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A heterophyllous fern from the Lower Cretaceous of Northern Spain

With 1 figure and 1 plate

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Abstract

Fronds of a heterophyllous fern tentatively assigned to the Pteridaceae, *Sphenopteris wonnacottii* sp. nov., are described from the Berriasian to Valanginian limestones of Santa Maria de Meia, Sierra del Montsech, Lérida Province, N-Spain. The small, mainly once-pinnate fronds are strongly catadromous and one of them shows evidence of morphological adaptation to an aquatic environment. The form of the pinnules in this frond changes from the proximal lobed pinnae of normal laminar form to larger pinnae distally which show progressive loss of mesophyll to become filiform and three dimensional, as in submerged leaves of the aquatic angiosperm *Ranunculus aquatilis* (Ranunculaceae). Such extensive modification of leaf morphology is seen in several submerged angiosperm leaves but rarely been recorded in ferns. Interpretation of *S. wonnacottii* as an aquatic or semi-aquatic plant, with partially submerged fronds, is consistent with current understanding of the palaeoecology of the Santa Maria de Meia flora and fauna.

Keywords: heterophyllous fern, aquatic plants, Lower Cretaceous, Spain

Kurzfassung

Aus den unterkretazischen (Berriasium-Valanginium) Kalksteinen von Santa Maria de Meia (Sierra del Montsech, Provinz Lérida, Nordspanien) werden die Wedel eines heterophyllen Farns, *Sphenopteris wonnacottii* sp. nov., beschrieben. Sie werden vorläufig zu den Pteridaceae gestellt. Die kleinen, einfach gefiederten Wedel sind streng katadrom gebaut, wobei sich in einem Falle Hinweise auf die Anpassuug au eine aquatische Lebensweise erkennen lassen. Die Form der proximalen Fiederchen ist in diesem Falle „normal" flächig-gelappt. Distalwärts lösen sich die Fiederchen in größere, dreidimensional-fädig gebaute Strukturen auf, wie sie ähnlich bei den untergetauchten Blättern der aquatischen Angiosperme *Ranunculus aquatilis* (Ranunculaceae) zu finden sind. Eine derart extensive Modifikation der Blattmorphologie ist zwar verschiedentlich bei untergetauchten Blättern vou Angiospermen zu beobachten, bei Farnen ist sie jedoch nur selten bekaunt geworden. Die Interpretation von *S. wonnacottii* sp. nov. als aquatische oder semiaquatische Pflanze mit teilweise untergetauchten Wedeln steht im Einklang mit den gegenwärtigen Vorstellung zur Paläoökologie der Flora und Fauna aus der Unterkreide von Santa Maria de Meia.

Schlüsselworte: Farn, Heterophyllie, Wasserpflanzen, Unter-Kreide, Spanien

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Introduction

Plant fossils from the famous Lower Cretaceous quarry at Rubies, near to Santa Maria de Meia in the Sierra del Montsech, Lérida, have been known since the time when the quarry was worked economically for lithographic limestone (MEUNIER 1902, VIDAL 1902). Early brief accounts of the flora by VIDAL (1902), AMOR (1951) and CONDAL (1951), however, have been expanded considerably and largely superseded as a result of recent collecting and descriptions by others (e.g., BARALE 1973, 1981, 1982, LACASA RUIZ 1981, BLANC-LOUVEL & BARALE 1983). Collections of exceptionally fine plant fossil material, deposited in the British Museum of Natural History (BMNH), were also made in 1955-1960, mainly by Mr. F. M. WONNACOTT and Dr. H. W. BALL. Some of this material has been documented by BARALE (1973) but the rest remains to be described. The object of this paper is to continue description of the BMNH material and thereby to contribute further to knowledge of this interesting flora.

The present paper describes some fragmentary but nonetheless morphologically and ecologically intriguing remains of a presumed fern which shows clear evidence of heterophylly very similar to that of several aquatic angiosperms and some extant aquatic ferns such as *Azolla*, *Salvinia*, and *Ceratopteris*. Indirect evidence indicates possible affinities to the Pteridaceae, a family that today embraces a wide range of diversity including the semi-aquatic genus *Ceratopteris*.

Systematic description

Filicales
?Pteridaceae

Sphenopteris (BRONGNIART) STERNBERG

Sphenopteris wonnacottii sp. nov.

Diagnosis: Fronds bearing sphenopteroid pinnules, mainly once pinnate but tending towards twice pinnate basally; of three different forms (trimorphic): form *A* has more or less uniformly lobed pinnae throughout; form *B* (the heterophyllous form) has lobed pinnae at the frond base changing distally to larger, filiform ones; and in form *C* the lobed pinnae change distally to become larger and kidney shaped (possible fertile pinnae). Sori, rhizome, scales and trichomes unknown.

Description: Form A (pl. 1 figs. 3, 4). Fronds up to 46 mm or more in length, pinnae more or less uniformly lobed. Rachis slender, 0.3-0.5 mm wide at base, mostly 0.2-0.3 mm, decreasing to about 0.1 mm at frond apex; bearing pinnae laterally in one plane at intervals of 2-3 mm, intervals rarely up to 4.5 mm towards frond base, decreasing to 1 mm near frond apex. Pinnae alternate, sharply constricted to point where attached either directly to rachis or to very short "petiolar" region; venation and lobing strongly catadromous, main vein departing from rachis at a low angle and curving outwards rapidly to enter pinna base at angles ranging from 10° to 70°. Pinnae mostly trilobed, lobes ranging from shallow near frond apex to deeply divided near frond base. At frond apex, lobing very shallow, occasionally bilobed, sometimes lacking; at frond base in some specimens (e.g. pl. 1 fig. 4) the pinnae have four to five lobes (a pair of proximal lobes or pinnules and a bilobed or trilobed distal portion resembling whole pinnae more distally on the frond). Dimensions of pinnae ranging from about 0.5-1 mm long x 0.5-1 mm wide at frond apex to 1-3 mm long x 1-3 mm wide over most of the frond; pinna length generally equaling the width at the widest point, which is

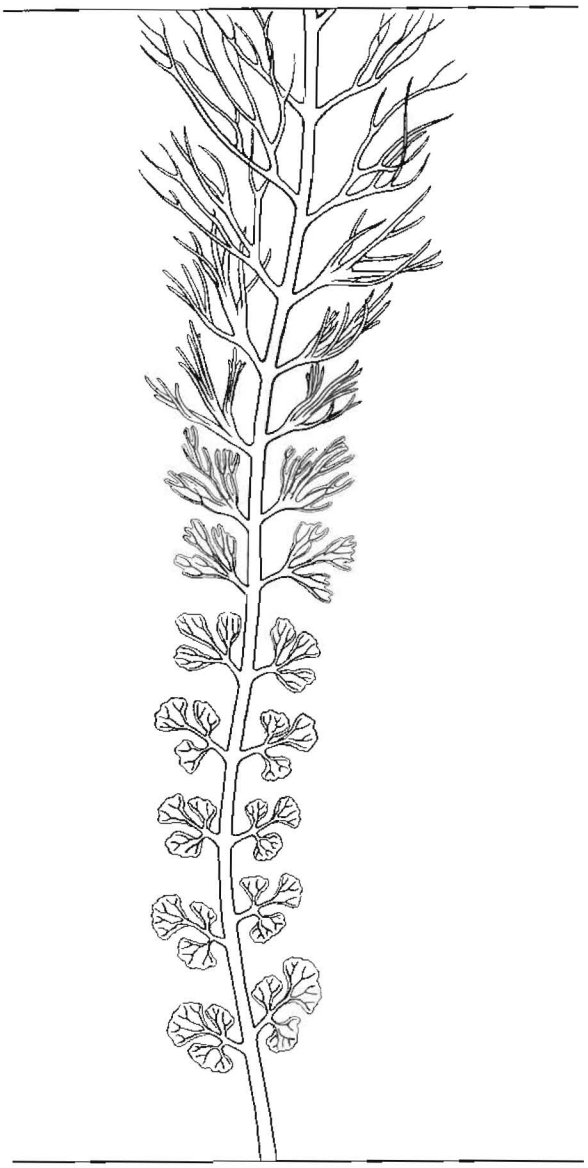

Fig. 1: *Sphenopteris wonnacottii* sp. nov. Reconstruction of heterophyllous frond form B, showing basal pinnae of normal laminar form becoming larger and filiform distally. Based on the holotype, V.41257; x 5.

near the pinna base, but towards the frond base tending to be slightly longer than wide; basal trilobed pinnae about 3 mm long x 2 mm wide, four to five lobed pinnae ranging from about 2.3 x 1.7 mm through 3.5 x 3 mm to 4 x 3 mm. Veins open dichotomous, in trilobed pinnae dichotomising two to four times between pinna base and margin at more or less equal or slightly increasing distances; where lobes are deeply divided - and also in four or five lobed pinnae – veins in each lobe dividing twice or occasionally three times, particularly in the distal portion. Number of vein dichotomies decreasing in pinnae towards the frond apex, together with the reduction in pinna size.

Form B (pl. 1 figs. 1, 2; text-fig. 1). Frond heterophyllous, more than 37 mm long, basal pinnae trilobed to faintly 4 or 5-lobed, becoming larger and filiform distally; in basal third the pinnae borne in one plane, opposite to subopposite, rachis and pinnae agreeing in all preserved features with those towards the base of form A fronds; towards frond apex, pinnae becoming progressively more linear-lobed, lamina also becoming progressively reduced and finally fully filiform, branching three to four times in three dimensions: pinnule size increasing from 2.5-3 mm long x 2-2.5 mm wide to 6-7 mm long in the most distal pinnae preserved.

Form C (pl. 1 fig. 5). Frond fragment (BMNH V.32313) 14 mm long, bearing proximally a small bilobed pinna, 1.5 mm long x 2 mm wide; distally five larger, entire, somewhat kidney-shaped (presumed fertile) pinnae, 1.5 mm long x 2-2.3 mm wide. Two other less well preserved specimens also known, one on the same block as V.32313; another, 1.8 cm long (V.41256), shows very clearly the transition from sterile to presumed fertile pinnae. The sterile pinnae in this specimen are identical to those of frond form A.

Holotype: BMNH V.41257, pl. 1 figs. 1, 2; text-fig. 1. Number of specimens examined 13.

Locus typicus: Santa Maria de Meia: La Pedrera de Meia, 0.8 km SW of Rubies in the Montsech Mountains of northern Spain (Lérida Province).

Stratum typicum: Lithographic limestones, Caliza con Caraceas Fm, Berriasian to Valanginian (SCHAIRER & JANICKE 1970, BRENNER et al. 1974, COURTINAT 1984).

Comparisons: We know of no Mesozoic fern resembling this species other than a specimen from the Rubies locality in the BMNH (V.11837) labelled *Sphenopteris* cf. *microclada* SAPORTA (SAPORTA 1894). This specimen however is about two to three times larger than both Saporta's species and ours; and the segments are entirely filiform and have angular branching unlike that of *Sphenopteris wonnacottii*. In our opinion it represents vegetative material of *Montsechites ferreri* TEIXEIRA (TEIXEIRA 1956, BLANC-LOUVEL 1984: pl. 3).

Name: *Sphenopteris wonnacottii* is named in honor of Mr. F. M. WONNACOTT, formerly curator of plant fossils at the British Museum of Natural History and who collected the specimens described here.

Habit: The fragmentary specimens include only one of frond form B and three of form C, none of which is complete from the extreme base to the apex. Several specimens show evidence of loss of pinnules and of decay before final preservation, as at the base and in the middle region of V.41257 (pl. 1 figs. 1, 2). Since there is no evidence of a rhizome, it is impossible to determine just how these fronds were borne, or indeed whether they were parts of fronds having a more complex architecture. In the absence of evidence to the contrary we suggest the simplest hypothesis, that the plant was small, with long and narrow, predominantly once-pinnate fronds - broadly like those of certain extant species of *Eriosorus*, *Jamesonia* and their hybrid X *Eriosonia*.

We suggest that the distal enlarged and highly dissected or filiform pinnae of frond form B were caused by submergence of the frond tip in water. Both the greater length of these distal pinnae and their good preservation argue against decay of intervening mesophyll as a causal factor (see also the account of rotting experiments on ferns in HILL 1987: 79, 88-89). In order to dip a frond in water, the plant must have been living at the very edge of a body of water, and since only one of several frond fragments has filiform pinnae, the entire plant was probably not fully aquatic but was more likely marginal aquatic.

Attribution to one species: The two forms A and B are considered to be fronds of the same species because the form of their basal pinnae is identical, the fronds are associated with one another at the same locality, and no other similar ferns occur in the flora. Frond form C (pl. 1 fig. 5) is attributed to the same species, based also on association and on its basal pinnae which resemble those seen at the base in form A fronds. Based on the general aspect of the reniform pinnae, we consider that this form perhaps represents the fertile frond but we cannot substantiate this as no spores could be prepared from the material, nor is there any direct evidence that the reniform pinnae bore sori. The pinnae are however, clearly modified.

Discussion

Sphenopteris wonnacottii occurs in association with a wide range of fossil plants and animals from Sierra del Montsech which indicate that the environment in which they lived was part of or very near a fresh water lake. The plants include algae, probable aquatic vascular plants such as *Montsechia* and *Montsechites*, and terrestrial vascular plants including *Weichselia*, *Frenelopsis*, and *Brachyphyllum*, among others, while the animals include fish, frogs, alligators, bird feathers, crustaceans, mollusks and insects (SCHAIRER & JANICKE 1970, LACASA RUIZ

1981, BARALE 1981, BARALE et al. 1984, WHALLEY & JARZEMBOWSKI 1985). Along the edges of a quiet lake there probably would be some ferns which grew with fronds dipping down into the water itself. We suggest that submergence of the frond tip occurred in this way while the fern was still growing because the differentiation of the terminal pinnae probably took place under water. The pinna enlargement and the change to filiform and three dimensional form resembles the leaf forms of several submerged angiosperms such as *Ceratophyllum*, *Myriophyllm*, and *Utricularia*. *Ranunculus aquatilis* has entire non-immersed or floating leaves while the immersed leaves are divided into narrow cylindrical lobes (SCULTHORPE 1967).

The finely divided leaves of the above mentioned angiosperms show a particular cylindrical form composed of closely arranged cells surrounding the vascular tissue, which reflects the basic vascular tissue of the venation in the unmodified aerial leaves (SCULTHORPE 1967, FAHN 1982). The very same situation is found in *Sphenopteris wonnacottii*, in which the filiform pinnae also reflect the basic venation pattern of the laminar trilobed pinnae. As is characteristic of many leaves which differentiate in a submerged aquatic environment, the filiform pinnae are larger than other pinnae on the frond. This is of special interest because they are distal on frond form B, of the fossil, whereas in form A fronds, the pinnae become reduced in size distally. In extant angiosperms, such increase in overall size of the lamina is thought to be related physiologically to the potential for nutrient uptake by the differentiating submerged leaves (SCULTHORPE 1967). The presumed fertile pinnae, like the filiform ones, also tend to be larger than the vegetative ones situated more proximally on frond form C.

Extant *Ceratophyllum* is also a heterophyllous aquatic fern. However, its fronds differ considerably from those of *Sphenopteris wonnacottii* (TRYON & TRYON 1982) and we do not know of any fern, living or extinct, that shows the type of heterophylly within a single frond seen in *S. wonnacottii* (KATO & IWATSUKI 1985). Some species of *Eriosorus*, *Jamesonia*, and *Eriosonia*, also in Pteridaceae, have comparably dissected fronds and similar pinnae (although often with an inrolled lamina), but the pinnae on an individual frond are not markedly heterophyllous.

It is impossible to determine a precise familial relationship for *Sphenopteris wonnacottii*. The evidence indicates merely general similarity to some species of the genera of Pteridaceae just mentioned, and although some grow in humid environments, none of these occur in aquatic habitats today. A major difference is the form of the venation which in most Pteridaceae appears to be dominantly anadromous or equal (TRYON & TRYON 1982, KRAMER 1987) whereas it is strongly catadromous in the fossil. It should be repeated that nothing is known about the sori of *S. wonnacottii*. *Platyzoma* is of some interest in also having once-pinnate trimorphic fronds and in its incipient heterospory, regarded by some as perhaps indicating a link between regular Filicales and the water ferns Marsiliaceae and Salviniaceae (TRYON 1964).

Conclusions

Sphenopteris wonnacottii is particularly noteworthy because it demonstrates heterophylly within a frond, the earliest occurrence of this type of heterophylly to be recorded among the fossil ferns. We suggest that it is the product of change in pinna development in the terminal portion of the frond as it dipped into water. Such changes in leaf morphology are well known in *Ranunculus aquatilis*. The morphological changes observed in the fossil fern parallel those seen today in *R. aquatilis* and lead to the conclusion that common physiological constraints of leaf development were operating in ferns during the lowermost Cretaceous.

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Plate 1

Sphenopteris wonnacottii sp. nov.

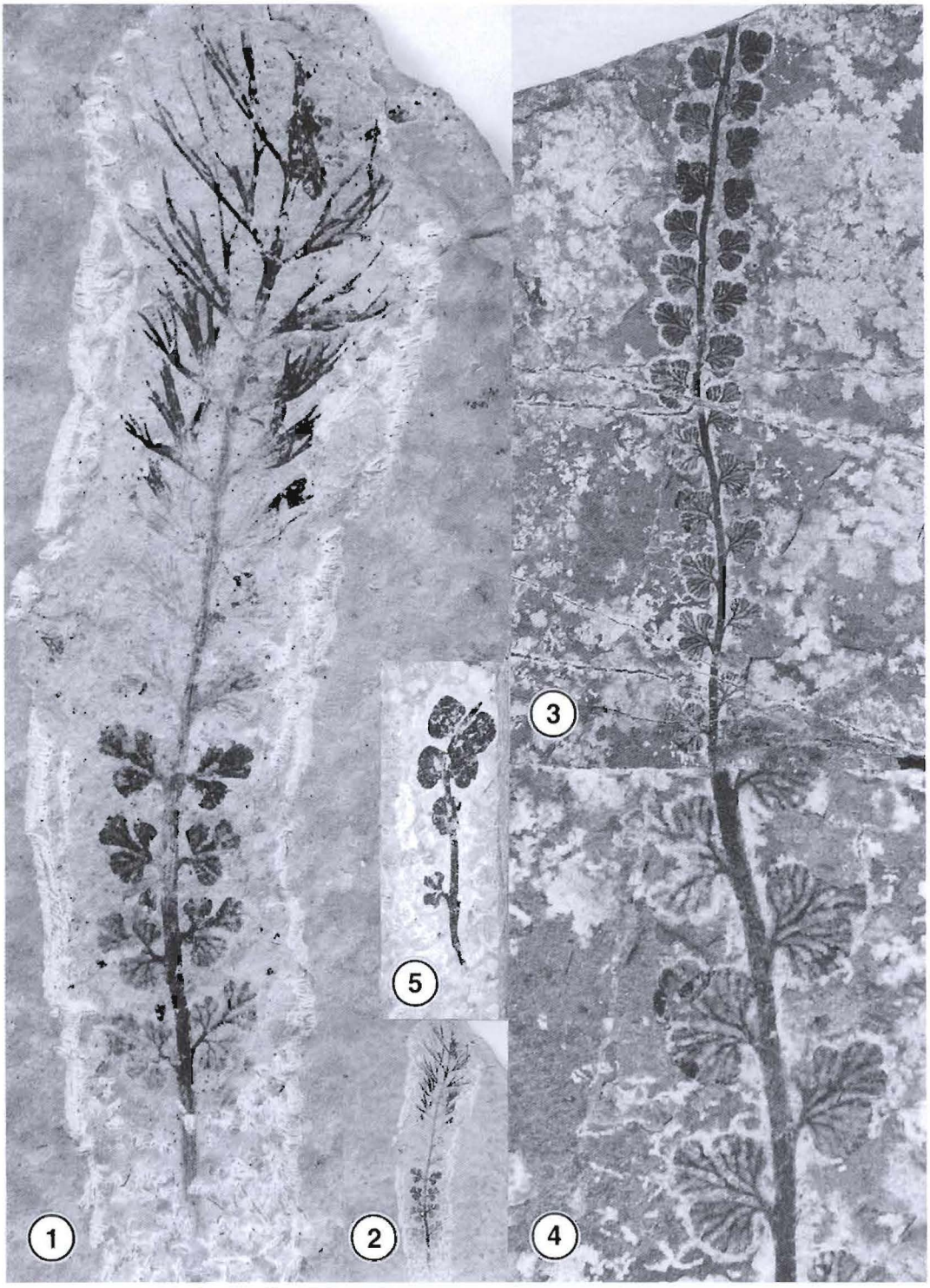
Fig. 1: Frond form B: Holotype, V.41257. – x 5.

Fig. 2: Frond form B: Holotype, V.41257. – x 1.

Fig. 3: Frond form A, showing pinna shape, attachment, and venation. V.41205. – x 3.

Fig. 4: Frond form A, showing pinna shape, attachment, and venation. V.41205. – x 7.5.

Fig. 5: Frond form C., V.32313. – x 3.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