Macrofloral remains from the Lower Cretaceous of the Leiva region (Colombia)

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Key words — Fossil plants, Lower Cretaceous, Leiva Region, Colombia.

Lower Cretaceous plant fossils are described systematically from marine deposits near Villa de Leiva (Boyaca region, Colombia). Specimens originating from the same localities kept at the Florida Museum of Natural History (Gainesville) were included in the systematic description. The plant fossils belong to the Pteridophyta, the Cycadophyta, the Coniferophyta, and to taxa of uncertain affinity which, following previous authors, are referred to the angiosperms. Two new species of Coniferophyta are described, viz. *Cupressinocladus hoedemaekeri* sp. nov. and *Brachyphyllum winklerprinsii* sp. nov. Also, *Thuites sutamarchensis* Huertas is transferred to the genus *Cupressinocladus*.

Contents

Introduction

Over a period of many years Mr P.H. Creuzberg collected Lower Cretaceous fossils from concretions in marine deposits near Villa de Leiva, in the Boyaca region in Colombia. A variety of macrofloral fossil remains were found in association with ammonites (see Pl. 4, figs. 1-2, Pl. 9, fig. 3). In this paper, these plant fossils and those obtained by D.L. Dilcher from the same sediments are described and identified.

Several authors studied macrofloral remains from the Lower Cretaceous of Colombia. Berry (1945) described *Thuites, Brachyphyllum* and *Pterophyllum* material and Huertas (1967, 1970, 1976) several other conifer and cycadophyte genera including cones, and even angiosperm fruits and seeds from the same area where the present material was found. More recently Pons (1982) published a preliminary paper on macroscopic plant remains from the Villavicencio area of Colombia. Lemoigne (1984)

Fig. 1. Sample localities of the Lower Cretaceous of Colombia plant macrofossils.

described a very diverse flora from the Lower Cretaceous of the Medellín area (Colombia) composed of ferns, Bennettitales, Cycadales, Ginkgoales, Caytoniales, and Coniferales collected during two expeditions to Colombia. In 1988 Pons defended her thesis on macro- and microfloral remains from the Lower Cretaceous of the northern

Table 1. Age of various localities described in the text.

Location	Age
Anapoima Apulo	Aptian
Loma Catalina	Aptian
Sutamarchán	Aptian
Verreda Chagüete	Aptian
Loma la Asomada	Barremian-Aptian
Sancto Ecce Homo	Barremian-Aptian
Villa de Leiva (various localities)	Barremian-Aptian
Loma Gonzales	Barremian
Loma Moniquera	Barremian
Santa Sofia	Barremian
Loma Blanca	Hauterivian-Aptian

part of Colombia belonging to most of the above cited groups. Other work on the Lower Cretaceous of the Equatorial Region (Vakhrameev, 1991) was done by Berry (1922, 1939) in Peru. Comparison with provinces in the 'Austral Region' is not expected to give results as the Equatorial region is separated to the south from the Patagonian Province by a desert (Archangelsky, 1966). We expect that a comparison of our data with those obtained by Pons (1988) will corroborate the identification of a distinct Equatorial Region during the Lower Cretaceous (Archangelsky, 1966; Vakhrameev, 1991).

Material

The plant fossils were found in calcareous concretions formed around fossils in silty marls and calcareous shales and mudstones. These concretions were found at the roadside, at the foot of 50 to 100 m high rock exposures in road cuttings. As a result, the age of the specimens can not be given more precisely than at the stage level and even sometimes less precisely. The ages range from Barremian to Aptian based on ammonites. The specimens were found in the Province of Boyaca in the vicinity of Villa de Leiva, at various localities (see Fig. 1). The localities are Villa de Leiva itself, Sancto Ecce Homo (a monastery), Loma La Asomada, Loma Blanca, Loma Catalina, Loma Gonzales, Loma Moniquera, Anapoima Apulo, Sutamarchán, Verreda Chagüete, and Santa Sofia. Several locations correspond to a single Lower Cretaceous stage, others represent several stages (see Table 1). The locality of the specimens in the University of Florida collection is only known approximately as the vicinity of Villa de Leiva.

The material consists generally of the impressions of twigs and leaves and a few permineralized cones and seeds. The specimens do not exceed 20 cm. The shoots are often preserved three-dimensionally in the concretions but anatomical details like epidermal structure could not be observed due to poor preservation and coarse grain size. No cuticles were preserved and neither could the internal structure of the slightly flattened cones be studied.

Little is known about the depositional area in which the cones and twigs were deposited. Ammonite associations indicate that it is a confined marine environment, in a back barrier or back reef area (pers. comm. Hoedemaeker, 1999). There is no clari-
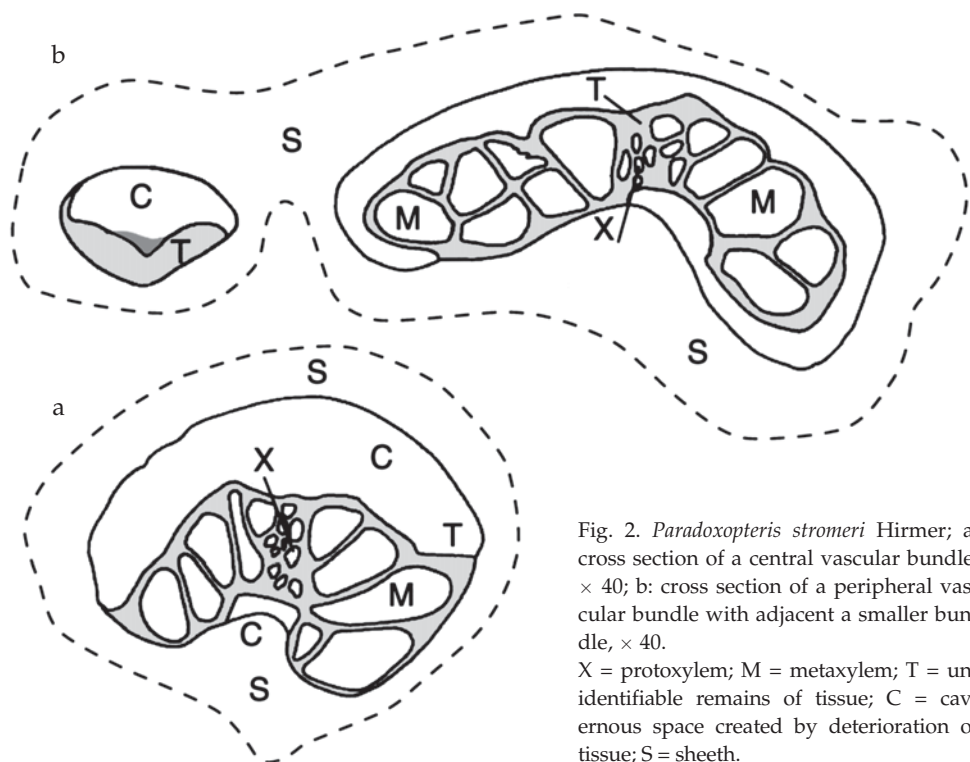
Fig. 2. *Paradoxopteris stromeri* Hirmer; a: cross section of a central vascular bundle, × 40; b: cross section of a peripheral vascular bundle with adjacent a smaller bundle, × 40.
X = protoxylem; M = metaxylem; T = unidentifiable remains of tissue; C = cavernous space created by deterioration of tissue; S = sheeth.

ty with respect to the depositional processes that led to the present assemblage.

Specimens coded with RGM are kept at the National Museum of Natural History in Leiden (The Netherlands), those with UF are kept at the Museum of Natural History in Gainesville (Florida, USA).

The synonymies are confined to Colombian material and to the basionyms.

Systematic descriptions

Class Pteridophyta
Order Filicales
Family Weichseliaceae
Genus *Paradoxopteris* Hirmer
Paradoxopteris stromeri Hirmer 1927
Pl.1, fig.1; Fig. 2.

Material — RGM 233 620 (Loma Gonzales).

Description — The stem is formed by a ground-tissue of isodiametrical parenchymatic cells. Within this ground tissue vascular bundles lie in concentric circles. Each vascular bundle is round to semi-circular with a central concave side and a

peripheral convex side. In the middle part of the bundle the protoxylem is centripetally situated, thus endarch. The metaxylem is situated periferally and especially laterally. The widest metaxylem elements are lying at the lateral ends of the xylem body: they are up to 130 µm wide in radial direction and up to 100 µm in tangential direction (Fig. 2).

Phloem, pericycle and endodermis could not be observed; they are mostly indicated by one or two large empty spaces, situated at the peripheral side of the vascular bundle, however in one case they are situated on the central side; sometimes these empty spaces are missing. Even then it was not possible to observe clearly anything that was not sclerenchymatised or lignified. The vascular bundle is surrounded by a sclerenchymatic sheath that is uneven in thickness. It is thickest at the centripetal side, more or less filling up the concavity of the vascular bundle. In one case a small vascular bundle, without xylem, lying laterally of a large one, was observed. It was still connected to the larger bundle by a common sclerenchymatous sheath (Fig. 2b). The longitudinal sections showed that the pitting of the wide xylem elements was scalariform. Due to the coarse cristallisation no more details could be observed.

Identification — The structure of the vascular bundles is comparable to that described for *Paradoxopteris stromeri* Hirmer. In several studies the anatomy of this type of fern-stem has been revealed. It is a construction of parenchymatous ground-tissue with concentric rings of vascular bundles with the same type of organisation as the above described. However, phloem, pericycle and endodermis are also described. Moreover, in several descriptions secretory canals are mentioned, which are absent in our material. But in some descriptions these structures are totally or partly lacking (Koeniguer, 1966). Although the precise structure of the stele is not yet known, it is considered a meristele by most authors, with stem bundles and smaller leaf-trace bundles.

Our material does not show the leaf-trace bundles in the longitudinal sections observed by Hirmer (1927), Edwards (1933), Zimmermann (1959) and Koeniguer (1966). However, in cross section a small bundle is observed which may be explained as a leaf-trace bundle. Since it is comparable and in some respects identical with *Paradoxopteris stromeri*, it is tentatively assigned to that species.

Discussion — *Paradoxopteris stromeri* has been compared with several families of ferns, e.g. Osmundaceae, Marattiaceae, Matoniaceae. The anatomy of the Osmundaceae is quite different. With regard to the stem-anatomy the choice between Marattiaceae and Matoniaceae is difficult. Alvin (1971) described fertile *Weichselia*-material in some detail. He made it clear, that the sporangia are small, annulate, in all probability leptosporangiate and covered by an indusium. This points to the Matoniaceae as the nearest relatives. Recent Matoniaceae possess a rhizome with only one or a few vascular bundles, comparable in structure with our material. A related genus, *Alstaettia*, described by Remy and Remy (1969), shows essentially the same type of vascular bundles, but here the bundles are fused to concentric vascular rings.

The leaf-fossil to which *Paradoxopteris* is linked is *Weichselia reticulata*, which is assigned either to the family Matoniaceae or is grouped in a separate related family,

the Weichseliaceae. This fern is found world-wide from the Upper Jurassic and Cretaceous up to the Cenomanian in subtropical and tropical areas (Vakhrameev, 1991). This may be the reason for the large amount of variation in stem structure and perhaps also in other organs.

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Class Cycadophyta
Form genus *Taeniopteris* Brongniart
Taeniopteris sp.1
Pl. 2, fig. 1.

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Material — RGM 233 577 (Villa de Leiva).

Description — The leaf fragment is simple, up to 2.5 cm wide and 10 cm long. It is incomplete and the leaf was clearly much longer. Its upper side is seen, therefore the midrib appears to be very narrow, just the intersection between the two leaf-halves. The secondary veins (c. 10/cm) are perpendicular to the midrib and hard to distinguish. No forking of the veins could be observed. The leaf has straight margins that are curved downwards.

Discussion — As no forking of the veins was observed, we think this leaf might be a *Nilssonia* but no confirmation through cuticles could be made. Therefore, we attribute this leaf to the form genus *Taeniopteris*. In Huertas (1970) a similar type of plant fossil has been described.
N.B. We use the generic name *Nilssonia* as the original spelling of *Nilsonia* by Brongniart was obviously a 'lapsus calami'.

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Taeniopteris sp. 2
Pl. 2, fig. 2.

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Material — RGM 233 574a/b (Villa de Leiva).

Description — This leaf is incomplete. We assume that it is up to 6 cm wide (the measured size is 3 cm but comprises only one half, as the midrib can not be observed) and 16 cm long. Secondary veins are finely spaced (12/cm) and perpendicular to the midrib. No bifurcation of the veins could be observed. No other features are clear enough to be described.

Discussion — As no forking of the veins could be observed, *Nilssonia* might be a possible genus for this specimen, but no confirmation through cuticles could be made. Therefore, this leaf is assigned to the form genus *Taeniopteris*. In Huertas (1970: 300, fig. 4) a similar type of plant fossil is described. This *Nilssonia* cf. *orientalis* leaf has about the same size (5.5 cm wide). The lateral veins are making an angle of 80° with the midrib. Considering that the identification of *Nilssonia* by Huertas is not substantiated by cuticle information, we believe that the leaf Huertas (1970) described should also be attributed to *Taeniopteris*.
Compared to *Taeniopteris* sp. 2, *Taeniopteris* sp. 1 is much smaller and longer, and

the general shape is very smooth. Moreover the vein density for *T.* sp. 2 is higher. *Taeniopteris* sp. 2 also has a less leathery leaf. The two specimens clearly belong to different species.

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Form genus *Macrotaeniopteris* Schimper
Macrotaeniopteris sp.
Pl. 2, fig 3.

</div>

Material — RGM 233 573 (Villa de Leiva).

Description — The leaf is incomplete. From the midrib to the leaf margin it is 13 cm wide. The leaf must have been at least 26 cm wide. The leaf fragment is 13 cm long but it is clearly a fragment of a much larger leaf. The veins are parallel and undivided, but folding of the leaf surface gives sometimes the impression that veins are bifurcating. Venation density is c. 8/cm.

Discussion — This fragment was placed in *Macrotaeniopteris* because this is a form genus for large, entire-margined leaves with parallel venation and without a known cuticle.

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Class Coniferophyta
Order Coniferales
Form genus *Cupressinocladus* Seward
Cupressinocladus lepidophyllus (Saporta, 1884) Lemoigne 1984
Pl. 3, fig. 1.

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Basionym: *Araucaria lepidophylla* Saporta, 1884: 443, pl. 187, figs. 2, 2a.
1967 *Thuites venustus* Huertas: 66, fig. 3 A-B.
1984 *Cupressinocladus lepidophyllus* Lemoigne: 684, pl. 8, figs. 5, 6, 10; not pl. 8, figs. 1-3, 9.

Material — RGM 233 562, 233 564, 233 566, 233 567, 233 570, 233 576a/b, 233 578a/b (Villa de Leiva); 233 580, 233 584, 233 585, 233 586, 233 596, 233 599 (Loma La Asomada); 233 601(Loma Catalina); 233 603a (Sutamarchán); 233 610 1/2/3 (Vereda Chagüete); UF 15876-28193, 15876-2897, 15876-28199, 15876-28196 (vicinity of Villa de Leiva).

Description — This species is the most common taxon in the assemblage. The largest specimen is RGM 233 584 with penultimate shoots of 16 cm and ultimate shoots of 6 cm, but many smaller specimens occur. In general the penultimate shoots are 5 to 16 cm long and c. 0.5 cm wide carrying ultimate shoots, 3 to 5 cm long and 0.5 cm wide. The distance between the ultimate shoots is about 1 to 1.5 cm. The ultimate shoots are alternating or opposed but always placed in one plane. All shoot types have the same width throughout. The ultimate shoots are attached to the penultimate shoot at an angle of 45° to 50°.
The leaves are placed at 35° to the axis, and are more or less needle-like, 0.3 cm wide and 0.5 cm long. The leaves have a decussate organisation. In transverse section the leaves are rounded to rhomboidally flattened. Their organisation is decussate. All leaves have about the same size except the much smaller distal ones.

The free part of the leaf is c. 0.3 cm long, the leaf base cushion is c. 0.2 cm long. The free part of the leaves is diverging from the stem but the leaf apices are falcate and acute. The original texture of the leaves was probably fleshy.

Discussion — Lemoigne (1984) described two forms of *Cupressinocladus lepido-phyllus* as being within the range of variation of this species. The first type has leaves that are nearly totally attached to the main axis and the second type has leaves forming an angle of nearly 90° to the axis. Clearly, the *C. lepidophyllus* found by Creuzberg belongs to the second form represented in Lemoigne's pl. 8, figs. 5, 6 and 10 (see further discussion under *C. leivanus*). Because Lemoigne described both types as variants of the plant originally described by Saporta (1884) as *Araucaria lepi-dophylla*, we had to go back to Saporta to see what the original material looked like. Clearly, the *A. lepidophylla* described by Saporta (1884) appears to be identical to Lemoigne's type 2 and to our material. Lemoigne's type 1 of *C. lepidophyllus* seems quite different and should probably be assigned to another species (see *C. leivanus* for further discussion).

Pons (1988) described a *Cupressinocladus leptocladoides* (Berry) Pons that shows some resemblance to our *C. lepidophyllus*. But the material described by Berry (1922) as *Thuites leptocladoides* on which the species is based, is clearly a much smaller specimen with leaves no longer than 0.2 cm and 0.1 wide, and with a shoot width of 0.3 cm. Consequently the name *C. leptocladoides* should be reserved to *Cupressinocladus* materi-al with very small leaves and narrow shoots, and it should not be used here.

Huertas 1967 described similar material from the Leiva region as *Thuites venustus*, but it should be attributed to the genus *Cupressinocladus* because of the decussate leaf arrangement, also *C. venustus* is a homonym of *C. lepidophyllus*.

N.B. For those *Cupressinocladus* species that belong to the Cheirolepidiaceae, Srini-vasan (1995) created the genus *Watsoniocladus*. This means that *Cupressinocladus* is now again only a form genus for conifer remains with a decussate leaf arrangement just as Seward (1919) intended.

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Cupressinocladus sutamarchensis (Huertas 1967) comb. nov

Pl. 4, figs. 1-2.

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Basionym: *Thuites sutamarchensis* Huertas, 1967, Caldasia X, 46: 66, fig. 3 c.

Material — RGM 233 582, 233 588 (Loma La Asomada) and 233 614a/b (Anapoima Apulo).

Description — The penultimate shoots (c. 5 cm long and 0.3 cm wide), lay in one plane and carry ultimate shoots, 2.5 to 3.5 cm in length at 0.3 cm width. The distance between the ultimate shoots is c. 1.0-1.5 cm. The ultimate shoots are alternating. All shoot types have the same width throughout. The ultimate shoots are attached to the penultimate shoot at angle of c. 45°.

The leaves are placed at 90° to the axis. The base of the leaf is cushion-like. In transverse section the leaves are rhomboidal. Their organisation is decussate. A leaf is usually c. 0.5 cm wide and 0.8 cm long, has the shape of a needle with a thick base,

and its acute apex is slightly falcate. All leaves have about the same size except the much smaller distal ones. The original texture of the leaves was probably fleshy to leathery.

Discussion — For the same reason as for *C. lepidophyllus* we place this material in *Cupressinocladus* rather than in *Thuites*.

Cupressinocladus leivanus (Huertas 1970) Pons 1988
Pl. 3, figs. 2-3.

Basionym: *Brachyphyllum leivanum* Huertas, 1970: 598, fig. 3.

Material — RGM 233 565, 233 579 (Villa de Leiva); 23 609a/b (Loma Blanca); UF15876-28195, 15876-28191(vicinity of Villa de Leiva).

Description — Specimen RGM 233 609 has a robust penultimate shoot, 14 cm long, 0.6 cm wide. It is carrying ultimate shoots of 2.5 cm long and 0.5 cm wide, in one plane. The ultimate shoots are narrower at the point of attachment to the penultimate shoot (0.4 cm). The distance between the ultimate shoots is c. 1 cm. The ultimate shoots are alternating and they are attached to the penultimate shoot at an angle of c. 60°.

The leaves are tightly imbricate (leaving less than 1/3 of the axis free). Their organisation is decussate. The leaves have a rhomboidal shape, twice as wide as high (0.4 cm to 0.2 cm). All leaves have about the same size except the much smaller apical ones. Apices are obtuse, slightly falcate. The original texture of the leaves seems to have been leathery. In the middle of the leaves a keel is running downwards from the apex.

RGM 233 579 has ultimate shoots that are 5 cm long and RGM 233 565 has relatively wider ultimate shoots: 0.7 cm; for the rest they agree with RGM 233 609.

Discussion — Huertas attributed his material to the genus *Brachyphyllum*, but the decussate arrangement of the leaves indicates *Cupressinocladus* (Seward, 1919), hence the combination *C. leivanus.* Pons (1988) described *C. pompeckji*, which resembles *C. leivanus*, but her species has a higher leaf density than our shoots have. Besides, the leaves on *C. pompeckji* have a larger free part, while *C. leivanus* has leaves that are nearly totally attached to the main axis.

Lemoigne (1984) combined many different species: *C. lepidophyllus* in which he recognised two forms: one with rhomboidal leaves attached to the axis and another with leaves nearly at a right angle to the axis. The latter is the 'real' *C. lepidophyllus* (see the discussion of *C. lepidophyllus*). Our *C. leivanus* resembles his first *C. lepidophyllus* type as figured on Pl. 8, fig. 2, while *C. pompeckji* (Salfeld) Pons 1982 (Pons, 1988, pl. 7, figs. 1-2), resembles his first *C. lepidophyllus* type as illustrated in pl. 8 fig. 3 (Lemoigne, 1984). This *C. lepidophyllus* is certainly different from Lemoigne's pl. 8, fig. 2 and does not resemble our *C. leivanus* as mentioned before. Until we know more about the general morphological variation of these South American *Cupressinocladus* species, we advise to use the different species names until it can be proven that they

should all be lumped together as *C. lepidophyllus* as Lemoigne has suggested on what appears to be insufficient evidence. Moreover, Pons (1988) seems to indicate that *C. leivanus* is typical for the Leiva region, while *C. pompeckji* is a dominant element of the northern Andean region in Early Cretaceous times.

Cupressinocladus hoedemaekeri sp. nov.
Pl. 4, figs. 3-4.

Holotype — RGM 233 608 (Pl. 4, figs. 3-4).
Type locality — Loma Blanca.
Type horizon – Barremian-Aptian.
Derivatio nominis — The species is named after Dr Ph.J. Hoedemaeker in recognition of his efforts to protect the Creutzberg collection by bringing it to the National Museum of Natural History of The Netherlands.

Diagnosis — *Cupressinocladus* species with ultimate shoots oppositely attached in one plane, at an angle of 70°; penultimate shoot wider than ultimate shoot, ultimate shoots decreasing apically in distance and width; leaves totally attached to the axis, hexagonal when placed between two ultimate shoots otherwise tetragonal in shape; apex placed centrally on the leaf.

Description — The holotype is an apical conifer fragment. The robust penultimate shoot is 8 cm long, 1.1 cm wide at the base, and 0.6 cm apically. The ultimate shoots are oppositely attached in one plane and show a gradual decrease in size from basal shoots 2.5 cm long and 0.5 cm wide to distal shoots 0.5 cm long and 0.3 cm wide. The distance between the ultimate shoots decreases distally from 0.8 cm to 0.2 cm. The ultimate shoots are attached to the penultimate shoot at angle of 70°.
The leaves are scale-like, totally attached to the axis. Their organisation is decussate. The leaves have a polygonal shape of an equidimensional rhomboid or a hexagone. The hexagonal shape occurs on the penultimate shoot in the area between two ultimate shoots. Basal leaves are larger (0.8 cm in diameter) than apical ones (0.2 cm). The apex is obtuse, blunt, small (0.1 cm high) and placed centrally on the leaves. Some leaves on the penultimate shoot seem to have two apices. The original texture of the leaves seems to be thick, leathery.

Discussion — This shoot is placed in the genus *Cupressinocladus* because the leaves are clearly organised in a decussate way. It differs from *C. leivanus* because no free part of the leaf could be observed; the whole leaf is attached to the axis, except for the tiny 0.1 cm high central apex. Moreover, hexagonal leaves can be observed on the penultimate axis at those points where ultimate shoots are placed oppositely. The specimen is reasonably well preserved but the bluntness of the leaf apices could be related to erosion during or after deposition.
Pons (1988: 63) describes *C. pompeckji* as having both hexagonal and tetragonal leaves, but she gives no details of where the hexagonal leaves were observed. In *C. hoedemaekeri* hexagonal leaves are observed on the penultimate shoot, between two ultimate shoots. Secondly *C. pompeckji* has ultimate shoots that are all of identical

size while our *C. hoedemaekeri* shows a decrease in ultimate shoot size and leaf size in distal direction. Clearly, *C. hoedemaekeri* and *C. pompeckji* are not conspecific.

Cupressinocladus sp. 1
Pl. 5, fig. 1.

Material — RGM 233 589 (Loma La Asomada).

Description — The robust axis is 7 cm long and 0.6 cm wide. It carries penultimate shoots of c. 3 cm length and 0.5 cm width. Some penultimate shoots bear small ultimate shoots, 0.5-1 cm long. The penultimate shoots are opposed while the ultimate shoots alternate. The penultimate shoots bear only one or two ultimate shoots placed at 0.5 and 1 cm from the main axis and are attached to the main axis at an angle of c. 70°. The ultimate shoots are attached to the penultimate shoots at an angle of 45-50°.
The leaves are scale-like, completely attached to the axis. Their organisation is decussate. The leaves have a more or less rhomboidal, equidimensional shape. Basal leaves are larger (0.5 cm) than distal leaves (0.2 cm). The leaf apex is a small mucro on a horizontal ridge placed on a leaf. The original texture of the leaves was leathery to woody.

Discussion — With respect to leaf size and shape, this specimen is comparable to *C. hoedemaekeri* but the organisation of the ultimate and penultimate shoots is different. Here the ultimate shoots are placed alternately, while *C. hoedemaekeri* has opposite ultimate shoots. Moreover *Cupressinocladus* sp. 1 has no hexagonal leaves between two ultimate shoots.

Cupressinocladus sp. 2
Pl. 5, fig. 2.

Material — RGM 233 612a/b (Loma Blanca, west of top).

Description — The specimen is a penultimate shoot, 11 cm long and 0.7 cm wide. Ultimate shoots decrease in length from 4 cm to 0.5 cm apically. The width of the ultimate shoots is 0.5 cm. The distance between the shoots is 1 cm. The shoots are oppositely attached to the main axis at an angle of 45°. The leaf organisation is decussate. The leaf scar is rhomboidal, leafs are attached to the axis at an angle of 90°. The leaf scar is 0.4 cm long and 0.2 cm wide. The scars suggest that the leaves were fleshy to leathery and very thick. The leaf appears slightly falcate, but too little can be observed to say anything definite.

Discussion — In many ways the present specimen resembles *C. sutamarchensis*, but in *C.* sp. 2 the leaves are smaller, and the ultimate shoots are opposed instead of alternating. More material is needed to decide if *C.* sp. 2 actually is a separate species or if it can be accounted for by the morphological variation of *C. sutamarchensis*.
For comparison of all *Cupressinocladus* species from this assemblage see Table 2.

Table 2. Comparison between the different species of *Cupressinocladus* (measurements in cm).

	C. lepidophyllus	*C. sutamarchensis*	*C. leivanus*	*C. hoedemaekeri*	*C.* sp. 1	*C.* sp. 2
Penultimate shoot width	0.5	0.3	0.6	0.6-1.1	0.6	0.7
Ultimate shoot						
Alternating or opposite	both	alternating	alternating	opposite	alternating	opposite
Length	3-5	2.5-3.5	2.5	0.5-2.5	3	0.5-4
Width	0.5	0.3	0.5	0.3-0.5	0.5	0.5
Distance between shoots	1-1.5	1-1.5	1	0.2–0.8	?	?
Angle to penultimate shoots	45-50°	45°	60°	70°	45-50°	45°
Leaves						
Length	0.5	0.8	0.2	0.2-0.8	0.2-0.5	0.4
Width	0.8	0.5	0.4	0.2-0.8	0.2-0.5	0.2
Free/attached part	1/2	2/3	1/3	totally attached	1/1	1/4
Apex	needle like	falcate	obtuse/ falcate	obtuse/ central	obtuse/ central	falcate
Shape	rhomboidal	rhomboidal	rhomboidal	hexagonal	rhomboidal	rhomboidal
Angle between leaf and shoot	35 °	90°	0°	0°	0°	90°

Genus *Brachyphyllum* Brongniart
Brachyphyllum winklerprinsii sp. nov.
Pl. 5, fig. 3; Pl. 6, fig. 1.

Type specimen — Holotype RGM 233 600 (Pl. 5, fig. 3; Pl. 6, fig. 1).
Type locality — Loma Catalina (southern flank).
Type horizon — Aptian.
Derivatio nominis — The species is named after Dr C.F. Winkler Prins, Head of the Palaeontology Department at the National Museum of Natural History, Leiden.

Diagnosis — *Brachypyllum sp*ecies with wide penultimate shoot (1.5 cm), ultimate shoots of c. 4 cm length and 1 cm width in one plane, oppositely arranged. Ultimate shoot placed at a distance of 4 cm. Leaves with rhomboidal cushions 0.8 cm long and 0.6 cm wide, imbricate and spirally arranged. One third of the leaf free, apex falcate. Keel present but not distinct. Penultimate shoot covered spirally by 6 leaves for a full circle.

Description — The penultimate shoot of specimen RGM 233 600 is 15 cm long, 1.5 cm wide and it bears ultimate shoots of c. 4 cm long and 1 cm wide in one plane, oppositely arranged. The distance between ultimate shoots is 4 cm. The apical part of the shoots can not be observed clearly.
The scale-like leaves are imbricate and spirally arranged. They show rhomboidal cushions, one third of the leaf is free and two-third remain attached. The leaf is 0.8 cm in length and 0.6 cm in width. The leaf carries a falcate apex. A light thickening of the leaf can be seen from the apex downwards but no distinct keel is observed.

Discussion — Specimen RGM 233 600 is considered to be a *Brachyphyllum* because the leaves are spirally arranged on the main axis and the ultimate shoots. It is similar to *B. leivanum* described by Huertas (1970) but the leaves, the axis, and the whole size

of the shoot are larger. Moreover, the distance between the ultimate shoots is c. 2 cm in our specimen and 0.2-0.5 cm in *B. leivanum*, and the leaves on the ultimate shoots of *B. leivanum* appear to be decussately arranged instead of spirally as in our specimen.

B. winklerprinsii also resembles *B. macrocarpum* Newberry 1895 (= *B. crassum* Lesquereux (1891) regarded as a homonym of Tenison-Woods, 1883) from the Cretaceous Dakota Group (USA) but is about twice its size in all aspects. We believe that this size difference is outside the natural variation within conifers species, therefore *B. winklerprinsii* is not conspecific with *B. crassum*.

Hollick and Jeffrey (1909, pl. 4, fig. 12) figured a *B. macrocarpum* specimen at natural size. Their specimen shows both the same characters and the size of our *B. winklerprinsii*. It is possible that this specimen is identical with *B. winklerprinsii*. Some caution with respect to this identification should be observed, as two fragments of the same species illustrated on the same plate 4 (figs. 13-14) are magnified 10 ×, but the illustrated features (like the twig width or the scale size) are not 10 × the size of the specimen at natural size resembling our *B. winklerprinsii*. The size indications on plate 4 from Hollick and Jeffrey (1909) cannot be trusted and we do not know with certainty if their specimen (pl. 4, fig. 12) can be assigned to *B. winklerprinsii*.

Berry (1939) has illustrated *B. peruvianum* Berry from the Lower Cretaceous of Peru, but the illustration is too poor to be judged properly for comparison. The specimen described by Berry (1939) is smaller with respect to its twig width, length, and also with regard to the distance between the ultimate shoots.

Brachyphyllum sp. 1

Material — RGM 233 563 (Villa de Leiva).

Description — The apical part of the penultimate shoot in specimen RGM 233 563 is not visible, but the shoot is c. 10 cm long. Ultimate shoots are 5 cm long. The shoot width is only 0.5 cm. Leaves are 0.4 cm wide, 0.6 cm long. The distance between the ultimate shoots is 2 cm. Here again, the apical part of the ultimate shoots can not be observed very clearly.

Discussion — RGM 233 563 is considered to be a *Brachyphyllum* because the leaves are spirally arranged on the main axis. Too few other features can be observed to give a more precise identification. Comparison to the other *Brachyphyllum* species is made in Table 3.

Table 3: Comparison between the different species of *Brachyphyllum* (measurements in cm).

	B. winklerprinsii	*B.* sp. 1	*B.* sp. 2
Penultimate shoot width	1.5	0.5	0.5
Ultimate shoot length	4	5	?
Ultimate shoot width	0.6	0.5	?
Distance between shoots	4	2	?
Leaf length	0.8	0.6	0.4
Leaf width	0.6	0.4	0.3
Free/attached part	1/3	?	1/2

Brachyphyllum sp. in Berry 1945 (Villeta Shale) is not a *Brachyphyllum* but a *Cupressinocladus* since the leaf organisation on the ultimate shoots is decussate. The leaves of the penultimate shoot are not decussate. The specimen is too poorly illustrated (and probably preserved) to attribute it to a particular species of *Cupressinocladus*.

<div align="center">

Brachyphyllum sp. 2
Pl. 6, fig. 2.

</div>

Material — RGM 233 602 (Loma La Asomada).

Description — This is a shoot 3 cm long and 0.5 cm wide. No lateral shoots can be observed. The leaves are spirally arranged. The rhomboidal leaves are strongly imbricate. The attached part of the leaf is 0.2 cm long, and the free part as well. Leaves are c. 0.3 cm wide.

Discussion — RGM 233 602 is considered to be a *Brachyphyllum* because the leaves are spirally arranged on the axis. Too few other features, such as leaf apices or leaf base cushions, could be observed to give a more precise identification. For a comparison with the other *Brachyphyllum* species see Table 3.

<div align="center">

Genus *Pagiophyllum* Heer
Pagiophyllum sp.
Pl. 6, fig. 3.

</div>

Material — RGM 233 604 (Sutamarchán, land of F. Castillo).

Description — The penultimate shoot is 13 cm long. A single ultimate shoot is visible but incomplete. The leaves are attached to the axis at an angle of 45°. The leaf cushion is 0.4 cm wide, the free part of the leaf is 1 cm long. The leaves are placed spirally. The leaf is slightly falcate.

Discussion — This specimen is identified as a *Pagiophyllum*, because of the spirally arranged leaves and the much larger size of the free part of the leaf in comparison to the leaf base. Too few data are available to attribute it to a species.
The genus *Geinitzia* is reserved for conifers with falcate leaves that are equally thick in horizontal and vertical directions.

<div align="center">

Coniferales incertae sedis
Genus *Podozamites* Braun
Podozamites sp.
Pl. 7, figs. 1-2.

</div>

1967 *Podozamites* cf. *lanceolatus* (Lindley & Hutton) Fr. Braun — Huertas: 69, fig. VII A.
1945 *Podozamites* sp. — Berry: 159.
1988 *Podozamites* sp. — Pons: 168.

Material — RGM 233 572a/b (Villa de Leiva, various locations), RGM 233 575a/b (Santo Ecce Homo); RGM 233 587, RGM 233 590, RGM 233 591 (Loma La Asomada); RGM 233 593 (Loma Catalina); RGM 233 595 (no indication of where it was found); RGM 233 605 (Sutamarchán, Land of Fernando Castillo).

Description — Leaves are varying in length between 8 cm and 12 cm. The leaf width is c. 1.2 cm. The leaves are constricted at the base (to 0.3 cm). The apices of the leaves are rather obtuse. The unforked veins (4-9 veins/cm) run parallel and converge near the base and the apex.

Discussion — Huertas (1967) described a *Podozamites* cf. *lanceolatus* that fits the present description except for the vein density, which is higher in the *Podozamites* described by Huertas (1967) than in the present material. We consider that the present material is too poorly preserved to assign it to a species. Similarly, Berry (1945) and Pons (1988) described several similar *Podozamites* leaves but found too few distinct characters to be able to assign them to a species.

Conifer fructifications
Genus *Araucariostrobus* Krasser
Araucariostrobus creutzbergii Huertas 1970
Pl. 7, figs. 3-4.

1970 *Araucariostrobus creutzbergii* — Huertas: 595, fig. 1.

Material — RGM 233 613 (Loma La Catalina).

Description — The sub-spherical female cone is 7 cm long and 6 cm wide. The base cannot be observed. The specimen is flattened. The bracts are 1 cm wide and 0.8 cm high. They are imbricate, striate and spirally arranged with a distinct keel ending in an acute apex.

Discussion — Shape and size of the cone, and shape and structure of the cone scales are similar to those described by Huertas (1970). The present cone cannot with certainty be assigned to the Araucariaceae as we do not know any details about the ovules. It is found in association with *Cupressinocladus lepidophyllus*, which has rather narrow twigs to carry the large cone found here, and with *C. leivanus*. The latter might have been better suited to carry such a large cone. Moreover, both the leaves in *C. leivanus* and the bracts in *A. creutzbergii* show a median keel, so attribution to *C. leivanus* is more probable than to *C. lepidophyllus*.

Araucariostrobus cf. *archangelskii* Huertas 1976
Pl. 8, fig. 1.

1976 *Araucariostrobus archangelskii* — Huertas: 21, fig. IV.

Material — RGM 233 597 (Loma La Asomada).

Description — The female cone is 7 cm long and 5 cm wide. The cone is sub-spherical but flattened. The cone scales (0.7 cm wide and 0.6 long) are totally attached to the cone (not imbricate). They are hexagonal, but sometimes also pentagonal or rhomboidal. Bracts are terminated by an apex placed centrally. Striations can be observed from the hexagonal edges to the apex.

Discussion — The size of this cone is comparable to that of *Araucariostrobus archangelskii* Huertas but the size of the cone scales is smaller than that in the description of Huertas 1976 (2 cm length at 0.8 cm width). However, judging from the illustration by Huertas, the cone scales in *A. archangelskii* have the same dimensions as in our cone. Most apices are eroded away and little structure can be seen in our specimen. The present cone cannot with certainty be assigned to the Araucariaceae.

<div align="center">

Pityostrobus sanctieccehomensis Huertas 1967
Pl. 8, figs. 2-3.

</div>

1967 *Pityostrobus sanctieccehomo* Huertas: 64, fig. II.

Material — RGM 233 583 (Santo Ecce Homo).

Description — The female cone is 9 cm long and 9 cm wide. The cone has been flattened. The cone scales are 2.5 cm wide. (Due to erosion of the cone scales, their length can not be measured.) The cone scales are loosely imbricate. The scar of the cone scale has a flattened rhomboidal shape. The lower edge is sometimes rounded.

Discussion — The size of this cone is slightly larger than that of the specimen found by Huertas. This can be explained by the strong flattening of the specimen or simply because of the variation within the species. The size of the cone scales is smaller than in the description of Huertas (1967); nevertheless, their shape is similar, so here again we believe that this difference relates to the variation within the species. At the location of Sancto Ecce Homo *Cupressinocladus venustus*, *C. sutamarchensis*, *C. leivanus,* and *Podozamites* were also found. Considering the sizes of these *Cupressinocladus* species, only *C. sutamarchensis* could have carried the cones.

Because no fructifications from *Podozamites* were described in the Cretaceous and because Early Jurassic *Podozamites* leaves have 2 different kinds of female fructifications types (*Swedenborgia* and *Cycadocarpidium*), we can conclude that *Podozamites* is a form genus with various affinities. From the Late Jurassic onwards, nothing is known about fructifications that might belong to *Podozamites* species. This means that *Podozamites* might also be a candidate for generating the cone. Consequently, both *C. sutamarchensis* and *Podozamites* are possible candidates as leaves and twigs from the trees that produced this *Pityostrobus sanctieccehomensis*.

<div align="center">

Genus *Conites* Sternberg
Conites sp.
Pl. 7, fig. 5.

</div>

Material — RGM 233 568 (Villa de Leiva).

Description — This cone is 2.8 cm long and 2 cm wide. The bracts are rhomboidal, flattened, 1 cm long and 0.8 cm high. Cone scales are imbricate.

Discussion — It is not clear if this is a female or a male cone. We therefore attribute this cone to the genus *Conites*, a genus for cones without characters indicating gender. The type species of Conites (*C. bucklandi* Sternberg) was based on an indistinct specimen that might even be a bennetitalean stem (Seward, 1904). However, the current practice is to use *Conites* in the sense applied here and indicated in the generic diagnosis of Sternberg, 1823 (see Farr et al., 1979).

<div align="center">

Putative Angiospermae
Genus *Sterculiocarpus* Berry
Cf. *Sterculiocarpus* sp.
Pl. 9, figs. 2-3.

</div>

Material — RGM 233 571(Villa de Leiva), RGM 233 598 (Loma La Asomada).

Description — Specimen RGM 233 571 is 6 cm long and 1 cm wide. It is curved and carries 6 longitudinal ridges, 0.3-0.4 cm wide. The hilus is 0.6 cm wide. The apex is not preserved. Preservation of RGM 233 598b is not as good as that of RGM 233 571. It is 5.4 cm long, 1.9 cm wide. One end is missing.

Discussion — Huertas (1967) described *Sterculiocarpus etayoi*, a slightly larger seed but relatively much wider (Length/Width: 2) than these seeds (L/W: 4). The ridges on the present seeds are much coarser than on *S. etayoi* described by Huertas. The curved shape of both seed species is however striking. It is entirely possible that this fossil is not an angiosperm but a gymnosperm with large seeds.

<div align="center">

Genus *Carpolithes* Brongniart
Carpolithes sp.
Pl. 9, fig. 1.

</div>

Material — RGM 233 607 (Loma Blanca).

Description — This is an oval seed with an apex on one side and a hilus on the other. The seed is 4.3 cm long and 3 cm in diameter. The apex is 0.4 cm long and 0.7 cm wide. Two layers are visible. This seed has an outer fleshy layer with longitudinal ridges, 0.2 cm wide and 0.05-0.1 cm high. This layer covers the whole seed, but the absence of an outer layer in one place shows a much smoother layer underneath. This layer also has ridges but these are much less conspicuous.

Discussion — This seed was assigned to the genus *Carpolithes* since nothing is known about its affinity. Because the Lower and mid-Cretaceous record consists of quite small angiosperm fruits and seeds (Dilcher, 2000) it is doubtful if the true affinity of these large seeds is angiosperm.

Wood
Stem casts
Pl. 1, fig. 2.

Material — RGM 233 569 (Villa de Leiva); RGM 233 581(Loma La Asomada); RGM 233 611 (Villa de Leiva, land of Fernando Castillo); RGM 233 615 a/b, RGM 233 619 (Loma Blanca); RGM 233 616 (Loma Moniquera); RGM 233 606, RGM 233 617 (Santa Sofia).

Description — Little can be said about the stem casts that were found in the Leiva area. They were infested by boring molluscs. The cast morphology did not show any detail and therefore did not allow identification at any taxonomic level.

Discussion

Age assessment

The preliminary field results and the age assessment of the associated ammonites (Hoedemaeker et al., in prep.) suggest that our fossil plants are Barremian to Aptian in age (see Table 4). A single fossil plant, *Carpolithes* stromeri, is possibly older, viz. Hauterivian-Barremian. According to field data, *Paradoxopteris* sp. and *Pytiostrobus sanctieccehomense* are of Barremian age. Most *Brachyphyllum* and *Cupressinocladus*, except for *C. leivanus* and *Brachyphyllum* sp. 1, indicate an Aptian age. The same holds for a *Pagiophyllum* sp. and *Taeniopteris* sp.1. All other fossils are of Barremian to Aptian age.

Comparison with the material described by other authors

Seven out of 20 species described here from the Leiva area (*Cupressinocladus sutamarchensis*, *C. lepidophyllus*, *C. leivanus*, *Podozamites* sp., *Araucariostrobus creutzbergii*, *A. archangelskii*, *Pityostrobus sanctieccehomensis*) are also found in common with the fifteen species described by Huertas (1967, 1970, 1976). We believe that from each species he probably had only a few specimens. Not all the species described by Huertas (1967,

Table 4. Age distribution of the various species.

Species	Age	Species	Age
Cupressinocladus sp. 1	Late Aptian	*Araucariostrobus creutzbergii*	Barremian-Aptian
Brachyphyllum sp. 2	Aptian	*Brachyphyllum* sp. 1	Barremian-Aptian
Brachyphyllum winklerprinsii	Aptian	*Conites* sp.	Barremian-Aptian
Cupressinocladus hoedemaekeri	Aptian	*Cupressinocladus leivanus*	Barremian-Aptian
Cupressinocladus lepidophyllus	Aptian	wood	Barremian-Aptian
Cupressinocladus sp. 2	Aptian	*Podozamites* sp.	Barremian-Aptian
Cupressinocladus sutamarchensis	Aptian	*Macrotaeniopteris* sp.	Barremian-Aptian
Pagiophyllum sp.	Aptian	*Taeniopteris* sp. 2	Barremian-Aptian
Taeniopteris sp. 1	Aptian	*Pityostrobus sanctieccehomensis*	Barremian
Cf. *Sterculiocarpus* sp.	Barremian-Aptian	*Paradoxopteris stromeri*	Barremain
Araucariostrobus cf. *archangelskii*	Barremian-Aptian	*Carpolithes* sp.	Hauterivian-Aptian

1970, 1976) were observed in the material described here. The following species were not identified in our collection: *Damarites yarzenii*, *D. kuckii*, *Pinostrobus caldasii*, *Nilssonia* cf. *princeps*, *Ficus* cf. *ceratops*, and *Sterculiocarpus etayoi.* Huertas (1967) found *Cupressinocladus sutamarchensis* and *C. lepidophyllus* in Barremian deposits while we find them in Aptian deposits. The age assessment of all the other plant fossils described by Huertas (1967, 1970, 1976) and those described here, is in agreement with our age assessments.

Cupressinocladus leivanus, and *Podozamites* sp. are the only two species from the Leiva region that were found in common amongst the twenty two species described by Pons (1988) from the areas North and Northeast of the Leiva region. Pons' (1988) palynological data indicate that the sediments in which her macrofossils were found are of Early Aptian age.

The Leiva region has only one species (*C. lepidophyllus)* in common with the twelve species found by Lemoigne (1984) in the Upper Valanginian of western Colombia. When considering that according to Vakhrameev (1991) the Late Jurassic age of the 'Valle Alto suite' flora identified by Lemoigne (1984) should be emended to Early Cretaceous, than only one out of more than thirty species is identical to the association found in the Leiva region. This macrofossil occurs in Aptian layers in the Leiva region.

Berry (1945) also described the *Podozamites* sp. from the Neocomian of Peru. The association he found is composed of 16 species.

Summarising, the age of most of the plant fossils described here ranges between Barremian and Aptian, only *Cupressinocladus lepidophyllus* (Valanginian to Aptian) and *Podozamites* sp. (Neocomian to Aptian) indicate a wider range. *Carpolithes* sp. could be a little older, viz. Hauterivian.

Taphonomy

During Barremian to Aptian times the Villa de Leiva region was situated in the middle of a shallow marine environment with a water depth of less than 200 m. More than 200 Km to the West of the Villa de Leiva region were the remains of an extinct volcanic arc and more than 200 Km to the East was the South American continent. To the North this sea was connected to the Proto-Atlantic Ocean, to the South, this epicontinental sea extended into Peru (Pindell & Tabutt, 1995). The lithology of the deposits in which concretions were found consists of calcareous mudstones, siltstones, limestones, shales, and sandstones (Etayo Serna, 1974) and indicated low energy levels of the depositional system. High concentrations of ammonites also indicate that sedimentation rate was low.

The cones from the assemblage are flattened. Inside the cones no structure could be observed as the core consists of a calcareous mass. This lack of structure might indicate that the core was degraded before it was lithified (pers. comm. Kerp, 2001) and consequently that the flattening indicates biodegradation. Furthermore ferns are only represented by a stem fragment and possible angiosperms by seeds. So although we do have information on the presence of plants with less resistant fronds, we do not find their leaves. Both the flattening and the absence of less resistant fronds might be the result from a long residence time in water.

On the other hand the conifer branches found in these deposits always are termi-

nal shoots still carrying penultimate shoots. Extant conifers such as Araucariaceae and Taxodiaceae shed their leaves by abscission of complete penultimate shoots. We expect that the *Cupressinocladus* species described here shed their branches in a similar way, which indicates that the means of transport was gentle enough not to dissociate the shoots. A long residence time in water and rough water transport would dissociate the shoots, so it is possible that a means of transportation other than exclusively water could be responsible for the presence of shoots at 200 km from the coast. It is suggested here that wind transport might have played a part in forming the assemblage found in the Leiva region. Conifer twigs with ultimate and penultimate shoots still attached have led to similar considerations on the taphonomy of an assemblage of the Rotliegend of Oberhausen (Kerp et al., 1990). The lithology in both areas is comparable but the depositional area is quite different: fluvio-lacustrine in the Rotliegend of Oberhausen while it is shallow marine in the deposits described herein.

In the Colombia flora described by Pons (1988), ferns are represented by *Phlebopteris* sp. and *Weichselia reticulata*, the latter preserved as leaf fragments rather than the stem from the Leiva flora. Cycadophytes were represented by *Zamites* cf. *Z. tenuinervis* and *Pseudoctenis sp.*, while we record *Taeniopteris* sp. 1 and 2 and one *Macrotaeniopteris* species. The conifers described by Pons (1988) are represented by *Brachyphyllum* sp., *Cupressinocladus pompeckji* and *C. leptocladoides* which is much less than the 13 conifer species from the Leiva region. On the other hand, Pons (1988) described five to six *Podozamites*-type leaves while only one such type was found in the Leiva flora. Similarly to the present study she found a single putative angiosperm.

This implies that the variety of the association found by Pons (1988) is more or less comparable to that from the Leiva region, which is, however, richer in conifers. The difference between the assemblage of Pons (1988) and the one we found can not be explained through different hinterland vegetations. Indeed the epicontinental sea is situated on the equator and must have been surrounded by a more or less uniform tropical flora. Neither can we expect the distance to the hinterland to favour a more complete representation of the assemblage in the Leiva region as the distance from the source area is approximately identical in both cases. Consequently we believe that the difference in assemblage between the flora studied by Pons and ours is to be assigned to the biodiversity within the original association. The differences in composition between our assemblage and that of Lemoigne (1984) can be explained similarly but will also reflect a difference in age (Valanginian versus Aptian-Albian) between the Leiva area deposits and those from the area studied by Lemoigne.

In conclusion the Leiva region fossil plant assemblage represents the distal macrofloral facies from possibly a rich and diverse association.

Palaeogeography

Vakhrameev (1991) described the association found by Pons (1988) and Lemoigne (1984) as belonging to the Equatorial Province of Gondwana.

When we compare our Coniferales to those reported by Archangelsky (1966) from the Patagonian province of the Gondwana area, no matches can be found, not even at the generic level. On the other hand we do find matches between our association and

the associations found by Pons (1988) and Lemoigne (1984). From this we conclude that the plants from the Leiva region belong to an Equatorial Province rather than to the Austral region (Patagonian association).

Acknowledgements

References

Alvin, K.L., 1971. *Weichselia reticulata* (Stokes et Webb) Fontaine from the Wealden of Belgium. — Mém. Sci. Nat. Belgique, 166: 33.

Archangelsky, S., 1966. New Gymnosperms from the Tico Flora, Santa Cruz Province, Argentina. — Bull. Brit. Mus. (Nat. Hist.), Geol., 13, 5: 259-295.

Berry, E.W., 1922. The Mesozoic flora of Peru. In: E.B. Mathews (ed.): Contributions to the Paleobotany of Middle and South America. — John Hopkins Univ. Studies Geol., 4: 44-65.

Berry, E.W., 1939. The fossil plants from Huallanca, Peru. In: E.B. Mathews (ed.): Contributions to the Paleobotany of Middle and South America. — John Hopkins Univ Studies Geol., 13: 74-93.

Berry, E.W., 1945. The *Weichselia* stage. In J.T. Singewald (ed.): The origin of land plants and other papers. — John Hopkins Univ. Studies Geol., 14: 74-93.

Dilcher, D.L., 2000. Toward a new synthesis: major evolutionary trends in the angiosperm fossil record. — Proc. Natl. Acad. Sci., 97: 7030-7036.

Edwards, W.N., 1933. On the Cretaceous Fern *Paradoxopteris* and its connexion with *Weichselia*. — Ann. Botany, 47: 317-341.

Etayo-Serna, F., G. Renzoni, & D. Barrero, 1979. Contornos sucesivos Del Mar Cretaceo en Colombia. — Congr. Colombiano Geol. 1, Bogotá, 1969.

Farr, E.R., J.A. Leussink & F.A. Stafleu, 1979. Index genericorum (Plantarum) Part I (A-E). — Bohn, Scheltema en Holkema, Utrecht & Dr W. Junk b.v., Den Haag.: 1-629.

Hirmer, M., 1927. Handbuch der Paläobotanik. — München: 1-609.

Hoedemaeker, Ph.J., T. Bogdanova, M.V. Kakabaze. & M.Z. Sharikadze, in prep. The ammonites of the Barremian and Aptian of Colombia. — Scripta Geol.

Hollick, A. & E.C. Jeffrey, 1909. Studies of Cretaceous coniferous remains from Kreischerville, New York. — Mem. New York Bot. Garden, III.

Huertas, G., 1967. Sertum Florulae Fossilis Villae de Leiva. Paleobotanica. — Caldasia, X, 46: 60-75.

Huertas, G., 1970. Sertum Florulae Fossilis Villae de Leiva. Paleobotanica. — Caldasia, X, 50: 596-602.

Huertas, G., 1976. Sertum Florulae Fossilis Villae de Leiva. Paleobotanica. — Caldasia, XI, 54: 18-23.

Koeniguer, J.C., 1966. Sur de nouveaux échantillons du genre *Paradoxopteris*. — Mém. Soc. Géol. France, n.s., 45, 2: 100-112.

Lemoigne, Y., 1984. Données nouvelles sur la paléoflore de Colombie. — Géobios, 17, 6: 667-690.

Lesquereux, L., 1891 (posthumously edited by F.H. Knowlton). The flora of the Dakota Group. — U.S. Geol. Survey, Mon. XVII: 1-400.

Newberry, J.S., 1895 (posthumously edited by A. Hollick). The flora of the Amboy Clays. — U.S. Geol. Survey, Mon. XXVI: 1-260.

Pons, D., 1982. Etudes paléobotaniques et palynologiques de la Formation de Giron (Jurassique Moyen-Crétacé Inférieur) dans la région de Lebrija, Département de Santander, Colombie. — 107 Congr. Nat. Soc. Savantes, Brest, 1982, Sci., I: 53-78.

Pons, D., 1988. Le Mésozoique de Colombie: macroflores et microflores. — Cahier Micropal., CNRS, Paris: 1-168.

Remy, W. & R. Remy, 1969. *Alstaettia andersoni* n.gen., n.sp. ein Matoniaceen-Sprossrest aus dem Mit-

tel-Barreme von Alstätte/Krs. Ahaus. — Argumenta Palaeobot., 3: 91-129.

Saporta, G. de, 1884. Paléontologie française. 2 Série. Végétaux III. Conifères. — G. Masson, Paris: 1-672.

Seward, A. C., 1919. Fossil plants 4. — Cambridge Univ. Press, Cambridge: 1-542.

Srinivasan, V., 1995. Conifers from the Puddledock locality (Potomac Group, Early Cretaceous) in eastern North America. — Rev. Palaeobot. Palynol., 89, 3/4: 257-286.

Sternberg, K., 1820-1838. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. — Fr. Fleischer, Leipzig & G. Haase Söhne, Prag. Pt.1 (1820): 1-24; Pt 2 (1821): 1-33; Pt. 3 (1823): 1-39; Pt. 4 (1825): 1-42. Pts. 5,6 (1833): 1-80; Pt. 7 (1838): 1-220.

Vakhrameev, V.A., 1991. Jurassic and Cretaceous floras and climates of the Earth. — Cambridge Univ. Press, Cambridge etc.: 1- 318.

Zimmermann, W., 1959. Die Phylogenie der Pflanzen. — G. Fischer, Frankfurt: 1-323 (2nd ed.).

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Plate 1

Fig. 1. *Paradoxopteris stromeri* Hirmer, RGM 233 620, Loma Gonzales, Barremian, neg. no. 35, × 1.

Fig. 2. Wood cast infected by boring molluscs, RGM 233 616, Loma Moniquera, Barremian, neg. no. 65, × 0.5.
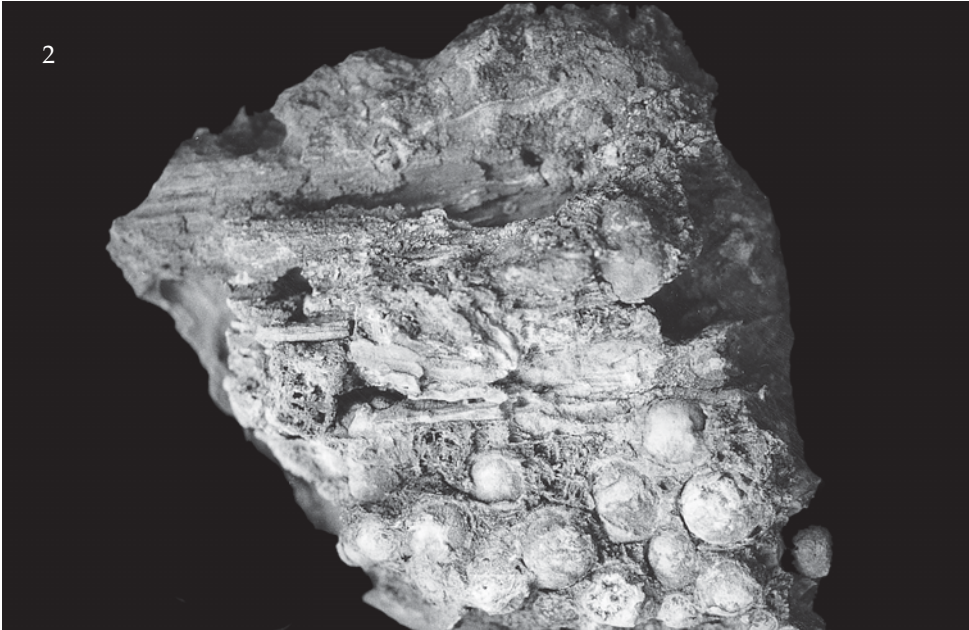
Plate 2

Fig. 1. *Taeniopteris* sp. 1, RGM 233 577, Villa de Leiva, Barremian-Aptian, neg. no. 48, × 1.

Fig. 2. *Taeniopteris* sp. 2, RGM 233 574, Villa de Leiva, Barremian-Aptian, neg. no 42, × 1.

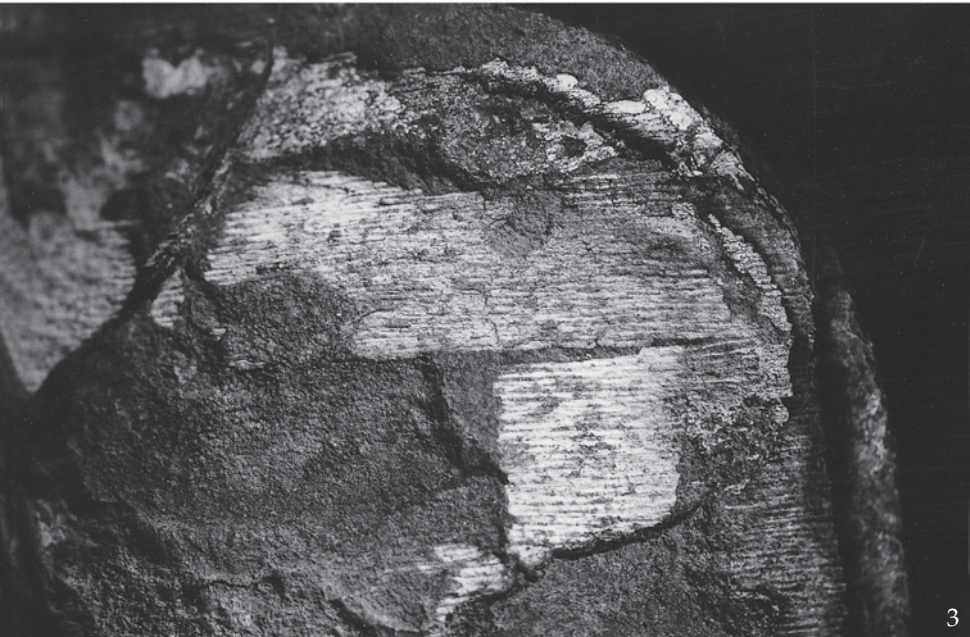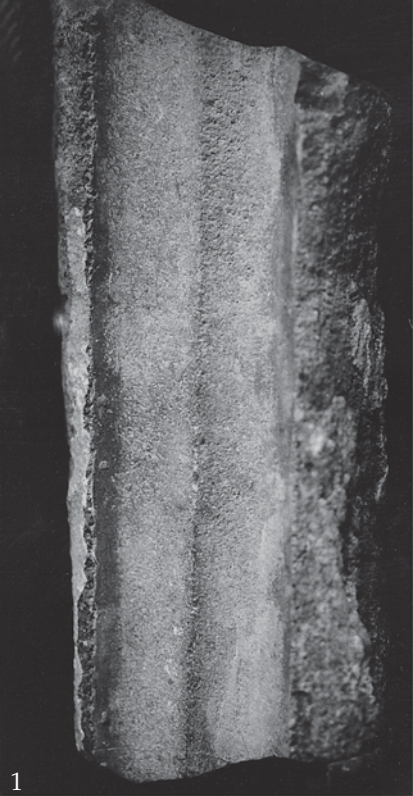Fig. 3. *Macrotaeniopteris* sp., RGM 233 573, Villa de Leiva, Barremian-Aptian, neg. no 38, × 1.

Plate 3

Fig. 1. *Cupressinocladus lepidophyllus* (Saporta) Lemoigne, RGM 233 599, Loma La Asomada, Barremian-Aptian, neg. no. 20, × 1.

Figs. 2-3. *Cupressinocladus leivanus* (Huertas) Pons, RGM 233 609, Loma Blanca, Hauterivian-Aptian; 2: neg. no. 139, × 1; 3: neg. no. 145, × 2.
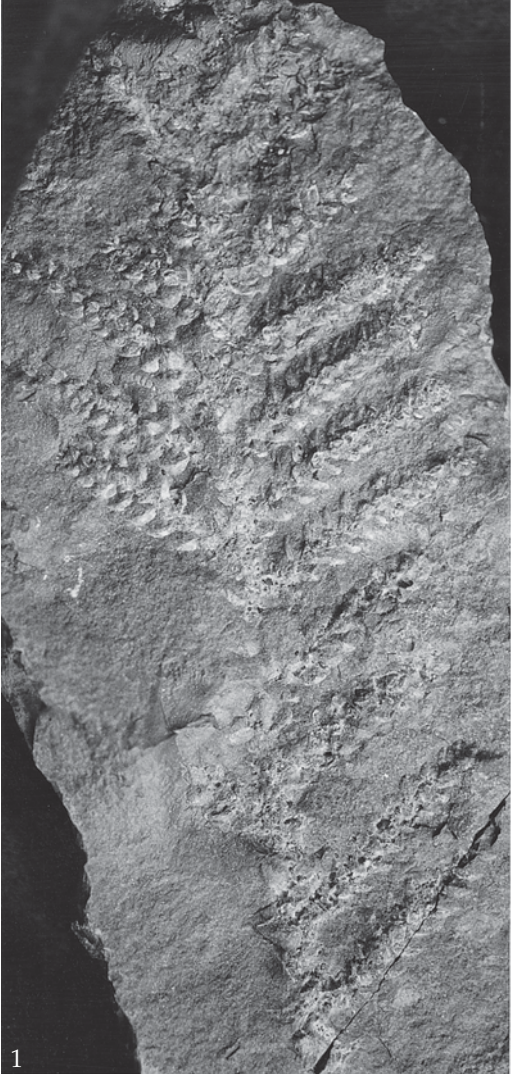
Plate 4

Figs. 1-2. *Cupressinocladus sutamarchensis* (Huertas) comb. nov., with an ammonite, Loma La Asomada, Barremian-Aptian; 1: RGM 533 588a, neg. no. 4, × 21; 2: RGM 533 588b, neg. no. 5, × 1.

Figs. 3-4. *Cupressinocladus hoedemaekeri* spec. nov., holotype, RGM 233 608, Loma Blanca, Hauterivian-Aptian; 3: neg. no. 13, × 1; 4: neg. no. 16, × 2.

Plate 5

Fig. 1. *Cupressinocladus* sp. 1; RGM 233 589, Loma La Asomada, Barremian-Aptian, neg no. 136, × 2.

Fig. 2. *Cupressinocladus* sp. 2, RGM 233 612, Loma Blanca, Hauterivian-Aptian, neg. no. 116, × 1.

Fig. 3. *Brachyphyllum winklerprinsii* sp. nov., holotype, RGM 233 600, Loma Catalina, Aptian, neg. 129, × 1.
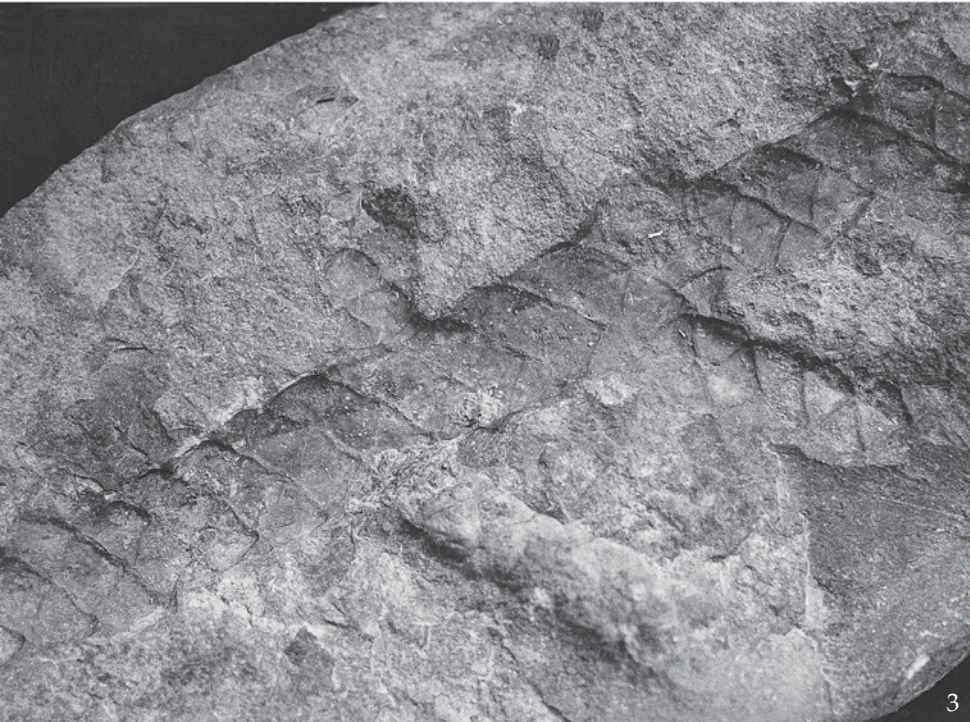
Plate 6

Fig. 1. *Brachyphyllum winklerprinsii* spec. nov., paratype, RGM 233 572a/b, Loma Catalina, Aptian, neg. no. 129, × 1.5.

Fig. 2. *Brachyphyllum* sp. 2, RGM 233 798, Loma la Asomada, Barremian-Aptian, neg. no. 126, × 2.

Fig. 3. *Pagiophyllum* sp., RGM 233 604, Sutamarchán, Aptian, neg. no. 124, × 1.

Plate 7

Figs. 1-2. *Podozamites* sp.
1: RGM 233 572a, Villa de Leiva, Barremian, Aptian; neg. no. 25, × 1.
2: RGM 233 593, Loma Catalina, Aptian, neg. no. 32, × 1.

Figs. 3-4. *Araucariostrobus creuzbergii* Huertas, RGM 233 613, Loma Catalina, Aptian, neg. no. 109; 3: ×
1; 4: × 2.

Fig. 5. *Conites* sp., RGM 233 568, Villa de Leiva, Barremian-Aptian , neg. no. 88, × 1.

Plate 8

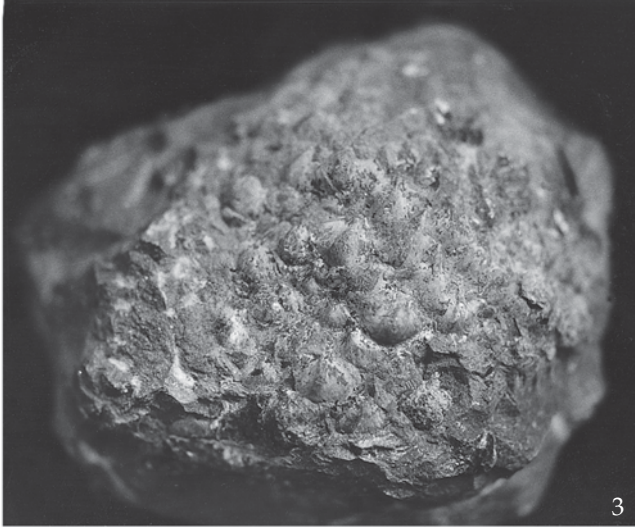Fig. 1. *Araucariostrobus* cf. *archangelskii* Huertas, RGM 233 597, Loma la Asomada, Barremian-Aptian, neg. no. 102, × 1.

Fig. 2. *Pityostrobus sanctieccehomensis* Huertas, RGM 233 583, Sancto Ecce Homo, Barremian-Aptian, neg. no 99; a: × 1; b: × 2.
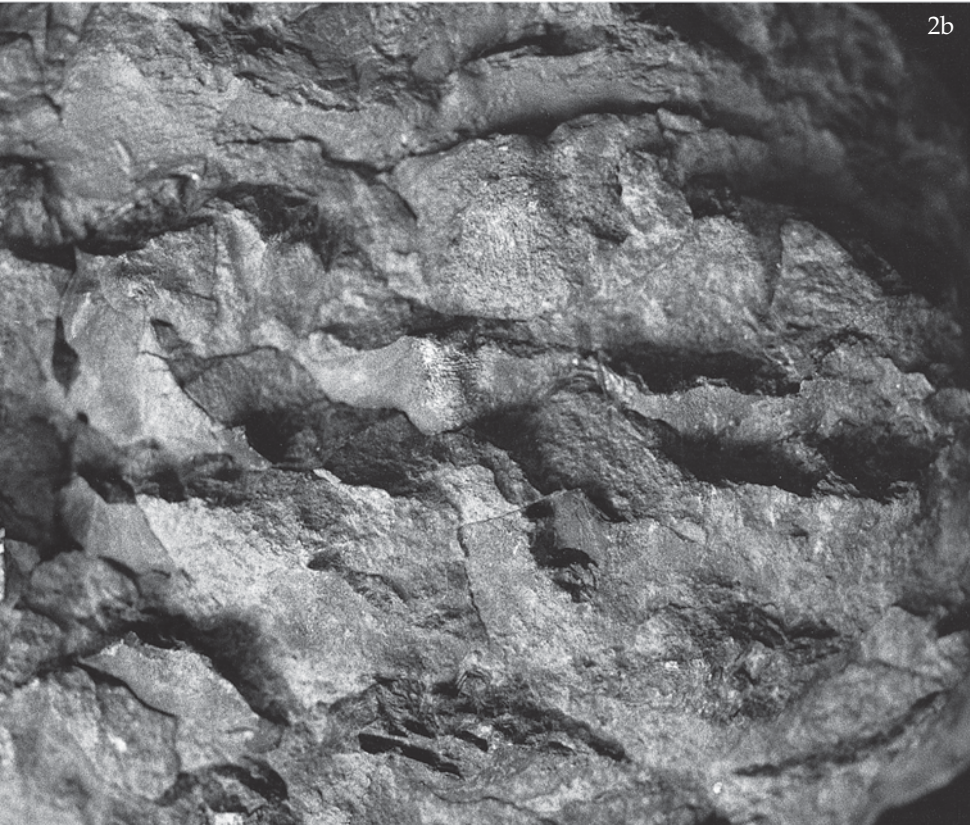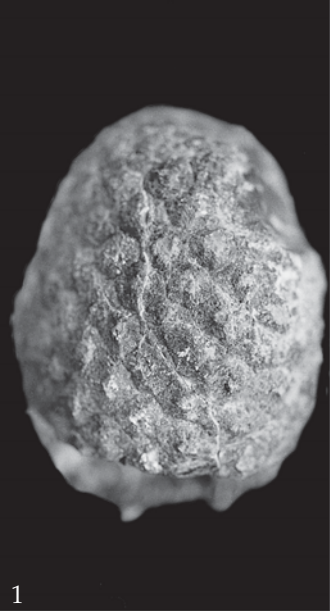
Plate 9

Fig. 1. *Carpolithes* sp., RGM 233 607, Loma Blanca, Hauterivian-Aptian, neg. no 78, × 1.

Fig. 2. *Sterculiocarpus* sp., RGM 233 571, Villa de Leiva, Barremian-Aptian , neg. no 84, × 1.

Fig. 3. *Sterculiocarpus* sp. with the ammonite *Karsteniceras aequicostatus*, RGM 233 598, Loma La Asomada, Barremian-Aptian, neg. no. 90, × 2.