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DIVERSITY, TAPHONOMY AND PALAEOECOLOGY OF AN ANGIOSPERM FLORA FROM THE CRETACEOUS (CENOMANIAN–CONIACIAN) IN SOUTHERN PATAGONIA, ARGENTINA

by ARI IGLESIAS*, ALBA B. ZAMUNER*, DANIEL G. POIRÉ† *and* FERNANDO LARRIESTRA*

*División Palaeobotánica, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n° 1900, La Plata, Argentina; e-mails: aiglesias@museo.fcnym.unlp.edu.ar; azamuer@museo.fcnum.unlp.edu.ar
†Centro de Investigaciones Geológicas, CONICET-UNLP 1 # 644, 1900 La Plata, Argentina; e-mail: poire@cig.museo.unlp.edu.ar

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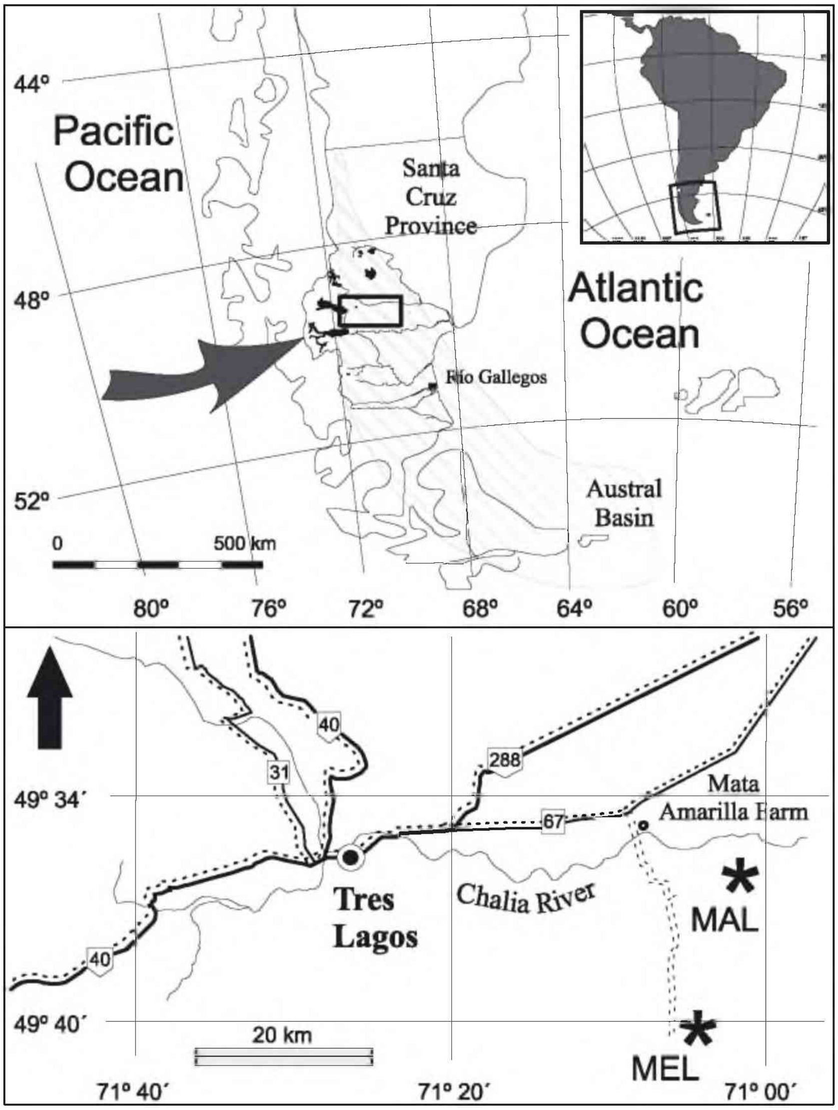
Abstract: This paper describes the diversity, taphonomy and palaeoecology of angiosperm leaves that dominate a palaeoflora of Cretaceous (Cenomanian–Coniacian) age from the Mata Amarilla Formation in the Austral Basin, south-west Patagonia, Argentina. Twelve morphotypes of angiosperm leaves are recognized based on foliar morphotype analysis of more than 500 specimens. These were divided into six morphological groups based on major architectural patterns. The relative dominance of these morphotypes, mode of preservation and relationship with sedimentary facies were evaluated from two levels within the formation. This analysis identified two different plant palaeocommunities. The lower, María Elena, level (MEL) was deposited in a marine coastal area on a subaerial delta plain; the dominant angiosperm morphotypes preserved in it are group 1 (MA100) and group 2 (MA101, 102); morphotypes MA109 and 110 are scarce but exclusive to this level. The upper, Mata Amarilla, level (MAL), accumulated inland in flood-plain environments; the most abundant angiosperm morphotypes are groups 3 (MA103–105), 4 (MA106) and 1 (MA100); morphotypes MA103–105 and 108 are exclusive to this level. Comparisons with other floras of similar age from Antarctica, Australia and New Zealand indicate that the Mata Amarilla flora has a slightly higher morphological diversity of angiosperm leaves, providing the first evidence for an angiosperm-dominated early Late Cretaceous macroflora in south-west Gondwana.

Key words: angiosperms, morphotypes, lower Upper Cretaceous, palaeoecology, South American floras, Patagonia.

CRETACEOUS angiosperms are less well known in the Southern Hemisphere than in the Northern Hemisphere. Nevertheless, in recent years the study of new mid and Late Cretaceous macrofloras from South America, Antarctica, South Africa, Australia and New Zealand has increased understanding of Cretaceous Gondwana floras (Pole 1992; McLoughlin *et al.* 1995; Cantrill and Nichols 1996; Rayner *et al.* 1997; Parrish *et al.* 1998; Passalía *et al.* 2001; Archangelsky *et al.* 2004).

In southern South America the earliest reported angiosperm leaves are from the lower Aptian (Romero and Archangelsky 1986). Although several floras are known from Patagonia, our understanding of angiosperm leaves from this region is still in its infancy (Romero and Arguijo 1981; Passalía *et al.* 2001; Archangelsky *et al.* 2004). Early studies by Berry (1928, 1937) and Frenguelli (1953) described a macroflora from the Mata Amarilla Formation in the Tres Lagos area, Santa Cruz Province (Text-fig. 1). A total of 21 genera and 25 species have been recognized for this flora, 14 genera and 18 species of which are angiosperm leaves. All of the taxa were based on limited descriptions, sometimes on fragmentary material, and with erroneous stratigraphic assignments (Frenguelli 1953). Field work in the area during 1999–2003 has yielded new fossiliferous localities in both the Mata Amarilla Formation (Iglesias *et al.* 2002, 2004; Zamuner *et al.* 2004) and the underlying Piedra Clavada Formation (Poiré *et al.* 2004*a*). These units are characterized by the presence of abundant impressions of angiosperm, fern and gymnosperm leaves, as well as permineralized conifer logs (Text-fig. 2).

A new (revised) macroflora of the angiosperm leaves recovered is described in this paper, and their taphonomy and palaeoecology evaluated with respect to the



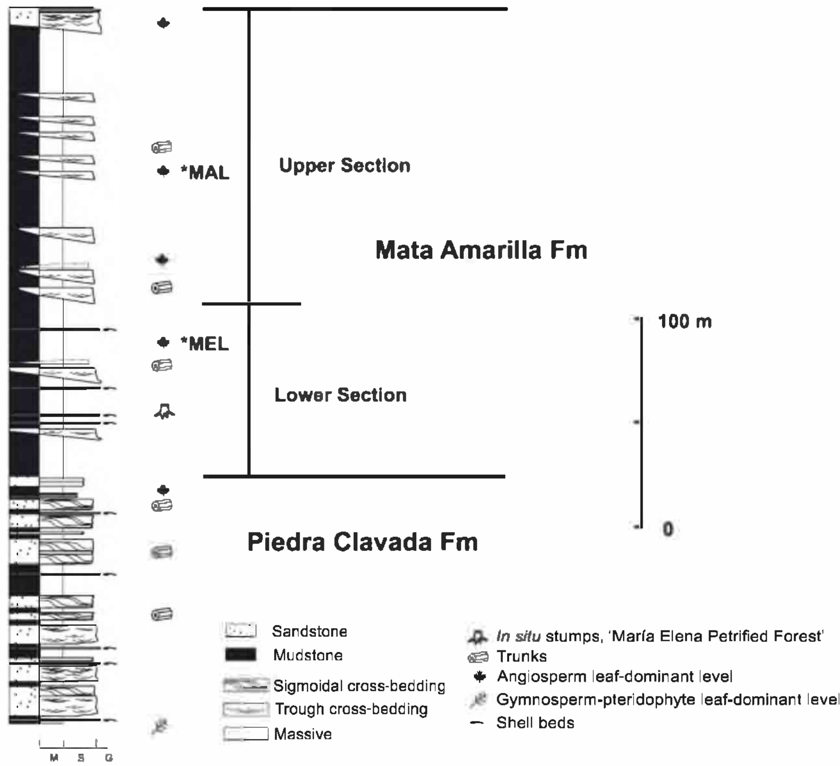
TEXT-FIG. 1. Map of the Austral Basin showing the location of plant-bearing levels MAL and MEL.

sedimentary facies, leading to a consideration of the community palaeoecology of the angiosperms. It is also compared with coeval floras in order to understand better the evolution of angiosperms in Gondwana during the Cretaceous Period.

GEOLOGICAL SETTING AND SEDIMENTARY FACIES

The macroflora discussed is present in clastic sediments of the Mata Amarilla Formation (Feruglio in Fossa Mancini *et al.* 1938; Leanza 1972) in the Austral Basin (= Magallanes Basin) of southern Patagonia. The Austral Basin is located on the southern edge of the South American Plate, and its history is related to the Triassic break-up of south-west Gondwana, which resulted in the formation of a small marginal sea behind a developing magmatic arch (Biddle *et al.* 1986). This marginal sea closed during the mid-Cretaceous and became a foreland basin during the Late Cretaceous.

The Mata Amarilla Formation is dated as Cenomanian–Coniacian based on ammonites found in associated marine facies (Riccardi and Rolleri 1980). It overlies the Piedra Clavada Formation, which is considered to be of Albian age based on palynomorph and ammonite occurrences (Riccardi *et al.* 1987), and underlies the La Anita Formation of Campanian age (Russo and Flores 1972; Riccardi and Rolleri 1980). It consists of beds of white sandstone and pale and dark grey mudstones, and includes four conspicuous plant-rich levels (Text-fig. 2). Three of these levels bear leaf impressions and the fourth consists of a petrified forest containing coniferous trees up to 1·20 m in diameter in life position (Zamuner *et al.* 2004).



TEXT-FIG. 2. Stratigraphic section of the Mata Amarilla Formation in the Tres Lagos area showing the location of plant-bearing levels MAL and MEL.

The formation comprises fluvio-deltaic deposits of the eastern margin of the Austral Basin (Arbe 2002). On the basis of facies analysis and associations (Text-fig. 3), a change in the sedimentary environment from a tide-dominated delta to a fluvial system has been inferred (Poiré *et al.* 2004*b*). In its lower part some coquinas are considered to represent sporadic marine transgressions (Goin *et al.* 2002; Poiré *et al.* 2004*b*).

Two localities contain levels of diverse, well-preserved fossil leaves. One of these is located in a ravine to the south of the Mata Amarilla Ranch (49°37′19″S and 71°07′55″W) (MAL in Text-fig. 1), next to outcrops studied by Berry in 1928. The other is located 10 km to the south on the María Elena Ranch (49°40′42″S and 71°08′51″W) (MEL in Text-fig. 1). Both are on the flanks (north and south, respectively) of a vast plateau that extends in an east–west direction. The fossiliferous levels represent different palaeoenvironments. The lower section is interpreted as part of a delta complex (Poiré *et al.* 2004*b*) and has sandstone horizons containing inclined coniferous stumps and fine-grained sediments containing marine bivalves, gastropods, sharks and stromatolites. The lower plant-bearing horizon, MEL in Text-figure 2, occurs just above this section in a heterolithic facies bearing abundant well-preserved angiosperm leaves and twigs. This level is interpreted as a part of a subaerial delta-plain deposit. The upper plant-bearing horizon, MAL in Text-figure 2, is found in extended lenticular deposits and mantle-like mudstone bodies with levels of dark mudstone. It is interpreted as a flood-plain deposit with meandering fluvial channels and large lacustrine bodies. The leaves are very well preserved, frequently with cuticles, degrees of fragmentation varying from low, in laminated mudstones, to very high in heterolithic facies with ripple marks. Permineralized coniferous logs in horizontal position are also found in this level. Both plant-bearing horizons are within a continuous sequence of white sandstones and light and dark grey mudstones. There is no abrupt lithological change, rather a transition in depositional setting from delta plain to a very low-energy fluvial system.

MATERIAL AND METHODS

Five-hundred and eighty specimens have been studied. More than 80 per cent of these are dicotyledonous leaves. The remaining 20 per cent consists of coniferous twigs and leaves, and fern frond fragments. Angiosperm leaves generally preserve the third, and sometimes up to the fifth, order of venation. The specimens studied are lodged in the palaeobotany collection of the Museo provincial Padre Manuel Jesús Molina, Río Gallegos, Santa Cruz province, Argentina (MPM-PB). Analysis and illustration of the fossil material were undertaken using a Wild M5 stereomicroscope and a drawing tube. The photographs were taken using a Leica DC150 digital camera system.

	Facies associations	Interpretation	Palaeoenvironment
Lower Section	(I-a) Assemblages of channel bodies composed of white, friable sandstones and pebbly sandstones, bearing fossil vertebrates and logs, and marine bioclastic lags. Sandstone bodies 4 m wide, 60–100 m long.	Facies of interdistributary ribbon channels	**Subaerial-delta complex and delta plain.**
	(II) Assemblages of massive sandstone lobes interbedded with fine-grained facies, heterolithic facies and bioclastic sandstones. Marine invertebrates, leaves and stumps in life position.	Facies of delta plain and interdistributary channels	
Upper Section	(I-b) Assemblages of channel sandstone bodies, with white, well-sorted sand in thin, long (extended lentiform) bodies bearing fossil vertebrates and logs.	Fluvial channel-fills of sinuous migrating streams forming extended lentiform bodies	**Meandering fluvial channels and large lacustrine bodies in flood plains.**
	(III) Assemblages of massive, light and dark grey banded mudstones, frequently showing slickenside structures, and abundant fossil vertebrates and logs.	Palaeosols developed in flood-plain and interfluvial zones	
	(IV) Assemblages of massive sandstone lobes interbedded with dark grey, massive mudstones bearing abundant vertebrate and charcoalified plant remains.	Crevasse-splays in flood plain	

TEXT-FIG. 3. Facies analysis, facies associations and palaeoenvironmental interpretation of the lower and upper sections of the Mata Amarilla Formation.

The angiosperm leaves exhibit a mixture of generalized characters in their foliar architecture, which hinders systematic assignments. To avoid this problem, an informal system of foliar morphotypes was adopted that enables the discrimination of angiosperm diversity based on distinctive vegetative morphological patterns without formal systematic assignment. This has previously proven to be an effective tool for the analysis of Cretaceous angiosperm floras, enabling analysis of palaeoecology, biostratigraphy and palaeoclimatology (Crabtree 1987; Johnson 1989; Johnson and Hickey 1990; Zastawniak 1994; Archangelsky *et al.* 2004).

For the description of the leaves we have used the terminology of Hickey (1973, 1977, 1979) and the corresponding updated version of the Leaf Architecture Working Group (1999). The leaves were divided into morphotypes following the criteria of Johnson (1989), and revised by the Leaf Architecture Working Group (1999). The morphotypes are named using two letters plus a three-digit number. Crabtree (1987) and Zastawniak (1994) proposed grouping Cretaceous foliar forms in morphotypes but using different criteria; however, use of either of these two terminologies that relate foliar forms to a biological group was in our experience unsatisfactory. For the analysis and comparison of the angiosperm leaves within this flora and other Gondwana floras, we group distinct and related morphotypes based on one feature or a set of architectural features.

The number of samples was considered sufficient to characterize and determine the relative abundance of the morphotypes in each plant-bearing horizon. In order to standardize comparisons between taphocoenoses from different levels with different numbers of samples, the data were converted to percentages of each plant-bearing horizon. Then for both of the plant-bearing levels MAL and MEL the relative abundance of each morphotype and the average foliar sizes were compared.

SYSTEMATIC PALAEONTOLOGY

ANGIOSPERMAE GROUP 1

Characteristics. Ovate to elliptical, entire-margin leaves. Primary venation pinnate, secondary venation camptodromous or brochidodromous.

MA100 morphotype
Text-figure 4A–E

Morphotype example. MPM-PB 1446.

Material. MPM-PB 1300(a–c), 1342, 1343(a–c), 1344(a–c), 1345(a–b), 1346(a–c), 1347(a–c), 1348(a–c), 1349(a–b), 1350–1355, 1356(a–c), 1357(a–b), 1358(a–b), 1359, 1445, 1446, 1455(a–b), 1462, 1463(a–b), 1464(a–c), 1465(a–b), 1466(a–b), 1467(a–c), 1468(a–b), 1469(a–b), 1470(a–b), 1471(a–b), 1472 (a–b), 1473(a–b), 1474(a–b), 1475(a–b), 1476(a–c), 1477(a–d), 1478–1498.

Description. Simple leaves, narrow ovate, microphyll to notophyll, 4 cm mean length, 2·6 cm mean width (2·8–11·5 cm length, 0·65–5·6 cm width), acute apex angle with convex shape. Base obtuse angle with rounded, rarely concave, shape. Entire margin, normal petiole, marginal insertion, 1 cm in length. Chartaceous texture. Primary venation pinnate, middle vein moderately thick, straight course, reaching foliar apex. Brochidodromous secondary venation. Secondaries subopposite, non-branching, vein spacing increasing towards base, arising at narrow (< 45 degrees), but decurrent base. Compound intersecondary veins. Tertiary veins of moderate thickness, with perpendicular angle to primary and decreasing angle exmedially, alternate and opposite arrangement in equal proportions. Distinguishable higher order of venation, moderate in thickness, random orientations. Moderately developed areolation with pentagonal and rombic forms, 6–7 areoles per interarea. Leaf rank 2r.

Remarks. With a total of 98 specimens identified from the Mata Amarilla Formation, MA100 is a co-dominant form in the lower level, MEL (24·6 per cent). Although easily recognized, it exhibits a great heterogeneity in shape and net-veined development. The leaves have a thick texture showing a well-preserved margin and venation. The petiole is generally attached. Foliar damage by arthropods (margin feeding) has been observed in some specimens as well as fructiferous bodies of epiphyllous fungi assignable to Microthyriales (Text-fig. 4).

Forms previously described by Berry (1928, 1937) as *Peumus clarki* and *Laurophyllum proteafolium* can be included in this morphotype: *P. clarki* Berry, 1928 based on shape and margin characters, its slightly asymmetric base, and the secondary vein pattern; *L. proteafolium* Berry, 1937 based on laminar size, the width-length ratio, base shape, mean vein thickness and secondary vein characters. *Laurophyllum kurtzi* Berry, 1937, although described from rare and fragmentary material, can also be considered to belong to this morphotype. MA100 is similar to species of the 'Laurophyll morphotype' of Zastawniak (1994) from the Campanian–Maastrichtian of King George Island, Antarctica, although it includes more complete and variable leaves of lower rank. Lauroid leaves of low rank illustrated from the Cenomanian of New Zealand (Parrish *et al.* 1998) could be related to it.

ANGIOSPERMAE GROUP 2

Characteristics. Leaves with three primary or strongly developed basal secondary veins running in convergent arches toward the leaf apex. Acrodromous venation.

MA101 morphotype
Text-figure 4F–K

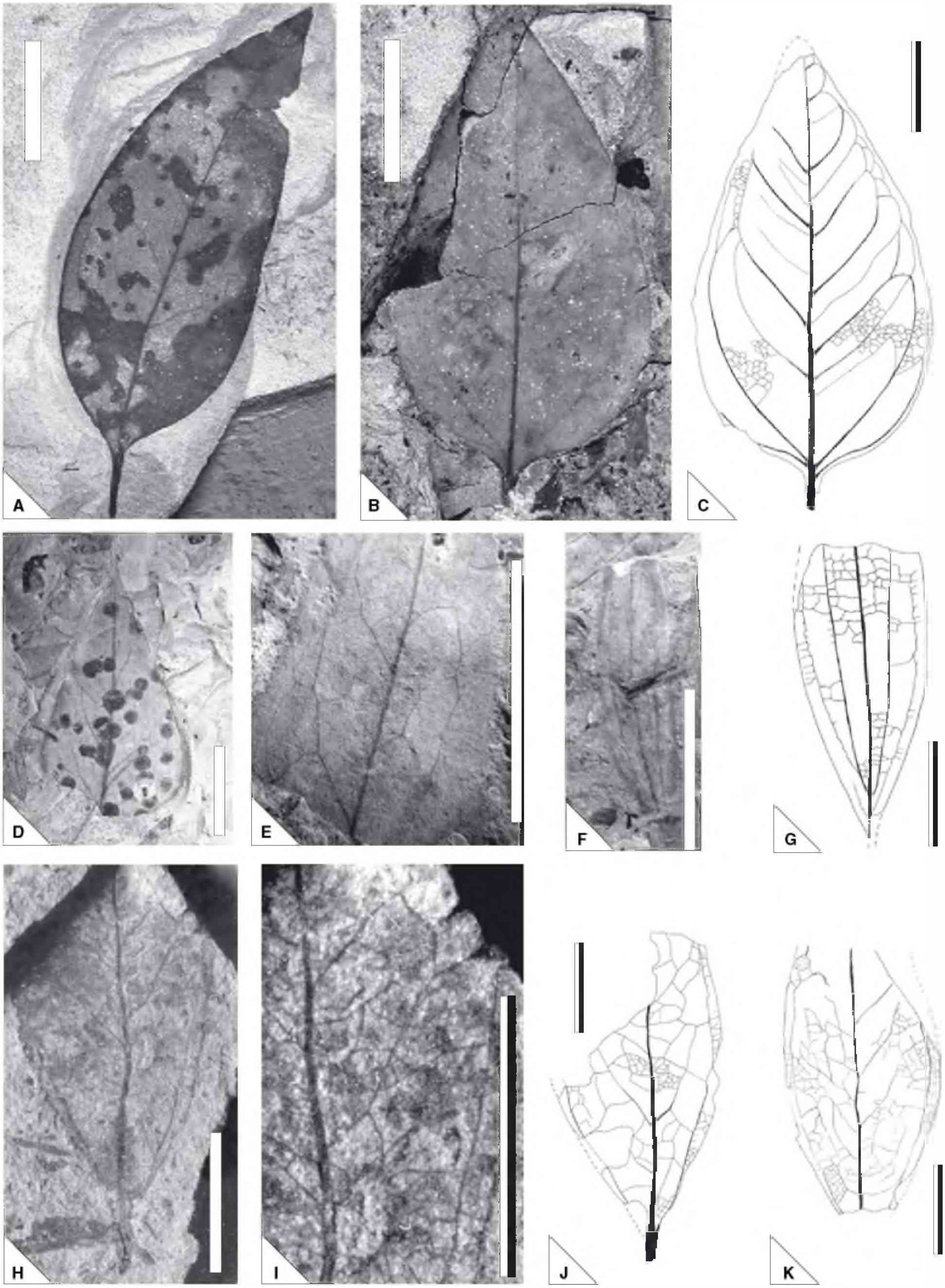
Morphotype example. MPM-PB 1330.

Material. MPM-PB 1318, 1324, 1325(a–c), 1326(a–b), 1327, 1328(a–c), 1329(a–b), 1330, 1331(a–d), 1332(a–e), 1333(a–b), 1334(a–c), 1335, 1336(a–b), 1337(a–b), 1338, 1339(a–b), 1340(a–b), 1341, 1503(a–c), 1504(a–b), 1505(a–b), 1506(a–b), 1507(a–c), 1508(a–c), 1509(a–g), 1510–1532.

Description. Simple leaves, elliptical or ovate in shape, notophyll to microphyll, 5·7 cm mean length and 2·8 cm mean width (3·7–9·8 cm length, 0·4–6·1 cm width), symmetrical or asymmetrical base, acute apex and base angles, decurrent base shape, entire margin, petiole *c.* 1 cm long and 1–2 mm wide, one specimen (MPM-PB 1318) shows an axis with two petioles oppositely arranged. Chartaceous texture. Imperfect basal acrodromous primary venation, with two strong secondary veins that arise close to petiolar margin and run parallel and close to leaf margin, acute angle from primary, forming the first great loops (about one-half length) or conspicuous intramarginal vein. Irregular, eucamptodromous secondary venation forming a weak intramarginal vein. Secondaries very sinuous and occasionally laterally anastomosed by a tertiary vein. Secondaries subopposite and decurrent, increasing in spacing toward base. Tertiary veins cross from acrodromous veins to middle vein. Tertiary venation random reticulate or ramified. Fourth order venation forming an irregular polygonal reticulation 7 mm in diameter. Distinguishable fifth order venation. Marginal ultimate venation looped. Leaf rank 2r.

Remarks. About 83 specimens of this morphotype have been identified and they are dominant forms in the lower level, MEL (more than 50 per cent). These forms show a great variation in length/width ratio and probably define different species. Fracturing and skeletonization has resulted in their poor preservation. Fructiferous bodies of epiphyllous fungi assignable to Microthyriales have been recorded on some specimens.

Bignonites chalianus Berry, 1928, created for specimens collected in the surroundings of Mata Amarilla Ranch, exhibit the same characters as the MA101 morphotype, which is also similar to the 'Acrodromophyll morphotype' of Zastawniak (1994) from the Campanian–Maastrichtian of Antarctica, but differs in its distinct basal acrodromous venation with two veins running near the margin.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MA102 morphotype
Text-figure 5A–E

Morphotype example. MPM-PB 1321.

Material. MPM-PB 1319–1323, 1499–1502.

Description. Simple leaves, orbicular or suborbicular (rarely elliptical), notophyllous, 5·6 cm mean length, 3·95 cm mean width (3·4–4·8 cm length, 2·8–5·8 cm width). Rounded or obtuse apex. Asymmetrical base with acute angle. Margin entire. Chartaceous texture. Marginal petiole 10 mm long, 1·5 mm wide. Perfect suprabasal acrodromous venation running at a distance from margin, subopposite, branching exmedially forming agrophic veins; exceptionally irregular agrophic venation. Primary vein changes towards apex, branching or diminishing in width, with a sinuous course. Secondaries brochidodromous, very curved, fewer than three pairs in middle vein, decurrent base. Tertiaries percurrent subopposite, sinuous in course, perpendicular to middle vein. Weak intramarginal vein formed by arcs of tertiary or higher order of veins.

Remarks. Nine specimens of this morphotype have been identified, seven in the MEL and two in the MAL. In spite of being relatively rare, they are easily distinguished from morphotype MA101 on the basis of their acrodromous vein pattern and length/width ratio. All of the specimens have a well-preserved shape, margin and venation; however, secondary and tertiary venation is often weakly defined. Chartaceous texture is also typical.

One specimen from the MEL (MPM-PB-1319) is closely related to *Menispermites piatnitzkyi* Berry, 1937, the remaining examples showing basal actinodromous venation with a different ordering of lateral veins.

MA102 is partly similar to the 'Acrodromophyll morphotype' of Zastawniak (1994) from the Campanian–Maastrichtian of Antarctica, showing a distinct subbasal or suprabasal acrodromous venation with two veins running at a distance from the margin up to the middle of the lamina, and acrodromous veins branching exmedially forming agrophic veins.

ANGIOSPERMAE GROUP 3

Characteristics. Leaves with pinnate primary venation, numerous and dense secondaries with a distinct intramarginal vein.

Remarks. Three morphotypes could be recognized based on architectural characters; they are easily differentiated by the shape of the lamina (lorate, obovate or elliptical) as well as by their size and secondary venation.

MA 103 morphotype
Text-figure 5F–I

Morphotype example. MPM-PB 1447.

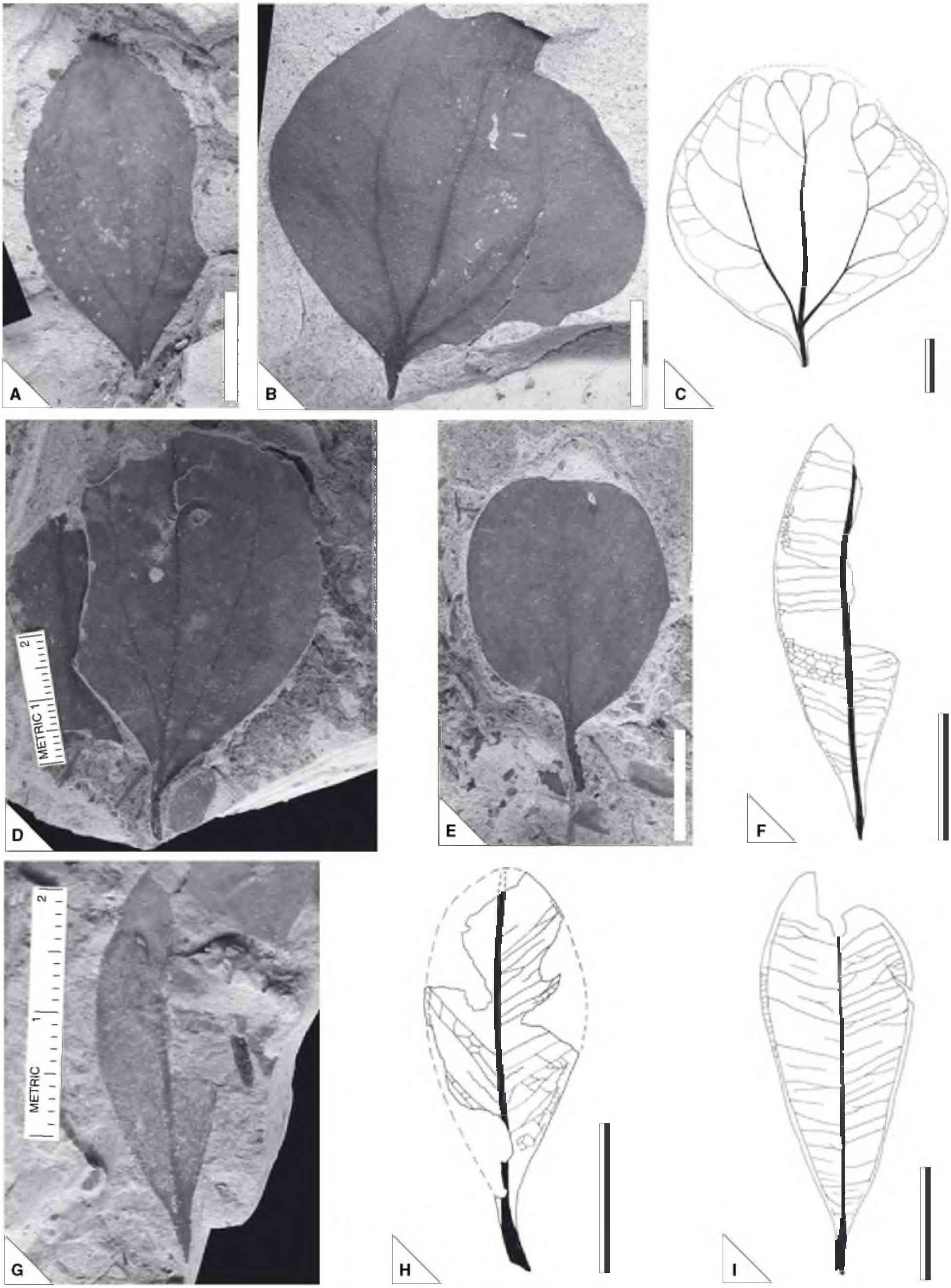
Material. MPM-PB 1361–1367, 1447–1449, 1503(a–b), 1504 (a–b), 1505–1512, 1513(a–b).

Description. Simple microphyll leaves, obovate or elliptical in shape, 2·85 cm mean length, 1·0 cm mean width (2·6–3·6 cm length, 0·6–1·4 cm width), obtuse apex angle, rounded or retuse apex shape. Acute base angle, cuneate or decurrent in shape. Entire margin, strong petiole 1 mm wide and *c.* 0·5 cm long. Coriaceous texture. Pinnate primary venation, strong middle vein up to apex. Brochidodromous secondary venation, secondaries straight, branching once or twice near margin, sometimes anastomosing laterally. Thin secondary veins, very dense and uniform in spacing, perpendicular or wide angle (60 degrees) to primary vein, can branch and anastomose with supradjacent before reaching margin. Angle of secondaries can be uniform, smoothly increasing or decreasing towards base. Compound intersecondary veins similar to secondaries in strength and thickness. One or two distinct or weak intramarginal veins, formed by secondary or tertiary arcs. Tertiaries similar to secondaries in thickness, mainly diverging perpendicularly, irregular course, forming a random reticulation, moderately developed areolation, five or more sided.

Remarks. Twenty-four specimens of this morphotype were recognized from the MAL. All show a typical coriaceous texture and good preservation of the margin and shape. The petiole is always present when leaf base is preserved. Two forms were found with a deformed apex, caused by the action of a folivore organism in stages of foliar primordium. Foliar damage suggesting margin feeding by arthropods was also found.

Forms previously assigned to *Myrcia acutifolia* Frenguelli, 1953 from the Mata Amarilla Formation can be included in this morphotype. *Myrtoidea patagonica* Passalía *et al.*, 2001 from the Albian of Patagonia shares with MA103 the presence of one or two intramarginal veins and numerous thin secondaries; however, the latter has ovate leaves and a rounded or retuse apex.

TEXT-FIG. 4. A–E, Group 1, MA100 morphotype. A, with skeletonization, MPM-PB 1445. B, MPM-PB 1455. C, camera lucida drawing of MPM-PB 1446. D, with epiphyllous fungi, MPM-PB 1344. E, MPM-PB 1462. F–K, Group 2, MA101 morphotype. F, MPM-PB 1374. G, camera lucida drawing of MPM-PB 1340. H, MPM-PB 1330. I, detail of H. J, camera lucida drawing of MPM-PB 1331. K, camera lucida drawing of MPM-PB 1330. White scale bars represent 1·5 cm; black and white scale bars 1·0 cm.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MA103 and the 'Myrtophyll morphotype' of Zastawniak (1994) from the Campanian–Maastrichtian of Antarctica show similar venation patterns, having up to two intramarginal veins, secondaries bifurcated near the margin and leaves that are obovate or elliptical in shape.

MA104 morphotype
Text-figure 6A–C

Morphotype example. MPM-PB 1451.

Material. MPM-PB 1368(a–c), 1369(a–c), 1370(a–b), 1371, 1372, 1373(a–c), 1374(a–c), 1375(a–c), 1376(a–d), 1377, 1378(a–b), 1450(a–c), 1451(a–d), 1514(a–b), 1515(a–b), 1516(a–b), 1517 (a–b), 1518(a–b), 1519(a–b), 1520(a–b), 1521(a–b), 1522(a–b), 1523(a–c), 1524(a–c), 1525(a–c), 1526(a–c), 1527(a–c), 1528 (a–d), 1529(a–d), 1530(a–d), 1531(a–c), 1532(a–c), 1533–1557.

Description. Simple leaves, oblong to lorate in shape, microphyll, 4·4 cm mean length, 0·8 cm mean width (2·2–6·8 cm length, 0·4–1·3 cm width). Acute apex angle, straight apex shape. Acute base angle, cuneate base shape. Entire margin, normal petiole. Margin thick. Chartaceous texture. Smaller leaves have acrodromous pinnate venation with two strong veins running at a distance from margin, larger leaves have pinnate primary venation with conspicuous intramarginal veins. Strong middle vein, straight or uniformly curved. Pinnate secondary venation, secondary veins moderately thin, very dense and uniform in spacing. Sinuous or curved in course, characteristically perpendicular or at wide angle to middle vein, alternate or semi-opposite, sometimes branched, fusing to intramarginal vein. Intersecondary veins similar to secondaries, distinct intramarginal vein running at a distance from, or fairly close to, margin, very straight in its course. Tertiary veins similar to secondaries in thickness, perpendicular angles to primary and secondary veins forming well-developed areolation near margin. Fimbrial vein inside margin.

Remarks. One hundred and nine specimens have been assigned to this morphotype from the MAL. Differences in the length/width ratio are very clear and may indicate a marked heterophylly, such as observed in *Eucalyptus*. The specimens show a wide range of preservation, but chartaceous texture and well-preserved venation is typical of all.

Two forms described previously from the Mata Amarilla Formation can be included in this morphotype: *Phyllites* sp. 6 Dusen, tentatively described by Berry (1928), is lorate, similar to MA104 in size, with an acute base and strong primary; *Myrcia santacruzensis* Berry, 1937 is similar in shape but lacks a fimbrial vein. 'Myrtophyll' leaves from the Campanian–Maastrichtian of Antarctica, assigned to *Myrciophyllum santacruzensis* (Berry) Zastawniak, 1994, differ because they lack a fimbrial vein.

MA 105 morphotype
Text-figure 6D–G

Morphotype example. MPM-PB 1452.

Material. MPM-PB 1306, 1379(a–c), 1380, 1381(a–b), 1382–1384, 1385(a–b), 1452, 1558(a–b), 1559(a–b), 1560(a–b), 1561(a–b), 1562(a–b), 1563(a–b), 1564(a–c), 1565–1572.

Description. Simple leaves, narrow elliptical in shape, microphyll, 3·2 cm mean length, 1·0 cm mean width (2·8–3·6 cm length, 0·7–1·3 cm width). Acute apex angle, convex apex shape; acute base angle, cuneate base shape. Entire margin, normal petiole. Membranous texture. Pinnate primary venation. Middle vein thinning towards apex. Brochidodromous secondary venation, strong secondaries, not branched, arising at a wide angle (65–80 degrees), curving smoothly or abruptly toward margin forming a conspicuous or diffuse intramarginal vein. Poorly developed compound intersecondaries. Tertiary veins perpendicular to primary vein in regular polygonal reticulation. Higher order of veins forming well-developed areolation; areoles 4–5 sided, in 5–6 lines by interarea.

Remarks. Thirty-six specimens of this morphotype have been recognized from the MAL. The membranous texture is characteristic and constant in all specimens; despite this, the margin appears well preserved in most cases. The intramarginal vein is not easily distinguished in some specimens although the curvature of the secondaries is. To date no leaf types from the Cretaceous of Gondwana have been found that are comparable with MA 105.

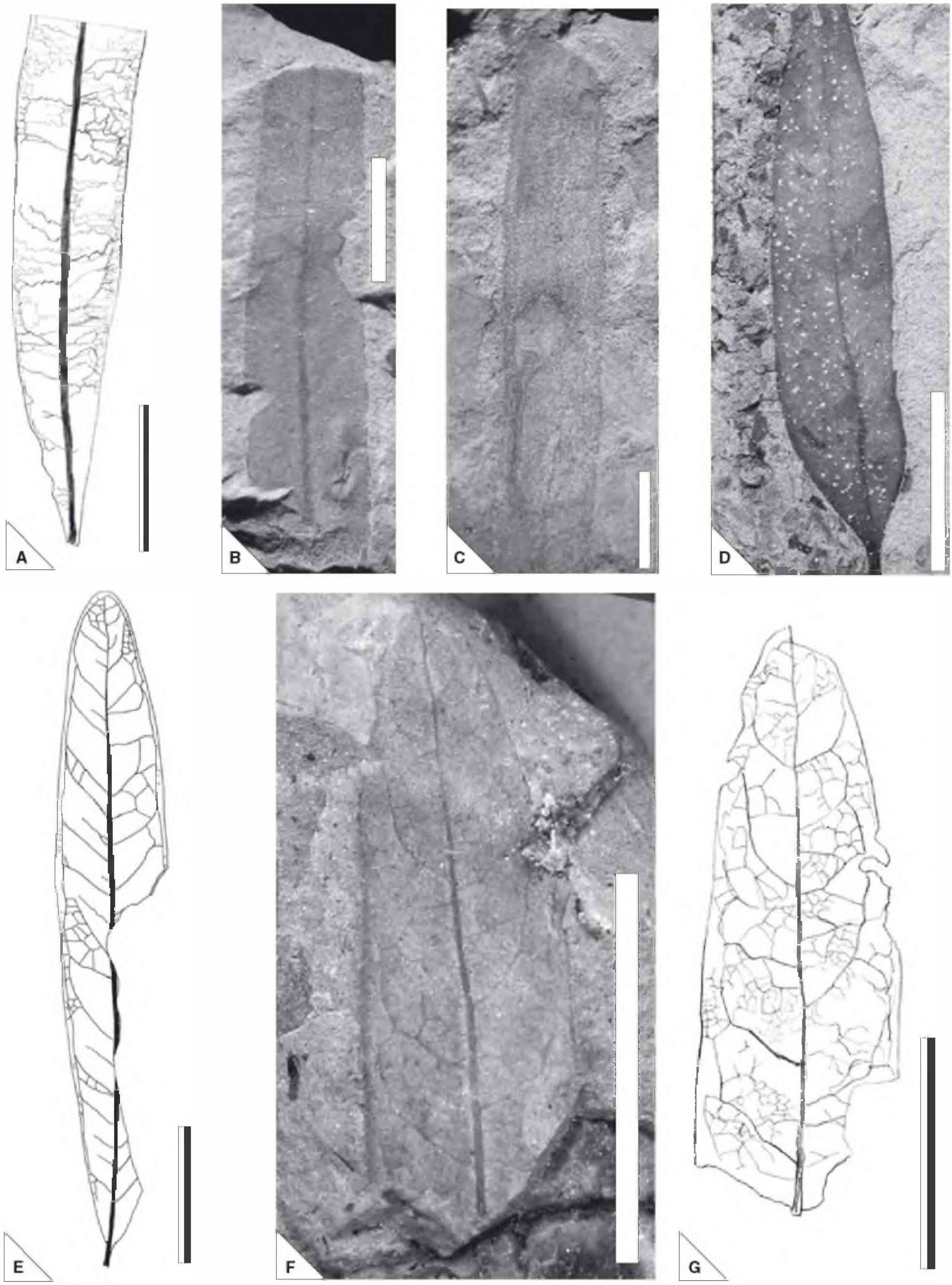
ANGIOSPERMAE GROUP 4

Characteristics. Elliptical or orbicular leaves, palmately lobed, entire margin. Actinodromous or palinactinodromous primary venation, secondary venation eucamptodromous, weakly developed.

MA106 morphotype
Text-figure 7A–I

Morphotype example. MPM-PB 1412.

TEXT-FIG. 5. A–E, Group 2, MA102 morphotype. A, MPM-PB 1322. B, MPM-PB 1321. C, camera lucida drawing of MPM-PB 1321. D, MPM-PB 1323. E, MPM-PB 1319. F–I, Group 3, MA103 morphotype. F, camera lucida drawing of MPM-PB 1449. G, MPM-PB 1449. H, camera lucida drawing of MPM-PB 1448. I, camera lucida drawing of MPM-PB 1447. White scale bars represent 1·5 cm; black and white scale bars 1·0 cm.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Material. MPM-PB 1386(a–c), 1387(a–c), 1388, 1389, 1390 (a–c), 1391, 1392, 1393(a–b), 1394–1396, 1397(a–d), 1398, 1399(a–c), 1400(a–b), 1401(a–b), 1402(a–d), 1403–1412, 1454, 1461, 1573(a–b), 1574(a–b), 1575(a–b), 1576(a–b), 1577(a–b), 1578(a–b), 1579(a–b), 1580(a–b), 1581(a–c), 1582(a–c), 1583 (a–d), 1584–1598.

Description. Simple leaves, very variable in shape and size, notophyll, microphyll, sometimes nanophyll or mesophyll, orbicular-elliptical in shape, 3·0 cm mean length, 3·3 cm mean width (1·3–9·5 cm length, 0·9–13·1 cm width), symmetrical or asymmetrical. Entire margin, palmately lobed, with 3–5 primary lobes (rarely seven or more). Very variable in odd-lobed apex angle, medial vein extending in a median lobe with convex apex shape (well-developed in trilobate forms). Lobes sometimes with subordinate lobules arising symmetrically or asymmetrically depending on the secondary vein. Convex or acuminate lobe sides, rounded or acute sinuses reaching one-half to two-thirds of distance to middle vein. Obtuse base angle, concave or complex in shape, normal petiole. Chartaceous texture. Perfect basal palinactinodromous primary venation. Strong middle vein, slightly sinuose in course. Lateral primaries from petiole frequently dichotomizing before the sinuses, thus forming subprimary veins. Branches of subprimaries innerving sinus and apical margin of leaf. Eucamptodromous secondary venation, arising in moderate or wide angles, uniform curved course, fusing in an intramarginal vein. Commonly thin, except when innerving the lobes. Intramarginal veins in sinuses arise by branching of subprimaries, running to lobe apex. Occasionally ascending subprimary branches innerve lobules. Weak tertiary veins, compound percurrent pattern (alternate-opposite in similar percentages), perpendicular to middle vein or increasing angle exmedially, with high density. Tertiaries develop rectangular and pentagonal areoles in a random arrangement.

Remarks. Eighty-seven specimens of this morphotype were identified in the Mata Amarilla Formation. They are co-dominants in the MAL. Trilobate forms with actinodromous venation are also included because they possess architectural characters that are similar to the palinactinodromous leaves.

Within this morphotype a continuous series of forms from actinodromous to palinactinodromous was determined and variable architectural characters were recognized including: number and development of lobes, presence of ascending branches of subprimaries, and sinus shape. The specimens show a typical chartaceous texture, which allows the first order of venation, but not the higher orders, to be clearly recognized, even in very small fragments.

Cretaceous palmately lobed leaves with palinactinodromous venation are abundant and well known in the Northern Hemisphere (Hickey and Doyle 1977; Crabtree 1987). In the Southern Hemisphere these forms are rare with records in Antarctica (Cantrill and Nichols 1996; Dutra and Batten 2000) and Patagonia (Berry 1925, 1928). Two species previously described for the Mata Amarilla Formation, *Sterculia sehuensis* Berry, 1937 and *Sterculia washburni* Berry, 1928, are included in this morphotype. *Sterculia sehuensis* corresponds to actinodromous trilobated forms; *S. washburni* includes leaves that vary in size, 3–5 palmately lobed, with actinodromous or palinactinodromous venation and camptodromous secondaries.

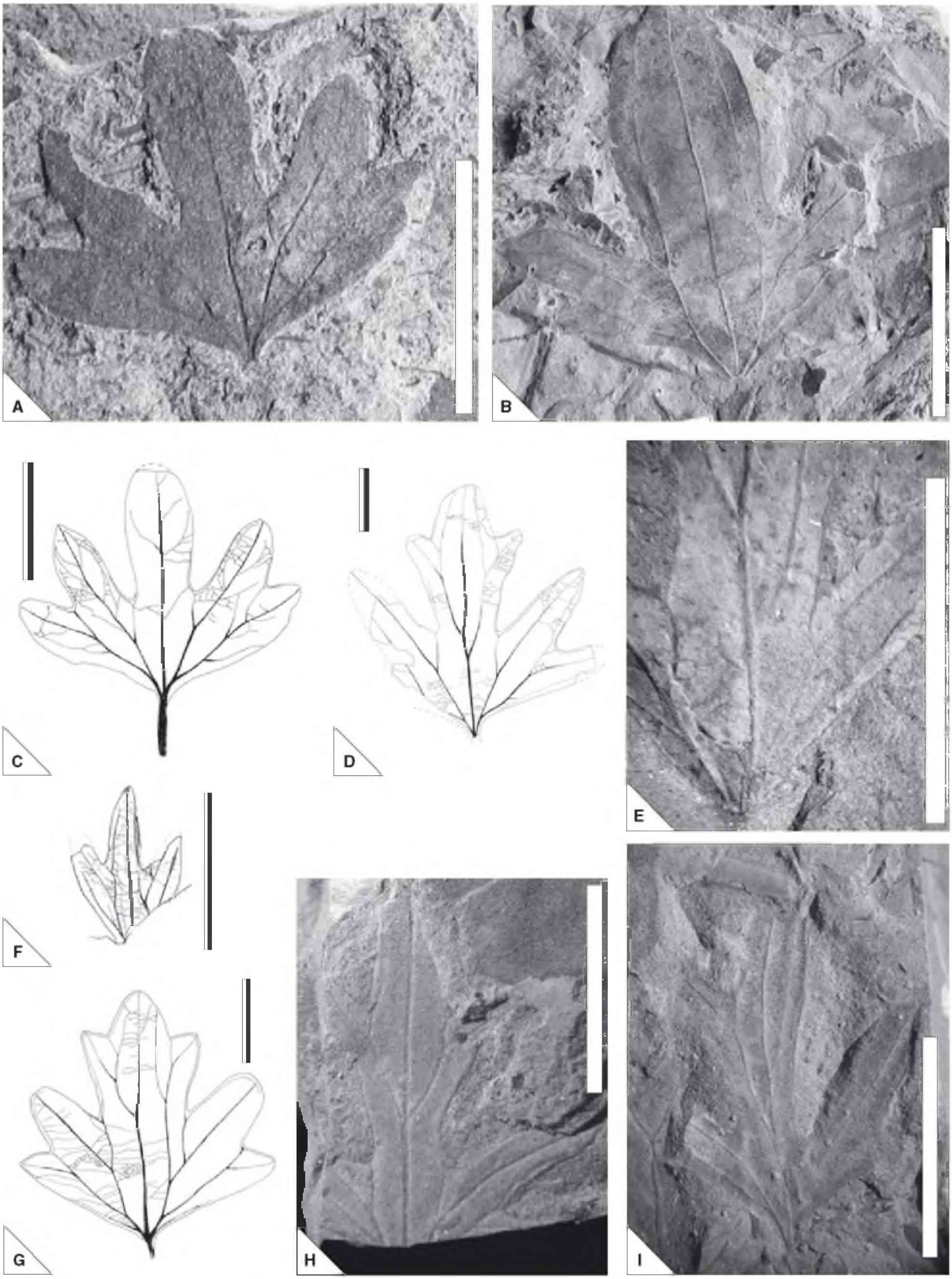
MA106 shares architectural features with the 'Pentalobaphyll morphotype' described from the Upper Cretaceous of the Rocky Mountains in western North America (Crabtree 1987) but it differs in having an elliptical shape, up to nine lobules, and leaf bases that are not always cuneated.

There are several records of palmately lobed leaves in the Cretaceous of Gondwana. *Araliaephyllum quinquelobatus* Cantrill, 1996 was described from the upper Albian of east Antarctica. This taxon resembles MA106 in having a 3–5-palmately lobed shape and palinactinodromous venation with a similar sinus and lobe venation, but differs in having suprabasal palinactinodromous venation, weakly incised rounded sinuses, ovoid lobes and secondaries diverging in angles between 45 and 60 degrees. Pole (1992) described two palmatilobate leaves from the Cenomanian of New Zealand: one of these, 'parataxon' TARA 28, resembles the small trilobate leaves with actinodromous venation of MA106; the other, OU29458, was only illustrated by Pole (1992, p. 199, fig. 89) but is similar to some specimens of MA106 with a more lobate blade. *Sterculiaphyllum australis* Dutra, 2000 is another Antarctic Cretaceous leaf from the Zameck Formation (Campanian–Maastrichtian) with venation patterns very similar to MA106, but the material is too scanty and fragmentary to enable full comparisons.

ANGIOSPERMAE GROUP 5

Characteristics. Leaves with pinnately lobed margin, pinnate primary venation and craspedodromous secondary venation.

TEXT-FIG. 6. A–C, Group 3, MA104 morphotype. A, camera lucida drawing of MPM-PB 1451. B, MPM-PB 1450. C, with an arthropod mining and pupation chamber MPM-PB 1368. D–G, Group 3, MA105 morphotype. D, MPM-PB 1453. E, camera lucida drawing of MPM-PB 1452. F, MPM-PB 1463. G, camera lucida drawing of MPM-PB 1463. White scale bars represent 1·5 cm; black and white scale bars 1·0 cm.



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MA107 morphotype
Text-figure 8A–C

Morphotype example. MPM-PB 1314.

Material. MPM-PB 1314(a–b), 1315, 1316(a–b), 1317, 1318, 1606–1608.

Description. Simple leaves, ovate in shape, notophyllous, 6·7 cm mean length, 6·0 cm mean width (4·8–7·8 cm length, 5·3–7·0 cm width). Obtuse apex angle, convex or retuse apex shape, obtuse base angle, complex or slightly cordate base shape with long petiole (*c.* 1·4 cm). Chartaceous texture. Pinnately lobed margin, 3–4 main lobes with accessory lobules more developed basally. Craspedodromous pinnate venation, straight main vein reaching apex, subopposite secondaries arising at moderate angle; first pair of secondaries are agrophic. Subopposite and percurrent tertiary venation, sinuous in course, some tertiaries innerve lobules. Tertiary veins are brochidodromous close to margin forming a weak intramarginal vein. Sinus innerved by two opposite tertiaries. Fourth order of venation develops irregular polygonal areoles. Looped marginal ultimate venation.

Remarks. Ten specimens were identified from the Mata Amarilla Formation, mainly from the MEL. These have a well-preserved outline, general venation and high order venation. They develop different degrees of lobules that are uniform in size and general outline.

McLoughlin *et al.* (1995) recovered pinnately lobed leaves (Angiosperm sp. C) from the Cenomanian of north-east Australia. These differ from MA107 because they have lobes with a mucronate apex, simple lobes, more secondaries and an ovate to elliptical shape. Pole (1992) described pinnate lobated leaves assigned to 'parataxon' TARA 15 from the Campanian of New Zealand that are similar to MA107 in lobation and secondary venation pattern, but differ in having a truncate base, more incised sinuses and more secondaries.

MA108 morphotype
Text-figure 8D–F

Morphotype example. MPM-PB 1301.

Material. MPM-PB 1301, 1307, 1360.

Description. Notophyllous leaves, 4·8 cm in length, 1·29 cm mean width (0·8–1·68 cm width), elliptical shape. Acute apex angle, convex in shape. Acute base angle, decurrent in shape. Stout petiole. Margin entire, pinnately lobed, with five pairs of alternate or subalternate lobes and one apical lobe. Lobes with greater development at base, convex margins and rounded apex. Lobe angles increasing towards leaf apex. Angular sinuses. Pinnate primary venation. Stout middle vein, thinning towards apex, slightly sinuous in course. Semicraspedodromous secondary venation, secondaries irregular, curved in course, decurrent, reaching medially to lobe or curving to lobe apex, 2–3 veins per lobe. Compound intersecondaries, irregular in course. Tertiaries arising perpendicular to secondaries, random reticulate pattern. Fourth order venation forms an irregular polygonal reticulum. Looped marginal ultimate venation. Low 2r rank.

Remarks. Even though only three specimens of this morphotype were found in the MAL, they exhibit distinctive architectural characters. In general, they show a state of preservation that makes recognition of higher order venation difficult, though the outline and margin are well preserved. MPM-PB-1307 appears to be a juvenile form owing to its small size and venation.

Similar forms have been described from the Campanian from New Zealand as 'parataxa' TARA 16 and TARA 21 (Pole 1992); MA108 differs in having a lower foliar rank with a more irregular venation pattern, fewer secondaries and distinct intersecondaries reaching the lobe apex.

ANGIOSPERMAE GROUP 6

Characteristics. Blade ovate or elliptical in shape, dentate margin.

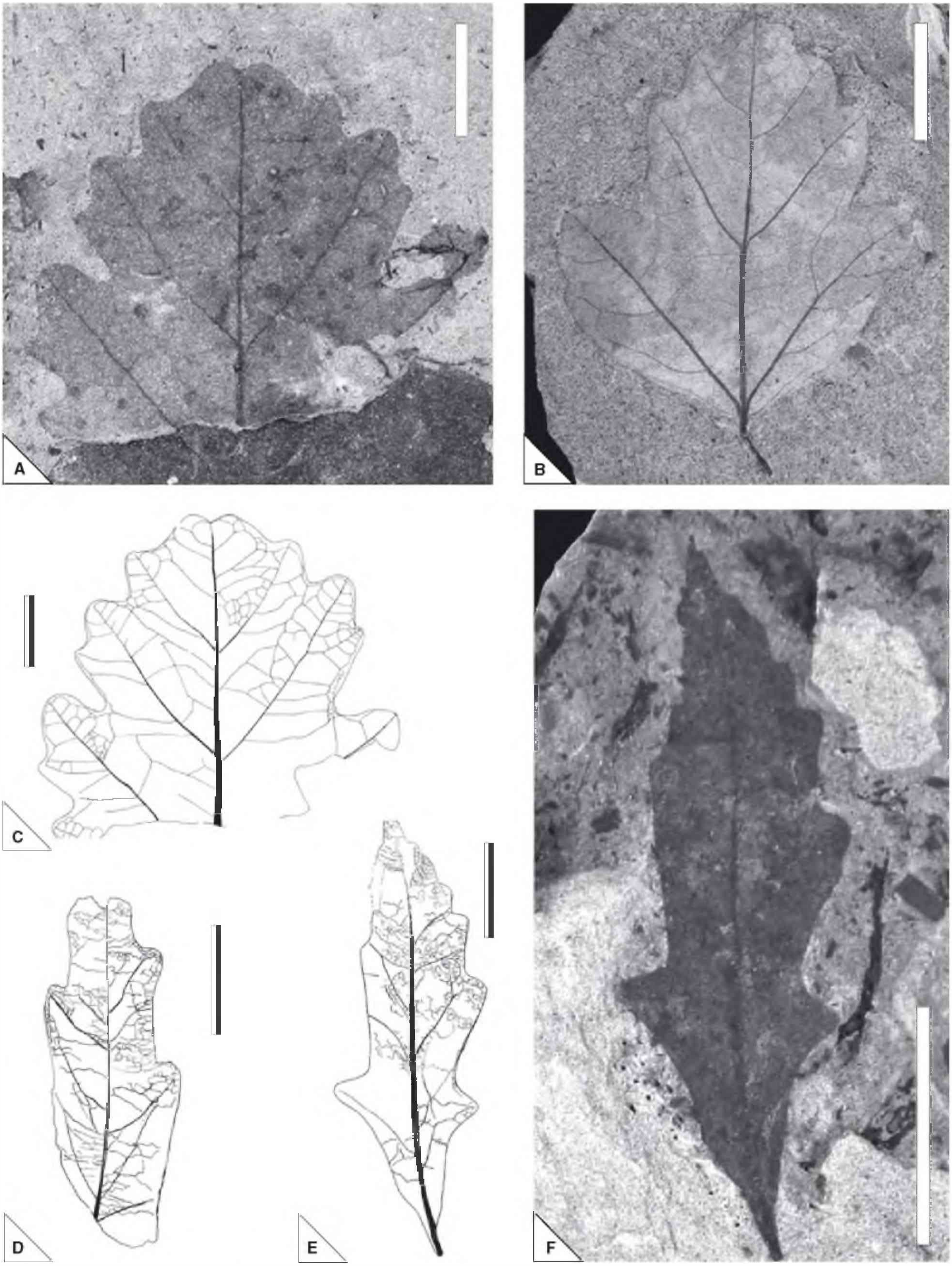
MA109 morphotype
Text-figure 9A–B

Morphotype example. MPM-PB 1309.

Material. MPM-PB 1308–1311.

Description. Microphyllous ovate leaves, 6·17 cm mean length, 4·15 cm mean width (2·9–7·5 cm length, 3·2–5·6 cm width). Apex not preserved. Concave base, generally symmetrical, acute base angle. Simple dentate-serrate margin, tooth spacing decreasing towards apex. Tooth shape basally convex and apically straight. Teeth innerved by a branch from a secondary loop, supplied by accessory marginal venation. Stout petiole. Chartaceous texture. Pinnate primary venation. Primary vein straight, strong at base and thinning to apex. Semicraspedodromous to festooned semicraspedodromous secondary venation.

TEXT-FIG. 7. A–I, Group 4, MA106 morphotype. A, five-lobed leaf MPM-PB 1410. B, MPM-PB 1452. C, camera lucida drawing of MPM-PB 1410. D, camera lucida drawing five-lobed leaf MPM-PB 1392. E, three-lobed leaf MPM-PB 1396. F, camera lucida drawing three-lobed leaf MPM-PB 1461. G, camera lucida drawing seven-lobed leaf MPM-PB 1412. H, seven-lobed leaf MPM-PB 1391. I, six-lobed leaf MPM-PB 1386. White scale bars represent 1·5 cm; black and white scale bars 1·0 cm.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Secondaries alternate at an acute angle, sinuous in course, vein spacing uniform, acute and uniform vein angle. Intersecondaries present. Tertiaries alternate percurrent, oblique, exmedially decreasing with respect to primary and forming polygonal areoles. In margin, they form loops, branching from secondary at an acute or right angle. Loops constitute smooth intramarginal vein at base of lamina. Fourth order venation forms irregular areolations. Looped marginal ultimate venation.

Remarks. Four specimens were assigned to this morphotype, all from the MEL. Preservation is good, showing high order venation, margin and tooth shape, which corresponds to the cunonioid type (Hickey and Wolfe 1975). *Laurelia amarillana* Berry, 1928 is included in this morphotype, although it differs in the development of secondary and tertiary brochidodromous arcs.

MA110 morphotype
Text-figure 9C–D

Morphotype example. MPM-PB 1312.

Material. MPM-PB 1304, 1312, 1313.

Description. Simple leaves, lanceolate-ovate or elliptical, more than 4 cm long and 1·3–2·6 cm wide. Serrated margin. Teeth concave/convex in shape. Angular sinuses. Simple craspedodromous venation, strong primary vein, decurrent secondary veins, curved in course, generating branches to margin that innerve teeth medially, 2–6 simple teeth per secondary.

Remarks. Although the material is fragmentary and scarce, the good preservation shows third order venation. No comparable forms are known from other Gondwanan Cretaceous floras.

MA111 morphotype
Text-figure 9E–I

Morphotype example. MPM-PB 1303(a).

Material. MPM-PB 1302, 1303(a–b), 1304, 1305, 1609–1611.

Description. Simple leaves, lanceolate-ovate. 7·9 cm mean length, 2·28 cm mean width (6·7–10·3 cm length; 1·6–3·0 cm width). Symmetrical to slightly asymmetrical. Acute apex angle, acute base angle and decurrent base shape. Serrated margin with spaced glandular teeth (fewer than five pairs). Normal petiole. Chartaceous texture. Pinnate primary venation. Strong primary vein, sligthly curved. Semicraspedodromous or festooned semicraspedodromous secondary venation. Secondaries dense (3–4 per tooth), thin, arising at a medium angle and decreasing smoothly towards apex. Intersecondaries present and similar to secondaries. Tertiaries alternate percurrent, sinuous, secondary angle decreasing exmedially to primary vein. Tertiaries and higher order venation form polygonal to irregular areoles. Weak intramarginal vein. Asymmetrical teeth with long basal sides and short apical sides, straight-flexuous in shape, rounded sinuses. Teeth with spherulate glandular apex, innerved by strong middle vein (from a secondary or a branch of it) with a pair of lateral accessory veins of higher order running to apex near tooth margin.

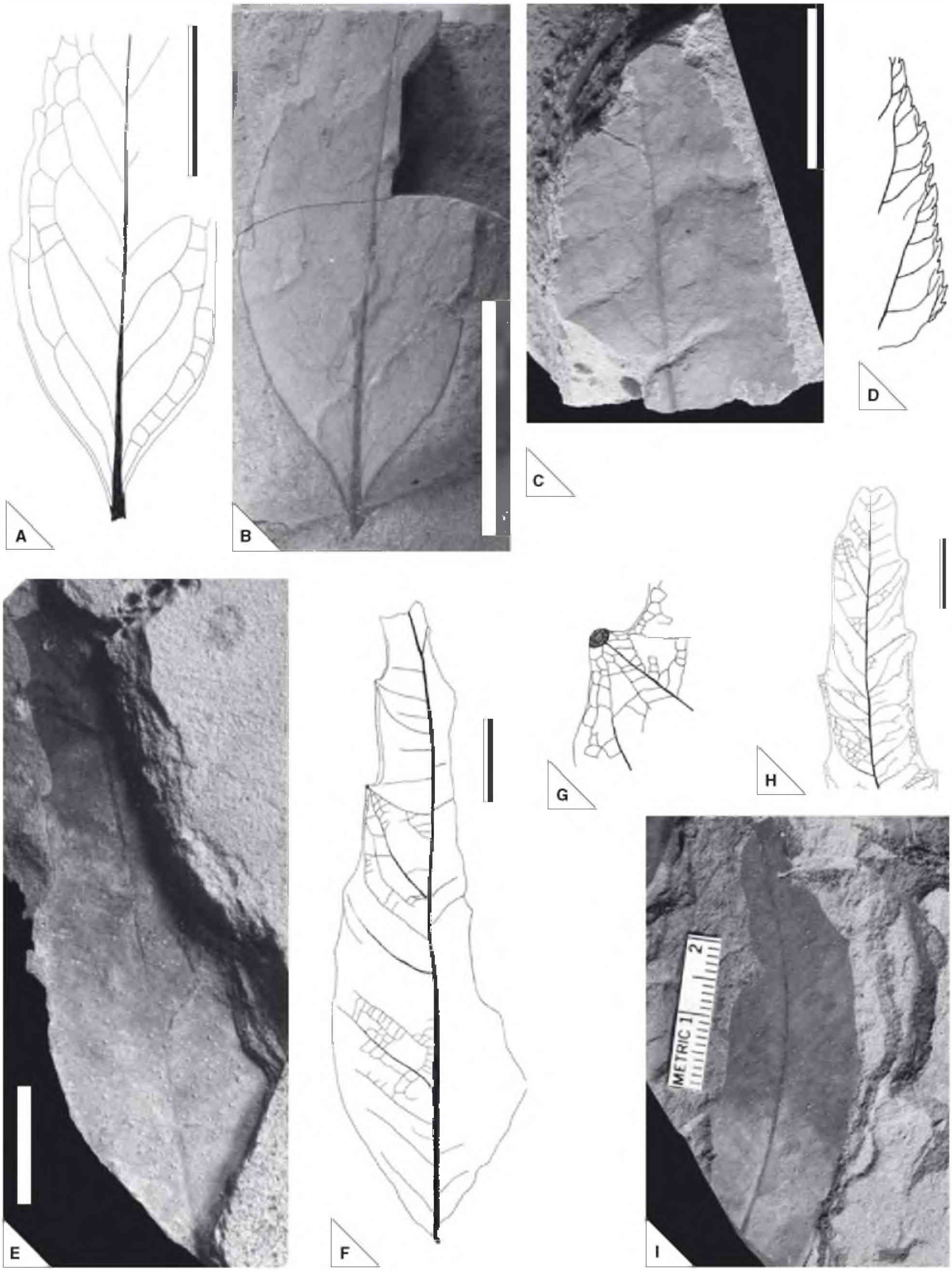
Remarks. Eight specimens have been assigned to this morphotype. Third order venation and tooth shape are distinct, although apex shape could not be determined. Likewise, the outline and margin are well preserved. The chartaceous texture is characteristic. The teeth are comparable with the chloranthoid type (Hickey and Wolfe 1975); no comparable forms are known from other Cretaceous floras from Gondwana.

DISCUSSION

Based on the characterization of 12 morphotypes and their association in six morphological groups, angiosperm leaf diversity has been estimated for sediments of Cenomanian–Coniacian age from the eastern margin of the Austral Basin, south-western Patagonia. Analysis of the abundance of major groups of plants indicates that the flora is represented by angiosperms (82 per cent), ferns (10 per cent) and conifers (8 per cent). This analysis has only been carried out for the MAL because, as discussed by Spicer (1980), continental flood-plain facies better represent the original content of the leaf-litter. Furthermore, fern and gymnosperm leaves (Text-fig. 10) in the MEL are too fragmentary and poorly preserved to enable quantification of the abundance of these groups. Nevertheless, the presence of coniferous stumps at this level proves that gymnosperms lived there.

Comparisons of the relative abundance of groups and morphotypes within and between levels show that the diversity of angiosperm leaves (Table 1; Text-figs 11–12) has a distinctive pattern of distribution in each palaeoenvironment. The relative abundance of each morphotype

TEXT-FIG. 8. A–C, Group 5, MA107 morphotype. A, MPM-PB 1316. B, MPM-PB 1314. C, camera lucida drawing of MPM-PB 1316. D–F, Group 5, MA108 morphotype. D, camera lucida drawing of MPM-PB 1360. E, camera lucida drawing of MPM-PB 1301. F, MPM-PB 1301. White scale bars represent 1·5 cm; black and white scale bars 1·0 cm.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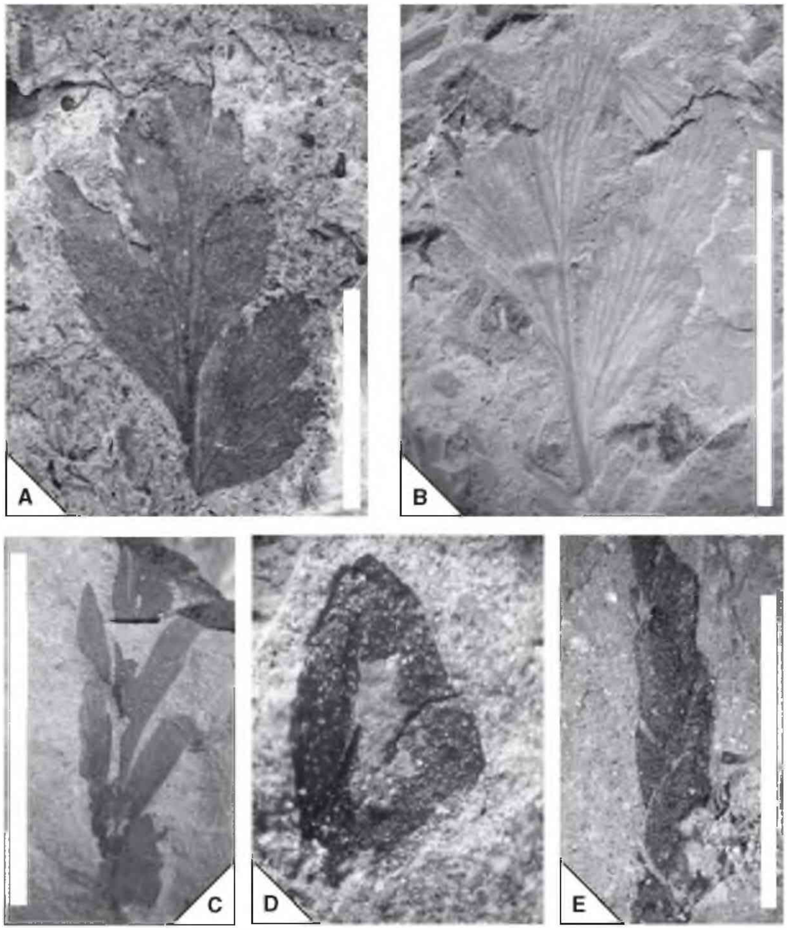


TEXT-FIG. 10. Ferns and conifers from the Mata Amarilla Formation. A–C, ferns. A, MPM-PB 1427. B, MPM-PB 1415. C, MPM-PB 1459. D–E, conifers. D, disarticulated scale-like leaf MPM-PB 1415; ×40. E, articulated MPM-PB 1438. Scale bars represent 1·5 cm.

and group shows different dominances for each plant-bearing level. Thus, in the MEL, Group 2 is dominant (48·26 per cent) with Group 1 co-dominant (23·78 per cent). In the MAL, Group 3 is the dominant group (48·96 per cent) with Groups 4 (22·9 per cent) and 1 (19·1 per cent) co-dominant. For each plant-bearing level the relative abundance of each morphotype (Text-fig. 11) shows a positive correlation with the group dominance and a discrimination of exclusive morphotypes. In this sense, morphotypes MA109 and 110 are exclusive to the lower level, while MA103–105 and 108 are exclusive to the upper level.

Regarding laminar sizes of the angiosperms: in the MEL leaves range from 400 to 2500 mm^2, with most falling between the microphyll (most frequent) and mesophyll size classes. In the MAL leaf size is mainly less than 500 mm^2, corresponding to nanophyll or microphyll size classes (Text-fig. 13). The pattern of size in each level could be related to different types of transport before deposition (Spicer 1980).

From a comparative study of fossil plants, taphonomy and sedimentary analysis of the Mata Amarilla Formation, significant preservational differences are apparent between the two plant-bearing levels. The leaves from the MEL show a predominant degradation of the lamina, which is consistent with organic decomposition, whereas in the MAL, the presence of fractures in the foliar margins suggests degradation by relatively high-energy sedimentary processes.

The degree of fragmentation in each level was estimated based on whether it was possible to measure the total length of each specimen. In the lower level the degree of fragmentation is low (29 per cent) whereas in the upper level it is very high (80 per cent). The percentage of coniferous leaf disarticulation is high in the lower level (where only dispersed scale leaves are found) and the fern leaves are more fragmentary. In the upper level conifer

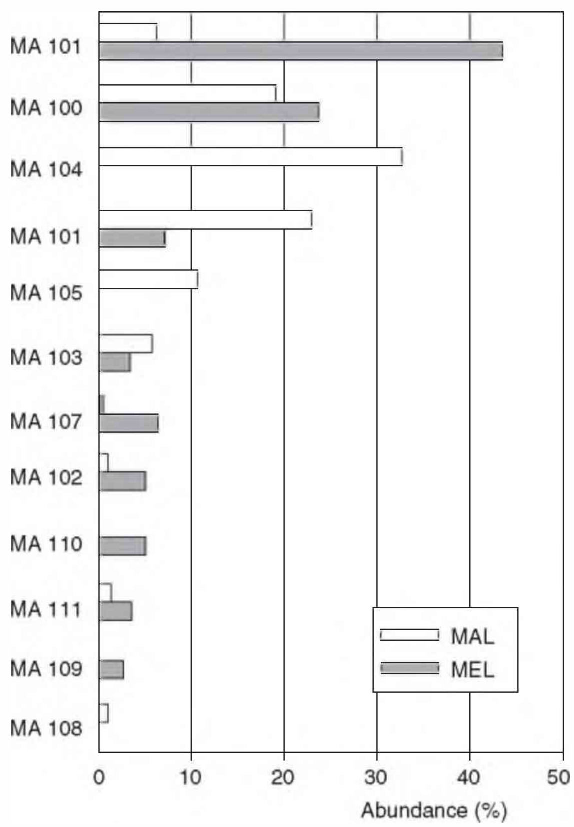
TEXT-FIG. 9. A–B, Group 6, MA109 morphotype. A, camera lucida drawing of MPM-PB1309. B, MPM-PB 1309. C–D, Group 6, MA110 morphotype, MPM-PB 1312. E–I, Group 6, MA111 morphotype. E, MPM-PB 1303. F, camera lucida drawing of MPM-PB 1303. G, detail of tooth venation of MPM-PB 1303. H, camera lucida drawing of MPM-PB 1304. I, MPM-PB 1305. White scale bars represent 1·5 cm; black and white scale bars 1·0 cm.

TABLE 1. Abundance of morphotypes and groups in the plant-bearing levels.

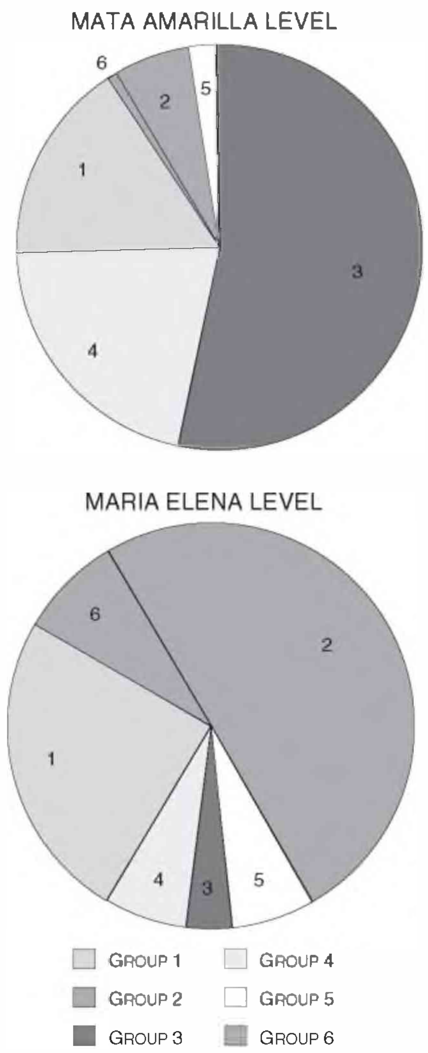
Group	Morphotype	MAL			MEL		
Group 1	MA100	64	19·10%	19·10%	34	24·46%	24·46%
Group 2	MA101	21	6·27%	6·87%	62	44·60%	49·64%
	MA102	2	0·60%		7	5·04%	
Group 3	MA103	19	5·67%	48·96%	5	3·60%	3·60%
	MA104	109	32·54%		0	0·00%	
	MA105	36	10·75%		0	0·00%	
Group 4	MA106	77	22·99%	22·99%	10	7·19%	7·19%
Group 5	MA107	1	0·30%	1·19%	9	6·47%	6·47%
	MA108	3	0·89%		0	0·00%	
Group 6	MA109	0	0·00%	0·89%	4	2·88%	8·64%
	MA110	0	0·00%		3	2·16%	
	MA111	3	0·89%		5	3·60%	

leaves commonly show organic connection and helical arrangement.

The MEL contains more angiosperms than gymnosperms and ferns. The good preservation of the angiosperm leaves and their larger size contrast with the upper level. The high degree of fragmentation of ferns, conifers and some angiosperms suggests considerable transport by water. This, together with the predominant degradation



TEXT-FIG. 11. Diversity of angiosperm morphotypes in the plant-bearing levels.



TEXT-FIG. 12. Abundance of angiosperm leaf groups in each plant-bearing level.

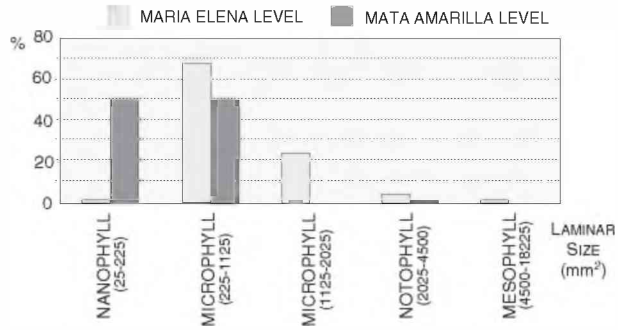
type present in some morphotypes, allows us to distinguish allochthonous or parautochthonous plant remains from those that were growing very close to the depositional site. Considering these taphonomic data alongside the information on sedimentary facies, which we interpret as representing a subaerial delta-plain, we infer that Groups 1 and 2 represent angiosperms that lived in the distributary complex on the plain. The groups of leaves that are scarcely represented (3 and 4) and only preserved in fragmentary form, reflect plants that lived inland beyond the depositional site.

Although the MAL is dominated by angiosperm leaves, the representation of gymnosperms and ferns is better than in the MEL. The degree of fragmentation and the selection of mainly lower sizes in the MAL indicate relatively high-energy sedimentary environments in a fluvial flood plain (Poiré *et al.* 2004*b*). As stated by Spicer (1981) for this type of setting, the fragmentary nature of the leaves is a result of transport of leaf-litter by relatively high-energy water, perhaps during flood events.

The numerous permineralized logs in the succession are all coniferalean (Poiré *et al.* 2004*a*); fragments of branches and twigs have also been found as impressions and compressions associated with angiosperm leaves. This may suggest that the angiosperms were not large trees and that they formed part of the mid-canopy or shrubs and undergrowth.

Several mid Cretaceous macrofloras are known from Gondwana (Pole 1992; McLouglin *et al.* 1995; Cantrill and Nichols 1996). Mata Amarilla is coeval and located at the same palaeolatitude as the Cenomanian Winton Flora of north-west Australia, which was described by McLoughlin *et al.* (1995). The leaf morphotypes from Mata Amarilla resemble, but are not related to, the Winton flora. The latter is dominated by gymnosperms and has eight angiosperm leaves with prevailing dentate or deeply cleft margins and mucronate teeth. Winton angiosperms also have a different leaf-size distribution with notophyll size predominant and less representation of microphyll and mesophyll sizes. In contrast, the Mata Amarilla flora has 12 morphotypes, with microphyll and nanophyll sizes prevailing (Text-fig. 13). The Winton Flora represents the earliest record of a macroflora with slightly varied angiosperm leaves for eastern Gondwana. For south-western Gondwana, Mata Amarilla represents the first evidence of a flora containing abundant and more diverse angiosperm leaves.

Pole (1992) described several taphofloras from the Upper Cretaceous of New Zealand. They are dominated by conifer leaves, but angiosperm representation comprises 21 leaf types (seven from the Cenomanian and 16 from the Santonian–Maastrichian). The Mata Amarilla Formation contains only two morphotypes (MA106 and 108) that may be related to some of the Campanian



TEXT-FIG. 13. Comparative laminar size in the plant-bearing levels based on 164 measurements. Microphyll leaf size was divided into two size categories in order to delimit the two data populations more clearly: one between 225 and 1125 mm^2 and the other between 1125 and 2025 mm^2.

leaves from New Zealand. By the Cenomanian New Zealand angiosperm floras are dominated by mesophyll sizes and have a lower representation of notophyll and microphyll sizes (Pole 1992). This size distribution is markedly different from that of the Mata Amarilla flora (Text-fig. 13).

In southern Africa there is a flora of Cenomanian–Coniacian age from near the town of Orapa, north-central Botswana. This flora is known only in general aspect (Rayner *et al.* 1997). It is dominated by angiosperms. The leaves are mostly microphyllous and 45 per cent of them have an entire margin. Biodiversity of the Orapa flora is apparently higher than at any other site in Gondwana, in including 29 foliar types from simple to pinnately lobed. They are very different from those of Mata Amarilla; this may be accounted for by the fact that the African flora is from lacustrine sediments that accumulated in a volcanic environment.

Cantrill and Nichols (1996) described seven angiosperm foliar types from the upper Albian of the west of the Antarctic Peninsula. Only one of these, *Araliaephyllum quinquelobatus*, is comparable with a morphotype in the Mata Amarilla flora (MA106), but the distribution of size classes is similar.

Taking into account generalized leaf types known from Gondwana (Zastawniak 1994; Archangelsky *et al.* 2004), Mata Amarilla Groups 3–5 could be considered as 'Myrtophyll', 'Pentalobophyll' and 'Pinnatilobulophyll', respectively. 'Myrtophyll' leaves in southern South America appeared in Albian times, dominating poorly diversified floras (Passalía *et al.* 2001). This foliar type continues into the Cenomanian–Coniacian, diversifying and maintaining its dominance in some deposits such as the MAL. In Antarctica this type apparently first appears in the Campanian–Maastrichtian (Zastawniak 1994).

Palmately lobed palinactinodromous leaves are known for some Cretaceous localities in Gondwana. The first record is in late Albian deposits in Antarctica (Cantrill and Nichols 1996). In the Cenomanian–Coniacian they radiated to New Zealand (Pole 1992) and southern South America (Mata Amarilla Formation).

Pinnately lobed leaves are known from the Upper Cretaceous in South America and north-east Australia. The earliest record is from early Aptian beds in Patagonia, and is of dentate to serrate forms (Romero and Archangelsky 1986). They continue with entire margins in the Cenomanian–Coniacian Mata Amarilla Formation (MA107 and 108) following later with different characteristics in the Campanian of south-west New Zealand (Pole 1992).

CONCLUSIONS

The composition, characteristics and preservation of the foliar remains of the two plant-bearing levels, MEL and MAL, and their sedimentary facies suggest that two different types of plant community are represented in the Mata Amarilla Formation. The lower level (MEL) accumulated in a marine coastal area over the subaerial delta plain where the canopy was represented by conifers (Zamuner *et al.* 2004) and the herbaceous, shrub and small tree flora was represented by angiosperm groups, with leaves of Groups 1 and 2 dominant. The upper level (MAL) accumulated in an inland, flood-plain setting and is characterized by a good representation of both herbaceous and arboreal taxa. The herbaceous component mainly consisted of ferns along with a canopy of conifers (Poiré *et al.* 2004*a*). The most abundant angiosperms with leaves of Groups 1, 3 and 4 represent the low arboreal and/or herbaceous/shrub vegetation.

The different states of biological degradation in the foliar assemblage indicate that leaf fall was constant and that the plants were not deciduous. The presence of fungal activity suggests high temperatures and high relative humidity.

The Cenomanian witnessed one of the main diversifications in angiosperm foliar types and plasticity with adaptation of the plants to different environments. As in the rest of the world, the Cenomanian of Patagonia contains the beginnings of angiosperm domination of macrofloras. Compared with other middle–lower Upper Cretaceous taphofloras known from the Southern Hemisphere, the Mata Amarilla Formation shows a slightly greater morphological diversity of angiosperm leaves, providing the first evidence of an angiosperm-dominated macroflora in south-west Gondwana.

More research is needed to gain a better understanding of the evolution and diversification of angiosperms in Gondwanan Cretaceous macrofloras and the palaeobiogeography of Gondwana. Future analyses of Cretaceous macrofloras from Patagonia, currently under way, will contribute to this.

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