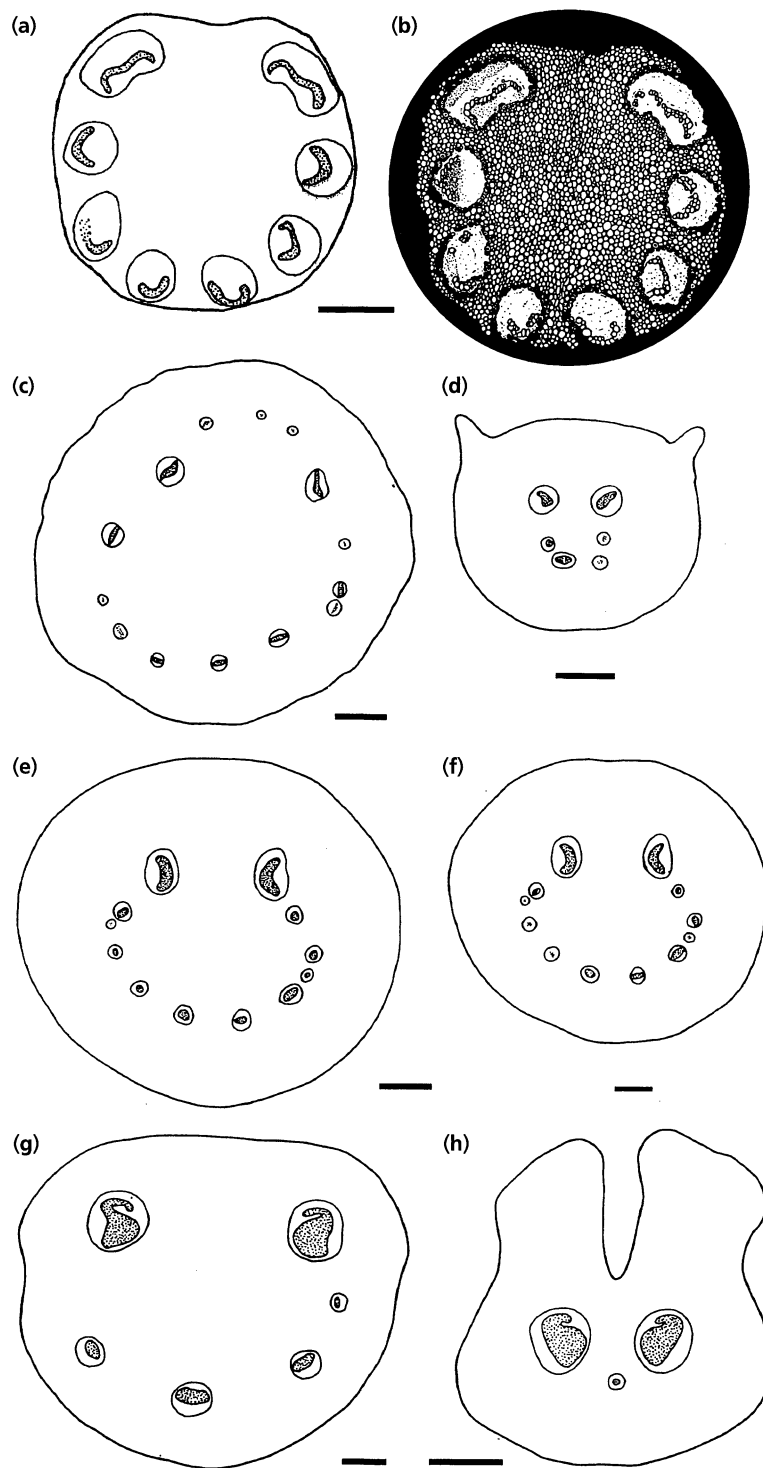
Fossil deposits of Eocene age (Ypresian, 52 million years BP) from southeast England contain abundant fern remains in the form of isolated axes associated with numerous woody angiosperm and conifer

fragments, collectively forming the 'twig' component of the London Clay flora. It is material from this source which is the focus of this study.

The London Clay flora paleohabitat is an allochthonous accumulation of material derived from an inland palaeovegetation source interpreted to be a rainforest flora (Reid & Chandler, 1933) with a suggested minimum mean annual temperature somewhere between 20 and 27°C (Collinson, 1983). This fossil flora has been likened most closely to the present flora of the Indo-Malaysian region (Reid & Chandler, 1933; Collinson, 1983; Poole, 1993a), with important higher plant elements such as dipterocarpaceous wood and frequent fossil *Nyssa* palm fruits emphasizing this link. The fern flora of modern Malaya and adjacent regions has been studied by Copeland (1907, 1958–1960), Holttum (1954), Amoroso *et al.* (1996), Parris (1985, 1986) and Roos (1996), who have emphasized species richness and ecological diversity.

Since the fern component of the London Clay flora indicates that catchment from a number of different habitats is involved, we feel it would be presumptuous to consider that elements in this fossil flora are exclusively genera still living solely in the Indo-Malaysian region. Thus, a broader comparison is drawn with ferns still occurring throughout the whole Malesian region (*sensu van Steenis*, 1950, which stretches from the Philippines and Malaya to north Queensland and the southwest Pacific Islands), as well as with some modern fern genera in other

\*Author for correspondence (tel +31 30 2535068; fax +31 30 2535050; e-mail i.poole@geo.uu.nl).

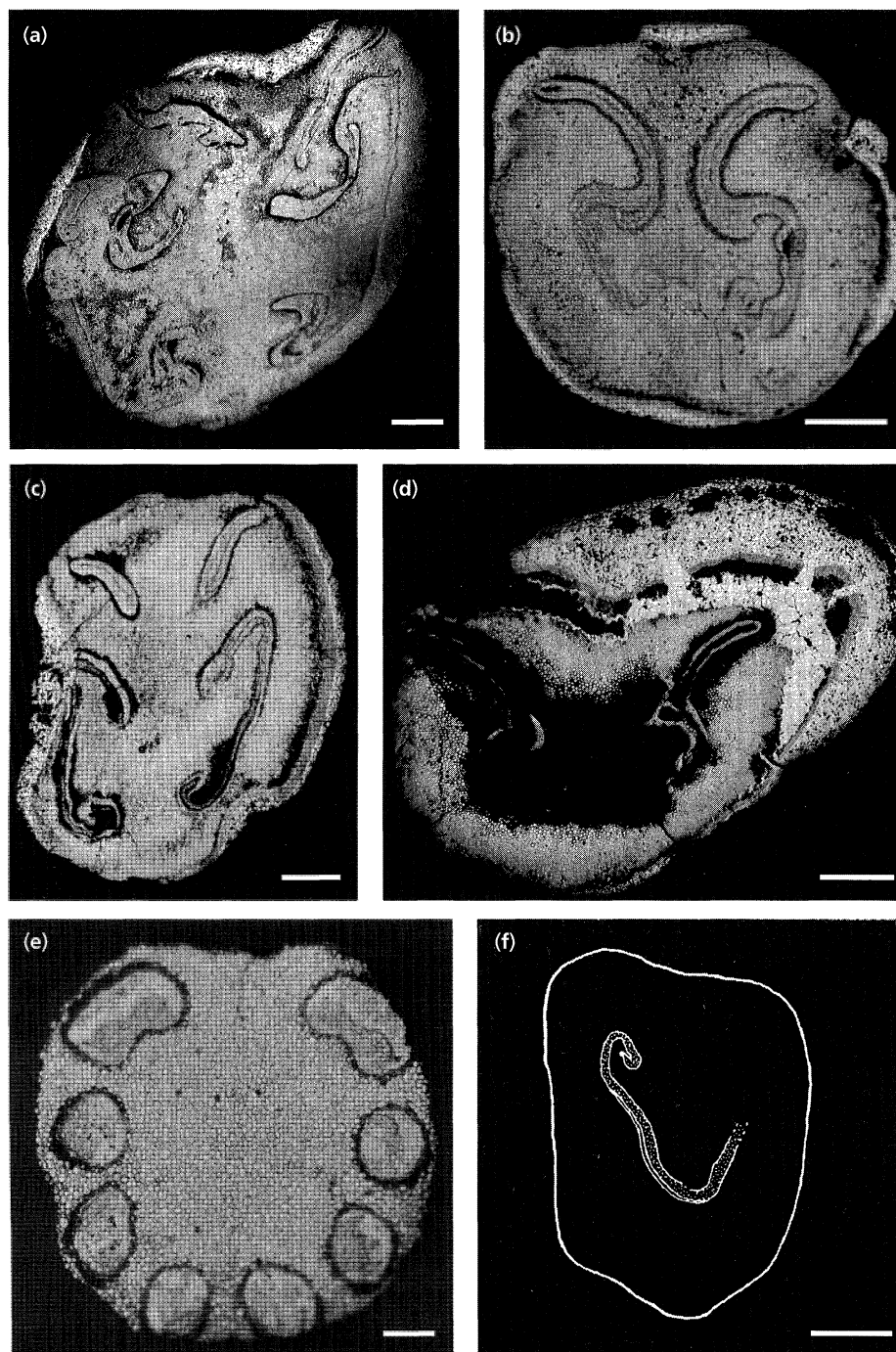


**Fig. 1.** Tissue plans of fossil Rachis type E (V.64716) and extant fern axes; a, c–h drawn from thin sections. (a) Low-power tissue map of Rachis type E (V.64716). Bar, 0.5 mm. (b) high-power diagram drawn from a photomicrograph of the individual cell distribution of the same specimen. (c) *Polypodium loriceum*, petiole. Bar, 1 mm. (d) *Polypodium loriceum*, upper rachis. Bar, 1 mm. (e) *Phlebodium aureum*, petiole. Bar, 0.5 mm. (f) *Phlebodium aureum*, upper rachis. Bar, 0.5 mm. (g) *Dryopteris odontoloma*, petiole. Bar, 0.5 mm. (h) *Dryopteris odontoloma*, upper rachis. Bar, 0.5 mm.

parts of the tropics. Significantly, perhaps, this broad region equates closely with the overall extant range of *Nypa* (Good, 1961).

The total diversity of the hitherto known fossil fern rachis assemblage from the London Clay represents remnants of one or more of an array of

possible families which include Dennstaedtiaceae, Athyriaceae, Thelypteridaceae, Onocleaceae and Pteridaceae (Poole, 1993b). Significantly, the extant members of the genera of these families are predominantly forest-floor-inhabiting taxa and, together with other woody components, might have



**Fig. 2.** Vascular morphology in transverse section of the six different types of fern rachides found in the London Clay: a–e, polished faces; f, drawn from Ribbins & Collinson (1978). (a) Rachis type A. (b) Rachis type B. (c) Rachis type C. (d) Rachis type D. (e) Rachis type E (V.64716). (f) Rachis type F. a–d and f, bar, 1 mm; e, bar, 0.25 mm.

been washed from such a forest floor during a sudden flooding outwash period into the rivers which drained into the shallow London Clay Sea to the east. In this respect, observations (C. N. Page, unpublished) of contemporary tropical fern vegetation suggest that the concentration of stipe and rachis material seen in these fossil deposits is typical of that which is seasonally shed from the more persistent rhizomes of ferns. The apparent absence of any laminar material might suggest a period of

initial frond decay which in ferns, especially in moist tropical habitats, proceeds very rapidly after death. Decay, especially from the distal regions of the frond, can reach virtual completion before the dying rachis either becomes detached from the rhizome or finally decays back to the rhizome without detachment.

The anatomical similarity within much of the fern axis material coupled with its relative abundance (2–4%) in the total twig flora and regular presence in

the fossil flora suggests that a terrestrial fern component was a comparatively important part of the parent vegetation. This is analogous to the abundance (and typical diversity) in which ferns contribute to the flora of virtually all moist tropical rainforests. The new find of a single additional specimen is of clear fern affinity (Figs 1a,b, 2e) and nothing closely similar to it has been found in any fossil flora. Its scarcity compared with the other fern types suggests that it was either a species of comparative rarity in the parent flora or that it belonged to another part of the same forest community but had less taphonomic potential.

Fern rachides have been noted from the lower Tertiary deposits of southern England. Carruthers (1870) describes a silicified 'fern stem' of *Osmunda* L. from the Lower Eocene of Herne Bay, Kent, UK. The transverse section exhibits abundant, discrete petioles with a gutter-shaped vascular trace. This specimen was added to three other closely allied forms from younger Tertiary strata. The *Osmunda* specimen described by Carruthers (1870) is very similar to the osmundaceous fern described by Arnold (1952) from the Upper Eocene Clarno Formation of western North America. Chandler (1961) described two distinct types of Eocene fern rachis which could be separated on vascular trace morphology. She named them 'Rachis 1' and 'Rachis 2'. Two of these specimens (Rachis 1 type) were from the Isle of Sheppey, the others were from Herne Bay, both in the London Basin. No further taxonomic assessment was made.

Collinson & Ribbins (1977) noted that 26 specimens of fern rachides represented about 1% of their total twig sample. These specimens could be divided into three basic types. Eight coincided with Chandler's Rachis 1 (to be designated 'Rachis B' by Collinson & Ribbins (1977) (Fig. 2b), 13 coincided with Chandler's Rachis 2 (to be designated 'Rachis C' (Fig. 2c) and five specimens were assigned to a previously unrecorded type, 'Rachis A' (Fig. 2a). They suggest that Rachis A (with inverted, convoluted omega-shaped traces with outwardly recurving adaxial arms) might be a primary rachis. Rachis B (with two traces of an S and mirror S shape) and C (with two adaxial arms and two C-shaped traces) would then be rachides of increasing order based on relative diameters. Ribbins & Collinson (1978) described a fourth rachis type which was initially included in Rachis A, but later assigned to a separate type, Rachis D, by Poole (1992) on the discovery of a rachis exhibiting the same trace morphology. Rachis D (Fig. 2d) is now represented by five specimens and is characterized by a smooth omega-shaped trace and very characteristic tightly and inwardly recurved adaxial arm. A fifth rachis type (Fig. 2f) was noted by Ribbins & Collinson (1978). Only one such specimen has been found; they describe this as having a 'pronounced

adaxial groove and a U-shaped vascular trace. The trace is more V-shaped and markedly less convoluted than specimens assignable to rachis type A. In addition, the adaxial arms are incurved to form adaxial hooks'. There was no evidence of compression and thus the V-shaped morphology could not have resulted from undue pressure on the fern rachis during fossilisation (M.E. Collinson, pers. comm.). Since this rachis vascular strand was described as being 'morphologically distinct' (Ribbins & Collinson, 1978) it has been suggested (Poole, 1993b) that this specimen be assigned the type-letter F for preliminary identification purposes and that the fossil with its distinctive vascular morphology described and discussed here represents a new rachis type, Rachis E (Figs 1a,b, 2e).

#### MATERIAL AND METHODS

Pyritised axes of small diameter (commonly referred to as 'twigs') can be found in abundance where the Lower Eocene London Clay outcrops around the southeast coast of England in both the London and Hampshire Basins (Collinson, 1983). Modern wave action washes the material out of the clay and concentrates the axes along the foreshore. The sample of pyritised twigs in which this specimen was found was collected from Warden Point (National Grid Reference TR996731) on the Isle of Sheppey, Kent.

The specimen is 3 mm in diameter and 17 mm long. Highly polished thick sections were obtained by cutting the specimen first transversely then longitudinally on a rock cutter with a diamond wafering blade. Sections were embedded in polyester resin and subjected to a fine-polishing technique (Kenrick & Edwards, 1988; Hass & Rowe, 1999). These surfaces were then studied with a mineralogical reflected-light microscope. This specimen (V.64716) is now deposited in the Natural History Museum, London, UK.

An initial survey to determine possible affinities was conducted through reference to illustrative and descriptive material (Bower, 1908, 1935; Ogura, 1972). Closer comparisons were then made using modern material of Polypodiaceae (e.g. *Polypodium lonicereum* L., *Phlebodium aureum* (L.) J. Sm. and *Platyserium hillii* T. Moore) and Aspidiaceae (e.g. *Dryopteris odontoloma* (Moore) C.Chr., *Dryopteris walliciana* (Speng.) Hyl, and *Dryopteris carthusiana* (Villars) H.P.Fuchs) supplied by the Royal Botanic Gardens, Kew, UK and the Royal Botanic Garden, Edinburgh, UK.

#### RESULTS

Rachis E, which is pyritised and is 3 mm in diameter and 17 mm long is characterized by an adaxial (dorsal) groove and eight discrete vascular traces,

two of which are reniform and the remaining six more or less circular (Figs 1a,b, 2e). The ground mass of the axis is composed of parenchyma and the outer layers of tissue have been eroded.

#### *Comparison with fossil material*

The diameter of Rachis E (3 mm) is much smaller than that of the other, more common, London Clay stipe material (mean approx. 6 mm) and exhibits major deviation from the common basic form of petiole vascular morphology shown by Rachis types A, B, C, D and F (Fig. 2a–d, f). These types are considered to include rachides increasing in order from A to C. Therefore, there are two lines of evolution, one line exemplified by Rachides A to D and F and the second by Rachis E.

A fern from the Princeton Chert (Middle Eocene) of North America is described (Basinger, 1976; Cevallos-Ferriz *et al.*, 1991) as being polypodiaceous, and resembles Rachis E. However, the North American fossil fern differs from Rachis E in that the former has a partially aerenchymatous vegetative body and somewhat larger adaxial traces which are C-shaped as opposed to reniform. Published records of ferns with a vascular trace morphology similar to that illustrated by Cevallos-Ferriz *et al.* (1991) have not been found.

#### *Comparisons with extant material*

Petioles which are adaxially grooved occur in other plant orders. Those which might carry petioles of similar size to those of the fossil include some conifers and *Ginkgo* (which can be distinguished from Rachis E by the presence of a single vascular trace or two traces, respectively) and some flowering plants. Very few angiosperm petioles are reported to have discrete vascular traces forming a ring (Metcalf & Chalk, 1980) and in those taxa which do, these traces are mostly small, relatively central within the tissue, with odd numbers of traces (i.e. 5, 7, 9) and lack the tendency for slightly larger adaxial traces and hooked sectional shapes to the strands – both features especially characteristic of fern stipe vasculature.

Thus, this new rachis type is characterized by its small diameter and the number, size and typically filicalean arrangement of the vascular traces. This specimen is similar to other fossil and extant fern rachides in its bilateral symmetry and small lengthwise groove, features which suggest that the fossil material represents a piece of fern stipe/rachis. The alternative interpretation is that this specimen is a fern rhizome, but this is less likely because of its small diameter. In addition, were it to be of rhizome origin it would probably possess the following characteristics: cross-sectional shape reflecting close adpression in life to a substrate; indications of

insertion points of dense root masses; indications or remnants of scale bases. Moreover, a groove is normally characteristic of the adaxial aspect of a fern stipe or rachis and not a rhizome. The distinctive vascular structure further suggests that it is not a small distal rachis fragment of another, already known, terrestrial fern but a fragment of stipe or rachis in its own right and of different taxonomic affinity.

Accurate identification of any material, including ferns, requires study of as many characters as possible. In the absence of reproductive structures, which are undeniably of paramount importance in fern classification, characters such as the gross morphology of (1) fronds, which can be of value in general family and sometimes generic attribution, (2) stems (including stipes and rachides), (3) epidermal structures such as hairs, spines, ramenta and glands, and (4) the arrangement of stomata and subsidiary cells which can be additionally diagnostic at a variety of levels. As many of these are absent or badly preserved in the fossil record, accurate identification of all material of a fossil fern to family or generic level can be difficult. The specimen described here is particularly slender (3 mm diam.) with a characteristic vascular trace composed of a ring of eight discrete sub-traces: six are smaller, almost circular in cross section; the remaining two are larger and almost reniform. Owing to the small diameter of the rachis and supposed tropical parent flora (Reid & Chandler, 1933), stipes and rachides of the other families were considered.

Of the fern taxa which also have slender stipes and are of modern tropical affinity very few exhibit close similarity in stipe vascular arrangement. Within the stipes of Gleicheniaceae (e.g. *Gleichenia*, *Dicranopteris* and *Sticherus*, which are common in tropical open areas near tropical forests, but which could be subject to flash floods), generally only traces of U, gutter or horseshoe shape occur. In the mostly slender-stiped *Pellaea* (Adiantaceae), *Matonia* (Matoniaceae), *Loxsonia* (Loxsoniaceae), *Onoclea* (Onocleaceae), Hymenophyllaceae, Grammitidaceae, Lindsaceae, Sinopteridaceae, Dennstaedtiaceae, Davalliaceae, Athyriaceae, Aspleniaceae, Aspidiaceae and Schizaeaceae families (the genera and many species of which can be numerous as individuals in various habitats within forests of the wet tropics) stipe stelar patterns are various, but none closely matches the morphology shown by Rachis E. In general the sectioned trace patterns of these groups present a variety of bilaterally symmetrical shapes: simple and circular; triangular; elliptical; of basin, horseshoe, urn, inverted  $\Omega$ , T, U, V, W or X shape; or more complex and convoluted than these, with or without incurved or outcurved marginal hooks. Alternatively, the vasculatures are either from all or part of wider, more arc-shaped distelic traces, or from even more

complex, two–three concentric, traces, the members of which might occasionally anastomose with each other to form more or less irregular concentric rings.

Other fern genera with cross-sectional patterns of broken vascular anatomy of multiple traces within the stipes occur in ferns of modern tropical affinity, most notably, for example, in *Dicksonia*, *Cyathea*, *Cibotium*, *Thyrsopteris*, *Acrostichum*, *Sadleria*, *Marattia* and *Angiopteris*. Thus, these taxa could have contributed to this type of fossil flora. However, in all these genera, trace numbers are much greater and differently arrayed, resulting in patterns of more complex structural type, involving multiple rings or forming distinctive overall cross-sectional patterns characteristic of all or part of those genera. Furthermore, fronds of all these genera are also typically large and robust, with stipe diameters considerably greater than that of the specimen in question. Moreover, many Blechnaceae, which are common by forest streams and thus might have contributed to such a fossil flora, have meristellar shapes (and stipe sizes) akin to those of Aspidiaceae (which can be distinguished from the fossil specimen by their far greater stipe diameters and differently emphasized meristellar patterns) or are more complex than these (e.g. *Stenochlaena*). Rings of separate traces are also present in the tropical fern genera *Platyzoma*, *Bolbitis* and *Maxonia*. In *Platyzoma* (now rare and monotypic in inland sandy floodplains) the trace components of the slender stipes, although of discrete vascular units inwardly hooked at their margins, are of more uniform small size and structure and usually occur scattered into two concentric rings (Ogura, 1972). *Bolbitis* (a tropical rainforest understorey and streamside fern) has vascular traces which are numerous and form a rather irregular ring tending towards urn shape, and the axis usually has two adaxial furrows (Hennipman, 1977). In *Maxonia* (a tropical climbing or epiphytic fern genus with scandent fronds) the anatomy approaches that of the fossil in the present study, except that the vascular traces of the stipe are relatively numerous (up to at least 24), the circular arrangement is more irregular and crowded (often partly in double rows) and the stipes are much more robust (Walker, 1972).

Single cross-sectional vascular trace stipe patterns of more than three components mostly of similar size arrayed in a single ring have only been found characteristically amongst modern material in *Ctenopteris*, *Dryopteris*, *Microsorium*, *Phlebodium*, *Polypodium* and *Platynerium* species, with a much sparser (though similar) ring in *Dictymia* (Walker & Page, 1982) and *Lecanopteris* (Jermy & Walker, 1975), and regular to irregular arrangement in *Pyrrosia* (Hovenkamp, 1986). The stelar configurations of virtually all these genera accord closely with those of this fossil specimen: they consist of several moderately sized traces arranged in a circle,

some of which are elliptical, but in all the size of the two adaxial traces varies between similar to, and slightly larger than, that of the other traces. In addition, all generally have small stipe diameters, closely comparable with those of this fossil. To demonstrate the degree of similarity between the fossil and some extant ferns, two representatives of the Polypodiaceae, *Polypodium loriceum* and *Phlebodium aureum*, and one from the Aspidiaceae (Dryopteridaceae; Kramer & Green, 1990), *Dryopteris odontoloma*, have been illustrated (Fig. 1c–h). The two members of the Polypodiaceae sectioned were very similar to each other, and all three members of the Aspidiaceae sectioned (but not all illustrated) were also similar to one other. Both groups had a number of separate traces, but their number, size and distribution differed between the two groups with closest anatomical similarity (especially in terms of a larger number of vascular units arranged in a gutter shape) lying with the Polypodiaceae (Fig. 1c–f). By comparison, the traces of *Dryopteris* spp. (also very similar to *Rachis* E) although discrete (Fig. 1g–h), are generally characterized by larger adaxial traces, together with a large central adaxial sub-trace with a series of smaller traces completing the U-shaped vascular trace. Despite the characteristic differentiation of the vascular trace of *Dryopteris* into large and small traces, a sequential diagram through the petiole and rachis of *Dryopteris lacera* published by Kramer & Green (1990) shows a similar vascular trace morphology to that of *Rachis* E. This extant species has up to nine discrete subtraces of more or less equal size, and two somewhat larger adaxial traces in cross section. However, at a section along the rachides of diameter similar to that of *Rachis* E, there are only two or three traces.

When such relative diameters are taken into consideration, the only close similarity to *Rachis* E is exhibited by the Polypodiaceae (illustrated in this study by *Phlebodium aureum*). Moreover, it shows such a match with a generic diversity of extant material within Polypodiaceae (*sensu stricto*) that it is proposed that this axis is one derived from this advanced fern family. Previously described stipe anatomical details of ferns (Bower, 1908, 1935; Ogura, 1972) from a wide range of genera, including several from this family, also support this conclusion.

#### DISCUSSION

This contribution confirms the importance of basing taxonomic interpretations of components from a Tertiary flora on joint palaeo- and neo-botanical approaches to produce detailed floristic conclusions and habitat signals.

Most species of the genera *Dictymia*, *Ctenopteris*, *Microsorium*, *Phlebodium*, *Polypodium* and *Platynerium*, as well as to a degree *Pyrrosia* and *Lecan-*

*opteris*, with which the general pattern of vasculature seen in Rachis E most closely compares, are members of the single Leptosporangiate fern family Polypodiaceae *sensu stricto* (Christensen, 1938; Ching, 1940; Copeland, 1947; Pichi-Sermolli, 1958, 1977; Crabbe *et al.*, 1975; *Platyserium* alone is sometimes put in a separate, although closely allied, family of its own). By contrast, Rachis types A, B, C, D and F seem to have greater affinity with other fern families such as Dennstaedtiaceae, Athyriaceae, Thelypteridaceae, Onocleaceae and Pteridaceae (Collinson & Ribbins, 1977; Ribbins & Collinson, 1978; Poole, 1993b). The family Polypodiaceae (and those closely allied to it) is regarded on many characters (including its dissected vascular anatomy, which is believed to be derived, e. g. Bower, 1908) as being distinctive, as well as modern, in terms of fern evolution as a whole (Mickel, 1974; Sporne, 1975; Lovis, 1977; Rothwell, 1996; Stevenson & Loconte, 1996).

In modern tropical rainforest communities, ferns with rachide diameters similar to that of the fossil specimen are rarely members of forest-floor communities but are often found in other niches such as emergent rocks or, especially, epiphytic sites within the overall vegetation community (Copeland, 1907; Holttum, 1938, 1954; Page, 1979a, b; Page & Clifford, 1981). Although forming an important part of analogous modern vegetation, members of such niches are rarely represented in fossil floras.

The polypodiaceous affinity (i.e. belonging to the family Polypodiaceae *sensu stricto*) is of special significance because it is indicative of a potentially epiphytic (and sometimes lithophytic) component of the Eocene vegetation community in which it occurred. Although epiphytism has been demonstrated for various other fern groups (Rothwell, 1996), this is the earliest record of probable epiphytic polypodiaceous fossil material, the scarce and isolated occurrence of which conforms with such an epiphytic interpretation because presence in such habitats is intrinsically less likely to contribute to fossil floras (van Uffelen, 1991).

Affinities between lithophytic and epiphytic ferns are close because of the requirement, in both sites, for such colonizers to have strong surface-clinging ability, as well as toleration of the consequent site nutrient disequilibrium. In modern rainforest environments there are, however, contrasting aspects between suites of ferns occupying epiphytic and lithophytic sites in the forest itself. For example on outcropping rocks, where moisture and humidity regimes are least limiting, intensity of light is often a constraint. Thus, colonisation is limited to members of more shade-tolerant genera, amongst which the Polypodiaceae have only a few specialists (e.g. members of *Belvisia* and *Selliguea*) whose individuals are usually scarce and scattered. By contrast, in the high-epiphytic sites within the same forest (i.e. the

upper trunks and tree-crown branches, where moisture and humidity regimes can fluctuate widely but light is not limiting), the light-demanding Polypodiaceae are diverse, and their members may be abundant and locally dominate the epiphytic communities. The main lithophytic analogues to these tend to occur only on outcropping rocks in other forest types where there is great penetration of light to ground level, such as around extreme margins of rainforest, within sclerophyll forests and on coastal rocks. Several of the polypodiaceous genera of these habitats are ecologically bi-modal with respect to sites in both the rainforest high canopy and rocks in other forest types. Some of these genera are also morphologically distinguishable by the possession of additional lithophyte-adaptive morphological modifications (e.g. rhizome-protective winged stipe bases in *Aglaoomorpha* and *Merinthosorus*, or fleshy frond structures in *Pyrrosia*). Thus, although, it cannot be ruled out that the fossil might originate from a lithophytic polypodiaceous member caught in a flash flood and deposited along with rainforest members, it is felt that this is the least likely explanation. By contrast, virtually throughout the area of the modern Indo-Malayan to Austro-Pacific regions, there is a far greater abundance of individuals of Polypodiaceae as high epiphytes within tropical rainforest canopies. Furthermore, a particularly large number of fronds is borne by plants in these sites since many have long creeping rhizomes sometimes bearing hundreds of fronds. Such fronds are shed onto the forest floor not only annually by abscission but also when branches, or whole forest trees, are felled by storms and epiphytes are often torn away by violent branch abrasion in the process. Therefore, there is a high probability that our polypodiaceous fern fossil originated in a rainforest high-canopy epiphytic site, and, having fallen, was swept away by passing groundwater, before decomposition, to its site of deposition, probably during the course of a violent storm.

It is perhaps easiest to make conjectures about the reasons for the rarity of epiphytic ferns in the fossil record when equivalent living taxa are studied. The great majority of the members of the Polypodiaceae today are pantropical to pantemperate in range. Most are predominantly epiphytic on trunks and especially branches of broadleaved trees and are characteristic of moist forests in which dry periods can occur (Holttum, 1954; Page, 1979a, 1988). In tall gallery forests especially, many grow high in the canopy. Observations on fronds of modern epiphytic Polypodiaceae show that each normally only persists for a single growing season.

Over the whole plant annually, as new fronds arise the old fronds are shed; this often coincides with the onset of annual drought periods. Prior to and during senescence, fronds undergo a relatively rapid pre-shedding period, when most of their reserves are



transferred back to the rhizomes for storage. Such fronds usually grow thin and pale from the tip downwards. Final shedding usually takes place suddenly and cleanly by breakage at a pre-formed morphologically distinct abscission zone at or very near to the base of the stipe which is marked by a point of externally observable articulation to the rhizome throughout the life span of the frond.

Epiphytic ferns are extremely numerous components of modern tropical rainforests, especially those in the Malesian region. Holttum (1938) notes that they rarely occur in such forests where the annual rainfall is less than 60 cm. In many sites such epiphytes can be part of complex epiphytic communities (Page, 1979a). They have succeeded in these sites largely because of the array of moist-surfaced trunk and branch habitats presented by arborescent angiosperm vegetation, in addition to the ability constantly to gain ready access to these habitats through the colonising mobility conferred by the minute airborne spores of ferns. Of the fern families involved, the Polypodiaceae are today one of the most extensively epiphytically committed, with many exacting, intricate and sometimes bizarre sporophyte life-form adaptations to the many variations in these sites. The identification of this fossil material as polypodiaceous is relevant to testing the hypothesis that Polypodiaceae are a recently radiated group (Rothwell, 1996). The existence of the Polypodiaceae in an Eocene palaeoflora is also of significance in that it signals the likely occurrence of epiphytic fern growth within these forests and indicates the occurrence of a generally moist climatic regime.

#### CONCLUSION

This fern specimen is assigned to the type *Rachis E* on the basis of its distinct vascular strand morphology. The discrete arrangement of the sub-traces in conjunction with the diameter of the material suggest that this is from an advanced fern of the family Polypodiaceae (*sensu stricto*). This family has already been identified as a component of European Tertiary floras (Depape, 1928; Collinson, 1978). This represents the first record of possible epiphytism in the Eocene London Clay flora; an important finding, as this specimen represents a floral component rarely preserved in any fossil record.

#### ACKNOWLEDGEMENTS

Members of the Geology Departments of University of Wales, College of Cardiff, and Royal Holloway College, University of London and the Electron Microscopy Unit (RHUL) are thanked for the use of their facilities. Dr K. Davies is acknowledged for useful discussions and comments. This research was funded by the NERC in

collaboration with the Royal Botanic Gardens, Kew, and their help is gratefully acknowledged.

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