BRIEF COMMUNICATION

**Karatophyllum bromelioides L.D. Gómez revisited:**
A probable fossil CAM bromeliad

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- **Premise of the study:** The fossil leaf *Karatophyllum bromelioides* L. D. Gómez found in Costa Rica was proposed by Gómez (1972) to belong to the Bromeliaceae and to date from the middle Tertiary. If the age and affinity of this specimen were proven to be correct, it would constitute the oldest record of this large and ecologically diverse monocotyledonous family.

- **Key results:** Morphological features of the fossil (leaf dimensions, marginal spines, cuticular traces) indicate a close affinity with the extant bromeliad *Aechmea magdalenae* (André) André ex Baker. Leaf thickness (1.6 mm at maximum) suggests that *K. bromelioides* L. D. Gómez performed CAM photosynthesis. The geological information does not corroborate the estimated age and location of the specimen; the fossil is suggested to be of more recent origin.

- **Conclusions:** The affinity of this fossil to Bromeliaceae was confirmed, but the uncertainties surrounding its age and collection locality mitigate against its use in inferences concerning the evolutionary history of the family.

**Key words:** *Aechmea magdalenae*; Bromeliaceae; CAM photosynthesis; *Karatophyllum bromelioides*; leaf morphology; travertine.

*Karatophyllum bromelioides* L. D. Gómez is the only mega-fossil considered to be convincingly attributable to Bromeliaceae (Smith and Till, 1998; Benzing et al., 2000). The type specimen was described in 1972 by the late Luis Diego Gómez Pignataro (1944–2009) in a paper in *Revista de Biología Tropical* (Gómez, 1972). This publication indicates that the fossil was collected in middle Tertiary deposits near the town of San Ramón, in the Alajuela Province of Costa Rica.

*Karatophyllum bromelioides* is an impression of a leaf embedded in a matrix of travertine (Fig. 1A-1), with external dimensions of 195 mm in length, 85 mm in breadth, and ca. 20 mm in depth. A medial cavity running longitudinally through the block, corresponding to the position formerly occupied by the leaf, has a maximum height of 1.6 mm (Fig. 1A-2) and a width of 84 mm. The imprint on the internal surface preserves traces of closely parallel but distally converging veins (Fig. 1B-3), cuticle (Fig. 1B-5), epidermal characters, and Bromeliaceae-like scales that are particularly prominent on the abaxial leaf surface (Gómez, 1972). The specimen was interpreted as possessing pronounced, curved marginal spines (Fig. 1B-4), 6 mm long, 3 to 3.5 mm wide at their base, and spaced 24 to 30 mm apart.

These characters, which we confirmed by inspection of the specimen, led Gómez (1972) to attribute the fossil to Bromeliaceae. He noted its possible affinity to extant genera such as *Aechmea* Ruiz & Pav. and *Bromelia* L. in subfamily Bromelioidae, but assigned the fossil to the new organ-genus *Karatophyllum*. *Karatophyllum bromelioides* has been regarded by various authors as the most plausible macrofossil attributable to Bromeliaceae (e.g., Smith and Downs, 1974; Smith and Till, 1998; Givnish et al., 2007). Six other possible bromeliad macrofossils were considered unconvincing by Smith and Downs (1974, p. 57), who described the tally as “one impossibility, one improbability, and four faint possibilities.” Graham (1985) also described pollen grain assigned to “cf. Tillandsia” from the Gatuncillo Formation of the middle (?) to late Eocene in Panama.

*Karatophyllum bromelioides* is of considerable interest because the inferred maximum leaf thickness of 1.6 mm suggests a degree of succulence in this organ. Leaf succulence in many families of angiosperms is closely associated with the occurrence of crassulacean acid metabolism (CAM), a photosynthetic adaptation to water-limited environments (Winter and Smith, 1996). This relationship to succulence also holds within Bromeliaceae (Smith, 1989; Pierce et al., 2002); data from a survey of 49 species show that a leaf thickness >1.0 mm is associated consistently with carbon-isotope ratios less negative than −20‰, indicative of full CAM activity (Fig. 2). The fossil record of CAM plants is poor to nonexistent because the dry, oxidizing conditions of arid environments are not generally conducive to preservation of macrofossils. *Karatophyllum bromelioides* could thus potentially be valuable in reconstructing the evolutionary history of CAM plants (Crayn et al., 2004; Givnish et al., 2007, 2011).
Plant remains preserved in travertine have been found in localities 40 km NNE from San Ramón (Pérez and Laurito, 2003) and have been dated to the late Pleistocene (50 to 13 ka). Given the importance of this fossil, we decided to re-examine the specimen. The fossil is held in the collections of the Museo Nacional de Costa Rica, Departamento de Historia Natural (collection number 46399). We discovered that Alvaro Castaing was the researcher who gave the fossil to Gómez to be studied. We contacted Prof. Castaing, who indicated that he found the fossil in a small collection of Liceo de Costa Rica (a high school in San José de Costa Rica, Costa Rica), and there was no associated information on their collectors, except the area where it was found. We contacted the principal of Liceo de Costa Rica, Milton Rojas, but the school did not possess any additional information on the fossil.

We searched the geological literature on the San Ramón area (Fernández and Sandoval, 1966; Denyer and Alvarado, 2007; Záček et al., 2010), where the fossil is supposed to have originated. Most of the outcrops in the vicinity of San Ramón are of igneous origin (Fig. 3). The few sedimentary deposits found in this area are tuffs and sandstones of Miocene age (Fig. 3) that do not have the kind of lithology observed in the fossil (travertine). Other sediments in the area include Pliocene deposits near the town of Palmares (7 km SE of San Ramón), where vertebrate fossils have been found, but do not contain travertine deposits (Laurito et al., 2005). There is a small outcrop of travertine deposits described by Fernández and Sandoval (1966) associated with hydrothermal springs on the eastern margin of the Barranca river, 10 km WSW from San Ramón (Fig. 3), from which the fossil could originate. We visited this outcrop, but unfortunately the entire outcrop has disappeared because the travertine has been quarried for ornamental stone. There is a small area with marine limestone that outcrops 24 km SE of San Ramón (Fig. 3), but the fossil does not seem to have accreted in a marine environment.

![Fig. 1. Images of (A–C) fossil Karatophyllum bromelioides L. D. Gómez holotype and (D–F) leaf sections of living material of Aechmea magdalenae (André) André ex Baker. (A) Cross section of the travertine matrix (1) showing the internal cavity remaining from the original leaf (2); maximum thickness of the leaf was 1.6 mm and 1.2 mm at the central furrow. (B) Internal view of the matrix showing imprint of the abaxial surface with close parallel venation (3), spines (note that the outline of the spine was drawn in ink on the specimen itself) (4), and cuticle traces (5). (C) External view of the matrix, adaxial surface. (D) Cross section of a fresh specimen near the widest point of the leaf blade. (E) Abaxial leaf surface. (F) Adaxial leaf surface. Scale bars = 10 mm.](image1)

![Fig. 2. Relationship between carbon-isotope ratio ($\delta^{13}C$ value) and leaf thickness for 49 species of Bromeliaceae, replotted from the data of Pierce et al. (2002).](image2)
Travertine forms by rapid precipitation of calcium carbonate from solution in surface waters, near hydrothermal springs or limestone deposits (Tucker and Wright, 1990). Fossil imprints and molds are often found in karstic topographies. Rain dissolves calcium from nearby limestones during the rainy season, and then calcium precipitates again along small creeks during the dry season, preserving leaves and other remains of the surrounding fauna and flora. Pleistocene volcanic activity in this region ca. 600 ka led to uplift of the Guanacaste range to its present-day elevation and was associated with a change in vegetation from tropical rain forest to a more seasonally dry landscape, more prone to producing travertine. This is also consistent with genetic evidence that tropical rain forest gave way to a seasonally dry climate dominated by oaks in Costa Rica in the mid- to late Pleistocene (Cavender-Bares et al., 2011). It seems more probable that *K. bromelioides* was collected from similar Late Pleistocene to Holocene travertine deposits (Pérez and Laurito, 2003) rather than Middle Cenozoic.

Despite uncertainty over its provenance and age, we consider that the fossil is convincingly assignable to Bromeliaceae on morphological grounds (leaf dimensions, cuticular imprint, and marginal spines). Although he chose to assign the specimen to a novel genus, Gómez (1972) noted the possible affinities of this fossil with *Aechmea* and *Bromelia*, which are represented by 17 species and 3 species, respectively, in the modern flora of Costa Rica (Morales, 2003). The *Bromelia* spp. in question do
not exceed 50 mm in leaf width, but several species of *Aechmea* possess leaves that are 80 mm or wider. One modern species provides a particularly convincing match to the fossil: *Aechmea magdalenae* (André André ex Baker), an understory plant possessing CAM photosynthesis that is often found in riparian habitats (Pitts and Smith, 1988; Skillman et al., 2005). The species is common from Mexico to Ecuador and Venezuela, and its distribution in Costa Rica is consistent with likely locations for the origin of the fossil (Rossi et al., 1997; Morales, 2003). *Aechmea magdalenae* is also known as the *pita* plant and has long been used for its fiber (Ticktin and Nantel, 2004; Lincoln and Orr, 2011).

The physical match of the fossil to both herbarium specimens and fresh material of *A. magdalenae* collected in the field (Fig. 1D–F) was striking. A leaf ca. 2.6 m long had a pronounced central furrow, a maximum thickness of 1.64 mm at the middle of the leaf, and of 0.64 mm between the middle and the edge (Fig. 1D), and a maximum width (without following the contour of the central furrow) of 80 mm, tapering toward the tip and more gradually toward the base. The marginal spines had a maximum spacing of 45 mm at the position of greatest leaf width, decreasing as the leaf tapered both toward tip and base (e.g., spacing of spines 4 mm at 100 mm from leaf tip and 14–16 mm toward the leaf base). The largest spines, at the point of maximum leaf width, were 4–5 mm long and 3–4 mm across at their base. Leaf ribbing on the abaxial surface can also be a useful taxonomic character in Bromeliaceae subfamily Bromelioidae (Tomlinson, 1969; Monteiro et al., 2011). Here again there was a close match between fresh material of *A. magdalenae* (16 to 17 parallel veins per 10 mm at the widest parts of the leaf, tapering to 21 per 10 mm at 100 mm from the leaf tip) and the fossil (18 ribs per 10 mm: Fig. 1D, E). All of these features indicate excellent concordance between the characteristics of *Karotophyllum bromelioides* and extant *Aechmea magdalenae*.

In conclusion, this fossil, although convincingly assigned to Bromeliaceae, is likely to be of relatively recent origin and should not be used for dating phylogenetic reconstructions of the family.

**LITERATURE CITED**


**Fernández, M., and F. Sandoyo. 1966.** Evaluación de un depósito de travertino localizado en la zona de Nagatac, región oeste de San Ramón. Ministerio de Industria y Comercio, Dirección de Geología, Minas y Petróleo [internal report], San José, Costa Rica.


**Monteiro, R. F., R. C. Forzza, and A. Mantovani. 2011.** Leaf structure of *Bromelia* and its significance for the evolution of Bromelioidae (Bromeliaceae). *Plant Systematics and Evolution* 293: 53–64.


