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Cover illustration: The inset cover image shows a well-preserved capitulescence of the newly designated genus and species *Raiguenrayun cura*, an extinct Eocene taxon of the daisy family, viewed under fluorescent light. The fossil was recovered from a 4.7 million-year-old formation in Patagonia, Argentina, and shares a mosaic of morphological features today recognized in taxa phylogenetically close to the root of the Asteracean tree. This new species is the oldest well-dated Asteraceae and perhaps the earliest indirect evidence for bird pollination in the family. See Barreda *et al*. (pp. 127–134).

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An extinct Eocene taxon of the daisy family (Asteraceae): evolutionary, ecological and biogeographical implications

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• *Background and Aims* Morphological, molecular and biogeographical information bearing on early evolution of the sunflower alliance of families suggests that the clade containing the extant daisy family (Asteraceae) differentiated in South America during the Eocene, although palaeontological studies on this continent failed to reveal conclusive support for this hypothesis. Here we describe in detail ***Raiguenrayun cura* gen. & sp. nov.**, an exceptionally well preserved capitulescence of Asteraceae recovered from Eocene deposits of northwestern Patagonia, Argentina.
• *Methods* The fossil was collected from the 47·5 million-year-old Huitrera Formation at the Estancia Don Hipólito locality, Río Negro Province, Argentina.
• *Key Results* The arrangement of the capitula in a cymose capitulescence, the many-flowered capitula with multiseriate–imbricate involucral bracts and the pappus-like structures indicate a close morphological relationship with Asteraceae. *Raiguenrayun cura* and the associated pollen *Mutisiapollis telleriae* do not match exactly any living member of the family, and clearly represent extinct taxa. They share a mosaic of morphological features today recognized in taxa phylogenetically close to the root of Asteraceae, such as Stifftieae, Wunderlichioideae and Gochnatieae (Mutisioideae *sensu lato*) and Dicomeae and Oldenburgieae (Carduoideae), today endemic to or mainly distributed in South America and Africa, respectively.
• *Conclusions* This is the first fossil genus of Asteraceae based on an outstandingly preserved capitulescence that might represent the ancestor of Mutisioideae–Carduoideae. It might have evolved in southern South America some time during the early Palaeogene and subsequently entered Africa, before the biogeographical isolation of these continents became much more pronounced. The new fossil represents the first reliable point for calibration, favouring an earlier date to the split between Barnadesioideae and the rest of Asteraceae than previously thought, which can be traced back at least 47·5 million years. This is the oldest well dated member of Asteraceae and perhaps the earliest indirect evidence for bird pollination in the family.

Key words: Compositae, capitulescence, fossil taxon, *Raiguenrayun cura* gen. & sp. nov., Eocene, Patagonia, southern South America.

INTRODUCTION

Asteraceae are an evolutionarily successful family of angiosperms with >23 000 species, occupying all continents except Antarctica (Jeffrey, 2007). One of the most important features of Asteraceae is the presence of flowers tightly packed into a condensed inflorescence, known as the capitulum. It resembles a single large flower and therefore acts as a single 'attraction unit' to pollinators. This morphological specialization has been postulated as one of the major determinants of the evolutionary success of the family (Stebbins, 1967; Broholm *et al.*, 2008). The evolution of floral display in the largely animal-pollinated Asteraceae is commonly attributed to pollinator-mediated selection (Lane, 1996): long corollas and high nectar secretion attract hummingbirds and sunbirds in some early branching groups [Barnadesiodeae, Mutisioideae and Carduoideae (Dicomeae)], whereas larger capitula or capitulescences attract solitary bees in more derived groups (Asteroideae).

The origin of Asteraceae has long been debated, with South America and the Palaeogene most frequently hypothesized as the place and time of their early evolution (DeVore and

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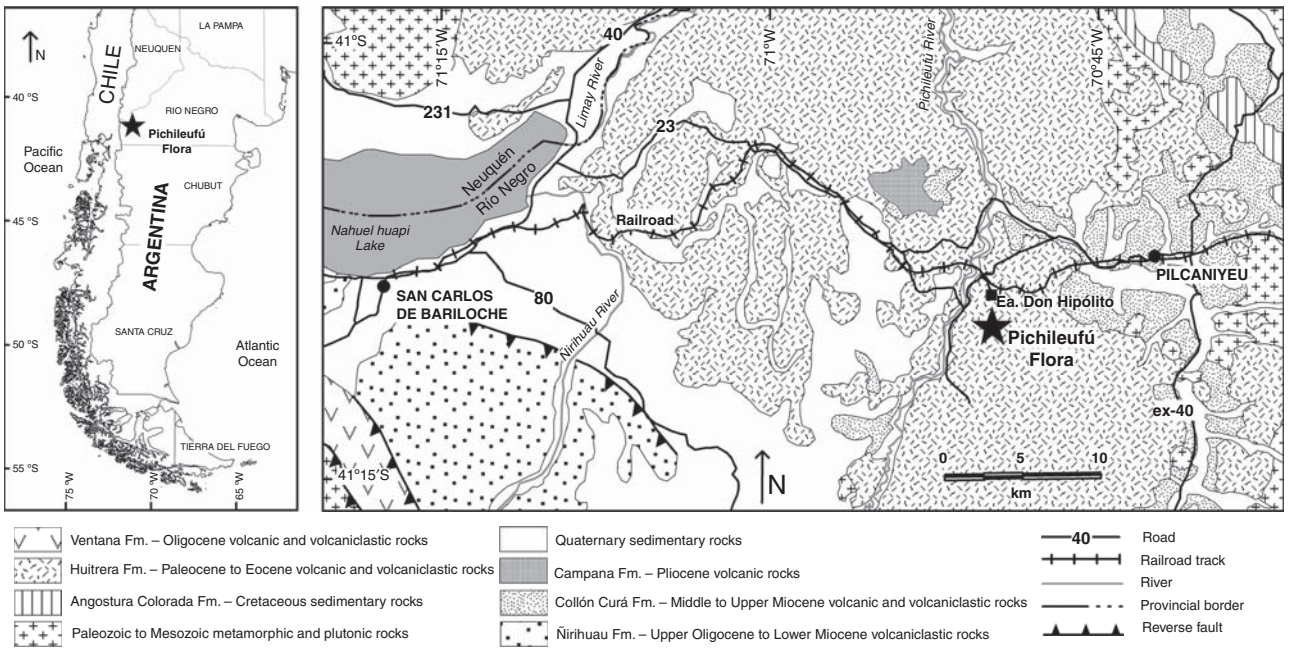

FIG. 1. Simplified geological map of north-western Río Negro Province showing the fossil locality (41°09′26·06″S, 70°49′57·11″W, WGS84). Modified from Giacosa *et al.* (2001).

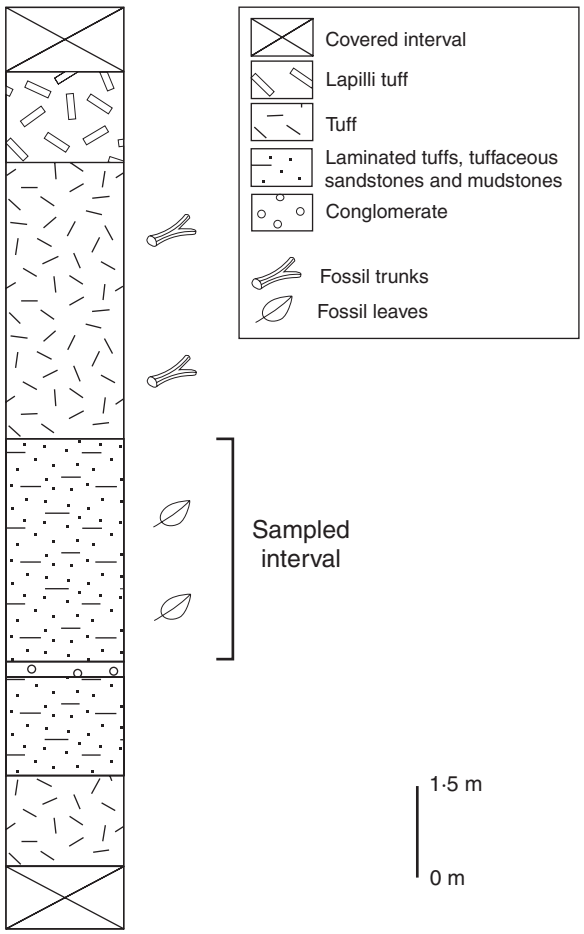

FIG. 2. Stratigraphic section of the Huitrera Formation at the Río Pichileufú flora site, showing the location of the fossil-bearing levels.

Stuessy, 1995; Stuessy *et al.*, 1996). More recently, Lundberg (2009) postulated an ancestral Asteraceae 'growing in what today is southern South America just north of Patagonia, sometime around middle or late Eocene'. Asteraceae underwent a worldwide explosive radiation during the Neogene (Graham, 1996; Barreda *et al.*, 2010*a*), but their scarceness in Palaeogene ecosystems is remarkable: in modern grassland, wooded grassland and montane vegetation, this family is a dominant component. This raises the question of whether Asteraceae were truly rare in Palaeogene communities or whether our picture of these ecosystems is incomplete.

Recently, the study of a fossil specimen from the Middle Eocene [47·5 million years ago (Ma)] Huitrera Formation of Río Negro Province, northwestern Patagonia (Figs 1, 2) resulted in the recognition of the first capitulum of Asteraceae in the fossil record (Barreda *et al.*, 2010*b*). This fossil displays several relevant features that we here present in detail for the first time; some may reveal past interactions with vertebrate pollinators. Furthermore, the age of the fossil-bearing strata suggests that the divergence between Asteraceae and its sister family Calyceraceae might have occurred far earlier than previously thought. In this contribution we formally describe *Raiguenrayun cura* gen. & sp. nov., the oldest well dated Asteraceae, and explore the evolutionary, ecological and biogeographical implications of this finding.

MATERIALS AND METHODS

The fossil specimen reported here was collected by one of us (R.C.) from the Río Pichileufú fossil-bearing strata (Huitrera Formation), near the Estancia Don Hipólito locality (41°09′26·06″S, 70°49′57·11″W, WGS84), Río Negro Province, Argentina (Fig. 1). The Huitrera Formation corresponds to laminated tuffs and tuffaceous mudstones and

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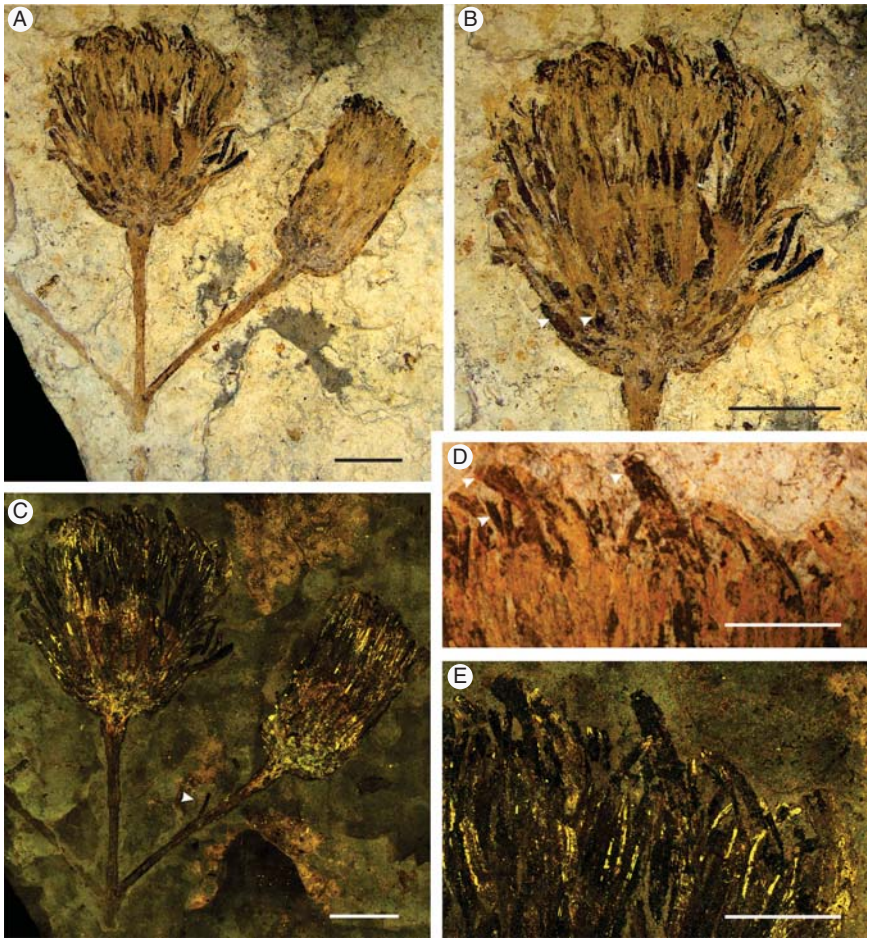

FIG. 3. *Raiguenrayun cura* gen. and sp. nov., fossil Asteraceae from north-western Patagonia, southern South America. (A) General view of the cymose capitulescence-like fossil showing two long-pedunculate head-like inflorescences. (B) Detail of the central capitula. Arrowheads show involucral bracts. (C) Capitulescence under fluorescent light taken with a confocal microscope. Note the slender projection (bract?) in the peduncle of the lateral capitula (arrowhead). (D) Apical zone of the central capitula showing individual florets (arrowheads). (E) The same detail of D, but under fluorescent light. Note the shining slender projections (pappus) among florets. Scale bars = 1 cm.

sandstones (Fig. 2), interpreted as deposited in an ancient shallow lacustrine or swamp environment (Aragón and Romero, 1984). The age of the Río Pichileufú flora-bearing strata is well constrained (Middle Eocene 47·46 ± 0·05 Ma) based on $^{40}Ar/^{39}Ar$ dating of sanidine phenocrysts from stratigraphically related tuffs (Wilf *et al.*, 2005).

The fossil capitulescence was examined under transmitted white light and fluorescent light. The fossil is housed in the palaeontological collection of the 'Museo del Lago Gutiérrez Dr. Rosendo Pascual de Geología y Paleontología' (San Carlos de Bariloche, Río Negro Province, Argentina): MLG 1156. Fluorescent photomicrographs were taken with a confocal Nikon microscope (objective PLAN UW 2 × /0·06) using a green filter. For non-microscope photographs a Nikon Coolpix 8000 camera was used. Fossil pollen was examined using a transmitted white light Leica microscope, and photomicrographs were taken with a Leica DFC 290 camera. Co-ordinates are referred to the England finder. Pollen terminology follows Punt *et al.* (2007).

The phylogenetic placement of the fossils (*R. cura* and *Mutisiapollis telleriae*) on the already available meta-tree (Funk *et al.*, 2009) was determined on the basis of their morphological characters (Barreda *et al.*, 2010*b*). We follow the terminology of Katinas *et al.* (2008), who considered tribes Onoserideae, Nassauvieae and Mutisieae within Mutisioideae *sensu stricto* and these, together with Stifftieae and Wunderlichioideae, within Mutisioideae *sensu lato* (*s.l.*) although Mutisioideae *s.l.* include a grade of around 12 clades according to the recent molecular phylogenetic analyses of Funk *et al.* (2009).

SYSTEMATICS

Genus. ***Raiguenrayun*** Barreda, Katinas, Passalia & Palazzesi **gen. nov.** (Figs 3, 4)

Type species. ***Raiguenrayun cura*** Barreda, Katinas, Passalia & Palazzesi **sp. nov.** (Figs 3, 4)

Generic diagnosis. Loosely cymose capitulescence with two or three, long pedunculate capitula. Central capitulum (mature?) globose in shape, with multiseriate–imbricate involucral bracts (phyllaries), the basal-most series decurrent onto the

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FIG. 4. Reconstruction of a hypothetical ancestral Asteraceae based on morphological features of both the fossil *Raiguenrayun cura* gen. & sp. nov. and the morphologically closest extant tribes.

long peduncle. Intermediate bracts widely oblong, with an apparent obtuse apex. Flowers numerous, large (approx. 1·5 cm long), with a developed ligule or lip. Slender projections like hairs present among flowers (pappus). Lateral capitulum (inmature?) oblong in shape.

Species. ***Raiguenrayun cura*** Barreda, Katinas, Passalia & Palazzesi **sp. nov.** (Figs 3, 4)

Specific diagnosis. As for the genus

Etymology. From the Aónikenk language used by native inhabitants of south-central Argentina. Raiguen-Rayún = flower, Curá = stone.

Holotype. Specimen MLG 1156 (Fig. 3)

Repository. 'Museo del Lago Gutiérrez Dr. Rosendo Pascual de Geología y Paleontología' Villa Los Coihues, San Carlos de Bariloche, Río Negro Province, Argentina.

Type locality and stratigraphic position. The material was collected by one of us (R.C.) from the Río Pichileufú fossil-bearing strata (Huitrera Formation), near the Estancia Don Hipólito locality (41°09′26·06″S, 70°49′57·11″W, WGS84), about 60 km east of San Carlos de Bariloche, Río Negro Province, Argentina (Figs 1, 2). This specimen comes from volcanic and volcaniclastic beds interpreted as deposited in a shallow lacustrine environment that contain the outstanding Río Pichilefú flora with exceptionally preserved compressions of leaves, flowers, fruits and seeds (Berry, 1938; Aragón and Romero, 1984; Wilf *et al.*, 2005).

Age. Middle Eocene – 47·5 million years – based on radiometric data (Wilf *et al.*, 2005).

Description. The fossil inflorescence reported here consists of a loosely cymose capitulescence, laterally compressed. It comprised two, probably three, capitula sustained by equally elongated peduncles (2·7–3·0 cm long, 0·15–0·20 cm wide). The three peduncles depart from nearly the same ramification point, apparently without pubescence. A slender projection (bract?) is observed in the peduncle of the lateral head. At least one of the fossil capitula (the central one) appears to be fully mature at the time of preservation. It is globoid in shape (3·0 cm long, 2·9 cm wide) and possesses several series (six or eight) of imbricate protective bracts (phyllaries of an involucre), the basal-most series decurrent onto the long peduncle. Intermediate bracts are widely oblong (approx. 0·15–0·20 cm wide and 1 cm long), with an apparent obtuse apex, although this could be the result of preservation. Flowers (approx. 80) are relatively large (approx. 1·5 cm long), apparently homomorphic [no clear difference between inner (disc florets) and outer (ray florets) flowers was observed, probably due to preservation bias], with a developed ligule or lip. Although the apex of individual flowers can be identified with relative accuracy (especially in the central head), their morphological nature is not so evident: they may be interpreted as the lobes of an actinomorphic corolla, lips of a bilabiate corolla or fused petals of a ligulate corolla (Fig. 3). Slender projections like hairs (somewhat flattened capillary bristles) are present among flowers. They are interpreted as remains of the pappus. The lateral capitulum (immature?) is oblong in shape. A third peduncle is also observed, inferring a third head.

Comparisons and remarks. There is no similar fossil taxon in the literature. Fossil capitula of possible asteracean affinity have been described from the Cretaceous (*Palaeanthus problematicus* Newberry) and Oligocene–Miocene (*Viguiera cronquistii* Becker) of North America, and from the Oligocene of France (*Hieracites nudatus* Saporta and *Hieracites stellatus* Saporta), but none of these specimens possesses features that conclusively link them to Asteraceae.

Palaeanthus problematicus, originally described as an asteracean head (Newberry, 1895), was later suggested as a possible cycadophyte (Cronquist, 1977) or, at most, as an unclassified angiosperm fruit with many follicles (Crane and Dilcher, 1984). The *Hieracites* morphotaxon was split by de Saporta (1889) into two species and interpreted by Small (1919) as possible Asteraceae: *H. stellatus* (heads with a subbiseriate involucre and a small receptacle) and *H. nudatus* (a mature receptacle with involucral bracts missing and achenes or florets densely packed). Despite the conviction of Small (1919) of the asteracean affinity of de Saporta's specimens, these are neither mentioned in fossil reviews (Cronquist, 1977; Crepet and Stuessy, 1978) nor accepted as Asteraceae (Martínez-Millán, 2010). *Viguiera cronquistii* is the megafossil most frequently attributed to Asteraceae. It was described by Becker (1969) who, following the observations of Cronquist (1977), remarked on some resemblances between the fossil and the extant genus *Viguiera* Kunth (Heliantheae). This fossil consists of a compressed head, completely covered by numerous helically arranged bracts,

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FIG. 5. Extant member of an early branching lineage of Asteraceae (Mutisioideae), *Cnicothamnus lorentzii* Griseb., that superficially resembles the Patagonian fossil capitula.

subtended by a short stalk (Becker, 1969) but, in contrast to *R. cura*, it lacks florets or floret-like structures. Although *V. cronquistii* was thought to be the first reliable megafossil of Asteraceae, Crepet and Stuessy (1978) re-examined the type specimen and concluded that this fossil 'cannot be considered unequivocally to be the remains of a Compositae'.

Botanical affinity. The above-described fossil is clearly a member of Asteraceae based on a combination of features diagnostic of the family (Barreda *et al.*, 2010*b*). It superficially resembles capitula of several modern Asteraceae, showing a mosaic of morphological features of Mutisioideae *s.l.* (Fig. 5), Carduoideae and even Barnadesioideae, but it does not match exactly any of these subfamilies and represents an extinct taxon (stem representative) (Fig. 6). The characteristics of the fossil capitulum match well with the features attributed to a hypothetical ancestor of Asteraceae proposed by several authors (e.g. Bremer, 1994; Funk *et al.*, 2009; Lundberg, 2009): inflorescence cyme-like; few heads per plant, heads indeterminate, each with many flowers; involucral bracts in several series, imbricate without hyaline or scabrous margins; florets mostly of one type, some differentiation in floral morphology in peripheral florets possible but without true rays; and pappus of capillary bristles.

The associated pollen grains (*Mutisiapollis telleriae* Barreda and Palazzesi) were helpful in determining the accurate taxonomic position of the megafossil within Asteraceae (Barreda *et al.*, 2010*b*). *Mutisiapollis telleriae* (Fig. 7) has morphological features currently found in early branching members of the family (Barreda *et al.*, 2009; Tellería *et al.*, 2010). In particular, the acaveate exine and the presence of well developed spines with an uneven arrangement characterize pollen of most members of genera of Stifftieae and Wunderlichioideae concentrated in the Guayana Highland, some Gochnatieae (Mutisioideae *s.l.*) and some members of Dicomeae and Oldenburgieae (Carduoideae) (Zao *et al.*, 2006; Blackmore *et al.*, 2010; Tellería *et al.*, 2010) (Fig. 6). Pollen characters clearly exclude subfamily Barnadesioideae. The microechinate (or almost spineless) pollen grains of the early branching Barnadesioideae and the related families Calyceraceae and Goodeniaceae may indicate that the presence of well developed spines is an evolutionary novelty (apomorphy) within Mutisioideae and Carduoideae (with subsequent reduction in some species).

DISCUSSION

New fossil discoveries from Patagonia, Argentina, have shed light on the emergence, early evolution and palaeobiology of Asteraceae. *Raiguenrayun cura* (capitulescence) and *M. telleriae* (pollen grains) do not match exactly any living member of the extant family and represent extinct taxa. Fossils show a mosaic of characters found in extant Stifftieae, Wunderlichioideae and Gochnatieae (Mutisioideae *s.l.*) and Dicomeae and Oldenburgieae (Carduoideae), tribes today endemic to or mainly distributed in South America and Africa, respectively (Ortiz, 2009; Ortiz *et al.*, 2009*a*, *b*; Sancho and Freire, 2009). Some prevalent shared features in modern representatives of some African Dicomeae and Oldenburgieae and South American Wunderlichioideae and Gochnatieae (e.g. apiculate anther appendages) led Panero and Funk (2008) to suggest a more direct African and South American connection. This connection might have been even stronger further back in time than that seen today: the documentation of highly similar asteracean fossil pollen grains from the Eocene on both continents (Zavada and DeVilliers, 2000; Scott *et al.*, 2006; Barreda *et al.*, 2010*b*; Zavada and Lowrey, 2010) reinforces the proposed link between western Gondwana lands. Floral interchange between South America and Africa occurred during the Late Cretaceous and continued into the Palaeogene in spite of the increasing distance between these land masses. Even by the Eocene, when South America and Africa were approx. 2000 km apart, a strong floristic affinity prevailed (Jaramillo and Dilcher, 2001). The latest palaeogeographic reconstructions suggested the existence of a series of islands and shallow terrain in the South Atlantic during the mid-Cenozoic, particularly between 40 and 50 Ma (Bandoni de Oliveira *et al.*, 2009). This palaeogeographic positive relief, which is underwater today, might have reduced considerably the distance of a possible biotic migration between South America and Africa. According to this scenario and previous biogeographical hypotheses, Asteraceae might have evolved in southern South America some time before the Eocene, and subsequently entered Africa, before the biogeographical isolation of these two continents became much more pronounced. In this context, the ancestor of Mutisioideae–Carduoideae might have occupied both continents during the Eocene, and ultimately diverged into two separate lineages when effective dispersal barriers had established. It remains unknown whether the current lack of pre-Eocene records of Asteraceae represents the true absence of the family, or whether our picture is incomplete due to the inevitable bias of the fossil record. The latter seems more likely in light of the facts that Mutisioideae–Carduoideae do not represent the earliest diverging branch of Asteraceae (a position occupied by Barnadesioideae) and that the appearance of Asteraceae in the current fossil record most probably documents the radiation of this lineage more than its time of origin. Previous divergence time estimates for the family (Kim *et al.*, 2005) are somewhat discordant

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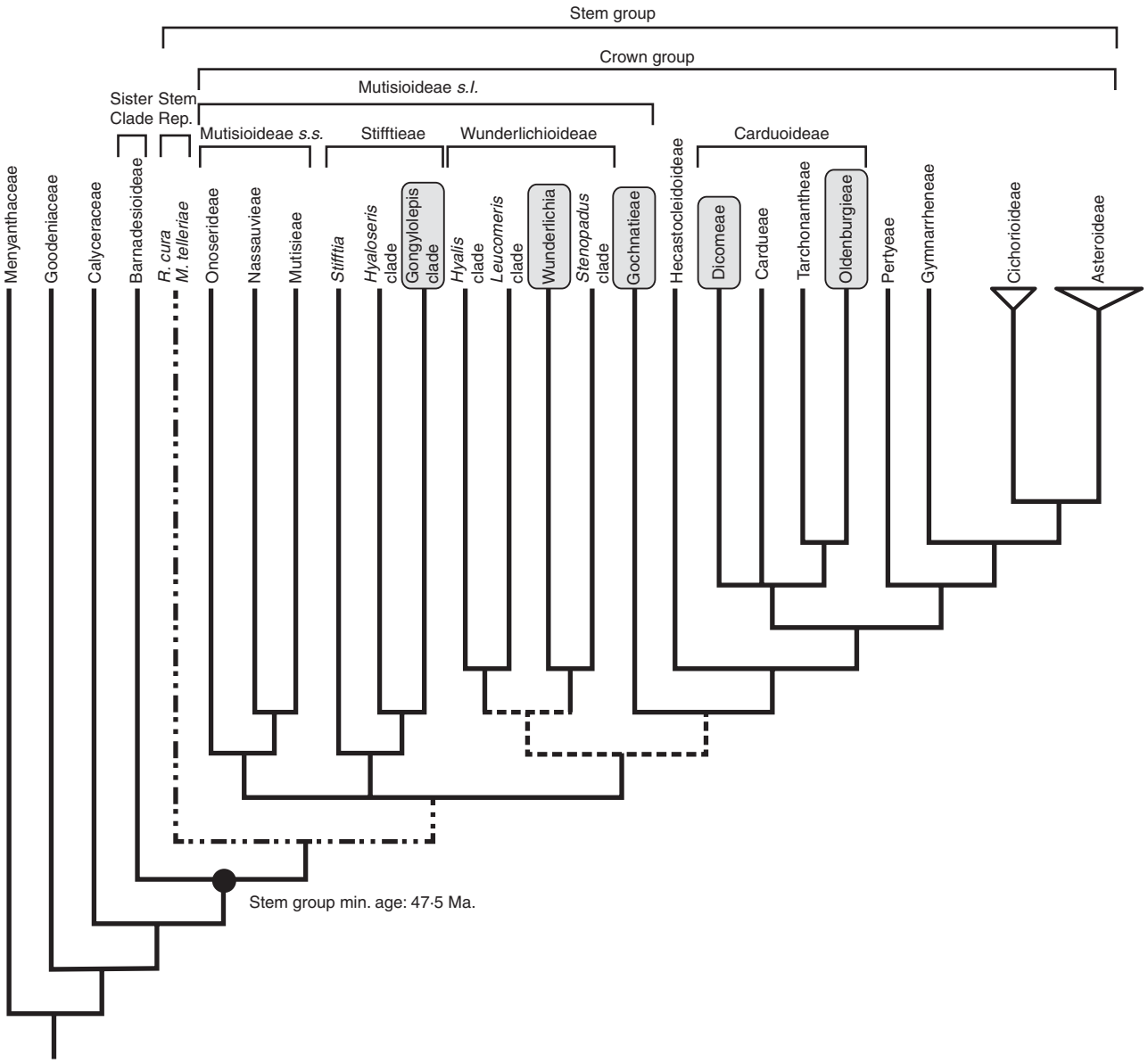

FIG. 6. Modified meta-tree of Funk *et al.* (2009) with the inclusion of the fossils *Raiguenrayun cura* gen. & sp. nov. and *Mutisiapollis telleriae* (dashed-dotted lines). In grey: taxa that share more characters with *R. cura* and *M. telleriae* than any other extant member in Asteraceae. Some branches are not well supported as compared with the remainder of the tree (dashed lines; Funk *et al.*, 2009). Crown group, stem group and stem representative definitions are based on Magallón (2004).

with the age of this Patagonian finding and previous African reports (Scott *et al.*, 2006; Zavada and Lowrey, 2010). Such a discrepancy can most probably be attributed to the lack of the oldest fossil calibration points of Asteraceae in most of the published molecular-based estimate attempts. *Raiguenrayun cura* is a stem representative (Fig. 6) because it displays some but not all the synapomorphies of the crown group. The radiometric age of the fossil-bearing deposits (Huitrera Formation) is here used to date the stem group (sister clade/stem group split). The split between Barnadesioideae and the rest of Asteraceae can be traced back at least 47·5 million years. The early evolution of Asteraceae may have occurred earlier than previously thought, and we think that it might have diverged from the sister family Calyceraceae by the Palaeocene or even by the Cretaceous, although this hypothesis needs new empirical studies.

The early evolution and past ecology of Asteraceae are probably best understood within the context of their source assemblage. The middle Eocene Río Pichileufú flora ranks among the most diverse compression–impression floras ever found in the fossil record (Wilf *et al.*, 2005). An equable climate with relatively warm and humid conditions may have supported highly diverse multilayered vegetation with canopy trees, vines, shrubs, ground cover and aquatic plants (Wilf *et al.*, 2009); in this scenario the earliest interaction between ancestral Asteraceae and pollinators may have occurred. Currently, most Asteraceae are pollinated opportunistically by a wide variety

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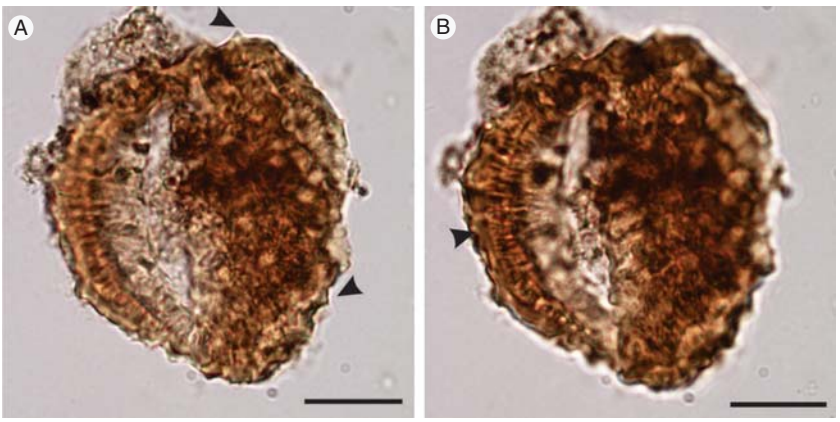

FIG. 7. *Mutisiapollis telleriae*, fossil pollen grain from the capitula-bearing sample. (A) General view, focus on well-developed spines (arrowhead). (B) Focus on exine structure (arrowhead). Specimen on slide MLG 1156: co-ordinates J51/J52. Scale bars = 10 μm.

of insects, but bird pollination has evolved in some lineages of the family (Lane, 1996). The main flower-visiting birds are hummingbirds (Trochilidae) in Barnadesioideae and Mutisioideae, and sunbirds (Nectariniidae) in Carduoideae (Lane, 1996; Anderberg *et al.*, 2007). Funk *et al.* (1995) considered the ancestor of extant Asteraceae to be bird pollinated because Mutisioideae, Barnadesioideae and Carduoideae (Fig. 5) are the earliest branching lineages of Asteraceae. The capitula of the ancestral Asteraceae, according to previous reconstructions (Bremer, 1992) and our interpretations on the fossil inflorescences (Fig. 4), could have been appropriately shaped (elongated corollas) and sized (large capitulum) for bird visitation. Bird pollination appears to have evolved in the Palaeogene (Mayr, 2004, 2009; Louchart, 2008; Tambussi, 2011) and occurs in aseasonal tropical and sub-tropical regions where flowers and nectar are available all year to support nectarivorous birds (Cronk and Ojeda, 2008). This climatic context agrees with that inferred for the middle Eocene of northwestern Patagonia (Melendi *et al.*, 2003; Wilf *et al.* 2005, 2009). However, the most important floral traits that are usually associated with bird pollination are virtually missing in the fossil record; many clues are not preserved at all (e.g. colour and nectar) and others only under the most extraordinary of circumstances (e.g. shape of the flower). However, because of ambiguity regarding the past pollination biology in Asteraceae, and the inherent bias of the fossil record, it is not possible for us to confirm whether or not *R. cura* was bird pollinated. Nevertheless, we can extrapolate our inductive inference into the unobservable past: if the closest living relatives of *R. cura* are today pollinated by hummingbirds (e.g. *Gongylolepis*) in South America or sunbirds (e.g. *Dicoma*) in South Africa, we can then infer that it might have been a bird-pollinated flower in the Eocene of Patagonia. Furthermore, families such as Proteaceae, Myrtaceae and Bombacaceae, with many of their current ornithophyllous members, were important elements of the Eocene ecosystems of northwestern Patagonia (Melendi *et al.*, 2003; Wilf *et al.*, 2005) coexisting with ancestral Asteraceae.

We have shown throughout this study the questions that can be answered as a result of the discovery of this fossil, but which questions remain unanswered? Much remains to be learned about the rapid radiation of Asteraceae since it is still unclear how its members rapidly colonized all habitats and became so incredibly diverse in a relatively short time interval (Stuessy, 2010). For example, this enormous family possesses one of the highest rates of diversification among all flowering plants, generating >23 000 species in a comparatively short period of time (Magallón and Sanderson, 2001). Such explosive radiation has been associated with innovations, particularly new traits (chemical and morphological) that made the reproductive process more efficient (Calabria *et al.*, 2009). The capitulum existed in Patagonia 47·5 Ma, far earlier than the ecological dominance of the family at least 20 million years later.

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