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A new calymmate mimosoid polyad from the Miocene of Argentina

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Abstract

A palynomorph with an unequivocal relationship to the eight-grain polyads of the mimosoid genus *Calliandra* Benth., is described from the Miocene sediments of San Juan Province, Argentina. Comparison of the fossil palynomorph with polyads of the extant *Calliandra* species shows a resemblance to those which have one, highly specialized, appendiculate monad. The new palynomorph has a rudimentary appendix, apparently transitional in the path leading to the more highly developed appendiculate forms in the extant *Calliandra* group. This specialized polyad type is considered to be one of the most highly evolved forms in subfamily Mimosoideae. The closest affinity of the new fossil polyad is with the eight-grain calymmate polyads of *Calliandra chilensis* Benth., a species which has developed in the extra-tropical, xerophilous shrub, habitat of north-central Chile. The disappearance of *Calliandra* species in San Juan Province is thought to be related to the culmination of the Andean rising, and the consequent interruption to the Pacific Ocean climatic influence. This new discovery is the first fossil record of *Calliandra* for Argentina, as well as being the most southerly and the oldest. It reinforces the hypothesis of an early origin and diversification for the Leguminosae in Tropical America.

Keywords: appendiculate; Argentina; *Calliandra*; calymmate; eight-grain polyad; Miocene

1. Introduction

The first records of Mimosoideae with compound pollen are from the Early Eocene of North America (Crepet and Taylor, 1985), while records for the Middle Eocene are many and the taxa diverse, see for example: Muller (1981); Herendeen (1992); Guinet and Ferguson (1989) and references cited therein. In the Neotropics the fossil pollen record of Mimosoideae is also abundant and varied: Lima and Salard-Cheboldaeff (1981), Lima and Amador (1985); Lima et al. (1985a,b); Caccavari and Anzótegui (1987); Barreda and Caccavari (1992); Graham (1992); Graham and Dilcher (1995). The available data show that the greatest diversification occurs during the Eocene to Oligocene (Caccavari, 1996).

The newly discovered *Calliandra*-like polyad is one component of a well-preserved and highly diverse palynological assemblage from the La Ollita Formation, that crops out of the Quebrada Salada, on the eastern slopes of the Cordillera de La Brea, Valle del Cura Region, San Juan Province, Argentina (Fig. 1). The fossil palynomorph has the characteristic appearance of the

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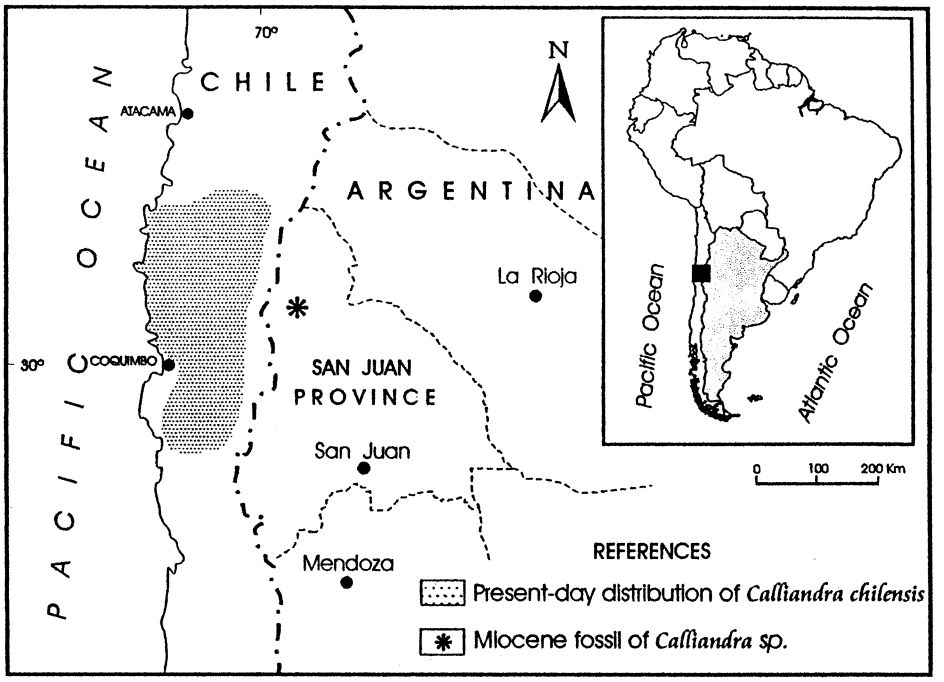


Fig. 1. Location map showing fossil locality of *Calliandra* sp. and present day distribution of *C. chilensis* Benth.

eight-grain polyads in the genus *Calliandra*: asymmetric ellipsoid shape, with a dissymmetrical tear-shaped outline. The eight grains which form the polyad are monoplanar. The affinity of the fossil polyad to recent *Calliandra* was determined with reference to Van Campo and Guinet (1961); Guinet (1965, 1969, 1981); Sorsa (1969); and Hoc (1989), as well as to our own reference slide collection (Table 1).

This is the first Argentinian record of a fossil

Table 1
Principal modern *Calliandra* polyads from the eight grains examined

Taxon	Country	Voucher collection	Herb.	BAPA	Polyad type with appendix
C. bijuga Rose	Mexico	Herb. Hinton GH 4099	SI	3054	
C. aff. *blanchetii* Benth.	Brazil	Lima 49.180	SI	3051	
C. brevicaulis Micheli	Argentine	Burkart 8125	SI	3057	
C. californica Benth.	Mexico	Chisaki y Bell 519	SI	3060	
C. chilensis Benth.	Chile (Dto. Elke)	Herb. Looseria 4328	SI	3064	+
C. chilensis Benth.	Chile (Coquimbo)	Jiles Col. 2423	SI	3065	+
C. foliolosa Benth.	Argentine	Cabrera et al. 28784	SI	3072	
C. linearis Benth.	Brazil	Willams y Assis 6972	SI	3082	+
C. longipes Benth.	Argentine	Burkart 15374	SI	3103	
C. mertensioides (Nees et Martius) Benth.	Brazil	Barreto Col. 9553	SI	3086	+
C. parvifolia (Hook et Arn.) Speg	Argentine	Hicken 5393	SI	1124b	
C. selloi (Spreng.) Mackbr.	Brazil	Mendez y Magalâes Col. 490	SI	3094	
C. cf. *squarrosa* Benth.	Brazil	Lima 50542	SI	3050	
C. twedii Benth.	Argentine	D. Cozzo (BA) 52259	BA	2997	

polyad with *Calliandra*-like characteristics. It is also the oldest record for the genus, since no records of *Calliandra* pollen exist prior to the Pliocene of Colombia (Hooghiemstra, 1984). The first published fossil record of *Calliandra* was for the Holocene of Panamá (Bartlett and Barghoorn, 1973).

The polyads of the Neotropical *Calliandra* are considered to be highly specialized in comparison to those of the Paleotropics (Guinet 1981). The presence of a similar polyad in a Miocene deposit is indicative that during this period the subfamily was probably already well-advanced in terms of evolution and dispersal.

Other components of the fossil pollen assemblage are representative of mainly herbaceous or shrubby species that have affinities with families Cyperaceae (*Cyperaceaepollis neogenicus*), Poaceae (*Graminidites* sp.), Asteraceae (*Tubulifloridites antipodica*, *Mutisiapollis viteauensis*), Ephedraceae (*Equisetosporites notensis*, *E. claricristatus*, *E. lusaticus*), Anacardiaceae (*Striatricolporites gamerroi*), Chenopodiaceae (*Chenopodipollis chenopodiaceoides*), Malvaceae (*Malvacipolloides* sp., *Baumannipollis variaperturatus*) and Symplocaceae (*Senipites patagonica*). At some levels, fresh-water algae are abundant, and a few dinoflagellate cysts are also recognized. Tree elements are very scarce: they are represented by the families Podocarpaceae (*Podocarpidites* sp.), Myrtaceae (*Myrtaceidites* sp) and Fagaceae (*Nothofagidites saraensis*) Pteridophyta and Bryophyta spores are also very scarce.

The range of palynomophs suggests a Middle Miocene age for the La Ollita Formation (Barreda et al., 1998). This age estimation is supported by a radiometric dating from an andesite outflow, interbedded near the base of the analyzed section, which gave a result of 16 ± 1 Ma (Limarino et al., in press). On both sedimentological and palynological grounds the development of pool systems under warm-temperate to warm, relatively dry climate conditions was deduced (Barreda et al., 1998).

2. Materials and methods

To recover the fossil material standard palynological techniques were followed, namely: treatment of the samples with hydrochloric and hydrofluoric acid, rinsing with diluted HCl, filtering the organic residue through meshes of different gauge $+25$ and -2.5 μm, and mounting (Brown, 1960). Slides of fossil material are housed at the Palynotheca of the Centro de Investigaciones en Recursos Geológicos (C.I.R.G.E.O.) under the catalogue number 1127, prefixed CIRGEO Palin.

Pollen material of 13 species (one collection for each, with the exception of *Calliandra chilensis*, two collections) (Table 1) was acetolyzed (Erdtman, 1960) for comparison. Slides of extant material are housed at the Actuopalynotheca of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", and prefixed BAPA (Buenos Aires, Palinologia, Actual).

All photomicrographs were taken using Agfapan 25 film, and the co-ordinates of the figured specimens correspond to the Leitz Dialux microscope No. 924193, from CIRGEO.

3. Results

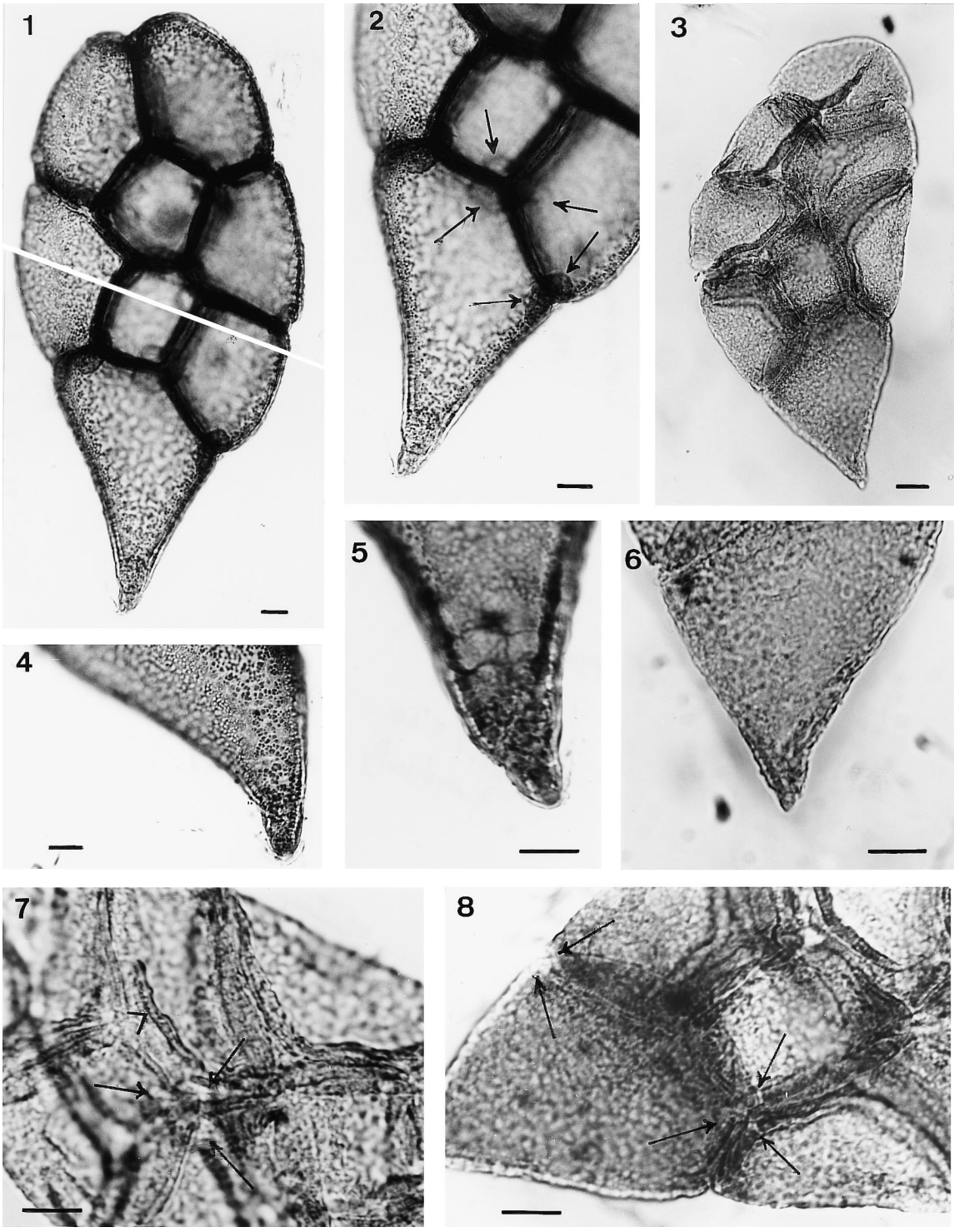
The studied material is comparable to the morphological features described for eight-grain calymmate polyads of Neotropical *Calliandra* (Guinet, 1965, 1969, 1981; Guinet and Barth, 1967), and to the appendiculate group sensu Guinet (1965).

The appendiculate polyads of all the Neotropical *Calliandra* examined were slightly to distinctly dissymmetric and large (100–200 μm). The eight grains comprising the polyad were monoplanar. Usually the pores of adjacent monads are positioned in groups of three on the equatorial-distal plane (Plate I,1 and 2). The structure of the exine is usually columellate and the outer layer surrounds all the grains (calymmate polyad). Some of the endemic species of the Amazonian basin showed the greatest degree of differentiation, with one highly modified peripheral grain which is tapered, culminating in an appendix [a modification which has been compared to the pollinia of Asclepiadaceae and Orchidaceae (Guinet, 1969, 1981)].

3.1. *Description of the fossil polyad* (Plate I,3,6–8)

Monoplanar calymmate eight-grain polyad, dissymmetrically ellipsoid, tear-shaped in outline, one

PLATE I



grain is highly modified: acuminate with the apex, modified into a small appendix. The other seven grains are irregularly polyhedric, with pores positioned at the junction of two or three adjacent grains, in an equatorial-distal position (Plate I,7 and 8). Exine tectate, columellate, with a smooth to slightly rugulose surface. Columellae distributed irregularly. Appendix comprised only of sexine.

3.1.1. Dimensions

Maximum length of the polyad: 135 μm; maximum width: 60 μm. Length of appendix: 9 μm. Thickness of exine: 2 μm.

3.1.2. Comparison

Calliandra sp., first reported from the Holocene of Panamá (Bartlett and Barghoorn, 1973), resembles our specimen in general features, but is much larger: 215 μm maximum diameter and lacks an appendix.

3.1.3. Observations

Although only one specimen was recovered, its distinctive characteristics confirm its affinity to the polyad structure of Neotropical *Calliandra* spp.

Between the eight-grain polyads of extant *Calliandra*, Guinet (1965) recognizes a small group of species where one of the monads is highly differentiated and, from an abrupt constriction, an appendiculate sexinous structure extends (Guinet and Barth, 1967; Guinet and Hernández, 1989). Although the fossil polyad does not have such a conspicuous appendiculate shape it, nevertheless, has a rudimentary sexinous appendix indicative of affinity with the 'appendiculate' group. The fossil specimen may represent a transitional form between the two morphological types recognized by Guinet (1965) for extant eight-grain polyads of Neotropical *Calliandra*.

PLATE I

Scale bar in all illustrations, 10 μm. *Calliandra chilensis* Benth.
1 General view.
2 Appendix detail and pores (arrows) of the Fig. 1
4,5 Other polyad appendices with different degrees of development. Note that these are comprised only of sexine.
Calliandra sp. Specimen on slide CIRGEO 1127, coordinates: 48,7/ 95,4.
3 General view.
6 Detail of incipient appendix.
7 Detail showing columellate exine (arrowhead) and pores (arrows).
8 Detail showing pores (arrows).

3.2. Botanical affinity

Of the extant *Calliandra* pollen material examined for comparison (Table 1), the most similar polyad to that of the fossil material is *Calliandra chilensis* Benth. (Plate I,1, 2, 4 and 5). Both the fossil and the extant polyads, have a similar shape, exine sculpture, and more particularly, the appendiculate condition. *C. chilensis*, however, is considerably larger (cf. Plate I,1 and 3) and there is a small degree of variation in the length of the appendix. Guinet (1965, 1969) includes *C. chilensis* in the 'non-appendiculate' group. However, both the material examined here (Table 1) and that figured by Heusser (1974) clearly show the appendiculate condition. It is possible that there is a mistake in the determination of the single specimen observed by Guinet (1965, 1969).

4. Discussion and conclusions

4.1. Paleobiogeographic considerations

Most species of *Calliandra* have a tropical distribution. However, *Calliandra chilensis* is one of a few species of the genus that thrive in an extratropical habitat (Bentham, 1875). This species grows in the Desierto phytogeographic Province, Coquimbo District (Cabrera and Willink, 1980), in the subtropical zone of dwarf and xerophytic shrubs as a stunted bush, covering the mountain area of the 'provinces' of Atacama and Coquimbo (now Regions III and IV, respectively) in the northern centre of Chile, between 28 and 31°S (Rummey, 1968) (Fig. 1). The climate is warm-temperate and arid, with an annual rainfall of between 40 and 80 mm, most frequent in winter. The oceanic influence of the cold Humboldt stream lowers the temperature slightly, making the summer drought less rigorous, often causing fog

in the mountain areas (Skottsberg, 1950; Walter, 1977).

Notably, the fossil species, is part of a diverse palynological assemblage suggesting similar climatic conditions (Barreda et al., 1998).

The habitat of extant *Calliandra*, as a rule, does not exceed 1000 m of altitude. This prompts the suggestion that, during the Middle Miocene, the altitude of the Valle del Cura region, where the palynomorph was found, may have been similar. Furthermore, the Pacific Ocean might still have had a slight climatic influence on the area.

Subsequent changes to the local environment due to the continued uplift of the Andes, with the consequent barrier to oceanic influence from the Pacific, may have been the underlying cause for the demise of *Calliandra* species in the area, and possibly also of the pollinators. In some species of extant *Calliandra* the principal legitimate visitors are bats and sphingid moths (Macqueen and Hernández, 1997).

4.2. Palynological considerations

The distinctive morphology of the fossil specimen, with a rudimentary appendix, places it in an intermediate position between the two types of extant eight-grain polyads of *Calliandra* described by Guinet (1965): 'appendiculate' and 'non-appendiculate'. Following Guinet's speculation, this palynomorph may represent a transitional evolutionary group. The extant species *Calliandra chilensis*, which has the closest palynological characteristics, presents a degree of variability in the morphology of the appendix, from rudimentary (Plate I,5) to conspicuous (Plate I,4).

4.3. Stratigraphical considerations

Fossil palynomorphs assignable to eight-grain polyads of the genus *Calliandra* are rarely found. Previously the only fossil records of *Calliandra* species are for the Holocene of Panamá (Bartlett and Barghoorn, 1973) and for the Pliocene of Colombia (Hooghiemstra, 1984).

This new fossil record for *Calliandra* is not only the first record for Argentina, but also the most southerly, and the oldest.

4.4. Evolutionary considerations

Guinet (1965, 1969, 1981), Guinet and Ferguson (1989) consider the eight-grain, appendiculate polyad one of the most specialized forms within the Mimosoideae.

On this basis, the fossil polyad may indicate that by the Miocene, the Mimosoideae had already attained a high degree of diversification and dispersal in South America, supporting the suggestions of Herendeen et al. (1992) and Caccavari (1996) about the early origin of the Leguminosae in tropical America.

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