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Research paper

Fossil Araceae from the Upper Cretaceous of Patagonia, Argentina, with implications on the origin of free-floating aquatic aroids

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ABSTRACT

Herein, we describe and name a new fossil genus and species, *Aquaephyllum auriculatum*, and report on the presence of *Pandaniidites* pollen grains from La Colonia Formation (Maastrichtian, Upper Cretaceous), Patagonia, Argentina. The new fossil taxon is based on leaf impressions and is morphologically similar to members of the family Araceae, subfamily Lemnoideae. The most important morphological characters comprise the adaxial venation with at least eight primary veins, the crenate margin, and the presence of an auricle with a floating function. Phylogenetic analysis places the new taxon in a close relationship within the subfamily Lemnoideae, which also includes the fossils *Limnobiophyllum scutatum*, *Cobbania corrugata*, and the extant *Pistia stratiotes*. *Aquaephyllum auriculatum* and *Pandaniidites* are the first fossil record of lemnaceous leaves and the oldest record for *Pandaniidites* pollen for the Southern Hemisphere respectively. The inclusion of *Aquaephyllum* and *Pandaniidites* within a phylogenetic context confirms the previously suggested hypothesis on the existence of close relationships between modern *Pistia*, and the fossils *Limnobiophyllum* and *Cobbania*.

1. Introduction

Among the monocots, the family Araceae comprises approximately 105 herbaceous genera and more than 3300 species world widely distributed mostly in tropical areas (e.g. Mayo et al., 1997; Stevens, 2012). Traditionally, the family was divided into eight subfamilies (Fig. 1) and it is characterized by the terrestrial, epiphyte or aquatic habit. Among its main morphological traits are the bractless flowers, the spike-like inflorescence called spadix (e.g. Arber, 1922; Grayum, 1990; Boyce, 1995; Mayo et al., 1997; Keating, 2004), and the simple leaves with parallel–pinnate, pinnate or pothoid venation patterns (e.g. Mayo et al., 1997; Wilde et al., 2005).

Fossils assigned to Araceae comprise mainly leaves, inflorescences, and pollen (see Stockey, 2006), and until now, they were restricted to the Northern Hemisphere. Its oldest fossil record was thought to go back to the Early Cretaceous of Portugal based on pollen grains described as *Mayoa portugallica* Friis, Pedersen et Crane (Friis et al., 2004, 2006). However, recent studies suggest that *Mayoa* pollen grains have affinities to gymnosperms and they do not belong to Araceae (Hofmann and Zetter, 2010; Nauheimer et al., 2012). Undisputable Araceae fossils occur during the Late Cretaceous. Numerous leaf remains have been described (Dilcher and Daghlian, 1977; Stockey et al., 1997, 2007; Kvaček and Herman, 2004; Wilde et al., 2005; Quang and Sun, 2008), but unfortunately reproductive organs are scarce and poorly understood. In this context, only a well-preserved permineralized aroid inflorescence, *Albertarum pueri* Bogner, Hoffman et Aulenback (Bogner et al., 2005) from the Late Cretaceous of Alberta, Canada, is consistent with Araceae. The Paleogene record is more abundant, including leaves, pollen, fruits, and seeds, from several localities in Europe, Asia, North America and South America (e.g. Van der Hammen, 1956; Van Hoeken-Klinkenberg, 1966; Van der Hammen and García de Mutis, 1966; Krassilov, 1973; Fedotov, 1975; Bogner, 1976; Hickey, 1977; Cevallos-Ferriz and Stockey, 1988; McIver and Basinger, 1993; Jaramillo and Dilcher, 2001; Zetter et al., 2001; Smith and Stockey, 2003; Wilde et al., 2005; Bogner et al., 2007; Hesse and Zetter, 2007; Herrera et al., 2008; Krassilov and Kodrul, 2009).

The best-known fossil taxa based on macrofossils are members of the subfamilies Lemnoideae and Aroideae. Stockey et al. (2007) described *Cobbania corrugata* (Lesquereux) Stockey, Rothwell et Johnson that corresponds to the fossil aroid originally described as *Pistia corrugata* Lesquereux (Lesquereux, 1878), a floating aquatic monocot from the Late Cretaceous Dinosaur Park Formation, Alberta, Canada. This taxon is represented by rosettes of leaves and roots attached to a short stem interconnected by stolons, and associated fruits with seeds (Stockey et al., 2007). Recently, Krassilov and Kodrul (2009) described remains of

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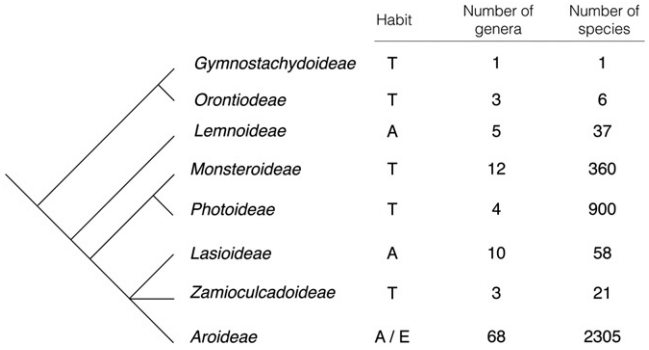

Fig. 1. Phylogenetic relationship among aroid subfamilies (modified from Stevens, 2012). T: Terrestrial, E: Epiphytic, and A: Aquatic habit.

Cobbania corrugata from the Amur Province (Russia) associated with *Cobbanicarpites amurensis* Krasslov et Kodrul fruits and seeds. Kvaček (1995) and Stockey et al. (1997) described fossils assigned to *Limnobiophyllum scutatum* (Dawson) Krassilov from the Paleocene Paskapoo Formation, Alberta, Canada. *Limnobiophyllum scutatum* includes stem and leaf remains characterized by one or two sessile suborbicular to reniform leaves forming small rosettes that were interpreted as free-floating organs. Staminate flowers with anthers containing echinate monoportae pollen grains that most closely resemble the sporae dispersae genus *Pandaniidites* Elsik are borne in the axils of second leaves. Based on root, seed and pollen morphology, venation patterns as well as habit, *Limnobiophyllum* is considered to be the "link-taxon" between the subfamilies Lemnoideae and Aroideae (e.g. Kvaček, 1995; Stockey et al., 1997).

In South America, the Araceae fossil record is based mostly on pollen but also on leaves from Late Cretaceous and Paleocene sediments of Brazil and Colombia. Among the pollen grains, one of the best recorded is *Proxapertites operculatus* Van der Hammen from the Paleocene of Colombia (Hesse and Zetter, 2007). The Colombian material is similar to the fully zonate pollen types of extant Araceae found in the subfamilies Monsteroideae and Zamioculcadoideae (Hesse and Zetter, 2007). The best recorded South American aroid leaves come from the Cerrejón Formation (Middle–Upper Paleocene), Colombia, and they are characterized by their oblong to sagittate–cordate shape with several primary veins running through the blade, and occasionally showing intersecondary and collective veins (e.g. Herrera et al., 2008).

Herein, we introduce and describe a new fossil taxon with affinities to free-floating aquatic aroids that represents the first fossil record of lemnaceous leaves for the Southern Hemisphere, and represents the oldest record for the subfamily Lemnoideae worldwide. We also report on the presence of *Pandaniidites* Elsik pollen grains associated with these leaves. This constitutes the oldest record of this pollen type for the Southern Hemisphere as well. In this context, we test the phylogenetic relationships among extant and extinct members of Araceae and discuss the origin of the free-floating aquatic habit for the family.

2. Materials and methods

2.1. Locality, repository information & specimen preparation

The La Colonia Formation outcrops on the SE slope of the Somuncurá Massif, exposed between Telsen and Gan Gan, in the Arroyo Mirasol Chico area, Chubut province, Patagonia, Argentina (Fig. 2). This formation was initially recognized by Pesce (1979), and later formally named by Ardolino and Delpino (1987). Pascual et al. (2000) recognized three facies associations, and more recently Navarro et al. (2012) suggest that basal deposits of the La Colonia Formation represent a transgressional surface (key surface) associated with the Maastrichtian–Danian Atlantic ingression, followed by a series of barrier-islands/lagoon complexes with a low sea level, and ends with tide dominated deposits suggesting a sea level rise (Navarro et al., 2012). Based on the diverse fossil content that includes macro and micro-vertebrates (reptiles and mammals), micro and macro-plant remains of aquatic alliance (including dinoflagellates), and micro and macro-invertebrates (including forams, ostracods and bivalves), the La Colonia Formation has been assigned to the latest Cretaceous (most probably Maastrichtian) (Ardolino and Franchi, 1996; Gandolfo et al., 2009; Guler et al., 2009; Navarro et al., 2012), although an earliest Danian age cannot be discarded for the uppermost facies (Pascual et al., 2000).

Fossil remains studied in this contribution were collected at the upper section of the stratigraphic sequence that outcrops at the Cañadón del Irupé locality, which corresponds to the middle portion of the La Colonia Fm. Specimens were trimmed in the field and additional preparations were performed as needed by Museo Paleontológico Egidio Feruglio (MEF) technicians. All fossil specimens are preserved as impressions and are housed in the paleobotanical collection of the MPEF (MPEF-Pb), Trelew, Chubut Province, Argentina. Extant leaves of Araceae used for comparisons were extracted from herbarium sheets

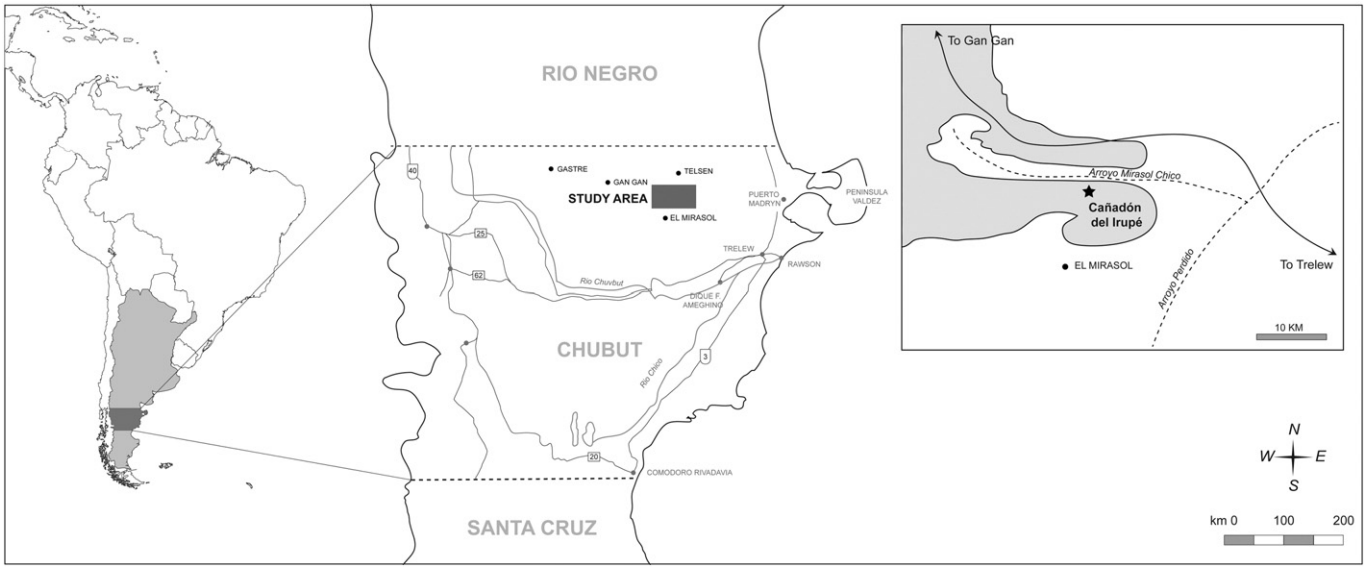

Fig. 2. Location of La Colonia fossil locality bearing remains of Araceae.