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Leaf and inflorescence evidence for near-basal Araceae and an unexpected diversity of other monocots from the late Early Cretaceous of Spain

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Phylogenetic analyses imply that monocots were a key group in the early radiation of angiosperms, yet they are much rarer than other major clades in the Early Cretaceous macrofossil record. Here we describe a well-preserved leaf and several inflorescences related to the near-basal monocot family Araceae and abundant monocot leaves of uncertain affinities from two latest Albian localities in north-eastern Spain. *Orontiophyllum ferreri* sp. nov. has a multistranded midrib, several orders of parallel-pinnate veins, two orders of transverse veins, and paracytic-oblique stomata. This suite of characters (but with both anomocytic and paracytic-oblique stomata) is characteristic today of *Orontium* in the near-basal araceous subfamily Orontioideae, and later Cretaceous and early Cenozoic leaves assigned to *Orontiophyllum* have similar architecture. Sedimentology and anatomy suggest a (semi)aquatic ecology. Other monocot leaves at the same locality are linear and parallel-veined but have similar stomata. Although anomocytic stomata have been proposed as ancestral in monocots, *O. ferreri*, the associated linear leaves, Albian–Cenomanian cuticles from Australia and Portugal, and extant data are consistent with the hypothesis that variable paracytic-oblique stomata are ancestral. *Turolospadix bogneri* gen. et sp. nov., from the other locality, includes spadices of ebracteate flowers with four tepals, a central gynoecium, and a long stipe (vs a spathe attached just below the fertile zone as in most Araceae). Phylogenetic analyses indicate that the character combinations seen in *O. ferreri* and *T. bogneri* are ancestral for Araceae, and they could be either sister to Araceae or nested within a basal grade of the family. Together with fossils from the Aptian–Albian of Brazil and Portugal, the Spanish fossils indicate that Araceae are among the oldest extant monocot families, but they were associated with diverse linear-leaved monocots of uncertain affinities.

Keywords: angiosperms; monocots; Araceae; phylogeny; Early Cretaceous; Spain

Introduction

Monocotyledons (monocots, Monocotyledoneae) are one of the most important extant plant groups, including *c.* 60,000 known living species, with an estimated 20,000 yet to be described (Joppa *et al.* 2010, 2011). They are one of the five major clades making up the core angiosperms or Mesangiospermae, which constitute *c.* 99.9% of angiosperm species, together with eudicots, Magnoliidae, Chloranthaceae and *Ceratophyllum* L. (Cantino *et al.* 2007; APG 2009). Monocots are distributed worldwide and are adapted to a great diversity of environments, from aquatic habitats to deserts and from the tropics to the high latitudes (Nauheimer *et al.* 2012). They are common in Late Cretaceous and Cenozoic macrofossil floras (e.g. Kvaček & Herman 2004; Stockey 2006; Smith 2013; Cúneo *et al.* 2014; Conran *et al.* 2015; Iles *et al.* 2015; and references therein), although usually not abundant, presumably because of the reduced fossilization potential of these largely herbaceous plants.

Despite the inferred early divergence of monocots in the mesangiosperm radiation, their Early Cretaceous fossil record is more meagre than that of magnoliids, eudicots and Chloranthaceae (Friis *et al.* 2006, 2011; Doyle & Endress 2010, 2014; Doyle 2015) and systematically confused. Two Early Cretaceous pollen types that Doyle (1973) and Walker & Walker (1984) compared with monocots, *Clavatipollenites minutus* Brenner and *Similipollis* Góczán & Juhász (then identified as *Liliacidites* Couper), have been associated with flowers (*Virginianthus* Friis *et al.*, 1994; *Anacostia* Friis *et al.*, 1997) that phylogenetic analyses place in other groups (Laurales and Austrobaileyales: Doyle *et al.* 2008). Friis *et al.* (2000, 2011) compared *Pennipollis* Friis, Pedersen & Crane and associated flowers with the monocot order Alismatales, but phylogenetic analysis links them with Chloranthaceae and/or *Ceratophyllum* (Doyle *et al.* 2008; Doyle & Endress 2014). Most confirmed Early Cretaceous monocot fossils have poorly defined affinities within the group. These include reticulate

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monosulcate pollen with finer sculpture at the ends of the grain (*Liliacidites sensu stricto*) and a stem bearing narrow leaves with sheathing bases and apically converging and fusing venation (*Acaciaephyllum* Fontaine) from the Aptian of the eastern USA (Fontaine 1889; Doyle 1973; Doyle *et al.* 2008), whose monocot affinities were questioned by Gandolfo *et al.* (2000) but confirmed by phylogenetic analyses (Doyle *et al.* 2008). Other remains of uncertain position within monocots are dispersed cuticles from the late Albian–early Cenomanian of Australia (Pole 1999). *Cratosmilax jacksoni* Lima, Saraiva, Silva, Bantim & Sayão, a leaf with acrodromous venation from the late Aptian of Brazil, was assigned to Smilacaceae by Lima *et al.* (2014) but differs in having much less regular venation (see Lima *et al.* 2014, fig. 5). C. Coiffard (pers. comm.) considers this species synonymous with *Hexagyne philippiana* Coiffard, Mohr & Bernardes-de-Oliveira, known as stems, leaves and flowers from the same formation, which has been placed in the magnoliid order Piperales by phylogenetic analysis (Coiffard *et al.* 2014).

A conspicuous exception to this uncertain systematic picture is presented by a growing number of Early Cretaceous fossils that have been compared with Araceae, the largest family of the order Alismatales, which diverged before all other monocots except the basal genus *Acorus* L. Araceae are divided into eight subfamilies, over 100 genera, and more than 3000 species, including both plants of freshwater aquatic habitats, like most other Alismatales, and more numerous terrestrial species, many of them climbers and epiphytes (Mayo *et al.* 1997). Friis *et al.* (2004) compared masses of pollen with striate (polyplicate) sculpture from the Aptian or early Albian of Portugal (*Mayoa* Friis, Pedersen & Crane) with *Holochlamys* Engler and *Spathiphyllum* Schott, although the angiosperm affinity of this pollen has been questioned by Hofmann & Zetter (2010). Other presumed Araceae are two unnamed inflorescences from the Aptian–early Albian of Portugal (Friis *et al.* 2010, 2011), and *Spixiarium* Coiffard, Mohr & Bernardes de Oliveira from the late Aptian of Brazil, which is known as dispersed leaves and a rhizome with attached leaves and roots (Coiffard *et al.* 2013).

In this paper, we report leaves and inflorescences of closely aggregated flowers that appear to be related to Araceae, plus a variety of other monocot leaves of less certain affinities, from two late Albian localities in north-eastern Spain. The leaves may constitute the oldest well-characterized foliar record of monocots in Eurasia. The most clearly araceous leaf, described here as *Orontiophyllum ferreri* sp. nov., may be one of the best-preserved fossil leaves of monocots in the fossil record, revealing the venation pattern down to the finest veins

and characters of the epidermal cells and stomatal apparatuses. This leaf is most similar in architecture to the genus *Orontium* L. in the subfamily Orontioideae. Orontioideae and the monotypic genus *Gymnostachys* R.Br. form the small (seven species) Proto-Araceae clade of Cusimano *et al.* (2011), which is sister to all remaining Araceae. Extant Orontioideae comprise *Orontium* L., *Lysichiton* Schott, and *Symplocarpus* Nutt. *Orontium* is a plant of aquatic habitats. *Lysichiton* grows in habitats ranging from shallow water to muddy soils, whereas *Symplocarpus* grows in muddy soils (Mayo *et al.* 1997; Kvaček & Smith 2015).

To evaluate the systematic position of the araceous fossils, we conducted phylogenetic analyses based primarily on the morphological dataset of Cusimano *et al.* (2011), which was used to reconstruct the evolution of morphological characters on the currently most comprehensive molecular phylogeny of Araceae. Because of the small number of characters available in the fossils and the need for more work on analysis of leaf characters (cf. Cusimano *et al.* 2011), our results are far from definitive, but we consider them heuristically useful. In particular, although the leaves resemble *Orontium* in all characters in the dataset, our analyses indicate that these features may be ancestral for Araceae as a whole, so the leaf could be in several positions near the base of the family. The inflorescences, described as *Turolospadix bogneri* gen. et sp. nov., come from a different locality than the leaves, and there is no evidence that they were produced by the same species. However, our analyses imply that they have a similar near-basal position in Araceae.

The other fossil leaves are less distinctive in being linear and parallel-veined, and no dataset for extant plants exists to place them phylogenetically. However, they demonstrate an unexpected diversity of monocot fossils at this time, and they share similarities in cuticle structure with *O. ferreri* that may have implications for the ancestral stomatal type in monocots.

Geographical and stratigraphical setting

The fossil leaves reported here were collected near the village of Huesa del Común, in Teruel Province (Aragón region), north-eastern Spain (Fig. 1). This locality is situated 100 km south of Zaragoza city and 113 km north of Teruel city in the Cuencas Mineras Comarcal. The leaves are from the Boundary Marls Unit, which overlies the Utrillas Formation (Aguilar *et al.* 1971). The Boundary Marls are an informal unit of greyish to green laminated marls and claystones containing fossil plants, with intercalated green clays and
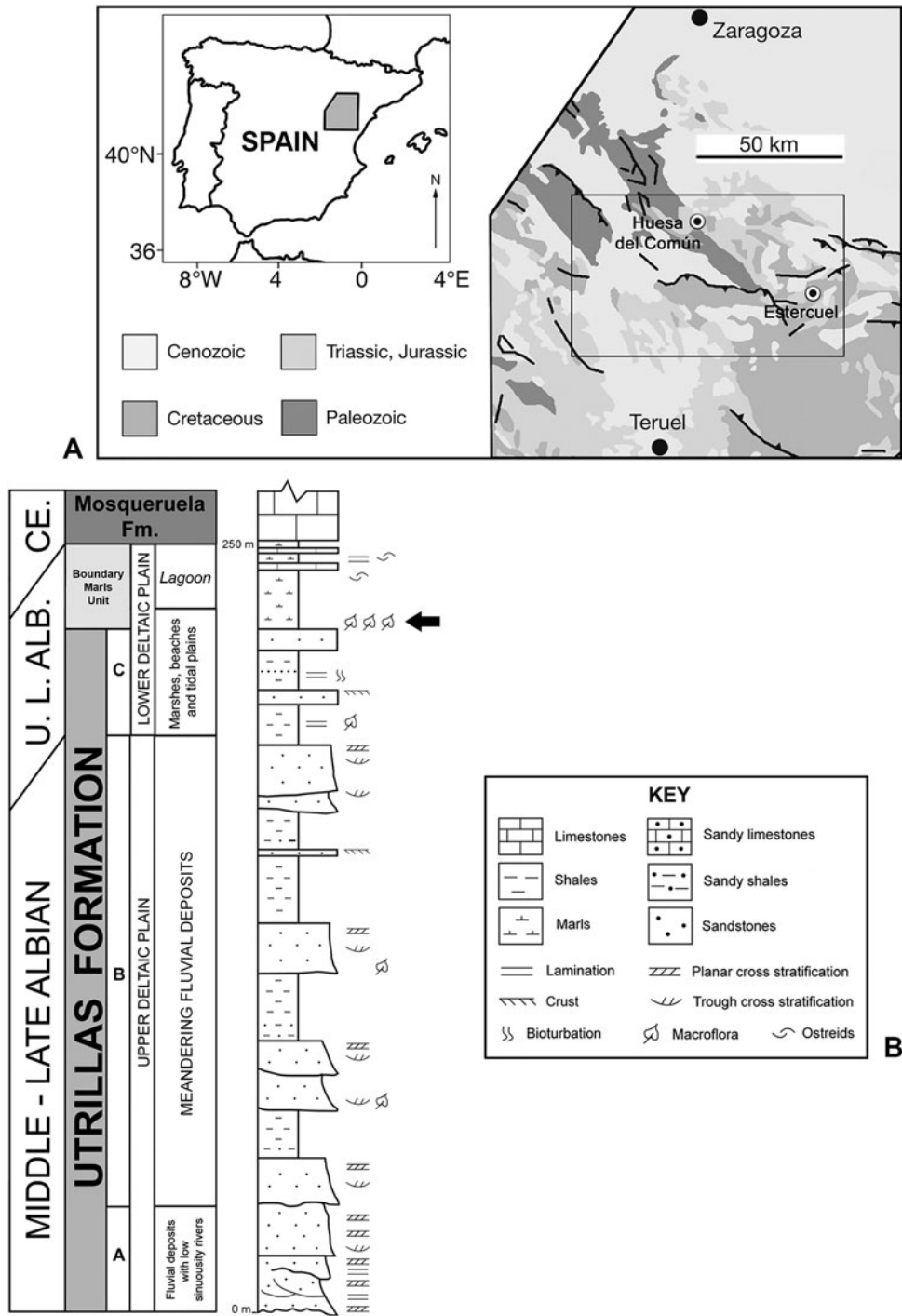
Figure 1. A, geographical location and geological setting of the two localities containing the studied monocot leaves and inflorescences. **B,** synthetic stratigraphical section of the Utrillas Formation and overlying beds in northern Teruel Province (northeastern Spain) indicating depositional environments and sub-environments. Abbreviations: U.L.ALB., uppermost late Albian; CE., Cenomanian. Black arrow in B indicates the position on the synthetic section of the levels containing the monocot remains from both fossil sites.

grey sandy claystones with bivalves and ostracods. Pardo & Villena (1979) interpreted this unit as deposited in freshwater swamps, marshes, beaches and lagoons within a wide coastal plain with marked tidal influence. It underlies shallow marine deposits of the Mosqueruela Formation (Canérot *et al.* 1982), which has been dated

as early Cenomanian at Huesa del Común using benthic foraminifera (Lendínez *et al.* 1989) and by orbitolinids in other areas of the Maestrazgo Basin (Schröder & Neumann 1985; Calonge 1989; García *et al.* 1989) (Fig. 1). Palynological assemblages from the Utrillas Formation in northern Teruel Province indicate a late Albian age (Villanueva-Amadoz *et al.* 2011; Sender *et al.* 2012). The Boundary Marls Unit has been correlated palynologically with the upper part of Subzone II-B or Subzone II-C of Brenner (1963) and Doyle & Robbins (1977) in the Potomac Group and dated as latest Albian, based on the association of *Cyclonephelium chabaca* Below, *Microreticulatisporites sacalii* (Deák & Combaz) Ravn, *Gabonisporis pseudoreticulatus* Boltenhagen, *Elaterosporites klaszii* (Jardiné & Magloire) Jardiné, *Equisetosporites ambiguus* (Hedlund) Singh, *Afropollis jardinus* (Brenner) Doyle, Jardiné & Doerenkamp, *Stellatopollis barghoornii* Doyle, *Liliacidites doylei* Ward, *Liliacidites inaequalis* Singh, *Senectotetradites varireticulatus* (Dettmann) Singh, and *Tricolporoidites* sp., plus other taxa that do not cross the Albian–Cenomanian boundary, such as *Impardecispora trioreticulosa* (Cookson & Dettmann) Venkatachala *et al.* and *Lophotriletes babsae* (Brenner) Singh (Villanueva-Amadoz *et al.* 2011; Sender *et al.* 2012).

The Boundary Marls Unit at Huesa del Común consists of nearly 30 m of finely laminated grey marls and clays with intercalated white to light brown sandstones. Sedimentological data on the stratigraphical level containing the plant fossils indicate a freshwater lacustrine subenvironment within a lower delta plain environment (Pardo & Villena 1979). The diverse floral assemblage includes conifers, ferns, aquatic lycophytes, aquatic angiosperm leaves, and several types of terrestrial angiosperm leaves, including *Sapindopsis* Fontaine (Sender *et al.* 2016).

The inflorescences studied here are from the 'La Dehesa' fossil site near the village of Estercuel, which is situated in the Andorra – Sierra de Arcos Comarcal 120 km south of Zaragoza city, 98 km north of Teruel city, and 40 km south-east of Huesa del Común (Fig. 1). This site is also located in the Boundary Marls Unit. However, sediments at Estercuel are much more detrital than those at Huesa del Común (for details, see Sender *et al.* 2012). The stratigraphical level containing the inflorescences is composed of grey claystones intercalated with fine- to coarse-grained yellow sandstones. This site also shows diverse macro- and microfloral assemblages composed of several types of terrestrial and aquatic angiosperms, conifers, ferns and aquatic lycophytes (Sender *et al.* 2012). These assemblages were deposited in a tidally influenced fluvial sedimentary environment of mainly freshwater coastal marshes and ponds.

Material and methods

The fossils described here include 112 leaves from Huesa del Común, ranging from fragments of various sizes to complete leaves, with preserved cuticle or natural replicas of the epidermal surface; and nine inflorescences from Estercuel, mostly complete spadices, some with the attached peduncle. The holotype of *Orontiophyllum ferreri* consists of a part and counterpart with exquisitely preserved venation and epidermal structure. The other monocot leaves, which are less well characterized and more difficult to place systematically, are designated as Leaf types 1 to 9.

The leaves range from compressions to impressions, both of which include some specimens with preserved venation and others with none. In all cases examined, some evidence of cuticular characters is preserved, either as natural replicas (moulds) of the outer cuticle surface, as cuticles of leaves viewed from the inside, or rarely as internal casts of mineral material between the two leaf surfaces. The inflorescences are preserved as impressions, with occasional remnants of organic matter.

The fossils were prepared using a micro-pneumatic hammer and sharp needles under a stereomicroscope. Photographs were taken using a Nikon D-90 camera with an AF-S Micro Nikkor 60-mm macro lens. Cross-polarized illumination was used following the technique of image acquisition described by Kerp & Bomfleur (2011). Photographs of epidermal features were taken using a JEOL JSM 6400 scanning electron microscope (SEM) and a Carl Zeiss MERLIN field emission scanning electron microscope (FESEM) at the Microscopical Image Service of the University of Zaragoza (Spain). The specimens are deposited at the Museo de Ciencias Naturales de la Universidad de Zaragoza, Zaragoza city, Spain (MPZ) under the numbers MPZ 2018/353 to MPZ 2018/363 and MPZ 2018/373 for Huesa del Común fossils, and MPZ 2018/364 to MPZ 2018/372 for those from Estercuel.

We have described the fossil leaves using the terminology of Kvaček & Smith (2015), who in turn adapted terms proposed by Hickey & Petersen (1978) and Mayo *et al.* (1997). The Hickey & Petersen (1978) terminology was a preliminary attempt to formulate an alternative to the dicot-centred system of Hickey (1973) for the very differently organized venation of most monocots, which they applied to fossil leaves assigned to Zingiberales. One modification of Kvaček & Smith (2015) concerned the term 'costa', which Hickey & Peterson used for a midrib consisting of either a single thick vein or numerous parallel veins, but which Kvaček & Smith restricted to the latter multistranded type. In addition, Kvaček & Smith (2015) adopted the term 'primary lateral veins' of Mayo *et al.* (1997) for major veins that diverge from the

costa. As discussed by Hickey & Peterson (1978), these might be considered secondary veins in the terminology of Hickey (1973), but they are often similar in thickness to the strands making up the costa. Furthermore, they are usually interspersed with finer veins, which might be called tertiaries but are like the thicker veins at their origin from the costa and have a similar parallel course. Such venation is called parallel-pinnate. Kvaček & Smith (2015) followed Hickey & Peterson (1978) in using the term 'set' for a group of parallel veins that form a recurring pattern. Every vein of equal thickness in a set is designated by a letter to compose the characteristic formula of the leaf. The thickest veins of the parallel vein set are designated A (or sometimes B, when a thicker vein or veins occur in the costa), with each subsequent vein order assigned the next letter of the English alphabet in order of decreasing thickness (B, C, D). Hickey & Peterson (1978) used no special term for the thickest veins, because in Zingiberales these and the finer veins of the same set are similar in having a parallel course and originating from veins in a multistranded costa. However, we find it more practical to follow Kvaček & Smith (2015) in using 'primary lateral veins' for the thickest veins, since they are more distinct from finer veins in most Araceae than they are in Zingiberales. The terminology used in the description of cuticular characters follows Dilcher (1974), with modifications by Keating (2002), Prabhakar (2004) and Rudall et al. (2017).

For some images of the fossil inflorescences we used the 'Invert values' tool in Adobe PhotoShop CS6 for better visualization of the original three-dimensional form of the flowers. This tool inverts the values in an image to produce a digital negative, which mimics producing a cast of the specimens (henceforth, 'virtual cast').

The dataset used for phylogenetic analyses is a modified subset of the IAS1 matrix of Cusimano et al. (2011, Supplemental data S1), which contained two outgroups (Acorus, the sister group of all other monocots, and Tofieldia Hudson, representing other Alismatales), 109 terminal taxa of Araceae (all of which are genera), and 81 characters. To reduce the sampling of taxa to a more convenient number, we collapsed 10 clades of two or more genera that have identical states in all the leaf characters of Cusimano et al. (2011) into single terminal taxa, resulting in 91 taxa of Araceae. All the collapsed taxa are in the large subfamily Aroideae (71 of the original 109 genera of Araceae), most of whose members differ markedly from the fossils in both leaf and floral characters. We reduced the character set to those characters preserved in the fossils, made one major change in character definition to allow more precise assessment of the position of the fossil leaf, and added two new characters, for a total of 17 characters. Character definitions,

a list of collapsed taxa, and the data matrix are presented in the Supplemental material. Modifications in scoring of leaf characters are based on descriptions and illustrations in Mayo et al. (1997) and our own observations on specimens in the University of California Davis Herbarium (DAV). As noted by Cusimano et al. (2011), there has been little work on comparative leaf architecture in living Araceae since the remarkable monograph of Ertl (1932), and much more comprehensive and critical analysis of leaf characters across the family is needed. However, we consider the Cusimano et al. dataset heuristically useful as a starting point for our analysis.

The definition change was in character 23 of Cusimano et al. (2011), "primary leaf venation – midrib", with two states, 0 for "midrib of primary veins ± absent with veins arcuate from the base", and 1 for "midrib of primary veins well developed, i.e. pinnate veins in anterior division" (the part of the blade above the petiole insertion, excluding basal lobes). Because state 0 included both conditions like that in the fossil and other conditions that are distinctly different, in our character 5 we split this state into three, which vary in the course of the primary lateral veins. The distribution of the resulting four states on the reduced tree of Cusimano et al. (2011) is shown in Figure 2. Leaves with our more narrowly defined state 0 have low-angle arcuate primary lateral veins, as in Orontium and the fossil Orontiophyllum ferreri described here. They may have several parallel veins at the middle of the blade, but although these veins form a costa in the sense of Kvaček & Smith (2015), they are not part of a thickened structure that runs the length of the blade. Following Cusimano et al. (2011), we also use this state for linear leaves with parallel venation (Gymnostachys and the outgroups). As in Cusimano et al. (2011), leaves with state 1 have a thickened and multiveined costa that gives rise to pinnately arranged primary lateral veins.

Of the two new states, we use state 2 for leaves with distinctly pinnate primary lateral veins that diverge from one or more medial veins, but no thickened costa. This state occurs in most Pothoideae: Anthurium Schott, Pedicellarum M.Hotta, and most species of Pothos L., but not the monotypic genus Pothodium Schott, which has low-angle primary lateral veins and no distinct medial vein(s) (state 0). In Pothos, species such as P. scandens L., P. junghuhnii de Vriese (Mayo et al. 1997) and P. loureiroi Hook. & Arn. (our observations) have arcuate primary lateral veins and fall in state 0, but other species have pinnate venation. Of these, some have a simple medial vein, but others, such as P. hellwigii Engler (our observations), have an unthickened medial zone of several veins. Both types fall in state 2 rather than state 1, which requires both thickening of the costa and several component veins. We therefore score Pothos as 0/2. State 2 also
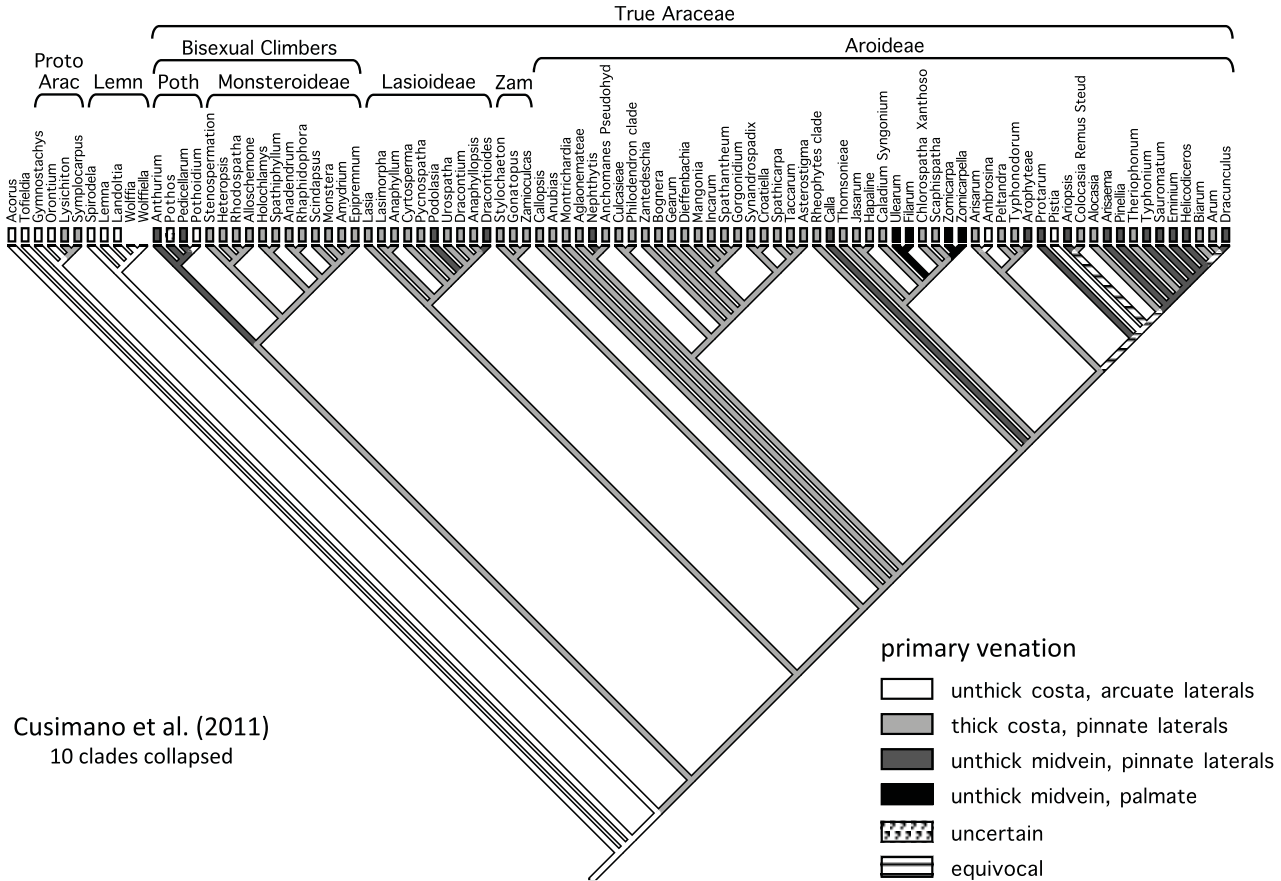
Figure 2. Backbone constraint tree of extant Araceae and two outgroups (modified from Cusimano *et al.* 2011), showing parsimony optimization of the primary venation character as redefined here. Abbreviations: Proto Arac = Proto-Araceae, Lemn = Lemnoideae, Poth = Pothoideae, Zam = Zamioculcadoideae, Anchomanes Pseudohyd = *Anchomanes + Pseudohydrosme*, Chlorospatha Xanthoso = *Chlorospatha + Xanthosoma*, Colocasia Remus Steud = *Colocasia + Remsuatia + Steudnera*.

occurs in some Lasioideae (*Podolasia*, *Dracontioides*) and many Aroideae. A problem concerns whether the apparent primary lateral veins in Pothoideae are equivalent to those in other taxa. In *Anthurium*, Ertl (1932) showed that these veins develop after the midrib and the arcuate outer veins, which suggests that they may be modified transverse veins. However, using development to define vein orders across Araceae would require extensive new studies, and even with such studies developmental differences might not be infallible as criteria for homology. State 3 is seen in four genera of Aroideae (*Ulearum* Engler, *Filarum* Nicolson, *Zomicarpa* Schott, *Zomicarpella* N.E.Br.), where the major veins have a strongly palmate pattern, with several primary lateral veins diverging from one point at much higher angles than the arcuate veins in *Orontium*.

The fine venation character of Cusimano *et al.* (2011) also needs discussion (their character 28, our character 8). Cusimano *et al.* defined this character in terms of secondary and tertiary veins, with these "forming mostly cross veins to primaries" in state 0 vs "parallel to primaries, joined by cross veins only" in state 1. States 2 and 3

correspond to two sorts of reticulate patterns. Cusimano *et al.* (2011) scored state 0 as occurring in *Acorus*, *Gymnostachys*, Orontioideae and Pothoideae. Orontioideae have more than one order of transverse veins, with thicker veins connecting primary lateral veins and thinner veins connecting only adjacent parallel veins, whereas in state 1, seen in most Monsteroideae and in Aroideae such as *Philodendron*, there is only one order of transverse veins connecting the thinnest parallel veins (taxa with venation of this type are listed and discussed by Coiffard & Mohr 2015). Although Pothoideae also have transverse veins of varying thickness, more detailed study is needed to evaluate whether their fine venation should be assigned to the state seen in Orontioideae. In *Orontium*, Ertl (1932) showed that the thicker transverse veins cross over the finer parallel veins. He described the same phenomenon in some Monsteroideae and Aroideae, but not in Pothoideae. However, presence or absence of vein crossing may not be a consistent difference between Orontioideae and Pothoideae, since Ertl (1932) did not report it in *Symplocarpus*. Because resolution of these

problems is beyond the scope of this study, we have pro-visionally retained the scoring of Cusimano *et al.* (2011) in Pothoideae.

There are also problems in scoring *Acorus*, *Tofieldia* and *Gymnostachys*, which have linear leaves and fine, closely spaced parallel veins. As a result, it is question-able whether distinctions recognized in the broad leaves of most Araceae can be applied. *Acorus* differs from other taxa in having laterally flattened, unifacial leaves with a set of parallel veins of varying thickness on either side. There is only one order of fine transverse veins, which connect only adjacent parallel veins but vary from perpendicular to oblique relative to the axis of the leaf (Ertl 1932; Kaplan 1970). Because this con-dition is not easily compared with states in broad-leaved Araceae, and because it is unclear whether the venation of a unifacial leaf can be compared with that of the bifacial leaves of other taxa, we have rescored *Acorus* as unknown. Cusimano *et al.* (2011) scored *Tofieldia* as having state 1, but because it has such fine, closely spaced parallel veins, we have also rescored it as unknown. By contrast, *Gymnostachys* has several orders of parallel veins, and although most transverse veins are of the finest order and connect only adjacent parallel veins, some are slightly thicker and more oblique and connect at least three parallel veins. We therefore con-sider its fine venation similar enough to that of *Orontium* to be provisionally scored as 0.

One of our two new characters is stomatal type (char-acter 10), not included by Cusimano *et al.* (2011), which we scored using primarily data of Keating (2002). Stomata in many Araceae are brachyparacytic (with a pair of short lateral subsidiary cells) or anomocytic (with no differentiated subsidiaries, as in Lemnoideae and *Pistia* L., and, mixed with brachyparacytic, in *Orontium*). Both stomatal types are common in other monocots (including *Acorus*, with brachyparacytic, and *Tofieldia*, with anomocytic: Zomlefer 1997; Rudall *et al.* 2017). Developmental processes leading to the brachyparacytic stomata, which Rudall *et al.* (2017) called paracytic-oblique, are discussed in detail below. Other Araceae have stomata with both lateral and polar subsidiary cells, designated brachypara-tetracytic, brachypara-hexacytic, and brachypara-octocytic. In these types the polar cells are elongated perpendicular to the stomatal axis. Two or more of these types often occur on the same leaf, usually along with brachyparacytic stomata; Keating (2002) described only *Pothos*, *Spathiphyllum*, *Anadendrum* Schott, *Anaphyllum* Schott, and members of the Rheophytes clade as having only stomata with polar subsidiaries. Because of this vari-ation, we combined all these conditions in state 2, defined by presence of polar subsidiary cells in some or all stomata on a leaf. It is possible that more detailed future studies will reveal useful distinctions in patterns of variation in this character.

The other new character is number of tepals (15), scored using data in Mayo *et al.* (1997). Cusimano *et al.* (2011) recognized only a character (2) for pres-ence or absence of a perianth (perigone in araceous usage), but the number of tepals varies within the family. Most other monocots (including *Acorus* and *Tofieldia*) have six tepals, in two whorls of three, but perigoniate Araceae more commonly have four tepals, in two opposite-decussate pairs (Mayo *et al.* 1997), reflecting a shift from trimerous to dimerous phyllotaxis. A problem is that Mayo *et al.* (1997) described many taxa as having four to six tepals; in fact, the only genera of Araceae that they described as having exclusively six tepals were *Orontium* and *Pothoidium*. In character 15, we define state 0 as six tepals and state 1 as four tepals, and we score taxa described as having four to six tepals as uncertain (0/1). Future studies of the systematic dis-tribution of the two perianth types in these variable taxa may allow inference of the ancestral state. Taxa with no perianth were scored as unknown (inapplicable).

We investigated the position of the fossils using a molecular scaffold approach, in which a morphological dataset is analysed with the arrangement of extant taxa fixed to a backbone constraint tree. The backbone tree used is that of Cusimano *et al.* (2011, fig. 1), based on six chloroplast markers, simplified as discussed above. We used PAUP (Swofford 1990) to search for most par-simonious and one step less parsimonious trees, with 10 replicates of random addition of taxa, tree bisection and reconnection (TBR) branch swapping, and *Acorus* speci-fied as outgroup to all other taxa. We also used MacClade (Maddison & Maddison 2003) and Mesquite (Maddison & Maddison 2011) to investigate character support, verify results obtained with PAUP, and test the relative parsimony of alternative arrangements.

Systematic palaeontology

Angiospermae (Lindley, 1830 *sensu* Cantino *et al.* 2007)
Monocotyledoneae (de Candolle, 1817 *sensu* Cantino *et al.* 2007)
Order **Alismatales** Dumortier, 1829
Family **Araceae** Jussieu, 1789 *nom. cons.* (total group)
Genus ***Orontiophyllum*** J. Kvaček & S.Y. Smith, 2015

Type species. *Orontiophyllum austriacum* (J. Kvaček & Herman) J. Kvaček & S.Y. Smith, 2015.

Orontiophyllum ferreri sp. nov.
(Figs 3–5)

Diagnosis. Leaf simple, entire-margined, lamina strap-shaped but expanded at apex and tapering at base, costa broad and weakly developed, distinct only in the basal portion of the lamina, multi-stranded, with veins spreading apically, primary venation parallel-pinnate, with three or four distinct orders of primary lateral veins, with the number of vein orders varying with the distance between the thickest veins, the thinnest order sinuous, the others straight, angle between primary lateral veins and costa ≤10°, with angle of divergence decreasing apically, two orders of transverse veins present, the first (thicker) order connecting different orders of primary lateral veins at angles ranging from 40° to 90° to the parallel veins, the second order thin, connecting only adjacent parallel veins to form rectangular to polygonal areoles. Epidermis with cells organized into rows, stomata restricted to one surface. Epidermal cells on stomatal surface predominantly four-sided, ranging in shape from rectangular to trapezoidal and rhomboidal; cell rows with stomata alternating with cell rows without stomata, non-stomatal rows 3–8 cells wide, stomatal rows one cell wide, anticlinal walls with thicker cuticle than those in non-stomatal rows, stomata longitudinally oriented, subsidiary cell arrangement brachyparacytic, subsidiary cells large, crescent- or kidney-shaped, often extending beyond ends of the guard cells, their ends often adjoining small rhomboidal to trapezoidal cells in the same ontogenetic row. Epidermal cells on non-stomatal surface wider and shorter than unspecialized cells of the stomatal surface, sometimes transversely elongate (i.e. wider than long in relation to the row).

Derivation of name. Dedicated to Prof. Javier Ferrer Plou of the University of Zaragoza (Spain) for his contributions to research in Spanish palaeobotany.

Material. Holotype (only known specimen): MPZ 2018/373 (part and counterpart).

Occurrence. Huesa del Común (Teruel Province, Spain), Boundary Marls Unit overlying the Utrillas Formation, latest Albian, Early Cretaceous.

Description. A single large leaf fragment 7.2 cm long and 2.8 cm in maximum width corresponding to the medial part of a lamina with apex and base missing (Fig. 3A–C). The leaf is simple and entire-margined. The preserved portion of the lamina is nearly strap-shaped but clearly widens from the base toward the apex and narrows slightly in the most apical preserved portion (complete blade possibly elliptic or obovate), with one side of the basal part slightly curved or folded inwards (Fig. 3B). Venation is parallel-pinnate, consisting of a weakly developed multi-stranded costa in the basal part of the lamina from which primary lateral veins depart (Fig. 3B, C, E). The primary lateral venation is organized in sets consisting of three or four orders of parallel veins, with narrower sets consisting of three orders toward the costa (Fig. 3D, F, G). The width of parallel veins decreases from *c*. 200 μm in the widest (first) order to *c*. 50 μm in the narrowest (third or fourth) order (Fig. 3D). The wider veins have a straight course, but veins of the last order are sinuous (Fig. 3D, F). The formula for arrangement of the primary lateral veins in a set (Hickey & Peterson 1978; Kvaček & Smith 2015) is AdCdBdCdA in the wider sets, AcBcA in the narrower sets, with 14 sets of primary veins in the leaf (Fig. 3G). The angle between primary lateral veins and the costa is ≤10°. The primary lateral veins are grouped near the costa at their bases, run parallel toward the margins, and then tend to curve slightly toward the apex of the lamina (Fig. 3B, C, E). Spacing of the first-order primary lateral veins varies from 2 mm in the first quarter of the leaf width from the margin toward the centre, to 1.3 mm in the second quarter, 2 mm in the third quarter, and 1 mm in the fourth quarter near the centre of the lamina (Fig. 3A, B). Spacing between first and second-order primary lateral veins decreases from 1 mm near the margin to 0.5 mm in the middle of the lamina. Spacing between second and third-order primary lateral veins increases from 0.3 mm near the margin to 0.5 mm in the third quarter of the lamina (Fig. 3B, D). Spacing between third and fourth-order primary lateral veins ranges from 0.2 mm to 0.15 mm (visible only in the third quarter of the lamina) (Fig. 3B, F, G). Two orders of transverse veins are present between primary lateral veins (Fig. 3D, F, G). The first-order transverse veins have variable orientations and widths (some are as thick as primary veins). They are irregularly and widely spaced (3 mm on average in vertical direction) and connect all orders of primary lateral veins. These veins are oriented oblique to the costa at variable angles ranging from 40° to nearly 90°. Second-order transverse veins are thin, straight to slightly curved, and oriented at nearly right angles to the primary lateral veins. These transverse veins are spaced 0.4–0.9 mm along the length of the primary lateral veins and connect veins of any order, forming rectangular to polygonal areoles that are elongated parallel to the primary lateral veins (Fig. 3F, G).

Stomata occur only on the side of the leaf seen in specimen B (Fig. 3B). In most plants that have stomata on one leaf surface, this surface is abaxial (i.e. the leaf is hypostomatic). However, the counterpart, specimen A (Fig. 3A), shows other typically abaxial features: greater protrusion of thicker veins and the costa into the matrix, and more
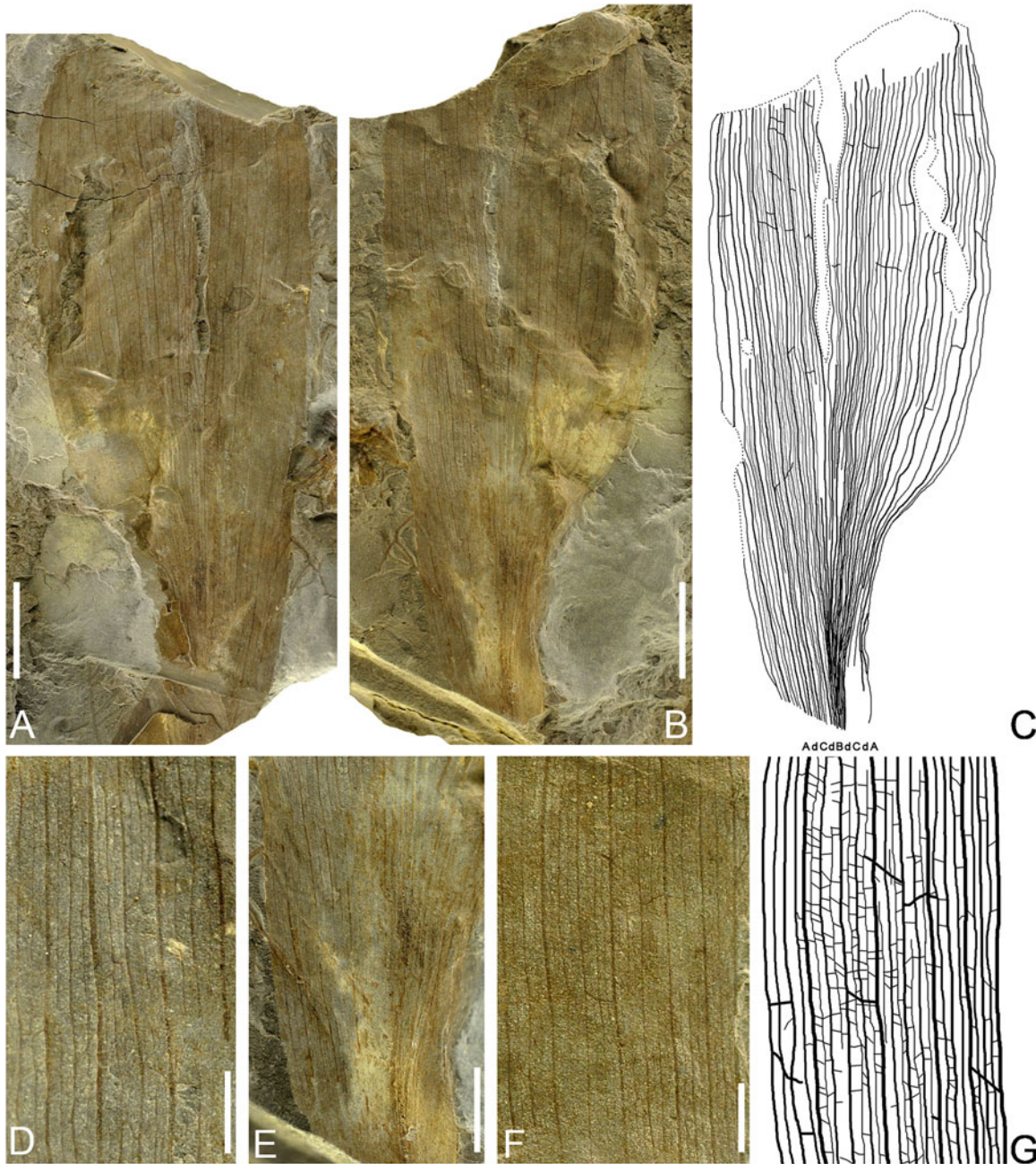
Figure 3. Leaf of *Orontiophyllum ferreri* sp. nov., holotype (MPZ 2018/373). **A, B,** part and counterpart; **C,** line drawing of the part in B; **D,** detail of venation from the centre-left zone of the surface in B; **E,** detail of the basal area with multi-stranded costa of the surface in B; **F,** detail of venation from the upper-right zone of the surface in B; **G,** line drawing of the detail in F, including formula for arrangement of the primary lateral veins in a set. Scale bars: A, B = 1 cm; D, F = 2 mm; E = 5 mm.

organic matter in the costa. These features would imply that the stomatal side in the fossil (B) is adaxial (i.e. the leaf is epistomatic). Because we do not consider this issue entirely resolved, we henceforth refer to the two sides of the leaf as stomatal (B) and non-stomatal (A).

On the stomatal side of the leaf (specimen B, Fig. 3B), we interpret the surface seen under FESEM as the inside

of the cuticle, based on the well-preserved flanges between epidermal cells that project toward the observer (Fig. 4). The cells are organized into distinct rows, some of which include stomatal complexes. Non-stomatal cell rows form zones 3–8 cells wide (Fig. 4B). Cells in these rows are rectangular to trapezoidal, with straight to weakly curved anticlinal walls, and measure 5–7 μm wide

(Fig. 4C–H). Cell length is ambiguous. Areas enclosed by distinct anticlinal walls are highly elongate and measure 64–93 μm long, but these are sometimes traversed by very narrow ridges (e.g. Fig. 4F–H, white arrowheads) that may represent weakly developed and poorly preserved cuticular flanges. If this is correct, cell length is probably much shorter than the above measures.

Stomatal rows are one cell wide (Fig. 4B, E). In these rows, unspecialized cells are predominantly rectangular, 21–49 μm long and 7–10 μm wide. They have wider and deeper anticlinal walls (cuticular flanges) than cells of the non-stomatal rows, and a more granular internal surface sculpture (Fig. 4B, E, F). The alternation of stomatal and non-stomatal cell rows is not related to the position of veins: for each 1 mm of leaf width, there are 5–6 parallel veins of various orders, but nearly 18–20 rows of cells bearing stomata.

Stomatal complexes are longitudinally aligned, parallel to both the lamina margin and rows of epidermal
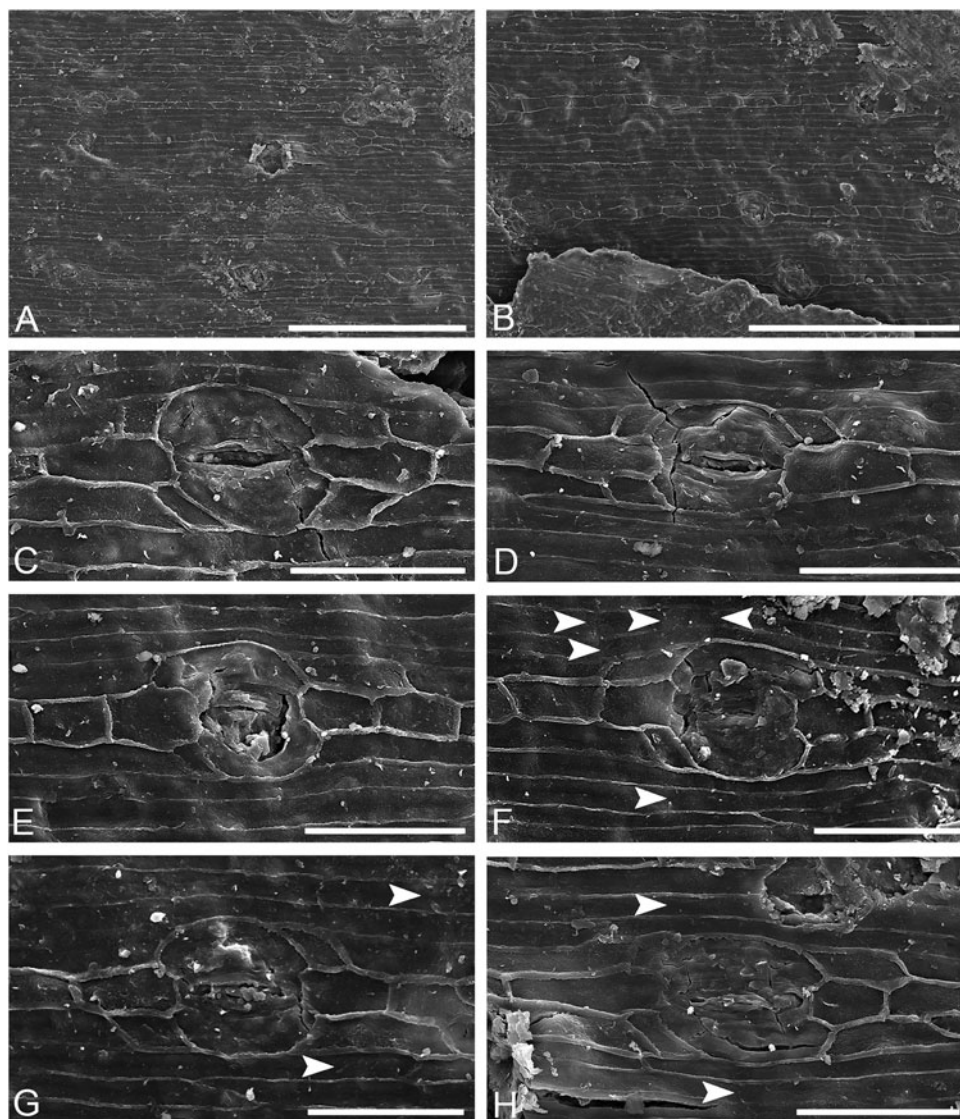
Figure 4. FESEM images of the inside of the stomatal cuticle of *Orontiophyllum ferreri* sp. nov. (surface in Fig. 3B). **A,** general view of rows of cells; **B,** view with more clearly visible cell rows bearing stomata alternating with cell rows without them; **C–H,** individual stomatal apparatuses of *O. ferreri* showing variation in the number, size and shape of subsidiary and neighbouring cells. White arrowheads in F, G and H indicate narrow ridges that may represent weakly developed end walls of epidermal cells. Scale bars: A, B = 200 μm; C–H = 40 μm.

cells. Spacing between stomata within a cell row ranges from 110 to 330 μm (average 140 μm) (Fig. 4B). The stomatal poles are level with the stomatal pore and have no polar extensions, and the guard cells have ridges that we interpret as inner stomatal ledges (Fig. 4C–H). The guard cell pairs are elliptic, with rounded to flattened poles, 29–34 μm long by 8–10 μm wide (Fig. 4C, D, G, H). The stomatal complexes are brachyparacytic, with a pair of lateral subsidiary cells that range from crescent- to kidney-shaped and usually measure 36–39 μm long by 10–12 μm wide (n = 10) (Fig. 4C–H). The subsidiary cells commonly extend beyond, but do not contact, the stomatal poles (Fig. 4C, G, H). Often associated with the subsidiary cells at one or both ends are small cells in the same ontogenetic row that are rhomboidal to trapezoidal in shape and oriented at oblique angles, usually parallel to the end wall of the adjacent subsidiary cell (Fig. 4C–H). Polar neighbouring cells range from similar in size and shape to unspecialized cells in the same row (Fig. 4E, G) to shorter (Fig. 4F, H) or longer (Fig. 4C, D), often with a truncated trapezoidal shape. These stomata conform to the paracytic-oblique type of Rudall *et al.* (2017).

The non-stomatal side of the leaf (specimen A, Fig. 3A) shows longitudinal rows of unspecialized epidermal cells of more poorly characterized size and shape (Fig. 5). It is likely that the surface seen with SEM represents a mould (impression) of the outer cuticle surface, rather than the inner surface of the cuticle, because the anticlinal cell walls do not project toward the viewer. The epidermal cells form rows parallel to the margins of the leaf, and vary from slightly raised (Fig. 5A, C) to sunken (Fig. 5B, D), both between rows and within the same row. Individual rows are 22–27 μm wide (Fig. 5C). Cell shape varies from square to transversely rectangular (Fig. 5C, D), with the long axis perpendicular to the long axis of the leaf, or trapezoidal (Fig. 5D), with the end walls oblique to the leaf axis.

Note on use of 'Araceae': Because our phylogenetic analysis indicates that *O. ferreri* may be a stem relative of Araceae rather than a member of the crown group (the most recent common ancestor of living Araceae and all its derivatives), we indicate that we are assigning it to Araceae as a total group; i.e. the crown group plus any fossils more closely related to Araceae than to any other extant taxa.

Other monocotyledonous leaves from Huesa del Común

All the other monocot leaf types from Huesa del Común (mostly preserved as fragments, except Leaf type 9) are
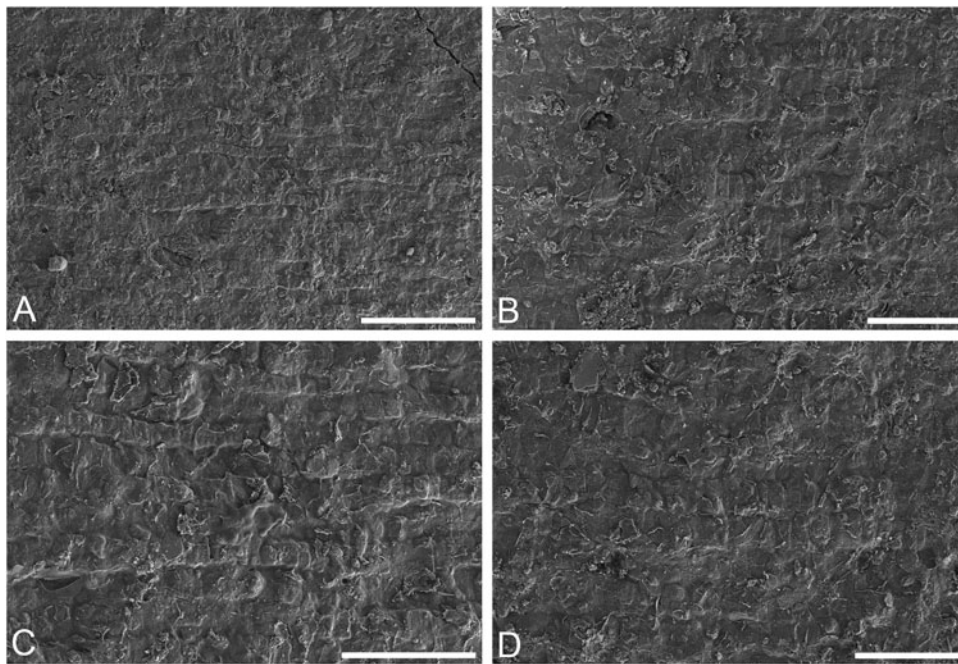
Figure 5. FESEM images of the outside of the non-stomatal cuticle of *Orontiophyllum ferreri* (surface in Fig. 3A). **A,** mostly raised longitudinal rows of epidermal cells. **B,** mostly sunken longitudinal rows of epidermal cells. **C,** detail of the area in A. **D,** detail of the area in B. Scale bars: A = 200 μm; B–D = 100 μm.

strap-shaped and entire-margined. Venation is parallel in all leaves in which it is preserved. There is no distinct medial vein or clustering of veins at the centre of the leaf, except possibly in Leaf types 8 and 9. Three leaf types show little or no preserved venation, but all show evidence of epidermal anatomy, with unspecialized cells in distinct longitudinal rows. Stomata are longitudinally aligned and restricted to special rows that are one cell wide. In most leaf types, unspecialized cells of the stomatal rows have much thicker walls than cells of non-stomatal rows. The number of stomatal rows varies from 20 to 40 per mm of leaf width, depending on the leaf type. Stomata are brachyparacytic and conform to the paracytic-oblique type. Subsidiary cells have rounded to flattened lateral walls and are commonly associated with cells in the same ontogenetic row that are smaller than unspecialized cells. These smaller cells generally have oblique end walls and are rhomboidal to trapezoidal in shape. Polar neighbouring cells are usually shorter than other non-stomatal cells in the same ontogenetic row. Nine leaf types can be distinguished by differences in the structure, shape and size of elements.

Leaf type 1
(Fig. 6A, C, E)

Material. MPZ 2018/253 to MPZ 2018/263 (Huesa del Común).

Description. Wide lamina, with at least two (possibly three) orders of parallel veins, six veins per mm (Fig. 6A). One order of slightly oblique transverse veins joining both orders of parallel veins (Fig. 6A, black arrowheads). Formula for parallel veins in a set is AbA, AcBcA if a third order is present, with at least 20 sets in the leaf. Zones of non-stomatal cell rows 3–6 cells wide (Fig. 6C). Number of cell rows of containing stomata 40 per mm of leaf width. Spacing between stomata within a row 60–200 μm (average 120 μm). Guard cell pairs are elliptic, with flattened or rounded poles, 26 μm long by 13 μm wide (n = 9) (Fig. 6E). Stomata with rhomboidal subsidiary cells, elongate polar cells that vary from shorter to longer than other epidermal cells, and up to four shorter cells with obliquely oriented end walls at the ends of the subsidiary cells (Fig. 6E).

Leaf type 2
(Fig. 6B, D, F)

Material. MPZ 2018/264 to MPZ 2018/272 (Huesa del Común).

Description. One order of parallel veins, three veins per mm; no cross veins observed (Fig. 6B). Internal cuticle surface shows parallel cell rows of a sinuous course, consisting of irregularly rectangular cells of variable sizes with somewhat sinuous walls (Fig. 6B). Zones of non-stomatal cells 3–8 cells wide (Fig. 6D). Number of cell rows containing stomata 30 per mm of leaf width. Spacing between stomata within a row 165–225 μm (average 195 μm). Guard cell pairs are elliptic, with rounded poles, 25 μm long by 9 μm wide (n = 16). Stomata with crescent- or kidney-shaped subsidiary cells, polar cells that are usually shorter than the other epidermal cells, and 2–4 shorter cells with oblique end walls at the ends of the subsidiary cells (Fig. 6F).

Leaf type 3
(Fig. 6G, I, K)

**Material.** MPZ 2018/273 to MPZ 2018/287 (Huesa del Común).

Description. Thin lamina slightly tapering toward one end. One order of thin parallel veins, four veins per mm; no cross veins observed (Fig. 6G). Zones of non-stomatal cells 4–7 (usually seven) cells wide. Number of cell rows containing stomata 30 per mm of leaf width. Spacing between stomata within a row varies greatly, from 106 to 242 μm (Fig. 6I). Guard cell pairs are elliptic, with flattened to rounded poles, 31 μm long by 11 μm wide (n = 9). Stomata with kidney-shaped subsidiary cells, polar cells that often vary in length by a factor of two but are shorter than other epidermal cells, and up to four (usually three) shorter cells with transverse to oblique end walls at the ends of the subsidiary cells (Fig. 6K).

Leaf type 4
(Fig. 6H, J, L)

Material. MPZ 2018/288 to MPZ 2018/290 (Huesa del Común).

Description. At least three orders of parallel veins, with six parallel veins per mm (Fig. 6H, J). Formula for parallel veins in a set is AcBcA, with at least 20 sets in the leaf (total width of lamina incomplete). Spacing of the first-order parallel veins is inconsistent, ranging from 700 μm near the margin to 400 μm toward the centre of the lamina (Fig. 6H). Spacing between first- and second- and between second- and third-order parallel veins decreases proportionally from the margin to the middle of the lamina. Two orders of transverse veins. First-order transverse veins are thicker than the finest parallel
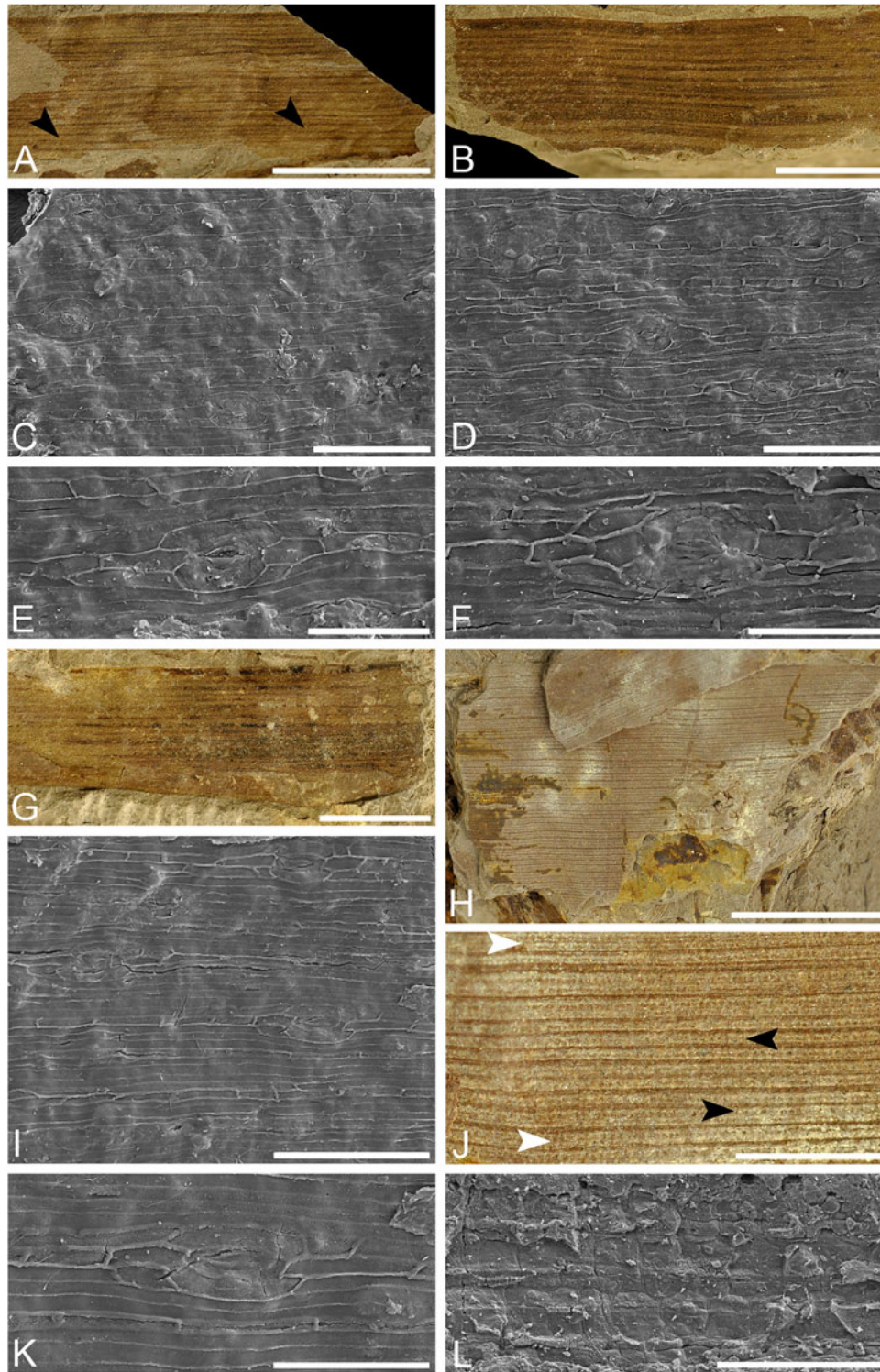
Figure 6. Leaves and related cuticles of other monocots from Huesa del Común. **A, C, E,** Leaf type 1 (MPZ 2018/253); **A,** fragment of leaf with primary parallel veins and transverse veins (black arrowheads); **C,** general view of rows of cells; **E,** stomatal apparatus and associated cells. **B, D, F,** Leaf type 2 (MPZ 2018/264); **B,** fragment of leaf with primary parallel veins; **D,** general view of rows of cells; **F,** stomatal apparatus and associated cells. **G, I, K,** Leaf type 3 (MPZ 2018/273); **G,** fragment of leaf; **I,** general view of rows of cells; **K,** stomatal apparatus and associated cells. **H, J, L,** Leaf type 4 (MPZ 2018/288); **H,** fragment of leaf with primary parallel veins and transverse veins; **J,** detail of venation of leaf in Figure 6H; white arrowheads indicate first-order transverse veins and black arrowheads point to second-order transverse veins; **L,** view of epidermal cells in rows. Scale bars: A, H = 1 cm; B, G = 5 mm; C, D, I, L = 100 μm; E, F, K = 50 μm; J = 2 mm.

veins and connect thickest parallel veins at angles from 55° to nearly 90° (Fig. 6J, white arrowheads). Second-order transverse veins are predominantly oblique, oriented at 45°, spaced 400–900 μm apart, and connect only adjacent veins, forming rectangular to polygonal areoles (Fig. 6J, black arrowheads). Only impressions of the epidermis are preserved, with cells arranged in alternating grooves and ridges, and with cells in the ridges twice as wide as those in grooves. Grooves composed of at least four parallel rows of rectangular to polygonal epidermal cells (Fig. 6L). No stomata observed.

Leaf type 5
(Fig. 7A, C, E)

Material. MPZ 2018/291 to MPZ 2018/327 (Huesa del Común).

Description. Venation poorly preserved, with only hints of numerous very thin parallel veins (Fig. 7A). Epidermal cell rows sinuous in course. Zones of non-stomatal cells 6–8 (usually six) cells wide. Number of cell rows containing stomata 40 per mm of leaf width. Spacing between stomata in a row 140–222 μm (Fig. 7C). Guard cell pairs are elliptic, with rounded poles, 23 μm long by 8 μm wide (n = 7). Stomata with kidney-shaped to sometimes flattened subsidiary cells, polar cells that vary in size, and up to four (usually three) smaller cells with oblique end walls at the ends of the subsidiary cells (Fig. 7E).

Leaf type 6
(Fig. 7B, D, F)

Material. MPZ 2018/328 to MPZ 2018/338 (Huesa del Común).

Description. Venation not preserved (Fig. 7B). Zones of non-stomatal cells 2–8 (usually five) cells wide. Number of cell rows containing stomata 20 per mm of leaf width. Spacing between stomata within a row varies greatly, from 196 to 348 μm (Fig. 7D). Guard cell pairs are elliptic, with rounded poles, 28 μm long by 15 μm wide (n = 10). Stomata with rhomboidal subsidiary cells, nearly equal polar cells that vary from shorter to often longer than other epidermal cells, and up to four (usually three) smaller cells with oblique end walls at the ends of the subsidiary cells (Fig. 7F). These latter cells and the polar cells are often similar in shape and size, so together with the subsidiaries they may form an imperfect ring around the guard cells (Fig. 7F).

Leaf type 7
(Fig. 7G, I, K)

**Material.** MPZ 2018/339 to MPZ 2018/354 (Huesa del Común).

Description. Venation not preserved (Fig. 7G). External cuticle surface with parallel cell rows of a sinuous course, composed of rectangular to elliptical to trapezoidal cells of varying sizes, 20–38 μm long by 5–6 μm wide (Fig. 7I). Internal surface of the cuticle shows zones of non-stomatal cells 4–8 (usually six) cells wide and single cell rows containing stomata. Number of cell rows containing stomata 30 per mm of leaf width. Spacing between stomata within a row 190–250 μm. Guard cell pairs are elliptic, with flattened poles, 33 μm long by 14 μm wide (n = 9). Stomata with relatively narrow subsidiary cells, polar cells that are similar in size and rectangular to polygonal in shape, either shorter or longer than other epidermal cells, and 1–4 smaller cells with oblique end walls at the ends of the subsidiary cells (Fig. 7K).

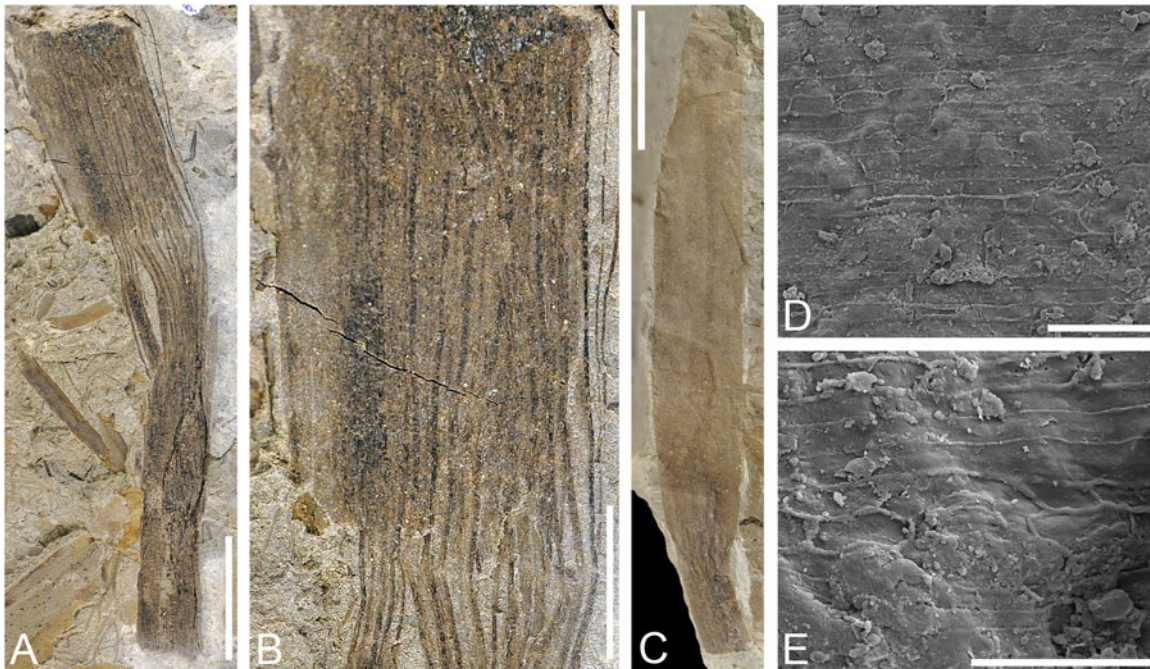### Leaf type 8
(Fig. 7H, J, L)

Material. MPZ 2018/355 to MPZ 2018/361 (Huesa del Común).

Description. Leaf with a central concentration of dark cell files suggesting a multi-stranded midrib 1.2 mm wide, but no visible primary lateral veins or transverse veins (Fig. 7H). External cuticle surface with straight to slightly sinuous parallel cell rows. Zones of 5–6 rows of narrow rectangular to trapezoidal cells with sinuous walls (total 40 μm wide) alternate with rows of much wider (20 μm) cells showing sporadic stomatal apertures. In some areas the rows of wider cells grade laterally and longitudinally into rows of the first type (Fig. 7J). Internal surfaces of the cuticle show zones of non-stomatal cells that are five cells wide. Number of cell rows containing stomata 30 per mm of leaf width. Spacing between stomata within a row more than 500 μm. Guard cell pairs are elliptic, with rounded or flattened poles, 32 μm long by 14 μm wide (Fig. 7L) (n = 6). Stomata often with narrow subsidiary cells, polar cells that are usually equal in size and shape in a given stoma but differ in size among stomata, and 2–4 smaller cells with oblique end walls at the ends of subsidiary cells (Fig. 7L).
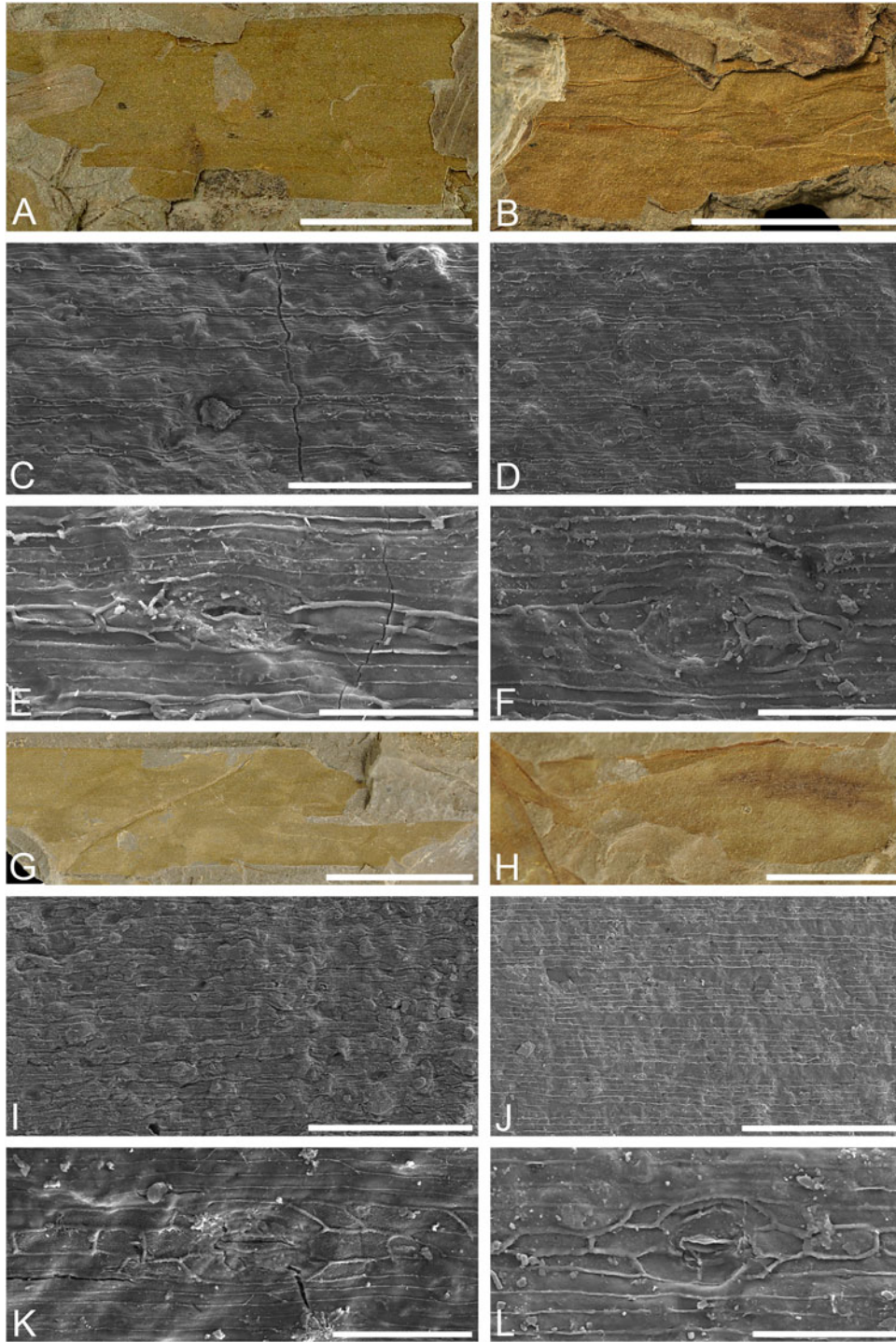
Figure 7. Leaves and related cuticles of other monocots from Huesa del Común. **A, C, E,** Leaf type 5 (MPZ 2018/291); **A,** fragment of leaf; **C,** general view of rows of cells; **E,** stomatal apparatus and associated cells. **B, D, F,** Leaf type 6 (MPZ 2018/328); **B,** fragment of leaf; **D,** general view of rows of cells; **F,** stomatal apparatus and associated cells. **G, I, K** Leaf type 7 (MPZ 2018/339); **G,** fragment of leaf; **I,** general view of rows of cells from the outside of the cuticle; **K,** stomatal apparatus and associated cells. **H, J, L,** Leaf type 8 (MPZ 2018/355); **H,** fragment of leaf with possible medial vein or clustering of veins at the centre of the leaf; **J,** general view of parallel rows of cells from the outside of the cuticle; **L,** stomatal apparatus and associated cells. Scale bars: A, B, G = 1 cm; C, D, I, J = 200 µm; E, F, K, L = 50 µm; H = 5 mm.

Figure 8. Leaves and related cuticles of monocot Leaf type 9 from Huesa del Común. **A,** basal portion of leaf (MPZ 2018/362); **B,** detail of medial-upper zone of specimen in Figure 8A showing venation; **C,** nearly complete leaf (MPZ 2018/363) with possible medial vein or clustering of veins at the centre; **D,** general view of rows of cells in cuticle from the basal part of specimen in Figure 8A; **E,** stomatal apparatus and associated cells in cuticle from the specimen in Figure 8A. Scale bars: A, C = 1 cm; B = 5 mm; D, E = 50 μm.

Leaf type 9
(Fig. 8)

Material. MPZ 2018/362 and MPZ 2018/363 (Huesa del Común).

Description. One leaf fragment, expanding apically to a width of 1 cm (Fig. 8A, B, D, E), and a nearly complete leaf, 4.6 cm long and 0.7 cm in maximum width (Fig. 8C). In the first specimen, no veins can be distinguished in the narrow base (Fig. 8A), but in the truncated apical portion there are more than 15 sets of at least two orders of straight parallel veins, with a formula AbA (Fig. 8B). No transverse veins are visible. The nearly complete leaf is oblanceolate, broadening slightly from a strap-like, possibly sheathing base, with a rounded to sub-acute apex (Fig. 8C). Numerous crowded parallel veins in the base appear to continue apically as a costa that runs straight up the lamina and becomes indistinct near the apex (Fig. 8A). Zones of non-stomatal cells consist of 3–5 (usually five) rows of cells. Number of cell rows containing stomata 30 per mm. Spacing between stomata within a row 300–360 μm (Fig. 8D). Guard cell pairs are elliptic, with rounded poles, 30 μm long by 12 μm wide (n = 6). Stomata with kidney-shaped subsidiary cells, polar cells that are usually nearly equal in size and shape, and up to four smaller cells with transverse to oblique end walls at the ends of subsidiary cells that are similar in size to the polar cells (Fig. 8E).

Family **Araceae** (total group)
Genus *Turolospadix* gen. nov.

Type. *Turolospadix bogneri* sp. nov.

Diagnosis. As for the type and only species.

Derivation of name. From the Latin name for Teruel and Greek/Latin spadix, the inflorescence type.

Turolospadix bogneri sp. nov.
(Figs 9, 10)

Diagnosis. Spadices bearing tens of small polygonal flowers arranged alternately in vertical rows (orthostichies) on a thick axis. Flowers of similar morphology and size along the spadix, with no floral subtending bracts. Spadices associated with a long stipe, up to greater than the length of the fertile portion, with no spathe or scar of a spathe. Four wedge-shaped tepals with a median ridge, arranged in upright cross
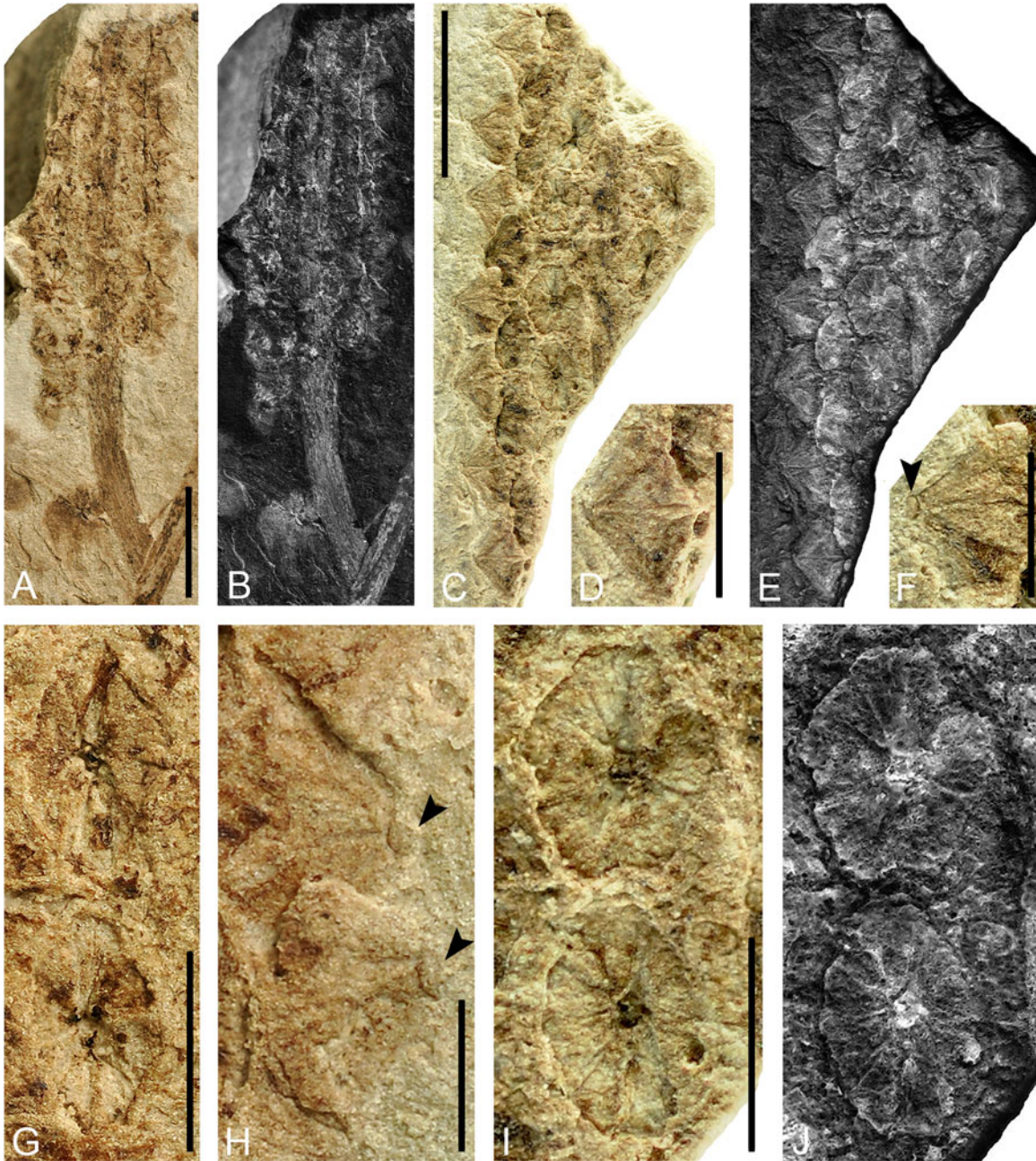
Figure 9. Spadices of *Turolospadix bogneri* gen. et sp. nov. from Estercuel. **A,** holotype MPZ 2018/364; **B,** virtual cast of specimen in A; **C,** paratype MPZ 2018/365; **D,** detail of lowest flower on the left margin of specimen in C showing tepals in lateral view; **E,** virtual cast of specimen in C; **F,** detail of flower halfway up on the left margin of specimen in C showing tepals in lateral view and the small disk-shaped stigma (black arrowhead); **G,** detail of the left margin of specimen in A showing two flowers with four tepals in frontal view; **H,** detail of the right margin of specimen in A showing two flowers with tepals in lateral view; the upper disk-shaped stigma shows clear relief (black arrowheads); **I, J,** detail of lower central part of specimen in C showing two flowers in a normal photo (I) and as a virtual cast (J). Scale bars: A, B, C, E = 5 mm; D, F, G, I, J = 2 mm; H = 1 mm.

configuration and forming a low cone, with round apex of gynoecium protruding from between tips of the tepals.

Derivation of name. In honour of Josef Bogner for his numerous and varied contributions to the systematics of living and fossil Araceae.
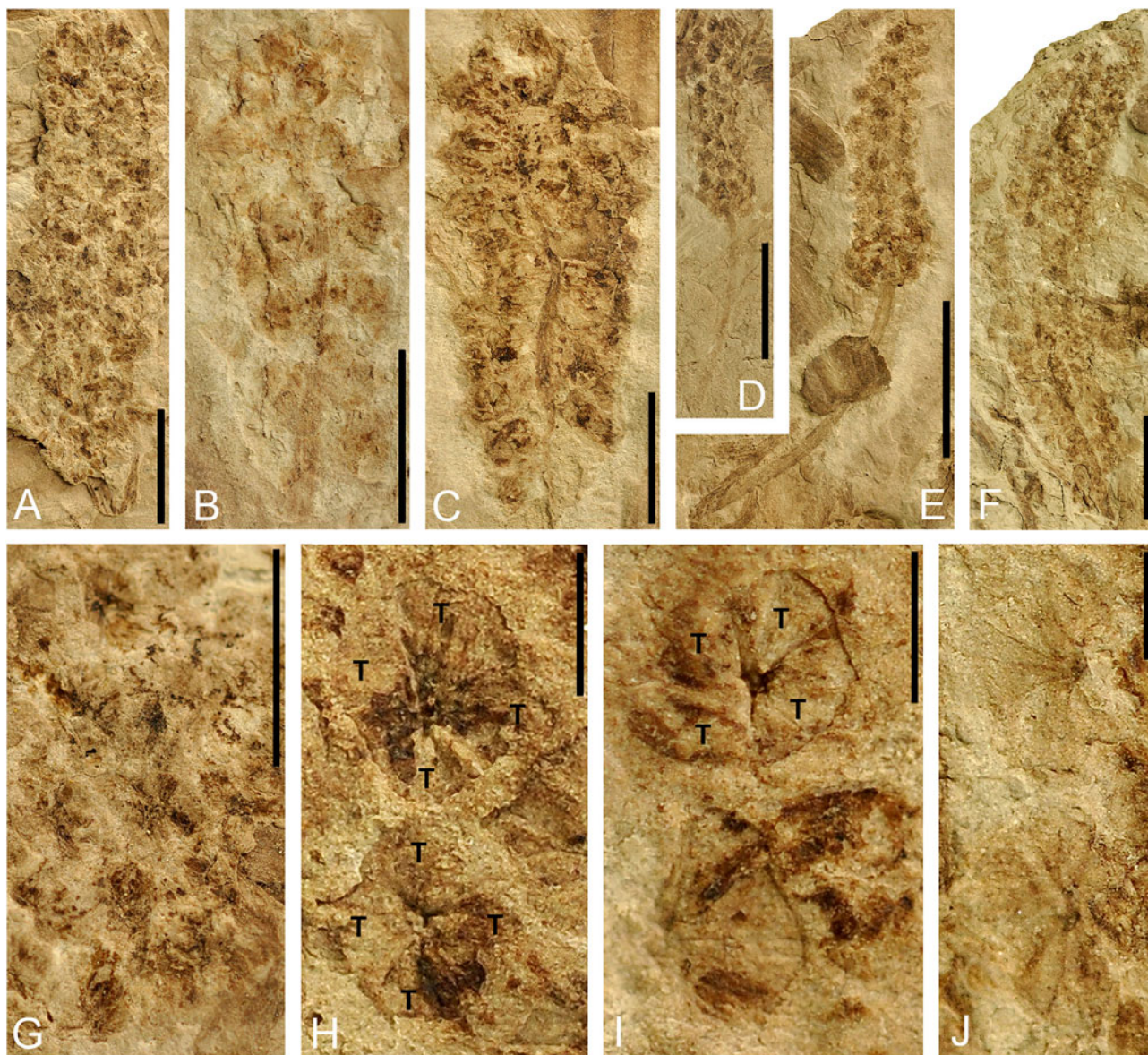
Figure 10. Spadices of *Turolospadix bogneri* gen. et sp. nov. from Estercuel. **A,** MPZ 2018/370; **B,** MPZ 2018/368; **C,** MPZ 2018/367; **D,** MPZ 2018/369, showing long stipe; **E,** MPZ 2018/371, showing long stipe; **F,** paratype MPZ 2018/366; **G,** MPZ 2018/372; **H,** two flowers from the lower right of the specimen in C, both bearing four wedge-shaped tepals; **I,** two flowers from the lower left of the specimen in C, with the upper flower showing four tepals (T) in frontal view and lower one partly tilted into lateral view; **J,** two flowers from the lower right centre of the specimen in F; three wedge-shaped tepals are visible in the upper flower and four in the lower flower, but in both flowers the tepals show the typical median ridge of the species. Scale bars: A, B, C, G = 5 mm; D, E, F = 1 cm; H, I, J = 1 mm.

Material. Holotype: MPZ 2018/364; Paratypes: MPZ 2018/365; MPZ 2018/366. Other material: MPZ 2018/367; MPZ 2018/368; MPZ 2018/369; MPZ 2018/370; MPZ 2018/371; MPZ 2018/372.

Occurrence. Estercuel (Teruel Province, Spain), Boundary Marls Unit overlying the Utrillas Formation, latest Albian, Early Cretaceous.

Description. Nine cylindrical spadices (MPZ 2018/364–MPZ 2018/372) (Figs 9, 10) are preserved as impressions (external moulds) retaining only small traces of carbonaceous material in localized areas (Figs 9A, G, 10A, C, G–I); we isolated minute fragments of cuticle from specimen MPZ 2018/370 (Fig. 10A), but these were degraded and showed no useful characters. Different specimens complement each other in demonstrating various aspects of their morphology, as detailed

below. Most variation among specimens seems related to differential preservation, but in two cases (MPZ 2018/369 and MPZ 2018/371) (Fig. 10D, E) it may be a function of stage of development.

The average length of the fertile portion of the spadix is difficult to estimate because one or the other or both ends are usually not preserved. However, the smallest spadix that appears to be completely preserved (MPZ 2018/368) (Fig. 10B) is 13 mm long, while the longest complete one (MPZ 2018/370) (Fig. 10A) is 21 mm long. The width of the spadix is similar through its length in some specimens but decreases slightly toward the apex in others (MPZ 2018/370, MPZ 2018/371) (Fig. 10A, E). Maximum width is 10 mm (MPZ 2018/366) (Fig. 10F). In most cases, the preserved length of the stipe (portion of the peduncle distal to any bract or spathe) is less than that of the fertile portion, usually much less, but in two specimens it is equal to or longer than the apparently completely preserved fertile portion: 18 mm stipe vs. 18 mm spadix in MPZ 2018/369 (Fig. 10D), 20 mm vs. 17 mm in MPZ 2018/371 (Fig. 10E). The stipe shows indistinct longitudinal striations that may represent vascular bundles.

Flowers are borne in vertical rows (orthostichies), at alternating levels between rows, resulting in oblique rows (parastichies) inclined in opposite directions at the same angle. This indicates a whorled arrangement (Endress & Doyle 2007). The number of vertical rows is clearest in specimens MPZ 2018/365 (Fig. 9C, E) and MPZ 2018/366 (Fig. 10F), which show a row of flowers seen in lateral view on both margins of the spadix (distorted on one margin in MPZ 2018/365), a row of flowers seen in face (apical) view in the middle, and one row of flowers seen in oblique view on either side of the middle row, between it and the marginal row. With five rows visible from the observed side of the spadix and the marginal rows shared with the opposite side, this implies a most likely total of eight orthostichies, or four flowers per whorl. Most flowers appear to be sessile, but some seen in lateral view may have a very short pedicel (e.g. Fig. 9C, E).

Flowers are 1.5–2 mm in diameter. In specimens MPZ 2018/364 (Fig. 9A, B, G) and MPZ 2018/366 (Fig. 10F, G), some flowers seen in face view clearly show four wedge-shaped tepals in an upright cross arrangement. The tepals narrow toward the centre of the flower, leaving a small, round indented area in the matrix in the centre, implying an original protruding structure that we interpret as the apex of the gynoecium (Figs 9A, C, G, I, 10C, H, I); the topography may be clearer in virtual casts made by producing a digital negative (see Material and methods) (Fig. 9B, E, J). The tepals show a usually lighter central line that is sometimes impressed into the matrix,

presumably representing a median ridge on the abaxial side of the tepal. This interpretation is supported by lateral views of flowers at the margins of some spadices (Fig. 9A, C, D, F–H), which show a low, slightly curved conical outline with a small thick disk at the apex, interpreted as the stigma (Fig. 9F, H). Converging lines near the apical and basal sides (with reference to the spadix axis) appear to represent the junctions between the lateral tepal and the apical and basal tepals, while an indented line near the middle of the lateral tepal corresponds to its median ridge (Fig. 9D, F). In specimens MPZ 2018/364 (Fig. 9A, B, G) and MPZ 2018/365 (Fig. 9C, E, I, J), flowers seen in face view appear at first sight to have more than four tepals. However, close examination and comparison with flowers that clearly have four tepals (Fig. 10G–J) and flowers seen in lateral view (Fig. 9C–F, H) indicate that the appearance of more tepals is caused by the lighter colour of the median ridge in some tepals. There is no sign of stamens in any specimen.

In specimens MPZ 2018/369 (Fig. 10D) and MPZ 2018/371 (Fig. 10E), the flowers are similar in size to those in the other specimens, and at least one flower shows four tepals, but they differ in being darker (because of more remaining organic matter) and more deeply impressed in the matrix, suggesting a thicker, more rigid consistency. This is unlikely to reflect a difference in compressibility of the matrix, which is similar in all specimens, so it may represent preservation at a later stage of development, such as early fruit vs flower stage, or late vs early fruit stage.

There is a conspicuous twofold difference in length between spadix MPZ 2018/366 (Fig. 10F) and the other specimens. However, all specimens conform to the same morphological type in terms of the size and shape of the flowers. We have observed comparable variation in length of spadices at the same developmental stage in living *Gymnostachys* (Royal Botanic Gardens, Melbourne; see also Mayo *et al.* 1997, pl. 1).

All flowers within the spadix of *T. bogneri* have the same organization, implying that they were either female or bisexual. In Araceae, all taxa with unisexual flowers have male and female flowers in different zones of the same inflorescence, rather than in different inflorescences (Mayo *et al.* 1997). If the fossils follow the same rule, the presence of one type of flower implies that the flowers were bisexual and the absence of stamens is a result of loss during development or preservation.

Phylogenetic analyses

Analysis of the phylogenetic position of *Orontiophyllum ferreri* on the molecular tree of Cusimano *et al.* (2011)
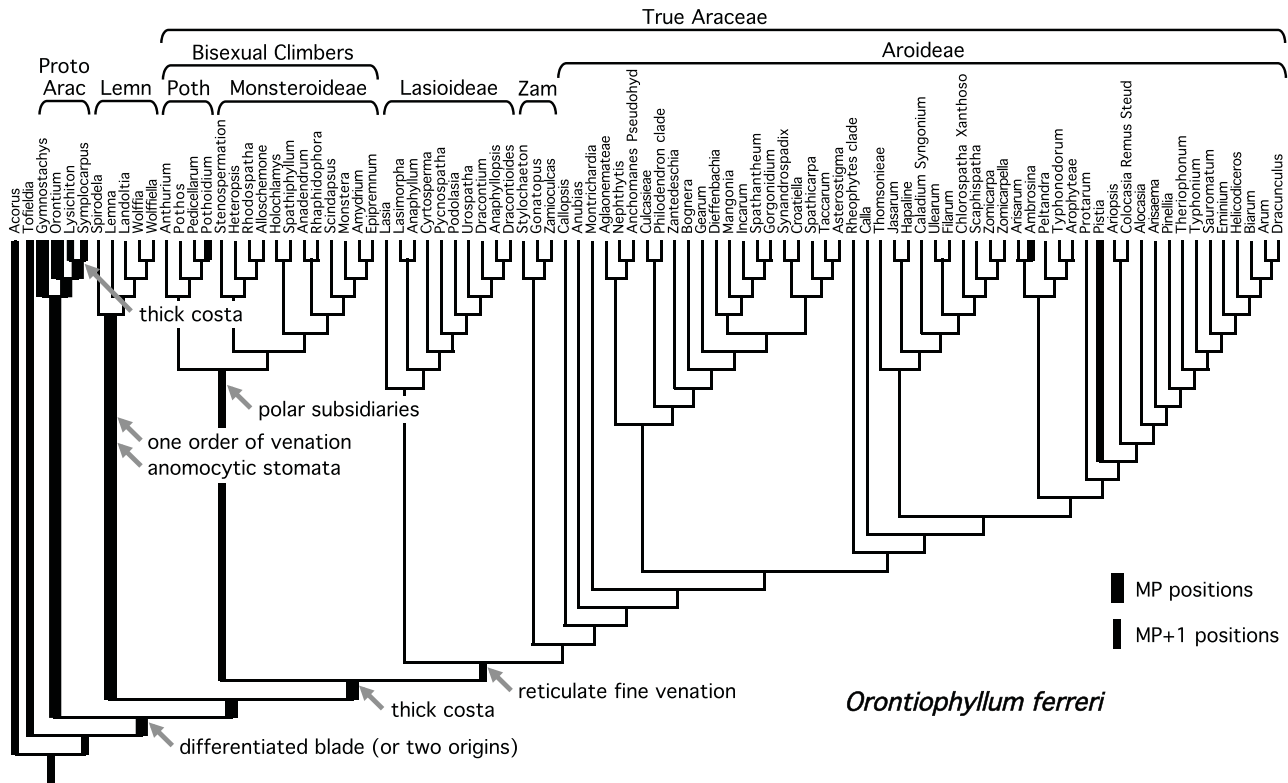
Figure 11. Results of the phylogenetic analysis in which *Orontiophyllum ferreri* sp. nov. was added to the backbone constraint tree (modified from Cusimano *et al.* 2011). Thick lines indicate all most parsimonious (MP) and one step less parsimonious (MP +1) positions for the fossil; arrows indicate synapomorphies that unite various relevant clades. Abbreviations as in Figure 2.

revealed nine most parsimonious positions, indicated by the thickest lines in Figure 11. These are sister to *Orontium*, on three other branches in the Proto-Araceae clade, attached to the stem lineage of this clade, on the stem of Araceae as a whole, on the internal branch leading to Lemnoideae and the True Araceae clade, on the stem of Lemnoideae, and on the stem of True Araceae. Synapomorphies of more derived clades that tend to exclude the fossil are indicated by arrows pointing to the relevant branches. These and other characters supporting the results are discussed further below. There are 11 positions that are one step less parsimonious, indicated by thinner lines: on the stem of monocots as a whole, linked with *Acorus*, on the stem of Alismatales as a whole, linked with *Tofieldia*, with *Lysichiton*, with *Symplocarpus*, on the stem of the Bisexual Climbers clade, on the stem of the *Podolasia* clade (Lasioideae, Zamioculcadoideae and Aroideae), and with *Pothoidium*, *Ambrosina* Bassi and *Pistia*.
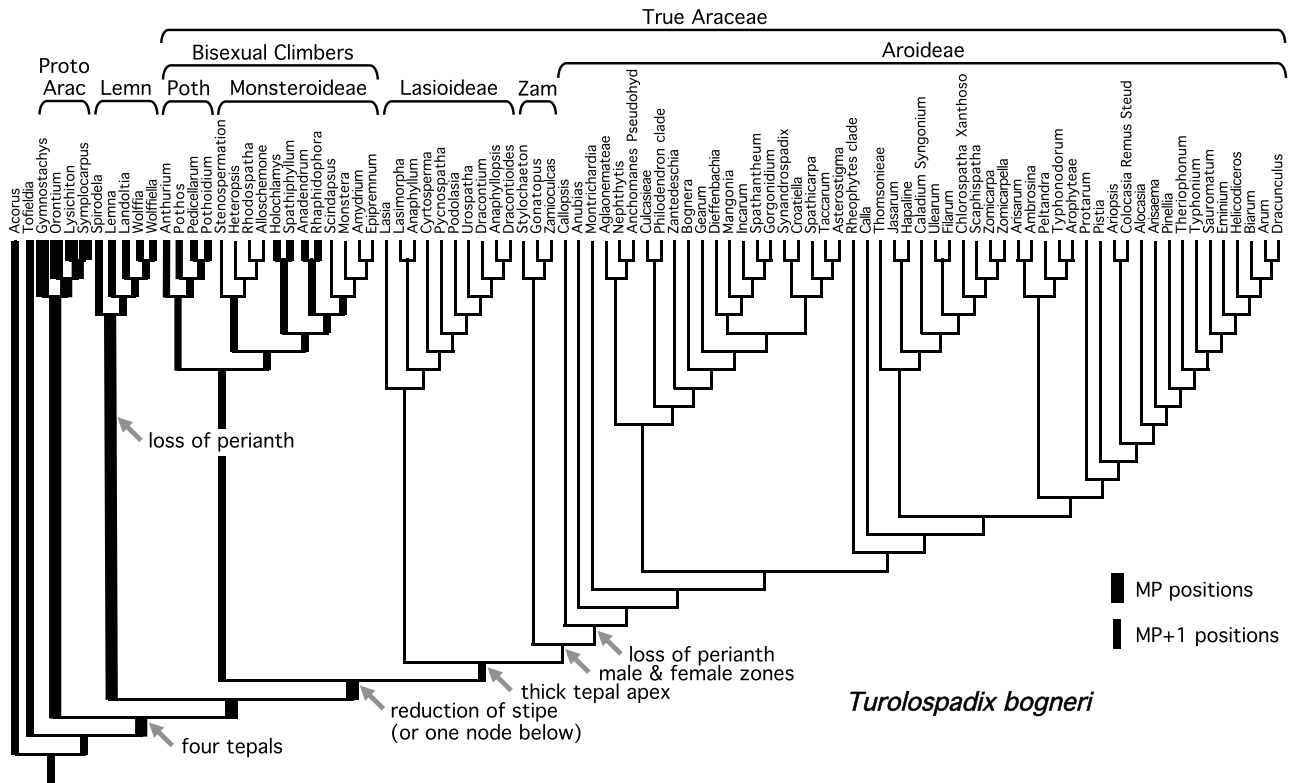
Results of the phylogenetic analyses of *Turolospadix bogneri* are summarized in Figure 12, using the same conventions as in Figure 11. This fossil has 11 most parsimonious positions, all near the base of Araceae: on the stem lineage of the family, on the stem of the Proto-Araceae clade, at all six possible positions within this

clade, on the internal branch leading to Lemnoideae and the True Araceae clade, on the stem of Lemnoideae, and on the stem of True Araceae. It has 32 positions that are one step less parsimonious: on the stem of monocots as a whole, linked with *Acorus*, on the stem of Alismatales, linked with *Tofieldia*, on the stem of the Bisexual Climbers clade, on the stem of Pothoideae, on the stem of Monsteroideae, at all 14 positions within Lemnoideae and Pothoideae, at 10 positions within Monsteroideae, and on the stem of the *Podolasia* clade.

Discussion

Comparison of *Orontiophyllum ferreri* with extant and non-araceous fossil taxa

Some gymnospermous groups have superficially 'parallel' major venation, such as multi-veined conifers and Gnetales, but *Orontiophyllum ferreri* differs from these and resembles modern monocots in several important respects (Doyle *et al.* 2008). Multiveined conifers, cordaites and ginkgophytes have basically open dichotomous venation, whereas *O. ferreri* and most extant monocots have cross veins and a midrib (whether a single medial vein from which veins diverge on either side

Figure 12. Results of the phylogenetic analysis in which *Turolospadix bogneri* gen. et sp. nov. was added to the backbone constraint tree (modified from Cusimano *et al.* 2011). Conventions as in Figure 11.

or a cluster of veins). In Gnetales, *Welwitschia* Hook.f. and Cretaceous fossils such as *Drewria* Crane & Upchurch (Crane & Upchurch 1978) and *Cratonia* Rydin, Mohr & Friis (Rydin *et al.* 2003) have cross veins, but they too have no midrib (although a midrib did arise in *Gnetum* L., associated with dicot-like secondary venation), and the cross veins form a chevron-like or inverted 'Y' pattern, in contrast to the simple transverse pattern seen in *Orontiophyllum* (chevrons do occur in some living monocots and the Aptian fossil *Acaciaephyllum*: Doyle 1973; Doyle *et al.* 2008). Another monocot feature is convergence and sequential fusion of major veins toward the apex, as noted in *Acaciaephyllum*. This is not established in *O. ferreri* because the leaf apex is missing, but the major veins do begin to converge apically in the preserved portion. Some non-monocotyledonous angiosperms (dicots) approach broad-leaved monocots in leaf form and acrodromous major venation (e.g. Piperales), but these lack parallel higher-order venation of the type seen in *O. ferreri* (Doyle *et al.* 2008; Coiffard *et al.* 2013, 2014).

Despite the large number of monocot families, the combination seen in *O. ferreri* of a multistranded but weakly developed costa, parallel-pinnate venation consisting of several sizes of veins, thicker transverse veins

crossing several orders of parallel veins, and finer transverse veins connecting the finest parallel veins is known today only in Araceae, and in particular the subfamily Orontioideae. Other monocots have broad leaves but differ in various venational characters. For example, Zingiberales have a similar parallel-pinnate major vein system, with a multistranded costa that gives rise to primary lateral veins and finer parallel veins between them, but they differ from *O. ferreri* in having a well-developed costa that extends to (or almost to) the leaf apex, and transverse veins of only one thickness, which in the majority of families connect only adjacent parallel veins (Hickey & Peterson 1978; Bogner *et al.* 2007; Coiffard *et al.* 2013; Kvaček & Smith 2015). Other members of the order Alismatales have broad leaves and arcuate primary lateral veins departing from a midrib, but these major veins, or next-order veins that run percurrently between them, are connected by numerous closely spaced fine parallel veins at various angles. As discussed by Coiffard *et al.* (2013), other taxa with broad leaves differ from Orontioideae and our fossil in various ways: in having one order of parallel veins and numerous fine transverse veins (*Pentastemona* Steenis, Pandanales; *Hosta* Trattinnick, Asparagales), more than one order of parallel veins but transverse veins only between adjacent veins (Tecophileaceae, Asparagales),

or more reticulate fine venation (*Tacca* J.R.Forster & G.Forster, Dioscoreales; many other Araceae). For this reason, we restricted our analysis to Araceae rather than attempting to compile a data matrix for all monocots.

Besides the combination of characters listed above, *O. ferreri* has suite of characters that in the extant flora is restricted to the genus *Orontium*, which is endemic to North America: an expanded to oblong lamina, a wide costa that ends well before reaching the apex of the lamina, closely spaced primary lateral veins, a similar range of angles between primaries and the costa, and widely spaced thick transverse veins very similar in width to the primaries, which are oblique to the costa (Bogner *et al.* 2007). However, the first-order transverse veins are both much less numerous and shorter in the fossil than in *Orontium*. The other genera of Orontioideae (*Lysichiton* and *Symplocarpus*) also have veins of several widths, but they differ from *Orontium* and the fossil in the greater length and thickness of the costa, more distinctly pinnate primary lateral veins, and a moderate to strong tendency for reticulate transverse veins (Bogner *et al.* 2007). In the subfamily Pothoideae, *Pothoidium* and some species of *Pothos* approach *O. ferreri* in venation, but the fossil lacks the distinctive apically geniculate and often alate petiole that unites this subfamily (Mayo *et al.* 1997). However, because our phylogenetic analysis indicates that the fossil has several equally parsimonious positions near the base of Araceae, we have assigned it not to *Orontium* but to the fossil-genus *Orontiophyllum*, which was proposed by Kvaček & Smith (2015) for fossil leaves with orontioid architecture.

Epidermal structure reinforces the leaf architectural evidence for the monocot affinities of *O. ferreri*. Guard cells are of the angiospermous type, with stomatal poles level with the stomatal pore, inner stomatal ledges, and no polar extensions. This contrasts with gymnospermous groups such as Gnetales, which have guard cells without well-developed stomatal ledges (all genera), and stomatal poles that are raised relative to the stomatal pore, often with polar extensions (*Ephedra* L. and *Welwitschia*) (e.g. Harris 1932; Upchurch 1995). Epidermal cell organization is much more like that of monocots than other angiosperms, particularly in having longitudinal rows of longitudinally aligned stomata and normal epidermal cells that alternate with rows of cells without stomata (Tomlinson 1974; Doyle *et al.* 2008; Rudall *et al.* 2017). These appear to be basic monocot features, although they are reversed in some derived groups with broad leaves and reticulate venation. Another typical monocot stomatal character seen in the fossil is the presence of an epidermal cell lateral to each guard cell and at each stomatal pole, so each pair of guard cells is contacted by four cells, whether or not these are differentiated into subsidiaries (Stebbins & Khush 1961; Dilcher 1974; Tomlinson 1974; Rudall *et al.* 2017).

Epidermal features are also consistent with a relationship of *O. ferreri* with Araceae, whose anatomy is documented most extensively in Keating (2002). Many Araceae differ from *O. ferreri* in having (1) anomocytic stomata (e.g. Lemnoideae, *Pistia*); (2) stomatal types with both lateral subsidiaries and specialized polar subsidiary cells, which are elongated perpendicular to the stomatal axis (brachypara-tetracytic); or (3) types with both polar subsidiaries and additional lateral or polar subsidiary cells (brachypara-hexacytic, brachypara-octocytic, etc.). Stomata in many Araceae with broad leaves also differ in being randomly oriented rather than aligned (e.g. Rudall *et al.* 2017, figs 3T, 5I–L). However, members of the Proto-Araceae clade (Cusimano *et al.* 2011) and many other groups resemble *O. ferreri* in having brachyparacytic stomata with unspecialized polar cells. *Orontiophyllum ferreri* is also like most Araceae in having no epidermal papillae or trichomes (Mayo *et al.* 1997).

Developmental studies on living monocots provide additional insights on the stomata of *O. ferreri*. In monocots with paracytic stomata, the lateral subsidiary cells are derived from cells in the longitudinal rows adjacent to the stomatal row: a perigenous pattern of development (Stebbins & Khush 1961; Pant & Kidwai 1966; Tomlinson 1974; Grayum 1990; Mayo *et al.* 1997; Rudall *et al.* 2017). As found in earlier studies of Poaceae, Stebbins & Khush (1961) showed that the lateral subsidiary cells in *Juncus* L. and *Sagittaria* L. are derived by asymmetric divisions of epidermal cells adjacent to the guard mother cell, parallel to the stomatal axis (longitudinal), with the resulting contact cells developing into subsidiaries. However, Tomlinson (1974) argued that Stebbins & Khush had overlooked a fundamental distinction within the perigynous paracytic stomatal class: between (1) types where the adjacent cells divide longitudinally, as in grasses; and (2) types where the adjacent cells first undergo oblique divisions, producing trapezoidal cells that give rise to the subsidiaries, either directly or after a longitudinal division. This distinction was endorsed by Rudall *et al.* (2017), who called the two types paracytic-nonoblique and paracytic/tetracytic-oblique, and documented development of the latter type in *Acorus* (which was assigned to Araceae until Grayum 1987). *Acorus* is like *O. ferreri* in the variable form of the cells contacting the subsidiaries in the same longitudinal row, which are often small and trapezoidal. Rudall *et al.* (2017) described the polar cells in *Acorus* as subsidiaries and therefore classified the

stomata as oblique-tetracytic, but its polar cells differ markedly from those of tetracytic Araceae in not being elongated perpendicular to the stomatal axis. For the purposes of our taxonomically more focused analysis, we restrict the term tetracytic to stomata of the araceous tetracytic type.

Despite these similarities, the relatively elongate shape of unspecialized cells on the stomatal surface of the leaf in *O. ferreri* contrasts with the generally shorter unspecialized epidermal cells in Araceae (Keating 2002), as well as with the shorter cells on the opposite surface of the fossil leaf itself. If our identification of the adaxial and abaxial surfaces is correct, *O. ferreri* is like *Orontium* in having stomata on the adaxial leaf surface, but the two taxa differ in shape of the unspecialized cells: long on the presumed adaxial surface, shorter on the abaxial surface in *O. ferreri*; but short on the adaxial surface, longer on the abaxial surface in *Orontium*. Reinterpretation of the leaf surfaces in the fossil would not eliminate the contrast in unspecialized cell shape on the stomatal surface.

Comparison of *Orontiophyllum ferreri* with other fossil monocot leaves

A considerable diversity of fossil leaves related to Araceae has been found in Late Cretaceous deposits of the Northern and Southern hemispheres (Stockey 2006; Bogner *et al.* 2007; Gallego *et al.* 2014; Coiffard & Mohr 2015; Iles *et al.* 2015). However, only a few of these fossils show the combination of strap-shaped to oblanceolate leaf shape with parallel-pinnate primary venation that occurs in *O. ferreri*.

Orontiophyllum riggauense (Knobloch) J. Kvaček & S.Y. Smith from the Turonian of Germany (Kvaček & Smith 2015) resembles *O. ferreri* in having parallel-pinnate venation, nearly constant spacing between parallel veins, and two orders of transverse veins. However, *O. riggauense* differs from *O. ferreri* in having five or six orders of primary lateral veins, rather than the three or four found in our fossil.

Orontiophyllum austriacum (J. Kvaček & Herman) J. Kvaček & S.Y. Smith from the lower Campanian of Austria (Kvaček & Herman 2004; Kvaček & Smith 2015), the type species of *Orontiophyllum*, resembles *O. ferreri* in most characters. However, *O. austriacum* has a much more strongly developed costa that extends the full length of the leaf and an incipient tendency toward reticulate higher-order venation, as in extant *Lysichiton* and *Symplocarpus* (Bogner *et al.* 2007; Herman & Kvaček 2010). This means that *Orontiophyllum* as currently delimited encompasses some deviation from the venation pattern in *Orontium*, *O. ferreri*, and other fossil species.

Orontium mackii Bogner, Johnson, Z. Kvaček & Upchurch from the upper Campanian (Amato *et al.* 2017) Jose Creek Member of the McRae Formation of the USA (Bogner *et al.* 2007) is like *O. ferreri* in having parallel-pinnate venation and a costa that is distinct only in the basal portion of the leaf. However, *O. mackii* has two, rather than three or four, distinct orders of primary lateral veins, and transverse veins of only one order, which are more irregular in orientation and cross both orders of primary lateral veins.

Orontium wolfei Bogner, Johnson, Z. Kvaček & Upchurch from the lower-middle Eocene of the USA and Canada (Bogner *et al.* 2007) resembles *O. ferreri* in having parallel-pinnate primary lateral veins and very widely spaced and oblique first-order transverse veins connecting all orders of primary lateral veins, higher-order transverse veins connecting higher-order primary lateral veins, and wide and elongate areolation. However, the thicker transverse veins in *O. wolfei* are admedially oriented in the central part of the leaf and subhorizontally near the margin, and the thinner transverse veins are often slightly curved and irregularly oriented.

A potentially related but less similar fossil is *Spixiarum*, described by Coiffard *et al.* (2013) from the upper Aptian Crato Formation of Brazil, known from isolated leaves and a rhizome bearing roots and several leaves. Like *Orontiophyllum*, *Spixiarum* has a multi-stranded costa that extends halfway up the blade, parallel-pinnate major venation, and transverse veins that connect both major parallel veins and thinner parallel veins. However, in *Spixiarum* the primary lateral veins are recurved, bending outward until near the margin, rather than curved toward the apex; the finer parallel veins diverge from the proximal (basal) side of the primary lateral veins, rather than from the costa; and the lower-order transverse veins are more nearly parallel than perpendicular to the leaf axis. A problem is that the lower-order transverse veins appear more distinct from the finer parallel veins in the drawings (Coiffard *et al.* 2013, fig. 2C, F) than they do in the photographic figures.

Several Late Cretaceous and Cenozoic leaves with a broad blade and parallel-pinnate venation have been assigned to Zingiberales (e.g. Hickey & Peterson 1978; Peppe *et al.* 2007; Kunzmann 2012). These differ from *O. ferreri* and other Araceae in the characters discussed under living Zingiberales (Coiffard *et al.* 2013; Kvaček & Smith 2015).

There are few reports of epidermal structure in mid-Cretaceous monocots (more are known from the later Cretaceous: Upchurch 1995; Herman & Kvaček 2010). In *Spixiarum* (Coiffard *et al.* 2013), the epidermal cells

appear to be preserved by iron oxide permineralization. *Spixiarum* differs from *O. ferreri*, *Gymnostachys*, and most Orontioideae (except *Orontium*, in which both anomocytic and paracytic occur on the same leaf: Keating 2002) in having anomocytic rather than brachyparacytic stomata. Teixeira (1948, 1950) reported numerous strap-shaped leaves with parallel venation from the Albian and Cenomanian of Portugal as (Monocotiledonea) sp. or *Phyllotaenia* Saporta sp.; the venation is too poorly characterized to say how many of these are monocots. However, specimens from Vila Flor (late Cenomanian: Kedves & Diniz 1981) yielded cuticles with paracytic-oblique stomata very similar to those of *O. ferreri* (Teixeira 1950, pl. 13, figs 1–4).

Pole (1999) reported dispersed fragments of two types of presumed monocot cuticle from the Mackunda and Winton formations of the Eromanga Basin in Australia, of latest Albian–earliest Cenomanian age, which he interpreted in terms of the scheme of Tomlinson (1974). His Monocot-1 cuticle type has longitudinally oriented stomata somewhat similar to those of *O. ferreri*, which he characterized as "essentially paratetracytic". As in *O. ferreri*, they show patterns apparently derived by oblique divisions of the adjacent cells, with smaller trapezoidal or rhomboidal cells adjoining one or both ends of the subsidiaries, but they are more variable, including patterns produced by intersecting oblique and longitudinal divisions that are not seen *O. ferreri*. Pole (1999) noted that the longitudinal divisions suggest a relationship with Arecaceae, but they are less constant than in palms and also occur in other families (Tomlinson 1974). Other differences from *O. ferreri* are the fact that the stomata are not restricted to special longitudinal cell rows and occur on both leaf surfaces. Pole's (1999) Monocot-2 cuticle type is more different from *O. ferreri* and has features suggesting that it may be gymnospermous. Some guard cells appear to have polar extensions and no well-developed outer stomatal ledges, as in gymnospermous seed plants. The combination of longitudinally aligned stomata and paracytic subsidiary cells suggests a possible relationship to the *Welwitschia–Gnetum* clade in Gnetales, prior to the origin of dicot-like venation in *Gnetum*.

Evolutionary implications of *Orontiophyllum ferreri*

Orontiophyllum ferreri has the same state as *Orontium* in all leaf characters in our phylogenetic dataset, except that stomata are brachyparacytic in *O. ferreri* but vary between brachyparacytic and anomocytic in *Orontium*. As expected, one of its most parsimonious positions (Fig. 11) is sister to *Orontium*. However, the fossil has eight other equally parsimonious positions, including

sister to the family as a whole, sister to *Gymnostachys*, and attached to six internal branches between the *Lysichiton–Symplocarpus* clade, Lemnoideae, and the True Araceae clade of Cusimano *et al.* (2011), which includes more than 98% of araceous species. This is because, given the current molecular phylogeny, all the characters of the fossil in our dataset may be ancestral for Araceae. Fossil leaves of this type may therefore represent a basal grade in the family, not just close relatives of *Orontium*, which supports their assignment to the fossil-genus *Orontiophyllum* rather than to *Orontium*.

Major venation and other characters tend to exclude *O. ferreri* from positions elsewhere in Araceae (see arrows in Fig. 11). Within Orontioideae, the *Lysichiton–Symplocarpus* clade is united by a shift from a weakly developed and unthickened costa and arcuate primary lateral veins, as in the fossil, to a well-developed and thickened costa and more strongly pinnate primary lateral veins (character 5, state 1). The same derived state arose convergently on the line leading to the True Araceae clade. Two synapomorphies of the floating aquatic subfamily Lemnoideae exclude the fossil from this clade: only one order of primary venation (character 8, state 4) and anomocytic stomata (character 10, state 0).

Reversals in the major venation character (5) explain the presence of three one-step-less parsimonious positions for *O. ferreri* within the True Araceae clade (Fig. 11). In Pothoideae, a reversal to the fossil state occurs in *Pothoidium* and some *Pothos* species, but a position with *Pothoidium* is counteracted by origin of stomata with polar subsidiaries (character 10, state 2) on the line leading to Pothoideae and Monsteroideae (the Bisexual Climbers clade). Splitting state 0 in the fine venation character (8) and scoring Pothoideae and Orontioideae as having different states, an alternative discussed in Material and methods, would further decrease the support for a position of *O. ferreri* in Pothoideae. Other reversals to the ancestral state in major venation occur in *Ambrosina* and *Pistia* (Aroideae), but linking the fossil with either of these taxa would require a reversal in fine venation (character 8), which becomes reticulate (state 3) on the line leading to Lasioideae and Aroideae (*Podolasia* clade) and is modified within Aroideae to additional derived states (1 and 2).

The nine most parsimonious positions of *O. ferreri* differ in their implications for the evolution of the broad, differentiated leaf blade characteristic of most Araceae, with the conspicuous exception of *Gymnostachys*, which resembles most other monocots in having a linear leaf (character 1). Considering extant

taxa only (Fig. 2), this is the single character of the fossil whose ancestral status in Araceae is equivocal: it is equally parsimonious to assume (1) that the linear leaf of *Gymnostachys* is retained from the first monocots and a differentiated blade originated independently in Orontioideae and the remaining Araceae, or (2) that a differentiated blade originated on the stem lineage of Araceae and the linear leaf of *Gymnostachys* is a reversal. However, if *O. ferreri* is sister to Araceae as a whole, to the Proto-Araceae clade, or to *Gymnostachys*, the hypothesis that the blade originated on the stem lineage of Araceae is favoured (it would require one origin of a blade and a reversal in *Gymnostachys*, rather than three origins of a blade). By contrast, with the fossil at its six other most parsimonious positions, the ancestral state of this character remains ambiguous.

Considering extant taxa alone, parsimony optimization reconstructs fine venation of the type seen in *O. ferreri*, Orontioideae, and provisionally *Gymnostachys* (character 8, state 0) as ancestral in Araceae. If Pothoideae were scored as having a separate state, the inferred ancestral condition in Araceae would be equivocal, and the orontioid state could be either ancestral or a synapomorphy of *Gymnostachys* and Orontioideae (the Proto-Araceae clade). However, a basal position of *O. ferreri* would favour the hypothesis that the orontioid state is ancestral.

If the relatively elongate shape of unspecialized epidermal cells in *O. ferreri* (compared to extant Araceae) is a plesiomorphic feature, this could be evidence that *O. ferreri* is a stem relative of Araceae rather than a crown group member. However, more information is needed on the distribution of cell shape in outgroups before this character can be polarized.

As emphasized by Mayo *et al.* (1997) and Cusimano *et al.* (2011), current definitions of leaf venation characters in Araceae are preliminary and deserve closer future investigation, informed by phylogenetic studies, as attempted in our reassessment of the major venation character. In addition to the difficulties in character definition discussed in this paper, a problem that needs more consideration is possible redundancy among characters treated as independent, such as the presence of basal ribs (character 6) and basal lobation of the blade (character 2). This may be more important in dealing with fossils that belong among more derived groups of Araceae.

Ancestral stomatal type in monocots

The paracytic-oblique stomata of *Orontiophyllum ferreri* and the other leaves from Huesa del Común are relevant to hypotheses on the ancestral stomatal type in monocots, which have been closely tied to the observations of stomatal development discussed above. Stebbins & Khush (1961) argued that stomata with more than two subsidiary cells were ancestral and anomocytic stomata were derived, based on the supposed relative advancement of taxa with the two types. In their comparative survey of monocots, Dahlgren & Clifford (1982) drew no conclusions on the ancestral stomatal type, but Dahlgren & Rasmussen (1983) suggested that it was anomocytic, based on the predominance of this type in Dioscoreales, Asparagales and Liliales, which have other characters that they assumed were primitive. However, this assumption is obsolete in light of present evidence that these taxa are nested within the core clade that includes all monocots other than *Acorus* and Alismatales, or Petrosaviidae of Cantino *et al.* (2007).

Rudall *et al.* (2017, fig. 11) reconstructed ancestral states by optimizing stomatal types on a composite molecular phylogeny of monocots and concluded that anomocytic stomata were most likely ancestral. When they considered only unambiguous character optimization, the ancestral state was equivocal: either paracytic/tetracytic-oblique or anomocytic. Although *Acorus* is paracytic-oblique, Tofieldiaceae (which the most recent molecular analyses identify as the sister group of all other Alismatales: Iles *et al.* 2013; Luo *et al.* 2016) are anomocytic, and Petrosaviidae are basically anomocytic (like *Japonolirion* Nakai in the basal family Petrosaviaceae: Rudall *et al.* 2017). However, when Rudall *et al.* (2017) used either ACCTRAN or DELTRAN criteria to resolve cases of ambiguous optimization (ACCTRAN favours origin of the derived state followed by reversal, DELTRAN favours more than one origin), they inferred that anomocytic was ancestral.

Our results suggest that these conclusions may not be definitive. First, with the Rudall *et al.* (2017) dataset and tree, character optimization using MacClade (Maddison & Maddison 2003) indicates that the most parsimonious ancestral state is still equivocal with both ACCTRAN and DELTRAN (Fig. 13A–C). A less consequential problem is the fact that Rudall *et al.* (2017) scored Araceae as either anomocytic or paracytic/tetracytic-oblique (0/2), but this was based on consideration of only a few derived taxa. With our broader taxon sampling and the data of Keating (2002), the inferred ancestral state in the family is paracytic (Fig. 14). Lemnoideae are anomocytic, but the Proto-Araceae clade is paracytic, and paracytic is reconstructed as ancestral in the True Araceae clade (which also includes taxa, particularly the Bisexual Climbers clade, or Pothoideae plus Monsteroideae, with polar subsidiaries). However, if the dataset of Rudall *et al.* (2017) is modified so that Araceae are represented by three taxa, Proto-Araceae, Lemnoideae and True Araceae, the ancestral state for monocots still remains equivocal under all three resolution criteria.
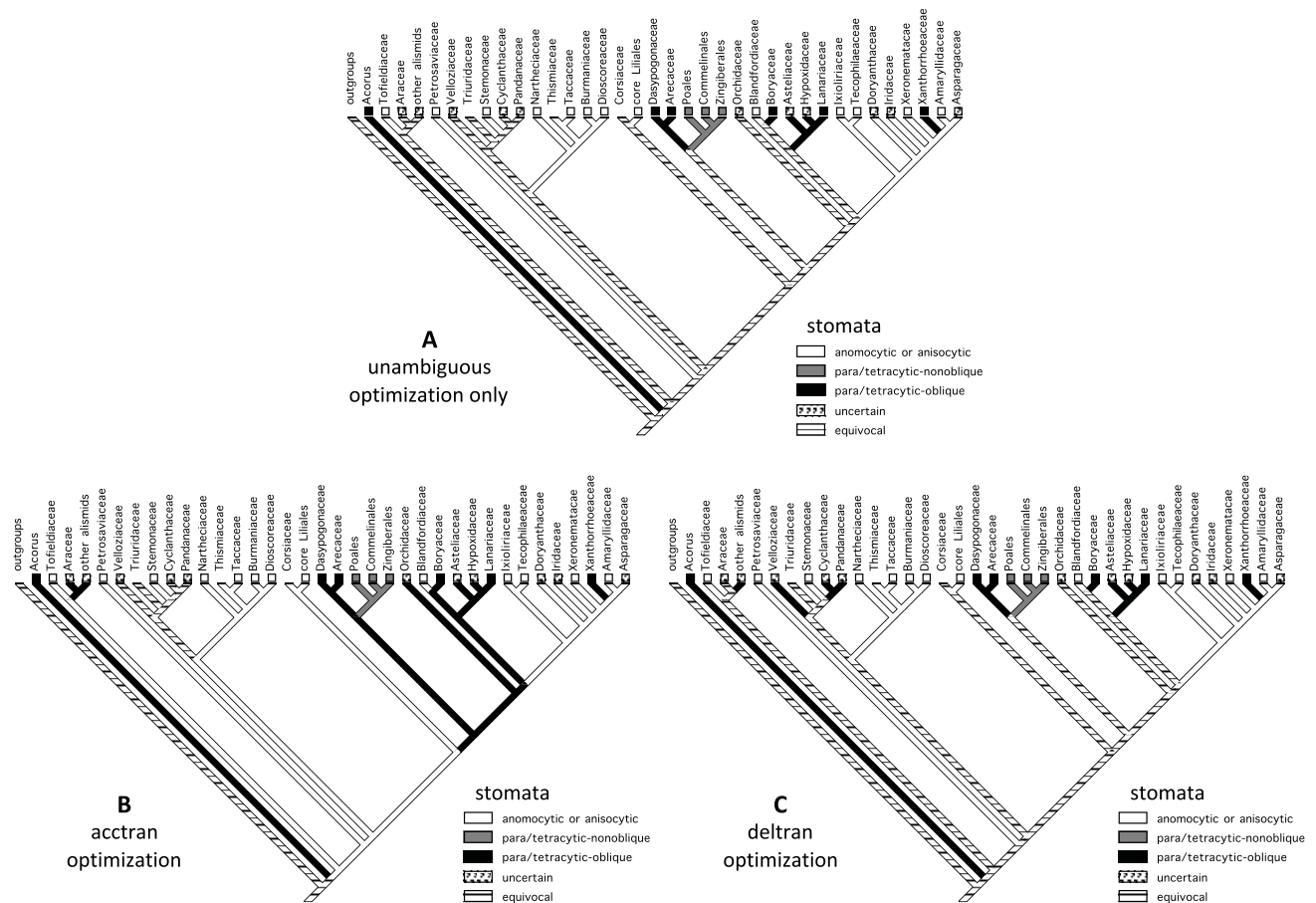
Figure 13. Phylogenetic tree of monocots of Rudall *et al.* (2017), showing parsimony optimization of the character of stomatal type as defined and scored in that article, using MacClade (Maddison & Maddison 2003), under three criteria: **A,** unambiguous optimizations only; **B,** assuming accelerated transformation (ACCTRAN); **C,** assuming delayed transformation (DELTRAN).

If *O. ferreri* and the other leaves from Huesa del Común are representative of late Albian monocots, the fact that they all have paracytic-oblique stomata, as do *Phyllotaenia* sp. of Teixeira (1950) from the late Cenomanian of Portugal and Monocot-1 of Pole (1999) from the late Albian–early Cenomanian of Australia, may appear to support the hypothesis that this stomatal type is ancestral in monocots. However, *Spixiarum* from the late Aptian of Brazil (Coiffard *et al.* 2013) has anomocytic stomata, negating any simple stratigraphical argument for polarity. Clearly more sampling of the diversity of Early Cretaceous monocot cuticles is needed, especially in the Aptian. From a phylogenetic point of view, more cogent evidence that paracytic-oblique stomata were ancestral would be demonstration that a fossil with such stomata was located at an appropriate position near the base of the phylogeny of monocots, for example attached to the internal branch between *Acorus* and the remaining monocots, or to the stem lineage of Alismatales as a whole. These considerations illustrate the general potential of fossils in testing hypotheses on character evolution based on extant plants, even if they do not affect inferred phylogenetic relationships.

Comparison of *Turolospadix bogneri* with living monocots

Unless otherwise indicated, statements here concerning the inflorescence and floral morphology of living Araceae are based on Mayo *et al.* (1997).

Turolospadix bogneri is like *Acorus* and Araceae in having a spadix with no floral subtending bracts. It differs from *Acorus* in having a dimerous rather than trimerous perianth. The dimerous condition is predominant in perigoniate Araceae but occurs only rarely in other monocots (e.g. Stemonaceae: Dahlgren *et al.* 1985). The fossils are quite unlike members of the large subfamily Aroideae, which have unisexual flowers with no perianth, and flowers of the two sexes in distinct zones of same spadix (except for an apparent reversal to bisexual flowers in *Calla* L.: Cusimano *et al.* 2011). In having a long stipe, *T. bogneri* is like *Acorus* and members of the Proto-
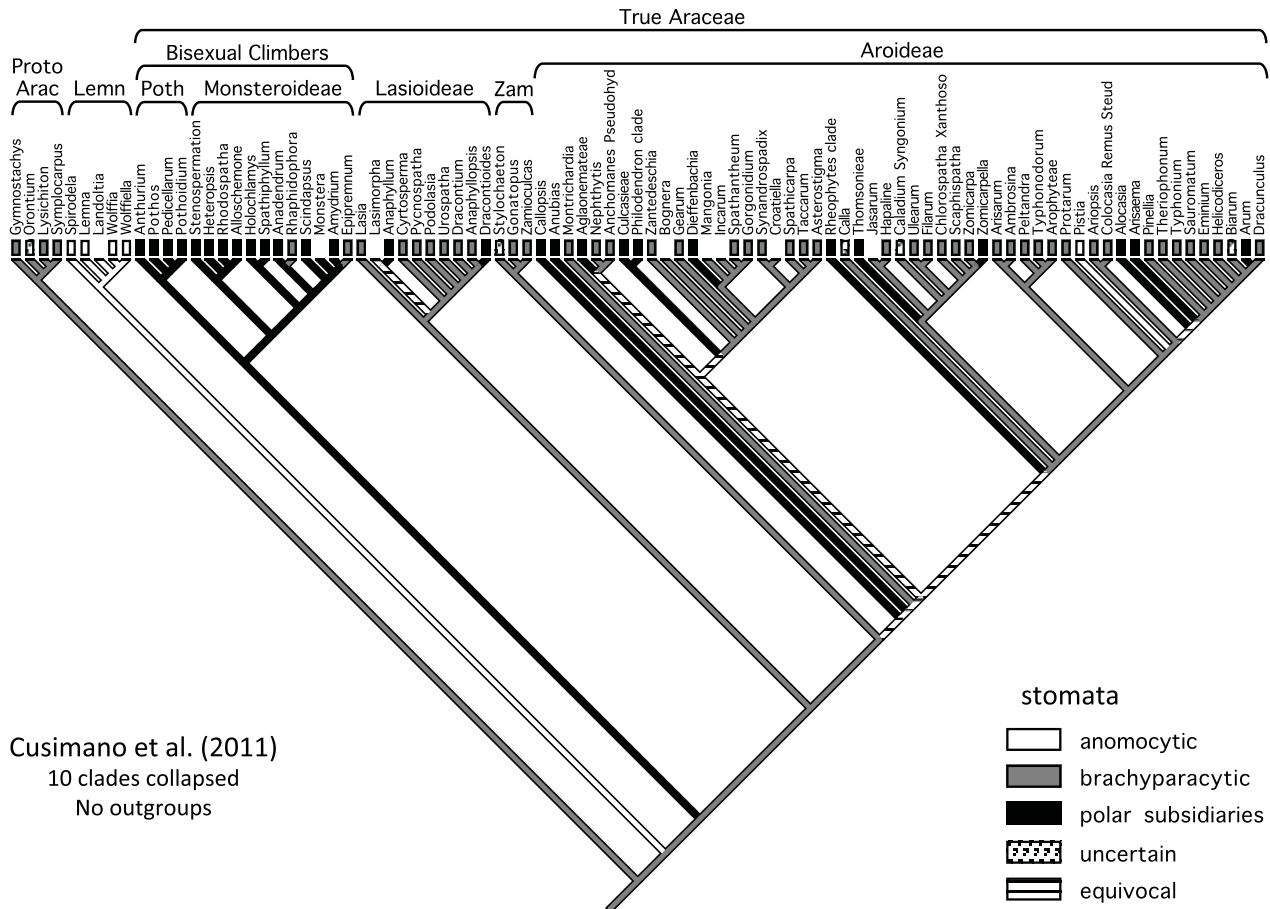
Figure 14. Backbone constraint tree of extant Araceae (modified from Cusimano *et al.* 2011), showing parsimony optimization of the character for stomatal type (data from Keating 2002). Abbreviations as in Figure 2.

Araceae clade (except *Symplocarpus*, which has a reduced stipe and a subglobose spadix). The inflorescences of Lemnoideae are too reduced to score this character, but in the remaining taxa, which make up the True Araceae clade of Cusimano *et al.* (2011), the spathe is attached near the apex of the peduncle, just below the fertile zone, as in *Symplocarpus*. In having a thin stipe, the fossil resembles *Gymnostachys* and *Lysichiton* and differs from *Orontium*, which has an unusually thick stipe.

Flowers with the most similar general morphology to those of *Turolospadix* occur in Proto-Araceae and Pothoideae. Among Proto-Araceae, *Lysichiton* is most like *T. bogneri* in having tepals with raised, pointed apices, giving the flowers a relatively conical shape; in the other genera, the top surface of the flower is flatter. In Pothoideae, *Pothos* and *Pothoidium* have thinner, even membranaceous tepals with a truncate apex; the tepals have a flat, thickened apex in *Anthurium* and are connate in *Pedicellarum*. Of those Monsteroideae that have a perianth (*Holochlamys*, *Spathiphyllum*, *Anadendrum*), the tepals are relatively thin, and in *Holochlamys*, *Anadendrum* and some *Spathiphyllum* species they are connate. Most Lasioideae have a perianth,

but the tepals have a thickened apex (as defined by Cusimano *et al.* 2011). Zamioculcadoideae and Aroideae have unisexual flowers in zones on the spadix, and Aroideae have no perianth.

Comparison of *Turolospadix* with fossil inflorescences

There is an extensive fossil record of spadices, fruits and seeds of Araceae, but it is mainly restricted to the Cenozoic (see Friis *et al.* 2011; Stockey 2006). Only a few Late Cretaceous reproductive structures have been confidently assigned to Araceae (Bogner *et al.* 2005; Stockey 2006), of which several are associated with whole plants placed in the lemnoid clade (Stockey *et al.* 2007, 2016; Krassilov & Kodrul 2009). The record of Early Cretaceous inflorescences has been even more restricted to a few incomplete specimens from south-western Eurasia. No described fossils show the combination of a cylindrical spadix, long stipe, and conical flowers with four tepals seen in *Turolospadix bogneri*, supporting its assignment to a new genus.

Friis *et al.* (2010, 2011) illustrated but did not formally describe two types of presumed araceous inflorescences from the Vila Verde 2 locality in Portugal (probably early Albian: Doyle & Endress 2014). Like *T. bogneri*, Araceae fossil sp. B, known as one large inflorescence fragment, which Friis *et al.* (2010) compared with Pothoideae, has flowers with four tepals in an upright cross configuration, the dominant state in living taxa that retain a perianth (vs. Lemnoideae, many Monsteroideae, and all Aroideae), but also stamens containing reticulate pollen. However, the tepals differ from those of *T. bogneri* and most members of the Proto-Araceae and Bisexual Climbers clades in having a thickened, flat-topped apex, as in *Anthurium* (Pothoideae), Lasioideae, and Zamioculcadoideae (Mayo *et al.* 1997; Cusimano *et al.* 2011). It is not known whether the inflorescence had a long stipe or a spathe attached just below the fertile zone, as in Pothoideae and other members of the True Araceae clade. Araceae fossil sp. A, known as smaller inflorescence fragments and isolated stamens, is more different from our fossils in having male flowers that lack a perianth, with one or two stamens. This would suggest a relationship to Aroideae, since the analysis of Cusimano *et al.* (2011) indicates that flowers became unisexual on the line leading to Aroideae and Zamioculcadoideae and lost the perianth in Aroideae. However, the pollen found in the stamens poses a problem, since it is monosulcate and reticulate, whereas Aroideae have inaperturate pollen (the sulcus is inferred to have been lost in their common ancestor with Zamioculcadoideae, after the shift to unisexuality but before loss of the perianth: Cusimano *et al.* 2011) and a highly reduced exine.

Later in the Cretaceous, the best-documented reproductive structure of Araceae is *Albertarum pueri* Bogner, Hoffmann & Aulenback, an incomplete silicified spadix described by Bogner *et al.* (2005) from the late Campanian of Alberta, Canada. This fossil, which Bogner *et al.* considered most similar to *Symplocarpus* in the Orontioideae, has flowers with six tepals and a gynoecium containing three ribbed seeds. It differs particularly from *T. bogneri* in having a subglobose rather than cylindrical spadix and six rather than four tepals. Only a scar of the stipe is preserved, so the length of the stipe is unknown.

In the Cenozoic, the inflorescence most similar to *T. bogneri* is *Acorites heeri* Berry from the Eocene of Tennessee, USA (Berry 1930), which was restudied by Crepet (1978) and compared with *Acorus*. This spadix resembles *T. bogneri* in having a stipe below the fertile portion, closely packed bisexual flowers, no floral subtending bracts, and paracytic stomata on the stipe, but although the number of tepals and stamens is not known,

there are three carpels, suggesting a trimerous rather than a dimerous floral organization. *Araceaeites friteli* Berry from the same flora was rejected by Crepet (1978) as showing no evidence of being a spadix-like inflorescence.

Evolutionary implications of *Turolospadix bogneri*

Turolospadix bogneri is scored the same as *Gymnostachys* and *Lysichiton* in the Proto-Araceae clade, but it has 11 most parsimonious positions around the base of Araceae (Fig. 12), because all of its character states are inferred to be ancestral in the family. These positions include all those found for *O. ferreri*, plus sister to *Lysichiton* and to *Symplocarpus*. As already noted, the fossil differs from *Orontium* in having four rather than six tepals and from *Symplocarpus* in having a long rather than a short stipe (which arose independently in the True Araceae clade). However, these features of *Orontium* and *Symplocarpus* are autapomorphies, so they do not exclude the possibility that *T. bogneri* is linked with one or the other genus. The same is true of the unusually thick stipe of *Orontium* (not included as a character in Cusimano *et al.* 2011), which is presumably derived relative to the thinner stipe of *Gymnostachys*, *Lysichiton* and *Turolospadix*.

With the present taxon and character sampling, the only unequivocal synapomorphy linking *T. bogneri* with Araceae is reduction from six to four tepals. With only *Acorus* and *Tofieldia* as outgroups, the fact that *T. bogneri* is like Araceae in having a spadix (not included as a character in Cusimano *et al.* 2011) does not necessarily support a relationship with the family. This is because *Acorus* also has a spadix, so it is equivocal whether a spadix evolved independently in *Acorus* and Araceae, or was ancestral in monocots and reversed in *Tofieldia*. However, if aquatic core Alismatales (traditional Helobiae) and core monocots (Petrosaviidae) are interpolated as additional outgroups of Araceae, it becomes most parsimonious to assume that a spadix arose independently in *Acorus* and Araceae, making this character additional support for a relationship of *Turolospadix* and Araceae.

Turolospadix bogneri is excluded from Lemnoideae by retention of a perianth, which was lost in these floating aquatics. All positions in Lemnoideae are only one step less parsimonious, but this is a function of the fact that six of the seven reproductive characters are inapplicable in these highly reduced plants. *Turolospadix bogneri* is excluded from the True Araceae clade by its long stipe, which was reduced in the shift of the spathe to just below the fertile portion of the spadix in True Araceae (this shift may have occurred one node lower, since Lemnoideae are too reduced to be scored for this character). *Turolospadix bogneri* matches many members of the

Bisexual Climbers clade in most other characters; as a result, it has 19 positions in this clade (including on its stem lineage) that are only one step less parsimonious.

It may seem problematic that definite monocot leaves have not been recognized in association with the inflorescences at Estercuel. However, this may be a function of the lack of organic preservation at the locality; there are fragments of strap-shaped leaves with only poorly preserved traces of venation that may represent monocots.

General evolutionary, palaeoecological and biogeographical implications

Orontiophyllum ferreri and *Turolospadix bogneri* confirm that characteristic derived leaf and reproductive features of Araceae, namely a broad blade and a spadix of ebracteate, dimerous flowers, had evolved by the late Albian, as already implied by *Spixiarum* from the late Aptian of Brazil (Coiffard *et al.* 2013) and Araceae fossil sp. B from the early Albian of Portugal (Friis *et al.* 2010). This is not surprising in light of the near-basal position of Araceae in molecular phylogenies of monocots, but such a position by itself would not necessarily imply that these features originated so early. The inferred ancestral character states and near-basal position of both Spanish fossils within Araceae are consistent with the hypothesis that the family was at an early stage of its radiation in the late Albian, but not indicative of it. As noted by Coiffard *et al.* (2013), the earlier occurrence of *Spixiarum* and Araceae fossil sp. B indicates that some diversification of Araceae had occurred by this time. Coiffard *et al.* (2013) suggested that *Spixiarum* is nested in or sister to Orontioideae, but its stomatal and venational differences suggest that it may belong elsewhere in the basal grade of Araceae. Its anomocytic stomata are a derived feature shared with the floating aquatic Lemnoideae, suggesting that *Spixiarum* could be a stem relative of this clade, representing a stage before evolution of the floating habit. If more detailed description and analysis confirm the suggestion of Friis *et al.* (2010) that Araceae fossil sp. B is related to Pothoideae, there must also have been some diversification of the Bisexual Climbers clade by the early Albian. However, it is entirely possible that stem relatives of the family, which might shed light on its origin, persisted alongside early crown group members, and *O. ferreri* and/or *T. bogneri* could represent such forms.

The fact that both *O. ferreri* and *T. bogneri* have several most parsimonious positions near the base of Araceae is presumably related to a relatively low number of morphological changes between branching events in the early radiation of the family. This is consistent with the fact that relationships among basal clades were poorly resolved when Cusimano *et al.* (2011, supplement S2) analysed the phylogeny of living Araceae using morphological data only.

Considering monocots as a whole, current fossil data imply that significant diversification in stomatal structure had occurred by the end of the Albian, given both the anomocytic type in *Spixiarum* (Coiffard *et al.* 2013) and the paracytic-oblique types in *O. ferreri*, the other monocot leaves from Huesa de Común, and Monocot-1 of Pole (1999) from Australia. However, the spectrum of stomatal structure is still narrower than that observed in monocot macrofossils and dispersed cuticles from the Campanian, Maastrichtian, and basal Paleocene of Austria, New Mexico, and Colorado (Kauffman *et al.* 1990; Upchurch 1995; Herman & Kvaček 2010). These younger assemblages include multiple taxa with tetracytic stomata with specialized polar neighbouring cells, transverse paracytic stomata, and paracytic stomata that have subsidiary cells with oblique end walls but no adjacent modified cells. Although the sample is still fairly small, this suggests increased diversification in stomatal structure through the Late Cretaceous.

The variable cell arrangements formed by oblique divisions in the stomata of *O. ferreri*, the other leaves at Huesa de Común, and Monocot-1 present an intriguing analogy with the variable stomatal structure in dicotyledonous angiosperm leaves from Aptian–early Albian horizons in the Potomac Group (Upchurch 1984). A possible explanation is that this variation reflects less canalization of stomatal development than in most extant angiosperms, which have more uniform stomatal structure.

Palynological studies provide additional evidence for a significant presence of monocots at the horizons containing *O. ferreri* and *T. bogneri*. Rich palynological assemblages in these beds (Villanueva-Amadoz *et al.* 2011; Sender *et al.* 2012) include graded-reticulate monosulcate pollen assigned to *Liliacidites* as strictly defined (*L. inaequalis* and *L. doylei*), a morphotype that is restricted to monocots and may or may not be ancestral in the clade (Doyle 1973; Doyle *et al.* 2008). The species *L. doylei* was used by Villanueva-Amadoz *et al.* (2011) as evidence for a late Albian age, but the fossil record shows that generally similar pollen persists through the Late Cretaceous (e.g. Couper 1953) to the present.

So far, *O. ferreri* appears to be the oldest well-corroborated monocot leaf in Eurasia, although the presence of *Acaciaephyllum* in the Aptian of Virginia (Fontaine 1889; Doyle 1973; Doyle *et al.* 2008), in the same Southern Laurasian province, implies that such leaves should be expected. There are fragmentary strap-shaped leaves with parallel venation in the Early Cretaceous of

Eurasia that have been tentatively related to monocots. The best preserved are remains assigned to *Phyllotaenia* from the Albian of Portugal (Teixeira 1948, 1950) and *Pandanophyllum* Hassk from the Aptian and Albian of Russia (Kryshtofovich 1929), which has marginal teeth suggestive of Pandanaceae. As already noted, the monocot affinities of *Phyllotaenia* from the late Cenomanian of Portugal (Teixeira 1950) are confirmed by cuticle evidence. However, although the external morphologies of the older leaves are consistent with monocot affinities, they are not known to have more than one order of parallel veins, cross veins, or cuticle features that would exclude them from being fragments of gymnospermous leaves of the sort assigned to *Desmiophyllum* Lesquereux, *Phyllites* Lesquereux and *Dammarites* Presl. Krassilov (1984, fig. 6D, G) illustrated 'grasslike' leaves from the pre-Albian of Mongolia with an arched groove at the sheath-blade junction that could represent a ligule, but they show only one order of parallel veins and no additional characters that would support a monocot affinity. Mohr & Rydin (2002) proposed that Aptian and Albian leaves now assigned to *Klitzschophyllites* Lejal-Nicol (from Portugal, as *Nymphaeites*: Teixeira 1948; Egypt: Lejal-Nicol 1981; Brazil, as *Trifurcatia*: Mohr & Rydin 2002; Tunisia: Mohr *et al.* 2006; Spain: Gomez *et al.* 2009) are monocots. However, Doyle *et al.* (2008) and Gomez *et al.* (2009) argued that these fossils are quite unlike monocots in their leaf architecture. Gomez *et al.* assigned them to eudicots, possibly Ranunculales, while Friis *et al.* (2011) suggested that they may be ferns rather than angiosperms. With its late Albian age, *O. ferreri* also represents the oldest record so far of the fossilgenus *Orontiophyllum*, which predates the next known record from the Turonian of Germany by 6–10 Ma (Kvaček & Smith 2015).

If the stomata of *Orontiophyllum ferreri* are on the adaxial surface of the leaf, this points to an aquatic habit of the plant. The epistomatic condition, typical of taxa with floating leaves (e.g. Kaul 1976), is seen in *Orontium*, whose leaves are held above the water or float on its surface (Mayo *et al.* 1997). Based on the sedimentology of the beds at Huesa del Común, *O. ferreri* was preserved in a freshwater lacustrine sub-environment within a deltaic plain environment (Pardo & Villena 1979; Sender *et al.* 2016). The exquisite preservation of both its venational and cuticular characters would indicate short transport and rapid burial, suggesting that the plant grew in or next to a small lake near the coast of the Tethys. The whole plant of *Spixiarum* described by Coiffard *et al.* (2013), with several leaves and numerous adventitious roots attached to a short rhizome, has a typical aquatic morphology and also occurs in lacustrine sediments. These data imply that members of Araceae have been adapted to aquatic environments for at least 113 Ma.

Whether *O. ferreri* and *Spixiarum* are nested in Araceae or stem relatives, these observations are consistent with the phylogenetic distribution of ecological characters in modern taxa. The fact that Proto-Araceae (except *Gymnostachys*) are largely marsh plants (helophytes) and Lemnoideae are floating aquatics is consistent with a more or less aquatic ancestral habit for Araceae (Cabrera *et al.* 2008; Cusimano *et al.* 2011; Nauheimer *et al.* 2012). This may also apply to monocots as a whole, as under the long-standing hypothesis that their distinctive apomorphies are related to an aquatic stage in their early evolution (reviewed in Les & Schneider 1995), independent of the now-obsolete hypothesis that monocots are related to Nymphaeales. *Acorus* is a helophyte, Tofieldiaceae are terrestrial but prefer boggy soils (Zomlefer 1997), and the remaining Alismatales (Helobiae, sister to Araceae in current phylogenies: Iles *et al.* 2013; Luo *et al.* 2016) range from emergent to submaquatics.

By analysing present-day geographical distributions on a molecular tree, Nauheimer *et al.* (2012) inferred that Araceae originated in Laurasia, with dispersal of *Gymnostachys* to Australia via West Gondwana and Antarctica. Earlier, Walker & Walker (1986) argued that monocots as a whole had a Laurasian origin, based on the diversity of presumed monocot pollen in the lower Potomac Group and the present distribution of taxa that they considered primitive (Liliales, Alismatidae, Araceae). However, some of their pollen types have been associated with non-monocotyledonous fossil flowers (Friis *et al.* 1994, 1997; Gandolfo *et al.* 2000; Doyle *et al.* 2008; Doyle 2015), and their phylogenetic assumptions need revision in the light of molecular phylogenetics. By contrast, Coiffard *et al.* (2013) argued that the late Aptian occurrence of *Spixiarum* in Brazil and the Australian distribution of *Gymnostachys* support a Gondwanan origin of Araceae, with dispersal into Laurasia via the transitional Iberian region, as indicated by the early Albian spadices from Portugal (Friis *et al.* 2010). *Klitzschophyllites* is another fossil that supports floristic exchange between Brazil and Iberia (Mohr & Rydin 2002; Gomez *et al.* 2009). Our new late Albian records from Spain would be consistent with this scenario, but together with the Portuguese fossils, which are almost as old as *Spixiarum*, they would be equally consistent with an initial centre of diversification of Araceae in Laurasia, as suggested by Nauheimer *et al.* (2012) and Kvaček & Smith (2015). It may be that the diversity of late Albian monocot leaves in Spain is an example of high speciation rates in island systems

(Comes *et al*. 2008; Crawford & Archibald 2017), since the Iberian area was an archipelago situated between North Africa, North America and Eurasia at this time.

Conclusions

This study has revealed a unique abundance and diversity of well-preserved monocot fossils in the late Albian of Spain, including leaves and inflorescences of Araceae and numerous linear leaves of uncertain affinities, plus pollen of the *Liliacidites* type. These results suggest that the fossil record has more potential for illuminating the history of this major angiosperm clade than is often assumed. The rarity of earlier reports must be partly a function of the herbaceous character of most monocots and the tendency of their leaves to degrade while still attached to the plant. In addition, if monocots were originally aquatic or semiaquatic, as appears to be the case for *Orontiophyllum ferreri* and *Spixiarum*, and their early radiation continued to be centred in aquatic habitats, they should be under-represented in well-studied Aptian–Albian sequences such as the Potomac Group, which is largely fluvial, and more common in lacustrine units such as the Boundary Marls or the Crato Formation of Brazil. Future study of such sediments may further extend the record of early monocots. Even if whole leaves continue to be poorly represented as fossils, our results and those of Pole (1999) indicate that leaf fragments and dispersed cuticles have potential for filling in the record of monocot diversity in time and space.

Our results add to growing evidence that the family Araceae was one of the earliest extant lines within monocots. Together with older mesofossil inflorescences from Portugal (Friis *et al.* 2010, 2011) and vegetative remains from Brazil (Coiffard *et al.* 2013), the Spanish leaves and inflorescences suggest that significant diversification of Araceae had occurred by the late Albian. However, much of this radiation may have involved splits near the base of the crown clade, and it may have included persisting stem relatives of the family. The problems encountered in evaluating the systematic position of the fossils also underline the importance of more detailed, phylogenetically informed surveys of leaf architecture and epidermal anatomy in extant Araceae and other monocots for future phylogenetic studies of such fossils. This information could enhance our understanding of the implications of fossils in reconstructing the course of morphological evolution in monocots, as illustrated by the still-unresolved problem of the ancestral stomatal type, and their ecological radiation into their present diverse habitats.

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Supplemental material

Supplemental material for this article can be accessed at: https://doi.org/10.1080/14772019.2018.1528999

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