EARLY CRETACEOUS FERNS FROM LACUSTRINE LIMESTONES AT LAS HOYAS, CUENCA PROVINCE, SPAIN

by CARMEN DIÉGUEZ *and* NIEVES MELÉNDEZ

ABSTRACT. A brief outline is presented of the geological conditions prevailing in the hard-water lake that produced the Las Hoyas fossiliferous site in the Serranía de Cuenca (north-east central Spain). The corresponding Barremian laminated limestones contain varied fossil remains including plants. The fern component of the assemblage is described in the present paper. Ten taxa are referable to the families Matoniaceae, Dicksoniaceae and Schizaeaceae, whilst eight are unclassified. A new species of Dicksoniaceae is described: *Coniopteris laciniata.* Three species, *Pelletixia valdensis, Cladophlebis albertsii,* and *Sphenopteris fontainei,* are recorded here for the first time outside the English Wealden; one species, *Acrostichopteris foliosa*, is new to the Barremian of Europe. The fern assemblage from the Las Hoyas site is most similar to that of the English Wealden. The xeromorph character of some species is noted.

Although the specimens from Las Hoyas are generally small, even tiny, most are still identifiable leaf fragments preserved as imprints on platy limestone. Epidermal detail has been obtained from a few impressions. Some rather delicate remains, such as indusia, a crozier with pinnules, and fragments of *Pelletixia valdensis* occur, thus suggesting limited residence time in water.

KEY WORDS: ferns, Early Cretaceous, lacustrine limestones, Las Hoyas, Spain.

ALTHOUGH Early Cretaceous floras are well known in Europe there are few records from Spain. Additional to the Las Hoyas site of Late Barremian age (Diéguez *et al*. 1995*a, b*), only three floras have been described, namely: from the limestones of Montsec, Lleida Province (Barale 1979, 1991; Barale *et al*. 1984), supposedly of Berriasian–Valanginian age; from Ortigosa de Cameros, Logroño Province (Depape 1953; Depape and Doubinger 1960); and from several other localities in Logroño, La Rioja (Agirrezabala *et al*. 1985; Barale and Viera 1989, 1991). The latter yielded mainly anatomically preserved wood remains. All were compared with Wealden floras. The Las Hoyas and Montsec floras are the only ones recovered from lacustrine limestones.

A wide-ranging palaeontological investigation of the extensively excavated Las Hoyas site has been carried out for about a decade by a multidisciplinary team. The first preliminary results, based on a limited number of specimens, were published by Sanz *et al*. (1988*a, b*). The fossil remains proved to be extraordinarily varied. Several groups of invertebrates (insects and crustaceans) were recovered as well as vertebrates including primitive birds (Sanz *et al*. 1988*a*; Sanz and Buscalioni 1992), and different ichnofacies have also been described (Fregenal-Martínez and Moratalla 1995). The floral remains are generally small and often indifferently preserved, although even very small fragments are identifiable, and indeterminable comminuted plant debris is not quite as abundant as might be expected. This suggests that residence time in water may not have been very long and raises the question of the size of the lake in which the remains were deposited. All the plant remains are imprinted on fine-grained limestone, and the preservation of organic material is restricted to certain groups with a resistant cuticle, e.g. the conifers. Later work (Sanz *et al*. 1990, 1994; Diéguez 1992; Diéguez and Martín-Closas 1995; Diéguez and Trincao 1995; Diéguez *et al*. 1995*a, b*; Martín-Closas and Diéguez 1996, 1998) showed the plant assemblage to be rather diverse, with charophytes, bryophytes, Filicales, cycadophytes, conifers and anthophytes being present. The present paper deals exclusively with the fern remains which represent 19 per cent of the total flora. Most of the fern remains are merely imprints on the limestone showing the general outline of pinnae

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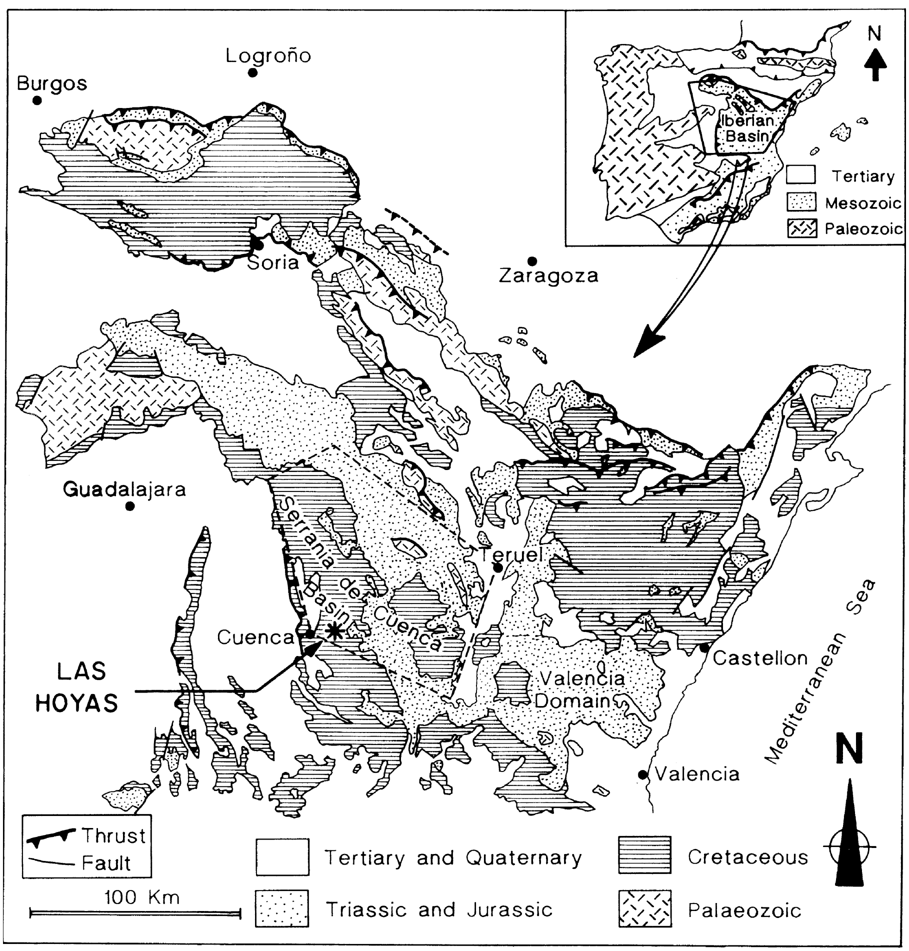
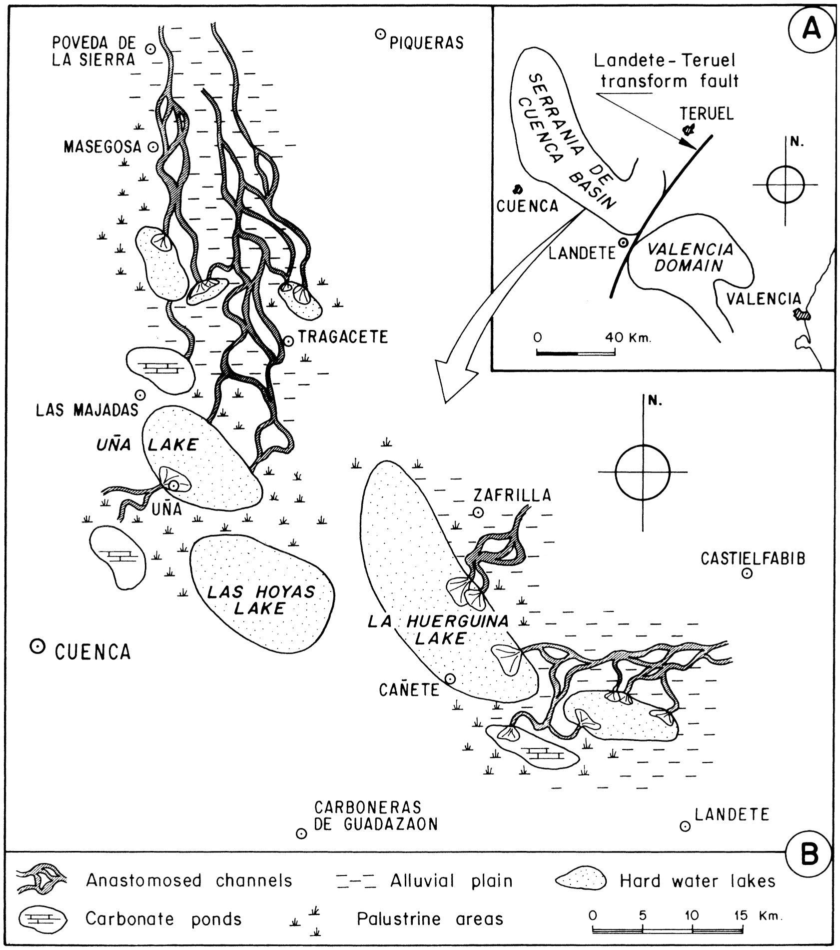
and pinnules, but some specimens are imprinted with sufficient detail to show epidermal features, thus allowing the preparation of silicone replicas for analysis under the scanning electron microscope (SEM). The fern remains appeared at first to be rather sparse and poorly diversified. In fact, only two fern species were recorded in the preliminary paper by Sanz *et al.* (1988*b*), namely *Cladophlebis browniana* and *Weichselia reticulata.* Further collecting showed the fern component to be more varied, with representatives of the Matoniaceae, Dicksoniaceae and Schizaeaceae being present. The entire fern assemblage is described in the present paper.

LOCATION OF THE STUDY AREA AND GEOLOGICAL BACKGROUND

Las Hoyas is situated in the Serranía de Cuenca, in the south-western part of the Iberian Range, east-central Spain (Text-fig. 1). This fossiliferous site of Early Cretaceous age occurs in a lacustrine succession laid down in a segment of the Iberian Basin during a Late Jurassic–Early Cretaceous rifting episode. This is the second of two rifting episodes, the first being of Late Permian–Early Jurassic age (Alvaro *et al.* 1979; Vilas *et al.* 1983; Salas and Casas 1993; Arche and López-Gómez 1996). As a result, a Valencian Domain



TEXT-FIG. 1. Location of the Las Hoyas Fossil Site in the Serranía de Cuenca (surrounded by a dark line) within the Iberian Ranges of east-central Spain; M, Madrid.



TEXT-FIG. 2. A, the Lower Cretaceous Iberian Basin showing subdivision into Serrania de Cuenca Basin and Valencia Domain owing to rifting and separation by the Landete-Teruel transform fault. B, diagram of the general palaeogeography of the Serranía de Cuenca showing the maximum lacustrine development during the Barremian (modified from Meléndez *et al.* 1989). A preferential rifting orientation of NW–SE for the alluvial system and deposits of shallow, hard-water, permanent lakes and ponds are present. The location of the main lakes (Uña, Las Hoyas, and La Huérguina) was related to the more subsiding areas of the different active half-grabens. Differential subsidence in the whole basin played a decisive role in the palaeogeographic distribution of lakes, as Meléndez *et al.* (1994) indicated in their isopach map.

in the south-east was separated from a more subsident Serranía de Cuenca Basin in the north-west (Text-fig. 2A) (Meléndez *et al.* 1994). The separation was due to a major transcurrent fault structure trending NE–SW, which Salas and Casas (1993) identified as the Landete-Teruel transform fault, a structure that was active during the earlier Late Permian–Early Triassic rifting episode (Arche and López-Gómez 1996). The Landete–Teruel transform fault seems to have acted as a barrier that halted the marine transgression from the Tethys which advanced from the south-east. The Serranía de Cuenca Basin was thus isolated from any marine influence during Barremian times (Poyato *et al.* 1998). Rifting on a smaller scale split the Serranía de Cuenca Basin into several sub-basins, which display a marked asymmetry of half-grabens with different rates of subsidence (Meléndez *et al.* 1989). The Las Hoyas fossiliferous site is located in the sub-basin which displays the highest rate of subsidence, and which accumulated up to 400 m of terrestrial sediments.

STRATIGRAPHY

The Lower Cretaceous stratigraphy of the Serranía de Cuenca is reasonably well documented (Meléndez 1983; Gómez-Fernández 1988; Meléndez *et al*. 1994). Everywhere, the Lower Cretaceous overlies Jurassic (Dogger) marine carbonates unconformably, indicating deposition after an episode of erosion and karstification. Sedimentation recommenced in Barremian times in the Serranía de Cuenca Sub-basin, this time under terrestrial conditions. The sedimentary record is represented by two time-equivalent lithostratigraphic units, i.e. the El Collado Mudstone Formation and the La Huérguina Limestone Formation, which interfinger.

El Collado Formation

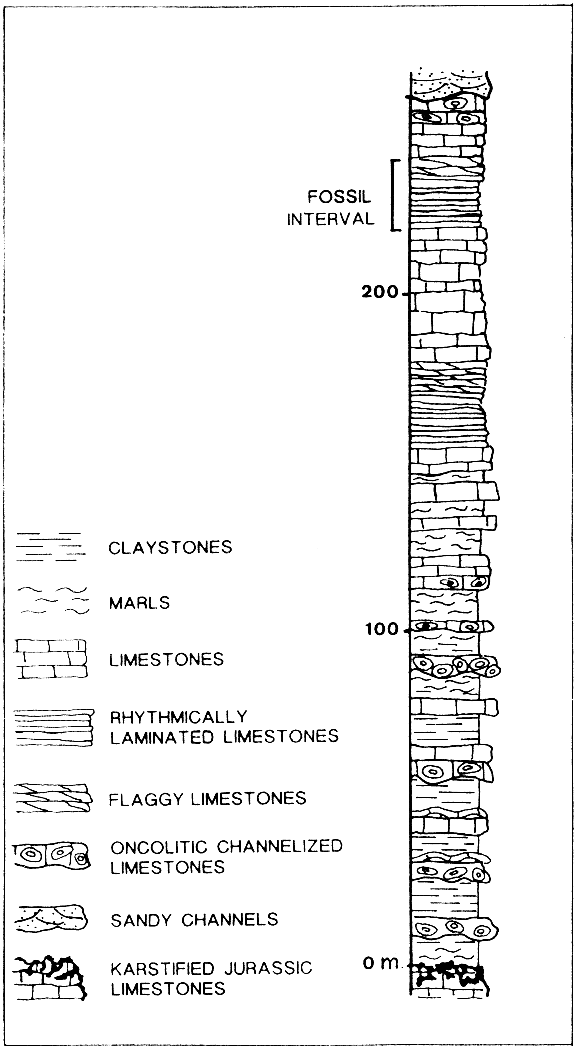
This siliciclastic unit, 0–50 m thick, consists mainly of coarse sandstones, with subordinate red mudstones and some conglomerates. Sandstones constitute channelised bodies up to 3 m thick; conglomerates are present as lag deposits; mudstones are massive and contain some palaeosol horizons. These deposits originated on a distal alluvial plain with anastomosed channels (Meléndez 1983; Gómez-Fernández 1988; Gierlowski-Kordesch *et al*. 1991; Meléndez *et al*. 1994).

La Huérguina Formation

This unit varies in thickness from almost 0 to 400 m; at the Las Hoyas site it shows the thickest development known for the Serranía de Cuenca Basin (Fregenal-Martínez 1998). It is a carbonate unit composed mainly of marls and massive limestones, but limestone conglomerates, oncolitic limestones, laminated limestones, lignites and clayey marls occur as well. Sedimentation took place in an extensive lacustrine system with several different environments, including shallow hard-water lakes and ponds, surrounded by paludal areas with hydromorphic palaeosols as well as distal alluvial carbonate plains (see Meléndez *et al*. 1989; Gierlowski-Kordesch *et al*. 1991; Gómez-Fernández and Meléndez 1991; Fregenal-Martínez and Meléndez 1993, 1994; Meléndez *et al*. 1994). Text-figure 3 shows the Rambla de Las Cruces section of Las Hoyas which has been measured where the maximum thickness of sediment is found; the fossiliferous interval is situated in rhythmically laminated limestones.

Palaeogeography of the Serranía de Cuenca Basin

The sedimentological characteristics and regional distribution of continental subenvironments in the Barremian of the Serranía de Cuenca Basin have been studied by Meléndez *et al.* (1989, 1994) and Gierlowski-Kordesch *et al.* (1991), among others. Text-figure 2B shows a palaeogeographic sketch, modified from Meléndez *et al.* (1989), that illustrates typical 'Wealden' seasonal-perennial wetlands and lake settings. Anastomosed channels of seasonal drainage and wide alluvial plains constituted an alluvial system located in the northern part of the basin (Gierlowski-Kordesch *et al.* 1991). Its source area was located to the north-east (Meléndez 1983). The main channels carrying siliciclastic material reached the Las Hoyas Sub-basin only occasionally (Fregenal-Martínez and Meléndez 1994; Fregenal-Martínez 1998). The channelised bodies are commonly composed of calcareous conglomerates and calcarenites, and are interpreted as the result of small streams incised on the distal alluvial carbonate plain (Gierlowski-Kordesch *et al*. 1991; Gómez-Fernández and Meléndez 1991). These small streams carried both carbonate material of the Jurassic basement outcropping on the margin of the Las Hoyas half-graben and reworked material from the contemporaneous alluvial carbonate plain and ponds. In the central part of the Serranía de Cuenca Basin extensive lacustrine systems were in place (Text-fig. 2B) with shallow lakes and ponds developing in the most subsident area of each half-graben (Meléndez *et al.* 1989, 1994). The extent of the surrounding paludal areas was apparently controlled by fluctuations in the water level of the lakes. These vegetated areas probably acted as a baffle with regard to the siliciclastic input, since the lake sediments are found to consist almost exclusively of limestones. Only the marls deposited in the early stages of infilling contain a small amount of clay.



TEXT-FIG. 3. Stratigraphic section at Las Hoyas, with the location of the fossiliferous interval in the rhythmically laminated limestone facies.

The fractured basement of these half-grabens was composed of Jurassic carbonate rocks, these being responsible for the high carbonate content of the lake waters. The palaeoclimate of the Iberian area during the Early Cretaceous has been regarded as tropical by Menéndez Amor (1970) on the basis of a palynological analysis of lignites. Rat (1982) used sedimentary and palaeogeographical data to suggest that the climate was warm, semi-arid, and seasonal. Ziegler *et al.* (1983) placed the Iberian Península during that time at latitude 30 degrees north. Sedimentological work by Gómez-Fernández (1988) and Gierlowski-Kordesch *et al.* (1991) suggested that the continental sediments of La Serranía de Cuenca were laid down under warm but fluctuating climatic conditions, with more humid and drier episodes. Gómez-Fernández and Meléndez (1991) discussed the genesis of rhythmically laminated limestones from the Las Hoyas fossiliferous site, which they related to the influence of alternating humid and dry episodes in a lake containing a large quantity of carbonate in solution. Fregenal-Martínez (1998) and Fregenal-Martínez and Meléndez (1998) studied varve-scale limestone laminae under the microscope and recognised the signs of fluctuations in the water level of the lake, which they explained as the result of alternating dry and humid episodes.

MATERIAL AND METHODS

At the Las Hoyas site a systematic method of excavation has been adopted so as to recover the maximum amount of information for evolutionary, palaeobiological, palaeoecological, taphonomic and sedimentological analyses. The following steps were taken (Fregenal-Martínez *et al*. 1995): (1) a random selection of the area to be exposed; (2) cleaning of the exposed area; (3) installation of a grid with a fixed datum point in order to obtain a set of coordinates for each fossil on a particular bedding plane; (4) recording of data for each specimen such as size, orientation, and taphonomic observations. Nearly half a square kilometre was excavated up to 1998. This kind of methodical excavation yields a smaller number of specimens than is obtained by the usual wholesale palaeobotanical collecting techniques, but it has allowed the determination of density and distribution patterns, and some idea of the way in which the fossil remains accumulated.

A total of 685 identifiable plant remains was collected, with a distribution as follows: charophytes (7 per cent); bennettitaleans (3·5 per cent); conifers (32 per cent); angiosperm-like plants (6 per cent); other minority groups such as bryophytes, lycopods or pteridosperms (3 per cent); and as much as 17 per cent of the intriguing plant *Montsechia vidali* of unknown taxonomic position. Unclassified remains (12·5 per cent) correspond to stems, bracts, roots, and seeds. Indeterminable plant fragments were relatively rare. Fern remains constitute only 19 per cent (112 specimens) of the total flora. These are mainly vegetative frond fragments, but a few fertile specimens were found as well, in addition to woody fragments. All are preserved as impressions and compressions, without a cuticle, although epidermal prints have been found.

A substantial part of the material belonged to the A. Diaz Romeral Collection (ADR) at Cuenca, which at present is deposited at the Museo de las Ciencias de Castilla-La Mancha (Cuenca) (LH), and at the Museo Nacional de Ciencias Naturales (MNCNV) in Madrid. Silicone RTV replicas were prepared of epidermal prints. These were coated with 15 μm of gold by a Sputter Bio-Rad SC515 and photographed with SEM. The specimens were measured with a Measuroscope Nikon. Direct comparison was made with British Wealden material at The Natural History Museum, London.

SYSTEMATIC PALAEONTOLOGY

Order FILICALES Engler and Prantl
Family MATONIACEAE Presl

Form-genus WEICHSELIA Stiehler

Weichselia reticulata (Stokes and Webb) Fontaine, *in* Ward emend. Alvin, 1968

Plate 1, figures 1–3

Description. Frond bipinnate. Rachis prominent, 1·3 mm wide, broad, rigid, channelled. Pinnae alternate to subopposite. Pinnules 4–10 mm long and 2–3 mm wide, alternate, thick, leathery, oblong, with entire margins and broadly rounded apices, broadly based but not confluent, sometimes slightly falcate and inclined forwards. Pinnules in the distal part of pinnae opposite, 2–3 mm long, generally subtriangular with rounded apices. Midrib prominent, straight and developed up to a little below the pinnule apex. Lateral veins anastomosing.

EXPLANATION OF PLATE 1

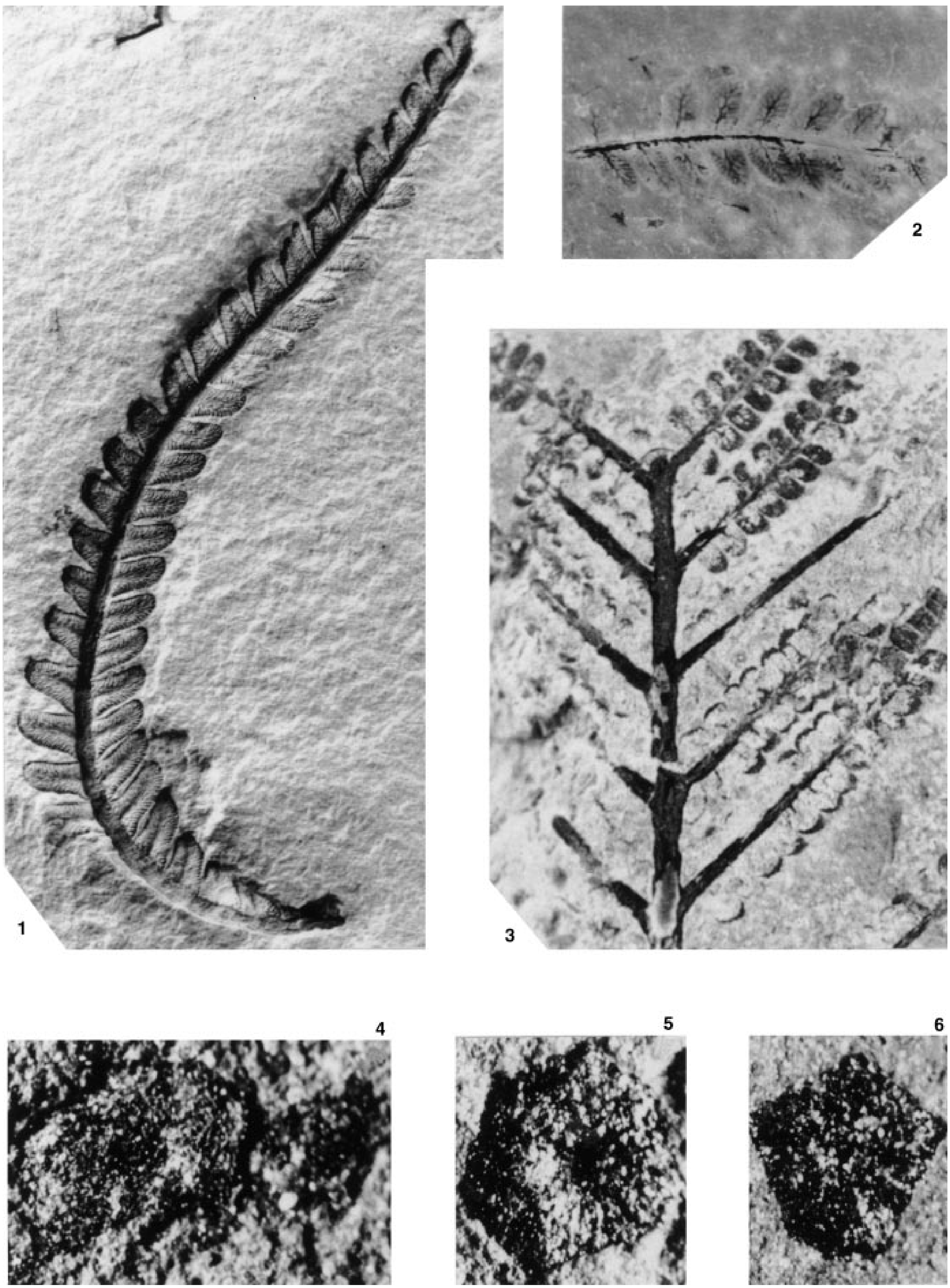
Figs 1–3. *Weichselia reticulata* (Stokes and Webb) Fontaine, *in* Ward emend. Alvin, 1968. 1, ADR 0054-P; impression of the underside of a pinna fragment; ×3. 2, ADR 0106-P; pinna segment with the pinnules showing the characteristic reticulate venation; ×4. 3, ADR 0126; the most complete specimen found which is a bipinnate fragment; ×3

Fig. 4. Matoniaceous indusia dispersae; the different sizes of the indusia are probably a result of different stages of development; ×45.

Fig. 5. Matoniaceous indusium; ×45.

Fig. 6. cf. *Weichselia reticulata* (Stokes and Webb) Fontaine, *in* Ward emend. Alvin, single indusium; ×45.

PLATE 1



DIÉGUEZ and MELÉNDEZ, *ferns*

Remarks. The fragments of *Weichselia reticulata* represent about 72 per cent of the fern remains recovered at Las Hoyas. Most are ultimate pinnae fragments from which the apical pinnule is lacking. Detached pinnules were disregarded, as were the abundant pinna rachises. Coalified compressions occurred almost exclusively in the darker limestone beds, whilst limonite-filled impressions were found commonly in the lighter coloured limestones. Two specimens are particularly well preserved. One of these is an impression which shows the pinnule contours as well as the venation (Pl. 1, fig. 1). The other, more fragmentary one (Pl. 1, fig. 2), shows pinnules in which the venation stands out almost in transparency.

The autecology of this species has been disputed for years. It was thought originally that some of the characters of *Weichselia reticulata*, such as the V-arrangement of the pinnules, could be an adaptation to copious rainfall (Nathorst 1890, *fide* Seward 1900). However, a very different interpretation was given by Seward (1900), Gothan (1910), and Alvin (1968), who regarded *Weichselia* as a xerophyte. Gothan (1910) assumed that it inhabited an arid dune region or even occurred in a maritime setting, and this opinion was shared by Daber (1968), Krassilov (1975), and El-Khayal (1985). According to Barale (1979), it was a xeromorphic plant that underwent periods of drought. Alvin (1971, 1974) merely stated that it dominated plant communities adapted to a peculiar habitat. All these interpretations coincide in highlighting the apparent adaptation to a stressed habitat. The occurrence of *Weichselia reticulata* at Las Hoyas raises some questions. In the first place it is noted that Las Hoyas represents a lacustrine carbonate environment without any apparent marine influence. Therefore, a coastal marine environment seems out of the question. Similarly, it does not really allow the assumption that *Weichselia* might have grown in dunes. Sedimentological studies on the Las Hoyas limestones, which are based on a large number of thin sections, show a total lack of siliceous material. The Las Hoyas sediments therefore either originated within the lacustrine system or were derived from the Jurassic limestones surrounding the lake. If one might wish to postulate that the *Weichselia reticulata* remains were brought in from a hypothetical dune area, the absence of any siliceous grains militates against this hypothesis. Although the remains of *Weichselia* at Las Hoyas are allochthonous, thus making inferences about habitat rather hypothetical, the general environmental conditions allow the possibility that it grew on calcareous soil. This is not the first time that *Weichselia reticulata* has been collected from carbonate sediments. Barale (1979) and Barale *et al.* (1984) recorded this fern from Montsec (Lleida, Spain). This site exposes limestones identical to those of Las Hoyas, but its environment was regarded as lagoonal by the authors cited; however, more recent sedimentological work by Fregenal-Martínez and Meléndez (1995) and Meléndez and Fregenal-Martínez (1997) suggests that the Montsec site belongs to a lacustrine system controlled by various allocyclic factors. It is noted in passing that other Lower Cretaceous sites in Spain (Guadalajara and Cuenca provinces), with similar lithologies and facies, also contain *Weichselia reticulata.*

The well-documented papers by Daber (1953, 1968) on apparently autochthonous material of *Weichselia* from Quedlinburg, Germany, allow the assumption that *Weichselia* might have been able to colonise both calcareous and siliceous soils. However, such a wide tolerance is very unusual in extant plants.

cf. *Weichselia*

Plate 1, figure 5

Description. Isolated peltate indusium, *c.* 0·82 × 0·93 mm, pentagonal in shape. Position of stalk marked by a hollow *c.* 0·015 mm wide in the top of the indusium. Indusium thick, apparently sclerotic. Although the indusium is comparable to that of *Weichselia reticulata,* the size does not fit the dimensions given by Alvin (1968) for the sori of this species, which has sporangia of *c.* 0·8 × 0·3 mm, i.e. a size that requires a much larger indusium.

Matoniaceae sp. 1

Plate 1, figure 4

Description. Isolated peltate indusium, elliptical, 0·82 × 0·5 mm. The position of the stalk of the umbrella-like indusium is marked by a deep central hollow, circular, 0·015 mm in diameter. Alongside this specimen, but not in connection, there is another smaller indusium, *c.* 0·46 × 0·2 mm, which is similar but less complete, with a central hollow of 0·011 mm in diameter. The relative position of these indusia suggests that they occurred in a row and were not clustered. In conjunction with their shape and general appearance this approximates them to certain specimens figured as *Matonia mesozoica* by Appert (1973, pl. 42, fig. 4; pl. 43, figs 2, 5), but their size is smaller. This fact is probably due to an earlier stage of development of the reproductive structures of the specimen studied.

Matoniaceae sp. 2

Plate 1, figure 6

Description. Isolated indusium, pentagonal, 0·71 × 0·6 mm, peltate. Indusium apparently thin-walled. Depression of stalk 0·004 mm in diameter. Although its shape suggests that it formed part of a cluster like those occurring in *Weichselia reticulata*, it differs by its size and delicateness.

Family DICKSONIACEAE Bower

Form-genus CONIOPTERIS Brongniart

Coniopteris laciniata sp. nov.

Plates 2–3; Text-figure 4A–B

Derivation of name. Refers to the shape of fertile distal pinnules which are cut into laciniae.

Type locality. La Huérguina Limestone Formation, 'Rambla de las Cruces II' Sequence, second lithosome of laminated limestones.

Holotype. ADR 0119-P, deposited in the Museo Nacional de Ciencias Naturales, Madrid.

Diagnosis. Polymorph tripinnate frond, partially fertile. Pinnae katadromically alternate, subperpendicular to axis. Pinnules polymorph, obliquely inserted, subopposite to opposite, deeply segmented. Basal pinnules trilobate. Intermediate pinnules partially fertile, cuneate and deeply incised with round sori covered by an indusium placed at the end of each pinnule segment. Pinnules in distal part of last order pinna skeletonised by apparent loss of lamina.

Description of holotype. Frond at least tripinnate, partially fertile (Pl. 2, fig. 1). Penultimate axis stiff, smooth, 0·86 mm wide, bearing katadromically alternate pinnae, 16–17 mm long, inserted at a wide angle (70–80 degrees) at intervals of 3·5–4·6 mm. Pinnules inserted obliquely, decurrent, quite variable in shape depending on their location in the frond, katadromically arranged, and joined at the base by a narrow flange.

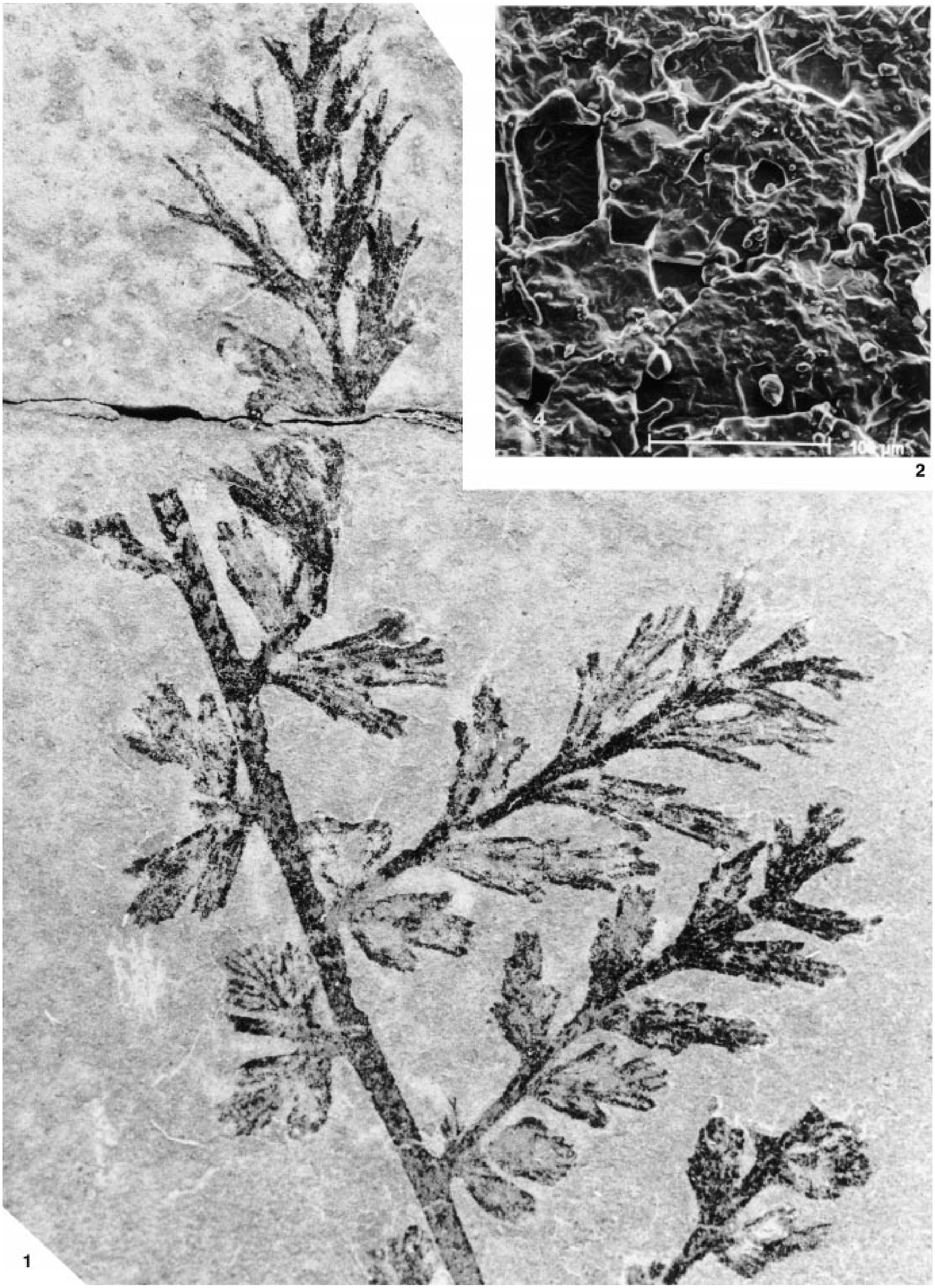
Vegetative pinnules broad, rhomboidal, trilobate, 3·7 mm long and 2·9 mm wide, with a stalked base (stalk 0·2 mm long and 0·6 mm wide). First pinnule basiscopic. Pinnules subopposite to opposite, departing from rachis at 46 degrees. Venation sphenopteroid, midrib katadromically forked four times (Pl. 3, fig. 4). Intermediate pinnae (Pl. 3, fig. 1) partially fertile with pinnules of variable shape from the base to pinna apex. Basal pinnules cuneate, 3·4 mm long and 2·8 mm wide, divided into three segments. Intermediate lateral pinnules rhomboid, 4·08–6·2 mm long and 1·4–2·2 mm wide, and cut into five segments with rounded indusium located at the tip of each segment; indusia 0·3 mm in diameter, with a small central hollow of 0·06 mm. Distal pinnules, 5·9 mm long and 1·9 mm wide, are deeply segmented to form laciniae, 2·5 mm long and 0·27 mm wide. A single vein occurs in each segment. More apical pinnae antler-shaped, 11·7 mm long; basal pinnules cuneate, stalked, 5·3 mm long and 3·6 mm wide. Stalk 0·36 mm long and 0·76 mm wide. Distal pinnules so deeply incised as to produce laciniae, 2·07–2·31 mm long and 0·26–0·39 mm wide. Venation indistinct. Abaxial epidermal impression shows isodiametric cells 28 μm in diameter with smooth, rather thick walls (3·6 μm) (Text-fig. 4B). The cells are disposed in a regular pattern in the interveinal areas, and are both larger and less regularly disposed over the veins (Text-fig. 4A). The midrib is marked by larger polygonal cells with thicker walls (6·5 μm) (Text-fig. 4A). Sparse anomocytic stomata occur randomly near the midrib (Pl. 2, fig. 2).

Remarks. Only one specimen (the holotype) is available and this consists of an incomplete pinna of the penultimate order which is preserved as an impression. The extremely fine-grained sediment has allowed the production of a replica for SEM analysis so as to observe the epidermal structure.

The specimen shows a twisted pinna at the tip, with a torsion of about 45 degrees, presumably as a result of dragging by currents. The most salient characteristic of this specimen is the marked polymorphism of the pinnules depending on the presence of sori and their stage of development. The basal part of the specimen shows the outline of the vegetative pinnules which possess a fully developed lamina. In the middle part the pinnules show a progressive loss of lamina which has produced a more stylised shape with pinnule segments following the outline of the venation. This is particularly noticeable in the distal parts of pinnae where the pinnules have become deeply dissected so as to produce narrow, almost linear pinnule segments (laciniae). A slight swelling at the tip of these segments apparently corresponds to the position of a sorus with indusium. Even though the preservation is not particularly good, Plate 3, figures 2–3 show a slight depression in the centre of what is likely to be an indusium, and this seems to correspond to the position of a stalk. Not all of the pinnule segments are tipped by an apparent sorus with indusium. Indeed, the most distal part of the pinnae and, in particular, the distal part of the twisted top pinna with entirely skeletonised pinnules, lack the swelling at the tip of pinnule segments and the segments even appear to be acute. The lack of a discernible sorus may mean that either the sorus fell off or, more likely, that it shrivelled after the release of spores from the sporangia, in which case it might become too minute for visible preservation. One might also regard the possibility that maceration in water degraded the tissues to the extent of leaving more acute pinnule segments to be imprinted on the sediment, but this seems less likely in view of the intermediate stages and the presence of non-skeletonised pinnules in the basal part of the specimen. The most interesting aspect of this specimen is the apparent progression in the development of sori, which implies a maturity series with the distal parts of pinnae showing a more mature stage of development than the more proximal parts. Among present-day ferns the genus *Adiantum* shows the apparent loss of sori in fertile pinnules which, after dispersal of the spores, retain merely a stain on the abaxial part of the pinnule lamina to mark their position. Of course, this would be rarely, if at all, detectable in fossil remains. In *Coniopteris* there are several species which are characterised by a loss of pinnule lamina associated with the development of fertile structures (sori) at the tip of skeletonized pinnules: e.g. *C. bella* Harris, and *C. hymenophylloides* (Brongniart) Seward. Other species of *Coniopteris* also show a marked differentiation in pinnule shape with a progressive loss of lamina in the fertile area. Intermediate to partially fertile pinnae occur in *C. embensis* Prynada (Baranova *et al*. 1975), *C. furssenkoy* Prynada (Baranova *et al*. 1975; Kiritchkova 1976), *C. vialovae* Turutanova-Ketova (Brick 1935; Baranova *et al*. 1975) and *C. minusculus* Kiritchkova (Kiritchkova 1976). Crabtree (1988, pp. 9–10), when describing *Coniopteris vinyardii* Crabtree, mentioned the existence of a gradation between vegetative and fertile pinnules as well as the presence of sori situated either individually on filiform pinnules or in groups of two or three on lobing pinnules which are in the process of being dissected into laciniae. As in the species from Las Hoyas, the reduction of lamina is observed in the pinnules situated in the apical parts of fronds, and in relation to fertile structures. *Cyathea termensis* (Seward) Krassilov, which is attributed to the family Cyathaceae but which is close to the Dicksoniaceae (it is noted in passing that the latter family is often regarded as merely a subfamily of the Cyathaceae), also presents four different kinds of pinnule shape. In this species the sori occur in partially fertile pinnules of linear-lanceolate or lanceolate shape. It also possesses distal pinnules which are subdivided into narrow segments served by a single vein, and this is very similar to the skeletonized pinnules of *Coniopteris laciniata* sp. nov. Krassilov (1978) described *Cyathea tyrmensis* as possessing demonstrable sori only in partially fertile pinnules. He mentioned that entirely fertile pinnae should be present but that no convincing evidence of such pinnae had been obtained. A comparison with the specimen to hand suggests that in both cases the fertile area was located in the most distal parts of the frond and graded into a partially fertile region lower down, showing a transition with the wholly vegetative part of the leaf. The skeletonized pinnules would thus most likely represent entirely fertile parts with shrivelled sori after the release of spores.

EXPLANATION OF PLATE 2

Figs 1–2. *Coniopteris laciniata* sp. nov., ADR 0119-P (holotype). 1, twisted pinna with skeletonised pinnules in the upper part; partially fertile pinnules with swollen tips of lobes representing small sori; fully developed pinnules in the lower part of specimen near the penultimate rachis; ×5. 2, epidermis of the abaxial surface of a pinnule showing an anomocytic stoma covered with lime; coated silicone replica (SEM).



DIÉGUEZ and MELÉNDEZ, *Coniopteris*

Coniopteris sp. cf. *Coniopteris murrayana* (Brongniart) Brongniart, 1849

Text-figure 4C

Description. Pinnae parallel-sided and gradually tapering towards the apex. Penultimate rachis grooved, 1 mm wide, with subopposite to slightly alternate last order pinnae inserted at angles of 50–65 degrees. Pinna terminals are entire to trilobate. Pinnules 28–36 mm long, with a sturdy limb, alternate to subopposite, arising in katadromic order, and characteristically trilobate with rounded lobes and a rounded, subtriangular apex. Pinnule bases are constricted. Sphenopteroid venation consists of a central midrib and lateral veins arising katadromically.

Remarks. Only two specimens have been collected at Las Hoyas. Both are pinna fragments lacking the basal part. The figured specimen (Text-fig. 4C) is an incomplete pinna of the penultimate order, 8·46 cm long and 2·93 cm in maximum width. It is densely encrusted with lime. The second, unfigured specimen is similar in all respects. Although closely comparable, these specimens differ from *C. murrayana* (Brongniart, 1849, p. 105) by the presence of trilobate pinnules as well as by the subopposite insertion of pinnae. Where alternating pinnae are observed, the intervals between pinnae are shorter than in Brongniart's species.

Genus DICKSONIA L'Heritier

Dicksonia sp.

Plate 4, figure 4

Description. The specimen attributed to *Dicksonia* sp. consists of a fertile pinna fragment with the shape and location of sori marked by concave impressions. The number of sporangia per sorus cannot be determined exactly, but seems to have been rather large. A description is as follows:

Partly fertile pinnae with a finely grooved, sturdy rachis about 2 mm wide. Last order pinnae arising opposite at intervals that decrease in length towards the apex (7·5–3·8 mm) and departing from the rachis at about 87 degrees in the lower part and 69 degrees higher up. Fertile and vegetative pinnules are similar in shape (no loss of lamina). Pinnules subopposite. The non-fertile basal anadromous pinnule is similar to the adjacent fertile one, broad, ovate (3 mm long, 2·6 mm wide); subsequent pinnules are trilobate, ovate, rather spaced out, but connected along the pinna rachis by a very narrow decurrent flange. Pinnule apex rounded, and with a base which is most constricted on the acroscopic side. Venation sphenopteroid. Basal pinnules on katadromous side fertile, ovate to roundish, each with a single sorus in the basal part on the basiscopic side. Sori ovate to rounded, 1·64 mm wide and 1·58 mm long, height and thickness unknown, and seemingly stalked as deduced from the different places that the sori occupy on compression; i.e. sometimes below the rachis of last order pinnae, and sometimes above the rachis and partially overlapping the penultimate rachis. Indusia, sporangia and spores not observed.

Remarks. Both the position and the stalked nature of the sori are indicative of *Dicksonia*. There is a fairly strong resemblance to *Dicksonia mariopteris* Wilson and Yates (1953, p. 930, text-figs 1–2) in regard to: (1) the main characteristics of the penultimate rachis, except for the presence of hairs; (2) the ovate shape of pinnules and the presence of a narrow connecting flange; (3) the presence of branches of the midrib

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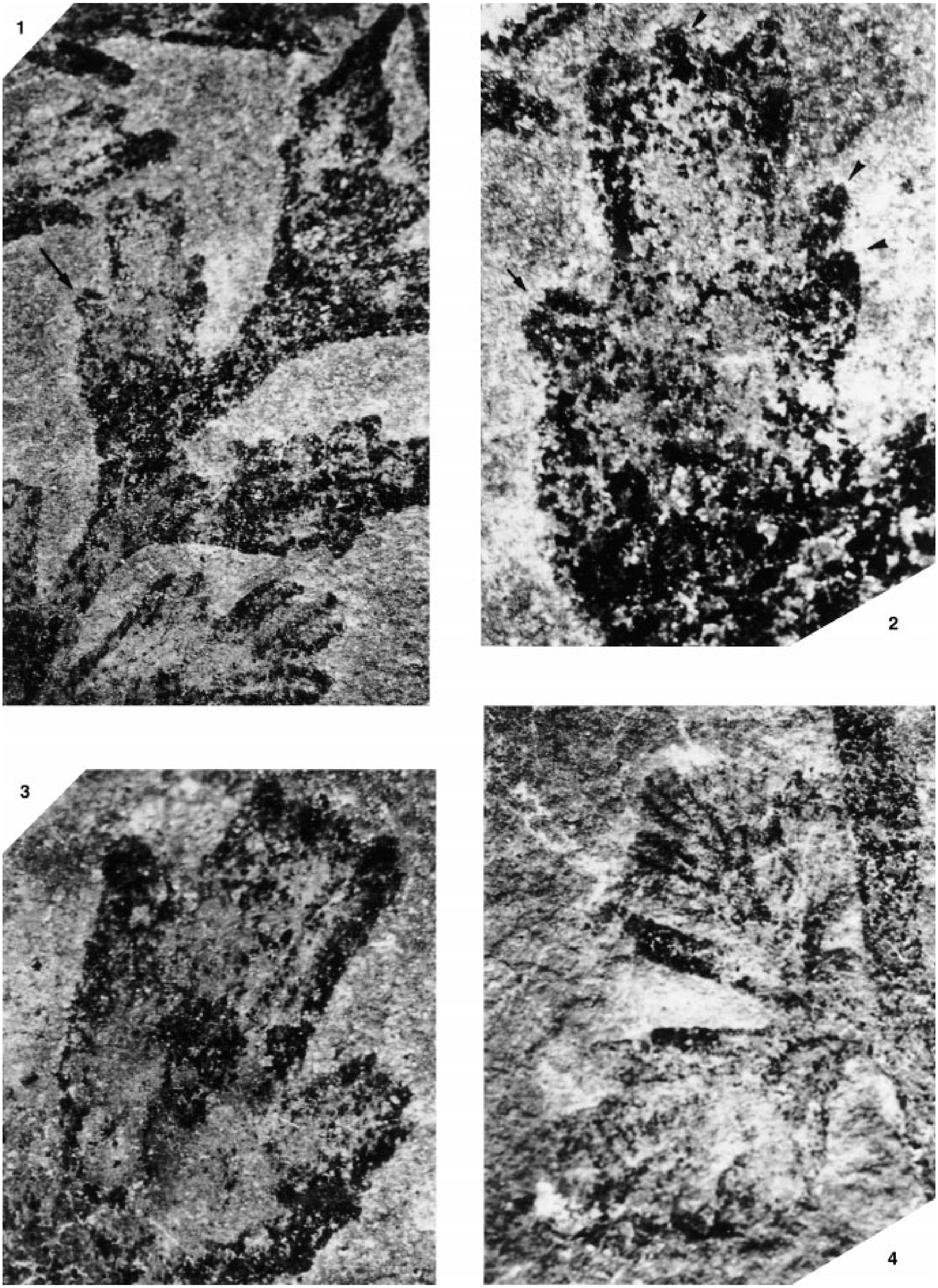
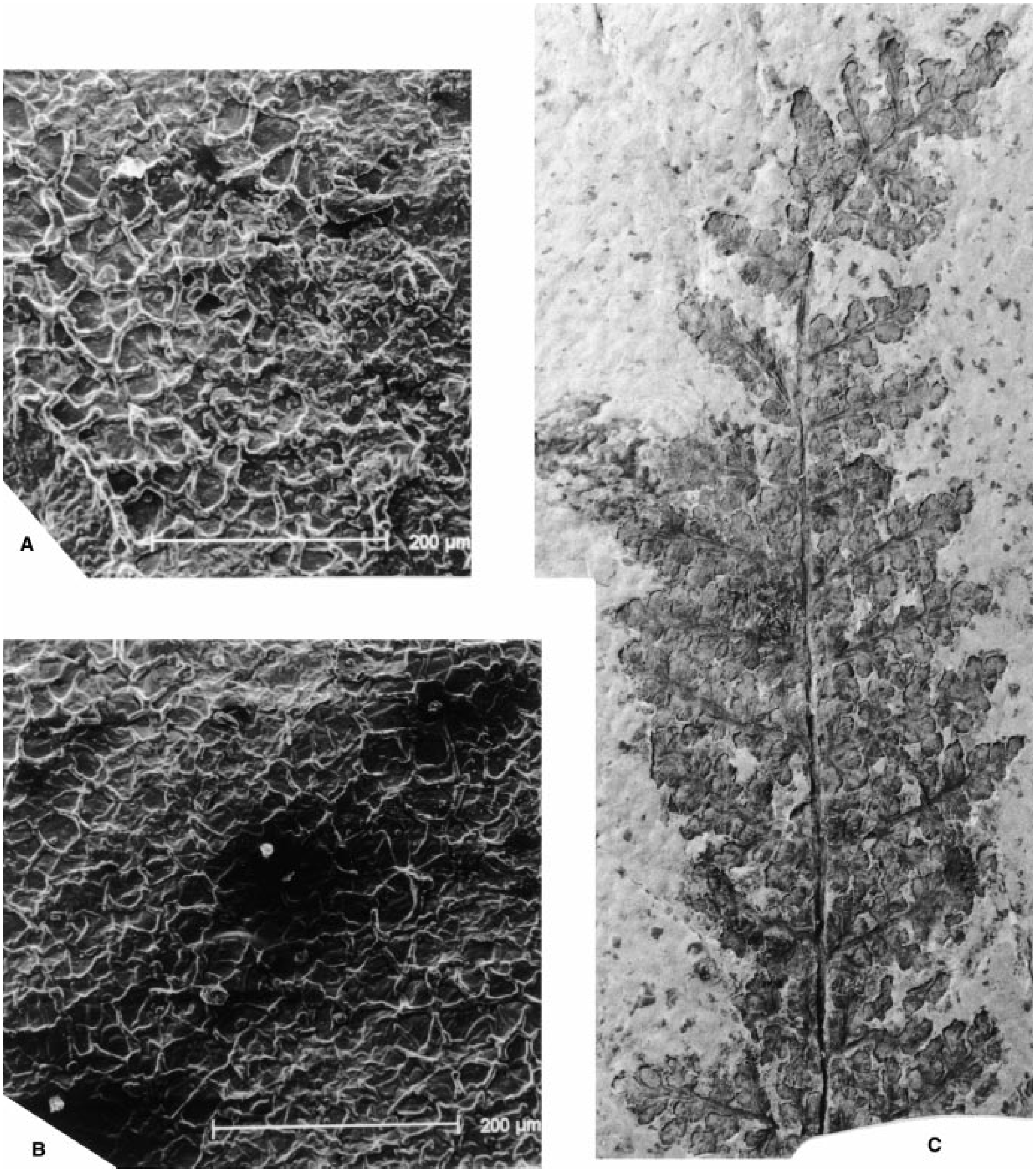
EXPLANATION OF PLATE 3

Figs 1–4. *Coniopteris laciniata* sp. nov. (holotype). 1, part of a last order pinna showing partially fertile pinnules with small sori at the tip of lobes (arrow); ×15. 2, close-up of pinnule in fig. 1 with a clearly developed indusium at the tip of a lobe (arrow) and three possible ones (arrowheads); ×24. 3, close-up of another pinnule of specimen in fig. 1 with indusium of sori at the tip of a lobe; ×24. 4, sterile pinnules at the base of lateral pinnae, showing a sphenopteroid venation; ×12.

PLATE 3



DIÉGUEZ and MELÉNDEZ, *Coniopteris*



TEXT-FIG. 4. A, *Coniopteris laciniata* sp. nov., ADR 0119-P (holotype); epidermis of the abaxial surface of pinnules showing the epidermal cells over the veins; coated silicone replica (SEM). B, *Coniopteris laciniata* sp. nov., ADR 0119-P (holotype); epidemis of abaxial surface of pinnules, coated silicone replica (SEM). C, *Coniopteris* sp. cf. *Coniopteris murrayana* (Brongniart) Brongniart, 1849, ADR 0059-P; ×2.

entering the lobes. However, it differs in having a single sorus per pinna, in possessing trilobate distichous pinnae and pinnules, and by the regular lobing of pinnules and the twice-forked lateral veins. The opposite positioning of the pinnae and pinnules as well as the presence of a single sorus in each pinna distinguish it from *Dicksonia kendallii* Harris (Harris 1961, pp. 179–181, text-fig. 66).

Form-genus ONYCHIOPSIS Yokoyama

Onychiopsis psilotoides (Stokes and Webb) Ward, 1905

Plate 4, figure 3; Text-figure 5B

Description. The material consists of five vegetative pinna fragments preserved as impressions (part and counterpart in one case). The most complete specimen (Text-fig. 5B) is 37·24 mm long and consists of a rachis 0·6 wide, with 12 lateral pinnules as well as the apical pinnule; these are coriaceous, alternately positioned, with adnate-decurrent bases, and are inserted at an acute angle of *c*. 25 degrees. Pinnules lanceolate, narrow, of almost constant width (0·6–0·7 mm), with acuminate apices. Pinnule length varies from 1·9 mm to 7·4 mm, diminishing rapidly distally. Additional specimens are generally similar to the one described, although possessing longer pinnules (8–13·5 mm long and 0·7–0·9 mm wide), which are positioned at a narrower angle (15 degrees) (Text-fig. 5B). One specimen, 14·24 mm long and 0. 5 mm wide, consists of an axis with eight incomplete pinnules, 0·5–0·8 mm long and 0·4–0·6 mm wide, parallel-sided with no preserved apices. Its general appearance is more delicate and looser than in the other remains studied; it is most comparable to a specimen figured by Seward (1900, pl. 2, fig. 20).

Remarks. The systematic position of this species has been disputed. Seward (1894, 1900) included it in the family Polypodiaceae. Tattersall (1961) agreed with Seward after studying fertile material from Ecclesbourne and Atherfield Bay in southern England. Skog (1986) transferred *Onychiopsis psilotoides* to the Lycopodiales. However, after the well-documented study by Friis and Pedersen (1990), its inclusion in the family Dicksoniaceae seems well established, thus vindicating Yokoyama (1889), who suggested this link by referring to *Thyrsopteris elongata* (a synonym) as *Dicksonia elongata.* The species *Onychiopsis psilotoides* has a wide stratigraphic and geographic distribution, and it is very common since it occurs in most of the known Cretaceous sites worldwide. In the Iberian Peninsule it has been recorded previously from various Portuguese localities (Teixeira, 1952), as well as from Montsec (Lleida, Spain; Barale, 1991). The record of *Sphenopteris mantelli* from the Upper Aptian–Albian of Pola de Siero (Asturias) by Alvárez-Ramis and Lorenzo (1979) and Alvarez-Ramis (1980) can also to be ascribed to this species. All the specimens recorded show coriaceous pinnules, which seem to be characteristic of this species. Tattersall (1961) mentioned that it is not a delicate fern, and it seems reasonable that Batten (1974) and Friis and Pedersen (1990) regarded the coriaceous pinnules as an adaptation to a high-stress environment.

Family SCHIZAEACEAE Kaulfuss

Form-genus RUFFORDIA Seward

Ruffordia goepperti (Dunker) Seward, 1894

Plate 5, figure 3

Description. The material from Las Hoyas assigned to this species includes vegetative pinnule fragments and scraps representing ultimate segments which are all preserved as impressions. A certain amount of polymorphism is apparent. A marked difference in the relative size and shape of pinnules or ultimate segments is apparent in the same manner as emphasised by Seward (1894). Three main types can be distinguished:

Representative of the first type is one of the most complete specimens found (Pl. 5, fig. 3) which consists of a compact pinna attached to a rhizome; it has a rhomboidal shape, and is 45·2 mm long, with a flexuous rachis 0·43 mm wide. Last order pinnae linear-lanceolate, 10–24·3 mm long, placed opposite at the rachis with a decurrent base, and arising at an acute angle (35 degrees). Pinnule or ultimate segments linear-acuminate or slightly lobed, opposite, decurrent, with a delicate, thin-limbed appearance and a coniopteroid venation, at least three times dichotomous. Other fairly complete specimens, 50·55 mm long and 54·89 mm in maximum width, belong to the second type. Although similar to the first type in general morphology, the rachises are more strongly developed (main axis 9 mm wide), and the pinnae are larger (25·51–48·20 mm long), and inserted at a wider angle (40 degrees). The pinnules are lanceolate, broad, and of more sturdy appearance. The general aspect is more compact.Venation is not preserved. One specimen is assigned to the third type. It consists of a pinna which bears a close resemblance to the specimen figured as *R. goepperti* var. *latifolia* by Seward (1894, pl. 6, figs 1, la), since it has wider ultimate segments, 1·4–2·4 mm, with entire margins.

Remarks. This species is a very common constituent of Lower Cretaceous floras worldwide. At Las Hoyas, it constitutes 9·7 per cent of the fern remains (12). Indeed, it is the most abundant element after *Weichselia reticulata.* The state of preservation is quite variable. Although all specimens are preserved as impressions, those imprinted on dark muddy limestones tend to show more detail than those preserved in lighter coloured rock. Some specimens are quite complete, including the rhizome (Pl. 5, fig. 3), but most are pinnule fragments which probably had a long residence time in water. *R. goepperti* has been recorded from the Lower Cretaceous in Spain by Barale (1991), and also by Alvarez-Ramis (1980) who identified it as *Thyrsopteris* aff. *nervosa* Fontaine.

Form-genus PELLETIXIA Watson and Hill

Pelletixia valdensis (Seward) Watson and Hill, 1982

Text-figure 5A

Description. Only a small fragment of a rather delicate fertile pinna has been found. It shows a slender axis, 0·28–0·47 mm wide, with a few thin branches bearing more or less spherical bodies (probably spore-masses), 2·7 mm long and 3·7 mm wide, which are located at the tip of ultimate branches by means of a short stalk, 0·2 mm long and 0·3 mm wide, corresponding to the constricted pinnule bases. Lamina consists of narrow, lanceolate, juxtaposed segments, 2·5–4·1 mm long and 0·4–0·5 mm wide. Sterile pinnules are composed of lanceolate segments, which conform in shape and arrangement to *Onychiopsis psilotoides* (Stokes and Webb) Ward.

Remarks. The original diagnosis of *Pelletieria valdensis* by Seward was emended by Watson (1969, p. 232) who described the spores masses as ‘capsules’. Watson did not describe the vegetative pinnules. Later, Watson and Hill (1982) proposed the new name *Pelletixia* for the genus *Pelletieria* Seward (Schizaeaceae). The authors considered that this name should be rejected under articles 64 and 75 of the Code of Botanical Nomenclature owing to the existence of the homonym *Pelletiera* Saint Hilaire (Primulaceae) and its confusing spelling; they therefore proposed the new combination *Pelletixia valdensis*. Although Seward (1913, pp. 92–93, text-fig. 4G) described the pinnules as split into cuneate segments, it may be that the original material was too poorly preserved to show the more lanceolate shape of segments displayed by the specimen from Las Hoyas.

The geographic distribution of this species is poorly known. Thus far it has only been reported from the English Wealden (Seward 1913; Couper 1958; Hughes and Moody-Stuart 1966; Watson 1969; Watson and Hill 1982).

UNCLASSIFIED FERNS

Form-genus ACROSTICHOPTERIS Fontaine

Acrostichopteris foliosa (Fontaine) Berry, 1911

Plate 4, figure 1

Description. Three vegetative pinnae, one of which is a little over 50 mm long. Last order pinnae display a broad rachis (1·5 mm wide) with alternate, oblique, rather spreading pinnules, rhomboidal or lanceolate in outline, and which are

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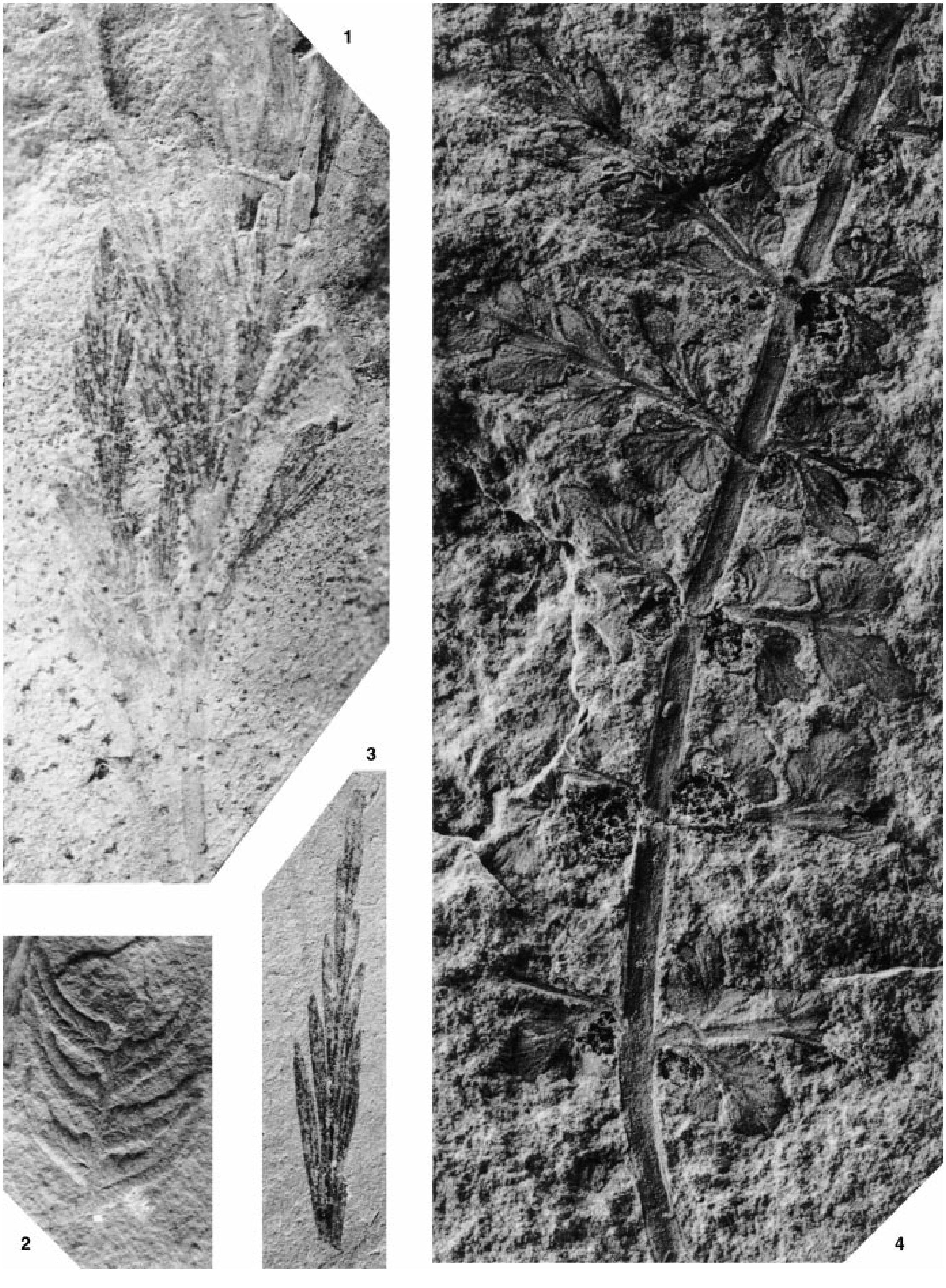
EXPLANATION OF PLATE 4

Fig. 1. *Acrostichopteris foliosa* (Fontaine) Berry, 1911, LH-5255; pinna fragment; ×3.

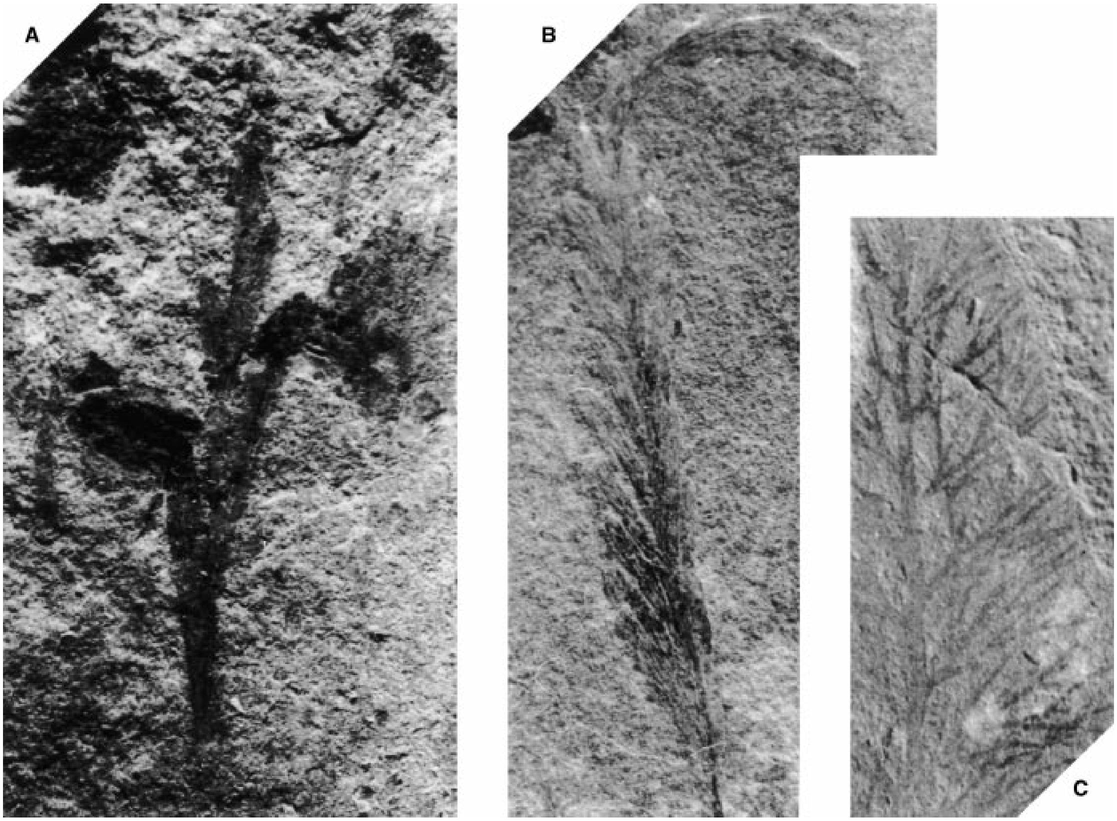
Fig. 2. *Dicksonia* sp., ADR 0050-P; pinna showing stalked spore masses overlapping basal pinnules and rachises; ×3.

Fig. 3. *Onychiopsis psilotoides* (Stokes and Webb) Ward, 1905, ADR 0020-P; pinna fragment with single-veined segments; ×3.

Fig. 4. *Cladophlebis albertsii* (Dunker) Seward, 1894, LH-154 A/B; last order pinna fragment with pinnules; ×3.



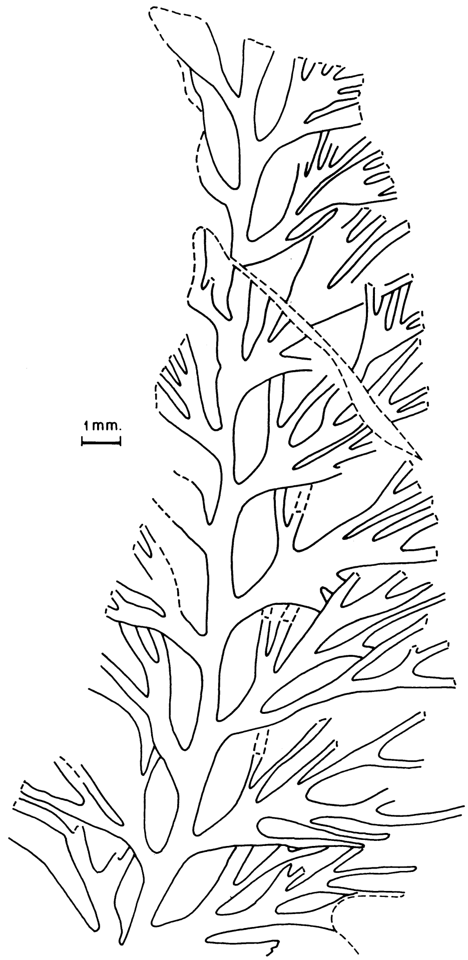
DIÉGUEZ and MELÉNDEZ, ferns



TEXT-FIG. 5. A, *Pelletixia valdensis* (Seward) Watson and Hill, 1982, MNCNV-7767; small fragment showing spore masses and lanceolate pinnule segments; ×12. B, *Onychiopsis psilotoides* (Stokes and Webb) Ward, 1905, MNCNV-7766; pinna fragment showing elongate terminal bent horizontally; ×3. C, *Sphenopteris fontainei* Seward, 1894, MNCNV-7771; ultimate pinna fragment with faintly imprinted pinnules subdivided into filiform segments; ×3.

split into lanceolate or obovate laciniae. Venation is faintly preserved, almost imperceptible, but some laciniae show dichotomous veins in the middle part.

Remarks. The three specimens collected are all preserved as impressions. They are very fragmentary since they consist only of portions of last order pinnae. There is a close similarity with the specimens figured by Bell (1956, pl. 25, figs 1, 3) from the Luscar Formation (Western Canada) of Aptian age. To some extent they also resemble *A. longipennis,* especially as figured by Fontaine (1889, pl. 160, fig. 10) from the Potomac Group (Virginia, USA). The Spanish material differs from *A. ruffordii* Seward from the Wealden of England (Seward 1894, pp. 61–62, pl. 6, fig. 3) and from the Portuguese species *A. nervosa* Teixeira (Teixeira 1948, pl. 19, figs 1–6) in that those species have cuneate laciniae. *Acrostichopteris* is a rare element of Jurassic and Lower Cretaceous floras, and where it does occur its specific diversity is low (Seward 1894; Berry 1911; Teixeira 1948; Bell 1956; Samylina 1976; Krassilov 1978, 1982; Lapasha and Miller 1985; Kimura 1987; Kimura and Ohana 1988; Kimura *et al.* 1988; Vakhrameev 1988; Gee 1989). The only exception is the Potomac flora which contains five different species of *Acrostichopteris*. This genus is apparently absent from the Lower Cretaceous localities of Belgium (Seward 1900), France (Carpentier 1927, 1929, 1934), and Germany (Schenk 1871; Pelzer 1984, 1987; Pelzer and Wilde 1987; Wilde and Schultka 1996). This is the first record from Spain.



TEXT-FIG. 6. *Sphenopteris fontainei* Seward, MNCNV-7771.

Form-genus SPHENOPTERIS Sternberg

Sphenopteris fontainei Seward, 1894 emend.

Text-figures 5C, 6

Original diagnosis. Frond delicate, pyramidal in form; pinnae alternate, approximate, on a slender rachis; pinnules deeply dissected, ultimate divisions narrowly linear, with bluntly terminated apices.Venation of *Sphenopteridis* type.

Emended diagnosis. Tripinnate frond with delicate looking pinnae, anadromically alternate at regular intervals; rachis slender, smooth, up to 0·6 mm wide. Pinnules constricted at the base, deeply dissected katadromically to form narrow, needle-shaped segments, with single veins. First segment on the acroscopic side of the pinnule is overlapped by the next acroscopic pinnule. Ultimate segments forked.

Description of new specimen. Fragment of a pinna of the last order bearing eight pairs of rather delicate looking pinnules, 6–12 mm long, which are deeply dissected into laciniae, 1·5–5·6 mm long and 0·2–0·3 mm wide. The pinnules are inserted at an angle of 58 degrees in the basal part of the pinna, whereas a narrower angle of insertion is found nearer the tip of the pinna where it is *c*. 48 degrees. Pinnules very constricted on the acroscopic side, forming a stalk 0·55 mm wide. The venation is too faint to be made out properly.

Remarks. The one specimen found is faintly imprinted on the limestone and the photograph (Text-fig. 5C) is correspondingly faint. This may well be because the lamina of this fern is very thin; Seward (1894, p. 106) called it 'delicate'.

Sphenopteris fontainei was described by Seward (1894, p. 106, pl. 7, fig. 2) from the English Wealden. Almost simultaneously, Saporta (1894) described two species from the Mesozoic of Portugal, viz. *S. microclada* (p. 23, pl. 6, figs 1–2; pl. 14, figs 3–5) from Granja and Vale do Gato, and *S. tenellisecta* (p. 25, pl. 13, fig. 1) from Salgueiro. After comparing the descriptions and figures of the two species described by Saporta and the one recorded by Seward, it seems that only one taxon is involved. Seward (1895, p. 229) observed that the specimens on which Saporta based his *S. microclada* were microscopic and he mentioned that this species was closely comparable to *S. fontainei.* After a revision of the type specimens Teixeira (1948, p. 15) expressed the opinion that Saporta's material was so poorly preserved that they could not be identified specifically. As a result, *S. microclada* and *S. tenellisecta* should be regarded as synonyms.

Sphenopteris fittonii Seward, 1894

Plate 5, figure 1

Description. Vegetative pinnae of the last order with pinnules 5 mm long, ovate-lanceolate, slightly lobed, alternate, decurrent, with acute apices, and inserted at angles of 46–63 degrees. Venation sphenopteroid, midrib straight to slightly flexuous. Lateral veins forked twice, ending at the tip of each lobe, one per lobe. In the case of dentate lobes there is one vein ending per tooth.

Remarks. This species is rare at Las Hoyas, only two pinna fragments having been recovered. They are preserved as impressions (part and counterpart). These remains compare well with that figured by Seward (1894, text-fig.11). Seward pointed out the morphological variation in this species, as this is also apparent in the specimens at Las Hoyas. *Sphenopteris fittonii* is widely represented in Lower Cretaceous floras.

Sphenopteris sp. cf. *Sphenopteris fittonii* Seward, 1894

Plate 5, figure 2

Description. A lanceolate vegetative pinna fragment with a slender rachis which is partially covered by pinnule bases. Pinnules alternate, with parallel margins and slightly tapering rounded apices; base slightly decurrent, very slightly lobate margins. Sphenopteroid venation, lateral veins departing obliquely and forking once.

Remarks. The one pinna fragment found is an impression filled by limonite which accentuates the venation pattern. Although resembling *Sphenopteris fittonii,* it is not a total fit.

Form-genus CLADOPHLEBIS Brongniart

Cladophlebis albertsii (Dunker) Seward, 1894

Plate 4, figure 4; Text-figure 7A

Description. The one specimen found is a pinna of the last order, with a flat, grooved axis bearing broadly attached,

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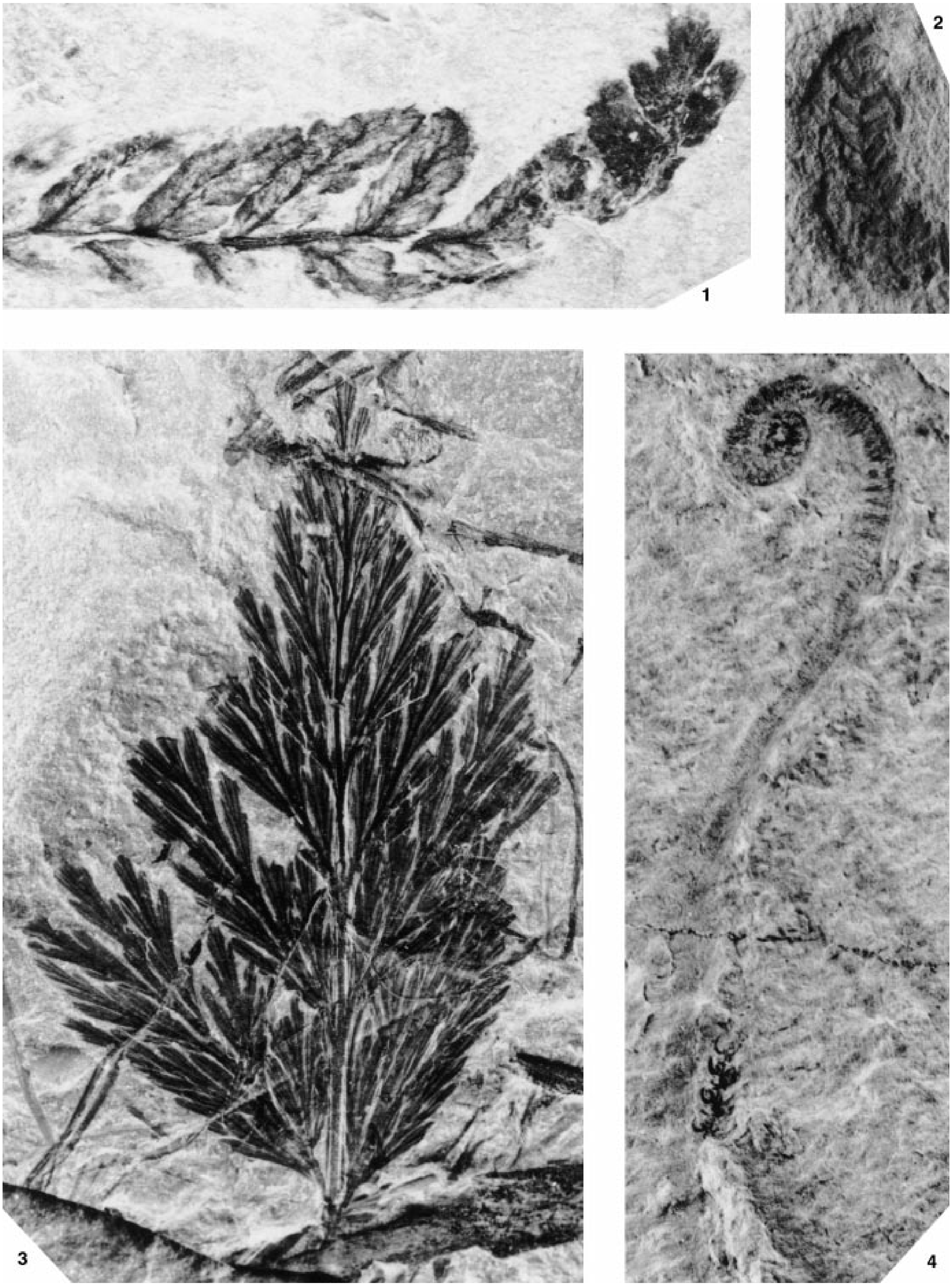
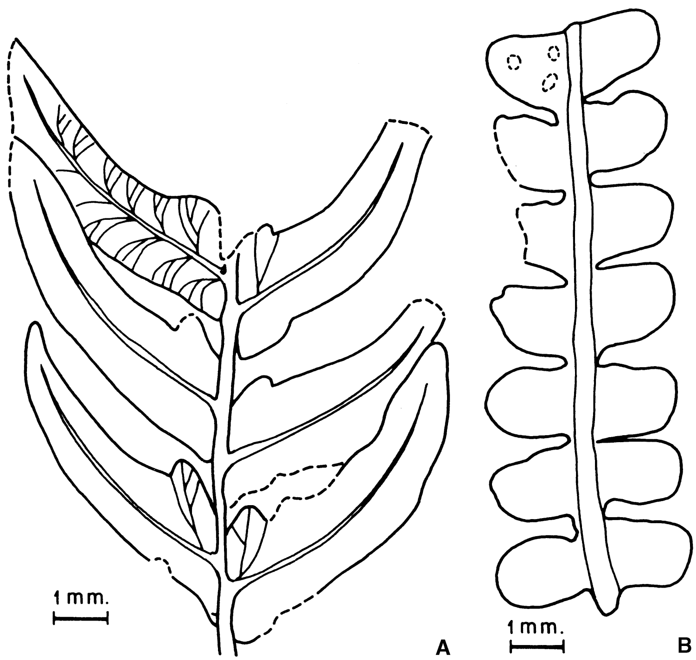
EXPLANATION OF PLATE 5

Fig. 1. *Sphenopteris fittonii* Seward, 1894, ADR 0041-P; ×7.
Fig. 2. *Sphenopteris* sp. cf. *Sphenopteris fittonii* Seward, 1894, ADR 0112-P; ×2.
Fig. 3. *Ruffordia goeppertii* (Dunker) Seward, 1894, ADR 0040-P; reasonably complete specimen showing pinna attached to rhizome?; ×3
Fig. 4. *Spiropteris* sp., ADR 0045-P; × 3.

PLATE 5



DIÉGUEZ and MELÉNDEZ, ferns



TEXT-FIG. 7. A, *Cladophlebis albertsii* (Dunker) Seward, LH-154 A/B. B, *Cladophlebis* sp. cf. *waltonii*, LH-5259.

subopposite pinnules inserted at 45 degrees, subtriangular, strongly falcate, margins slightly dentate, 7–8 mm long and 3–4 mm wide. Basal lobe on acroscopic side of the pinnule, which is very slightly decurrent on the basiscopic side. Midrib curved towards the obtuse apex and reaching almost to the pinnule apex. Lateral veins bifurcate twice with the first fork near the midvein. First acroscopic lateral vein with an accessory vein.

Remarks. This specimen has characters in common with *C. virginiensis* Fontaine and *C. falcata* Fontaine, but it differs from *C. virginiensis* in having longer and narrower pinnules. Some specimens of *C. falcata* (Fontaine 1889, pl. 4 fig. 8; pl. 5 fig. 3) possess pinnules of similar shape and venation, with undulating margins, but this similarity is cancelled out by the less rigid appearance of the overlapping pinnules.

Cladophlebis sp. cf. *Cladophlebis waltonii* Seward, 1927

Text-figure 7B

Description. Pinna fragment 1·14 mm long, with pecopterid pinnules 0·18 mm long and 0·12 mm wide, entire, with a broadly rounded apex, and inserted at right angles to a rachis 0·06 mm wide. Venation not preserved.

Remarks. One might regard the possibility that the specimen was fertile owing to the presence of three faint rounded marks similar to sori on one of the pinnules located in the most distal part of the pinna fragment (see Text-fig. 7B), but it is impossible to prove this because of its poor state of preservation.

The specimen from Las Hoyas differs from *C. waltonii* as figured by Seward (1927, p. 74, text-fig. 3) by possessing straighter pinnules without curvature towards the terminal pinna and by lacking the slight constriction of the pinnule bases. It resembles more closely the remains figured by Bell (1956, pl. 19, fig. 3) as *Cladophlebis waltonii.*

Form-genus SPIROPTERIS Schimper

Spiropteris sp.

Plate 5, figure 4

Description. Part and counterpart of a fragment, 8·2 cm long, of a young circinate frond showing pinnules 1 mm long, folded into a spiral position, and lacking hairs. It is similar in morphology to the croziers of the extant *Polypodium vulgare*.

Remarks. Young circinnate pinnae ('croziers') have been recorded from a number of Lower Cretaceous floras: Wealden of north-west Germany (Schenk 1871, pl. 30, figs 4–5); Kome Bed, North Greenland (Heer 1874, pl. 4, fig. 59); Vale de Lobos, Portugal (Heer 1881, pl. 11, fig. 4); Potomac Group (Fontaine 1889, pl. 21, fig. 5); Féron, France (Carpentier 1927, pl. 10, fig. 16; pl. 17, fig. 16); Snake River Canyon (Ash 1991, figs 4–5). Heer (1881, p. 129) and Fontaine (1889, p. 145) gave brief descriptions, but all the other authors merely figured croziers since they lack diagnostic specific characters. Heer (1881) assigned his specimen to a named species, *Sphenopteris mantelli,* an assignment that is difficult to verify. It comprises the circinnate pinnae and part of the rachis but lacks discernible pinnules and is even smaller than our specimen. On the other hand, Ash (1991, p. 325) attributed three croziers to *Phlebopteris tracyi* since they were found together with determinable fronds of this species, but this is by association only. The material from Snake River Canyon differs from the Las Hoyas specimen in their larger curly part and their shorter, less curved axis, that is almost perpendicular to the circinnate part. The pinnules are too faintly imprinted to be clearly discernible. The size and approximate shape of pinnules in our specimen suggest a possible attribution to *Weichselia reticulata*, but this is obviously speculative. From a taphonomic point of view the occurrence of croziers is significant due to the fact that fern fronds do not absciss but have to be detached by force (the pinnae of Recent ferns remain attached to the plant until they decay); this applies particularly to young fern fronds. The croziers represent young fronds and are very fragile, thus being unlikely elements to survive intact for a long time macerating in water or in a high-energy transport medium.

DISCUSSION ON FLORAL COMPOSITION

As noted by Watson (1969, p. 211), the main difficulty when comparing different Wealden floras resides in the fact that most of them were described a long time ago and are in need of taxonomic revision. The most recent work on the Wealden floras from Belgium, France, the Netherlands and Germany has focused mainly on the palynology (Delcourt and Sprumont 1955; Burger 1966; Levet-Carette 1966; Herngreen 1971), and there has also been interest in the sedimentology and environmental reconstructions (e.g. Allen 1959, 1967; Pelzer 1984, 1987; Pelzer and Wilde 1987; Wilde and Schultka 1996). There is little that is new on the macrofloras, and in this respect the observations to be made on the fern remains from Las Hoyas are of interest. The following comments can be made: (1) The presence of 18 different taxa shows the fern assemblage from Las Hoyas to be quite diverse. (2) It is noted that the high diversity of Dicksoniaceae is unusual for Wealden floras. (3) Fern remains attributable to *Cladophlebis* show a low specific diversity, whereas this genus is generally common in Lower Cretaceous floras. (4) Two of the species found at Las Hoyas, i.e. *Pelletixia valdensis* and *Sphenopteris fontainei*, were only known previously from the English Wealden. (5) *Acrostichopteris foliosa* is present, whereas it is absent from all the other known Wealden floras in Western Europe. (6) Las Hoyas shows a more diverse fern flora than the other Spanish Lower Cretaceous localities.

The ferns at Las Hoyas are similar to those of the English Wealden (Watson 1969), and the Las Hoyas locality differs in this respect from the other Iberian floras of broadly similar age. The differences with respect to the English Wealden flora reside in the absence of species of Dipteridaceae and Polypodiaceae and in the higher diversity of Dicksoniaceae. The broad overall similarity between the floral composition at Las Hoyas and that of the English Wealden may reflect similar environmental and climatic conditions. Taphonomy may also have played a role. The rather fragile remains of *Pelletixia valdensis* and

Sphenopteris fontainei possibly did not survive prolonged maceration and transport, and were thus preserved only exceptionally.

In the Portuguese floras considered as being of Valanginian and Aptian ages (Teixeira 1948, 1952) the conifers are predominant and the ferns are poorly diversified. Only three of the fern species of Las Hoyas are also known from Portugal, namely *Onychiopsis psilotoides, Weichselia reticulata,* and *Cladophlebis browniana.* In comparison with the flora from another limestone locality at Montsec (Lleida, Spain), we note that it shares four species with Las Hoyas, and that the latter contains a larger number of named taxa. Montsec was considered to be Kimmeridgian by Zeiller (1902) who reported only one fern, *Sphenopteris* cf. *microclada* Saporta (the figured specimen is unfortunately indeterminable). Additional taxa were recorded by Teixeira (1954) and by Barale *et al*. (1984), who assigned a Berriasian–Valanginian age to the Montsec flora. Barale *et al*. (1984) described seven fern taxa: *Weichselia reticulata*, *Onychiopsis psilotoides*, *Ruffordia goepperti*, *Cladophlebis* cf. *browniana*, *C.* aff. *alata*, *C.* sp., and cf. *Hausmannia.* Barale (1991, p. 39) used open nomenclature, which is due primarily to his conviction that only fertile fern specimens can be identified correctly. We do not share this conviction. Three of the Montsec ferns are found to be the same as at Las Hoyas.

The ferns found at Ortigosa de Cameros, La Rioja (Depape and Doubinger 1960) comprise *Cladophlebis browniana, Coniopteris nephrocarpa, C. hymenophylloides, Sphenopteris hispanica, S.* (*Ruffordia*) *goeppertii*, and *Gleichenites* sp. Only two of these species also occur at Las Hoyas. The other floras from La Rioja comprise reworked material of *Weichselia reticulata* and reworked permineralized stems of *Tempskya riojana* (Agirrezabala *et al*. 1985; Barale and Viera 1989, 1991). The relatively high diversity of fern taxa at Las Hoyas is probably because of intermingling of material from different habitats in what is clearly an allochthonous deposit.

SUMMARY AND CONCLUSIONS

Eighteen fern taxa are described from the Barremian Las Hoyas site. This is the first record of *Acrostichopteris foliosa* in Western Europe, whilst *Pelletixia valdensis, Sphenopteris fontainei,* and *Cladophlebis albertsii* are now recorded for the first time outside the English Wealden. One new species of Dicksoniaceae is described, namely *Coniopteris laciniata. Weichselia reticulata,* belonging to the Matoniaceae, dominates numerically with 72 per cent of the identifiable fern remains; Schizaeaceae as well as unclassified ferns constitute 10 per cent, and the Dicksoniaceae *c.* 8 per cent. The Dicksoniaceae are the most diverse specifically: *Coniopteris laciniata*, *Coniopteris* sp. cf. *C. murrayana*, *Dicksonia* sp., and *Onychiopsis psilotoides*. Apart from *W. reticulata,* the most common species are *Ruffordia goeppertii* and *Onychiopsis psilotoides*; both are widely distributed in Lower Cretaceous deposits throughout the world. Comparing the Las Hoyas fern assemblage with other Early Cretaceous assemblages from Europe, its similarity with the English Wealden flora is quite striking, despite the relatively small number of specimens collected, which makes comparison harder. The numerically poor record may ascribed to: (1) method of excavation; (2) the lacustrine environment; and (3) the probably rather high proportion of lime in the water in which the remains were soaked, causing cuticle decay and the general breakdown of plant material. Most of the ferns at Las Hoyas present xeromorph characters indicative of a stressed environment. On the other hand, there are a few species with very delicate foliage, i.e. *Pelletixia valdensis* and *Sphenopteris fontainei.* Most living ferns have xeromorphic characters regardless of their place of growth, and it is noted that Dicksoniaceae, Schizaeaceae and Matoniaceae grow today in tropical to subtropical areas under warm to hot climatic conditions. It may be supposed that similar conditions applied at Las Hoyas.

From a taphonomic point of view, it is noted that considerable fragmentation occurred. Remains are generally tiny, only a few cm in length, and larger specimens are rare. This suggests substantial residence time in water but the existence of some more complete specimens, such as that of *Ruffordia goepperti* attached to a rhizome (Pl. 5, fig. 3), and the occurrence of delicate remains such as indusia and a crozier with small pinnules, does not support the idea of prolonged maceration since this would lead to biodegradation. Fern cuticles are generally fragile, but the total absence of cuticle preservation is probably the result of biostratinomic processes in the carbonates. All the fern remains occur as impressions, and these are sometimes infilled with limonite. The extremely fine grain of the almost lithographic limestones has permitted preservation of sufficient epidermal detail to allow replicas to be made for SEM work. This detailed preservation also militates against substantial biodegradation.

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