Orontiophyllum, a new genus for foliage of fossil Orontioideae (Araceae) from the Cretaceous of central Europe

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Reinvestigations of fossil taxa are important to ensure that their affinities are well defined, providing important data bearing on biogeography and evolution. Here, we studied fossil leaves previously assigned to Araceae and Zingiberaceae, and found that the vein architecture is most similar to Araceae subfamily Orontioideae. The genus *Orontiophyllum* J.Kvaček & S.Y.Smith is proposed for leaves with orontioid venation, but lacking associated reproductive structures, which precludes us from knowing whether they represent an extant genus or an extinct taxon with a mosaic of features. Leaves are ovate and simple. Venation is parallel-pinnate, eucamptodromous, with at least three orders of primary lateral veins that leave the costa at acute angles. Higher order transverse veins are perpendicular to slightly oblique between the primary lateral veins, somewhat irregular, and the finest venation is generally reticulate. Two species are recognized, *O. austriacum* from the Campanian of Austria and *O. riggauense* from the Turonian of Germany. The vein architecture shows a mixture of features similar to both *Orontium* and *Lysichiton*. The two species differ from each other in the angle of departure of the primary lateral veins from the costa and details of the finer transverse veins. Both fossil taxa are found in sediments, suggesting a wetland environment, a habitat similar to that in which members of Orontioideae are found today. Combined with previous fossils for the subfamily, they show that members of Orontioideae were diverse and widespread across Laurasia in the Cretaceous. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **178**, 489–500.

ADDITIONAL KEYWORDS: *Lysichiton* – monocotyledons – venation – *Zingiberopsis*.

INTRODUCTION

As we seek to understand plant evolution, fossils are critical for providing hard data on past occurrences, both temporally and spatially, which have an impact on our interpretations of phylogenetic relationships, biogeographical patterns and morphological changes through time. This is limited by how well we understand the fossil record, and a key component of that is ensuring that fossils used in these synthetic analyses have had their affinities verified. Although pollen,

fruits and seeds typically have many useful characters to support their taxonomic placement, leaves can be more challenging because of their overall simplicity relative to three-dimensional reproductive structures, their often fragmentary nature and poorly preserved higher order venation and, in monocotyledonous flowering plants, convergences in form (e.g. parallel-veined linear leaves), but are nonetheless important when trying to piece together the fossil record.

Monocots are an early diverging group within angiosperms, with several orders having records extending into the Late Cretaceous (Herendeen & Crane, 1995; Gandolfo, Nixon & Crepet, 2000; Friis,

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Crane & Pedersen, 2011; Smith, 2013), but only Araceae has been tentatively reported from the Early Cretaceous (Friis, Pedersen & Crane, 2004, but see Hofmann & Zetter, 2010). Pollen named *Mayoa portugallica* E.M.Friis, K.R.Pedersen & P.R.Crane from the Early Cretaceous of Portugal was assigned to Araceae (Friis *et al.*, 2004), although Hofmann & Zetter (2010) suggested that this pollen was similar to *Lagenella martinii* (Leschik) W.Klaus, which is found from the Triassic to the Cretaceous, and is therefore unlikely to be angiospermous. In addition, inflorescences similar to Araceae have also been found in Early Cretaceous deposits from Portugal, but have not yet been formally described (Friis, Pedersen & Crane, 2010). Recently, the taxon *Spixiarum* Coiffard, Mohr, & Bernardes-de-Oliveira has been described from the Early Cretaceous Crato Formation of Brazil, and also closely compared with Araceae (Coiffard, Mohr & Bernardes-de-Oliveira, 2013).

Here, we reinvestigate two Cretaceous fossil monocots preserved as leaves. One was recently assigned to the extant genus *Lysichiton* Schott (Araceae) (Bogner *et al.*, 2007) and would represent the oldest material of that genus, whereas the other represents one of the earliest records of Zingiberales (Knobloch, 1979), and thus is of interest for understanding the evolution of that group. We find that these taxa both have venation typical of Araceae subfamily Orontioideae, confirming that this early-divergent aroid lineage was well established by the Late Cretaceous.

MATERIAL AND METHODS

The studied material comes from the Late Cretaceous localities Grünbach in Austria and Riggau in Germany. Fossil plants from both localities have been described in several papers (Knobloch, 1971, 1979; Herman & J.Kvaček, 2002, 2007, 2010; J.Kvaček & Herman, 2004a, b).

The Grünbach flora derives from the Grünbach Formation ('Coal-bearing Series' according to Plöchinger, 1961) of the Gosau Group in the Grünbach Neue Welt Basin in the eastern calcareous Alps, Lower Austria (Fig. 1). The predominantly terrigenous clastic fillings of the basin (Gosau Group) consist of lithostratigraphic units of late Santonian to Eocene age. The three lower units, several hundred metres thick, represent the Cretaceous part of the Gosau Group (Summesberger, 1997; Summesberger *et al.*, 2000, 2002). The Grünbach Neue Welt Basin of the eastern Alps represents a syncline with an overturned limb (Plöchinger, 1961).

The Grünbach Formation is composed of conglomerates, sandstones, siltstones, coaly siltstones and coal seams. Plant fossils are the most common fossils in the Grünbach Formation. Foraminifera from the Grünbach Formation at Aiersdorf belong to the Globotruncana elevata Zone (lower Campanian) and the nanofossil association has been assigned to the Campanian UC 15 Zone (Hradecká *et al.*, 2001). The Grünbach palaeoenvironment is interpreted predominantly as wetland with coal-forming peat swamp (J.Kvaček & Herman, 2004b).

Sediments occurring near Riggau belong to the so-called Hessenreuther Forst, which is a part of the 'Upper Danubian' Cretaceous. The terrestrial sediments in which fossil plants are found belong to the Parkstein Member. Because of its terrestrial nature, its stratigraphic position has been rather unclear. The first fossils from Riggau were described by Engelhardt (1905), who thought they were Cenozoic in age. Knobloch (1971) was the first to correctly identify the flora from Riggau as being Cretaceous and estimated a Cenomanian–Turonian age. Schweigert (1992) questioned this and, using his own identifications of fossil plants, suggested again a Palaeogene age of the strata. However, later studies (Niebuhr, Pürner & Wilmsen, 2009) argued again for a Cretaceous age and assigned the sediments to the Turonian–Campanian. The latest study by Niebuhr *et al*. (2011), using an integrated (sequence) analysis of the whole Danubian Cretaceous based on borehole sections and surface exposures, correlated the Parkstein Member of the Hessenreuth Formation with the Roding Formation of the Bodenwöhrer Senke, which is of Turonian age.

The specimens from Grünbach were photographed in alcohol immersion. The specimens from Riggau were photo-documented using ordinary light. Specimens from both collections were photographed using a Canon EOS 6D camera with a Canon 100 macro lens.

The material from Grünbach is housed in the Department of Geology and Palaeontology of the Naturhistorisches Museum (Natural History Museum, Vienna; NHMW). The material from Riggau was originally housed in the University of Erlangen, but is now housed in the State Natural History Collections, Museum of Mineralogy and Geology Dresden (MMG).

Modern leaves from many monocots were studied for comparison from the literature, the University of Michigan herbarium (MICH), the National Cleared Leaf Collection (Smithsonian National Museum of Natural History), the New York Botanical Gardens cleared leaf collection, the University of Michigan cleared leaf collection (MCL) and specimens cleared in the National Museum Prague.

The terminology used to describe the leaves follows that of Hickey & Petersen (1978) and Mayo, Bogner & Boyce (1997). Briefly, the term 'costa' is used for a
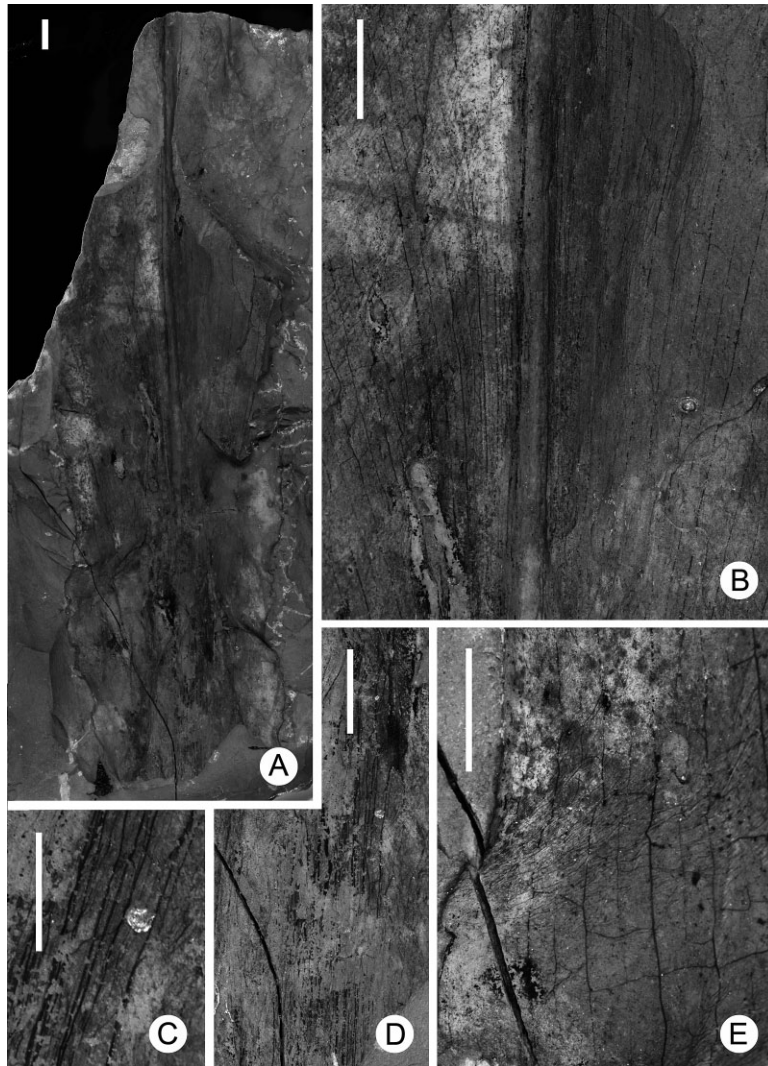
Figure 1. *Orontiophyllum austriacum* (J.Kvaček & Herman) J.Kvaček & S.Y.Smith **comb. nov.** Holotype NHMW 1999B0057/0183. A, Complete specimen. B, Semidetail. C, Veins in costa. D, Multistranded costa. E, Marginal part of leaf. Scale bars: A, B, 10 mm; C–E, 5 mm.

multi-veined midrib (*sensu* Hickey & Petersen, 1978), and 'primary lateral veins' refer to the veins both comprising the costa and diverging from the costa (*sensu* Mayo *et al.*, 1997). Different orders or vein thicknesses are recognized among lateral veins (equivalent to parallel longitudinal veins in other monocots) and transverse veins (which connect individual parallel veins). They tend to form a recurring pattern based on order (width), called a 'set' (Hickey & Petersen, 1978). Following Hickey & Petersen (1978), these different vein orders, or subsets, are each assigned a letter, with the thickest given the first letter of the sequence (e.g. B) and each subsequent vein order assigned the next letter in order of decreasing width (C, d, etc.).

SYSTEMATIC PALAEOBOTANY

FAMILY ARACEAE

SUBFAMILY ORONTIOIDEAE MAYO *ET AL.*, 1997

GENUS: *ORONTIOPHYLLUM* J.KVAČEK & S.Y.SMITH **GEN. NOV.**

Type: *Orontiophyllum austriacum* (J.Kvaček & Herman) J.Kvaček & S.Y.Smith comb. nov. = *Araciphyllites austricus* J.Kvaček & Herman 2005, p. 4, text-figs 1, 2A, B = *Lysichiton austriacus* (J.Kvaček & Herman) Bogner *et al.*, 2007, p. 142.

Diagnosis

Leaf lamina simple, entire-margined, midrib multistranded, venation parallel-pinnate, eucamptodromous. Primary lateral venation consisting of several well-defined vein orders departing from multistranded costa at acute angles. Higher order transverse veins perpendicular to slightly oblique to primary lateral veins forming a more or less square pattern.

Discussion

The fragmentary nature of fossil leaves that are entire-margined, parallel-pinnate, with transverse veins that cross multiple vein orders, combined with a lack of any reproductive structures, in the Cretaceous requires a definition of a taxon for fossil foliage of subfamily Orontioideae, and hence we introduce the genus *Orontiophyllum* gen. nov. to accommodate such fossils. In the fossil record, it is not uncommon to find mosaic taxa with leaves resembling one genus and reproductive structures resembling another, or organs that are similar to recent taxa in gross morphology but have different epidermal structure. Thus, without distinctive reproductive structures, it could be misleading to place a fossil leaf into an extant genus.

In a conservative sense, it differs from all genera of subfamily Orontioideae (*Orontium* L., *Lysichiton* Schott and *Symplocarpus* Salisb.) in lacking any reproductive structures. Leaves of Orontioideae are oblong-elliptic to ovate and are (sub)cordate in *Symplocarpus* (Mayo *et al.*, 1997). These three taxa also vary in the major venation, with *Lysichiton* having a wide robust costa with pinnate venation, *Symplocarpus* having a narrow costa with pinnate venation and *Orontium* being more or less actinodromous (Ertl, 1932; Mayo *et al.*, 1997). *Orontiophyllum* also accommodates fossil leaves lacking an apex with preserved central costa, without which it is difficult to ascertain whether a leaf is more like *Orontium* or *Lysichiton*. In *Lysichiton*, the costa reaches the leaf apex, whereas, in *Orontium*, it does not. *Orontiophyllum* differs from *Lysichiton* in having closely recurring vein subsets, primary laterals leaving the multistranded costa at low angles, and lacking an intramarginal vein. The new genus is different from *Orontium* in the presence of a multistranded costa and frequent perpendicular transverse veins forming areoles. There is also consequently a general need to establish a morphotype that would serve for an accommodation of this type of fossil orontioid foliage.

Orontiophyllum differs from the genus *Araciphyllites* V.Wilde, Z.Kvaček & J.Bogner in having a less pronouncedly defined costa and lacking marginal-submarginal veins. Further, it differs in having several well-defined orders of primary lateral veins leaving a multistranded costa at low angles.

Orontiophyllum differs from the genus *Zingiberopsis* Hickey in having transverse veins connecting more than two adjacent parallel veins, forming more or less square patterns with the lower order veins; in *Zingiberopsis*, the transverse veins only connect adjacent parallel veins.

ORONTIOPHYLLUM AUSTRIACUM (J.KVAČEK & HERMAN) J.KVAČEK & S.Y.SMITH COMB. NOV.
(FIGS 1, 2)

Basionym: *Araciphyllites austriacus* J.Kvaček & Herman. (2005). Validation of *Araciphyllites austriacus* J.Kvaček & Herman (monocotyledons: Araceae), Journal of the National Museum, Natural History Series 174, p. 4, text-figs 1, 2A, B.

Synonym

Lysichiton austriacus (J.Kvaček & Herman) Bogner *et al.* (2007), p. 142.

Holotype: NHMW 1999B0057/0183, published by Kvaček & Herman (2005, text-figs 1, 2A, B; refigured herein as Figs 1A–E, 2A, B)

Type locality: Grünbach am Schneeberg, Austria.
Type horizon: Early Campanian, Late Cretaceous.

Emended diagnosis

Leaf entire-margined, midrib multistranded, venation parallel-pinnate, eucamptodromous. Primary lateral venation consisting of three well-defined vein subsets leaving costa at low angles. Higher order transverse venation perpendicular to slightly oblique, reticulate. Transverse veins irregularly connecting all orders of primary lateral veins.

Description

The only specimen available is the holotype (Fig. 1A). It is an exceptionally large specimen of a leaf lamina, 260 mm long, narrowing from > 100 mm in the terminal part to 60 mm in the basal part. The leaf margin is entire and slightly undulate in the basal part. The base, petiole and apex are lacking. A multistranded costa (midrib; Fig. 1A, B) narrows from the base (12 mm wide) to the apex (3 mm wide). In some places of the costa, individual veins are visible (Fig. 1C, D). The primary laterals are arranged in three differentiated orders. They emerge at an angle of about 10° from the multistranded costa (Fig. 1B). Each vein order (indicated by a letter, the thickest 'B' to the thinnest 'd') has a specific width: B, 0.12–0.10 mm; C, 0.08–0.06 mm; d, 0.05–0.03 mm. Spacing of the primary lateral veins varies from 0.8 to 1.2 mm. Higher order venation is reticulate between them (Fig. 2C). Transverse veins vary in width (0.10–
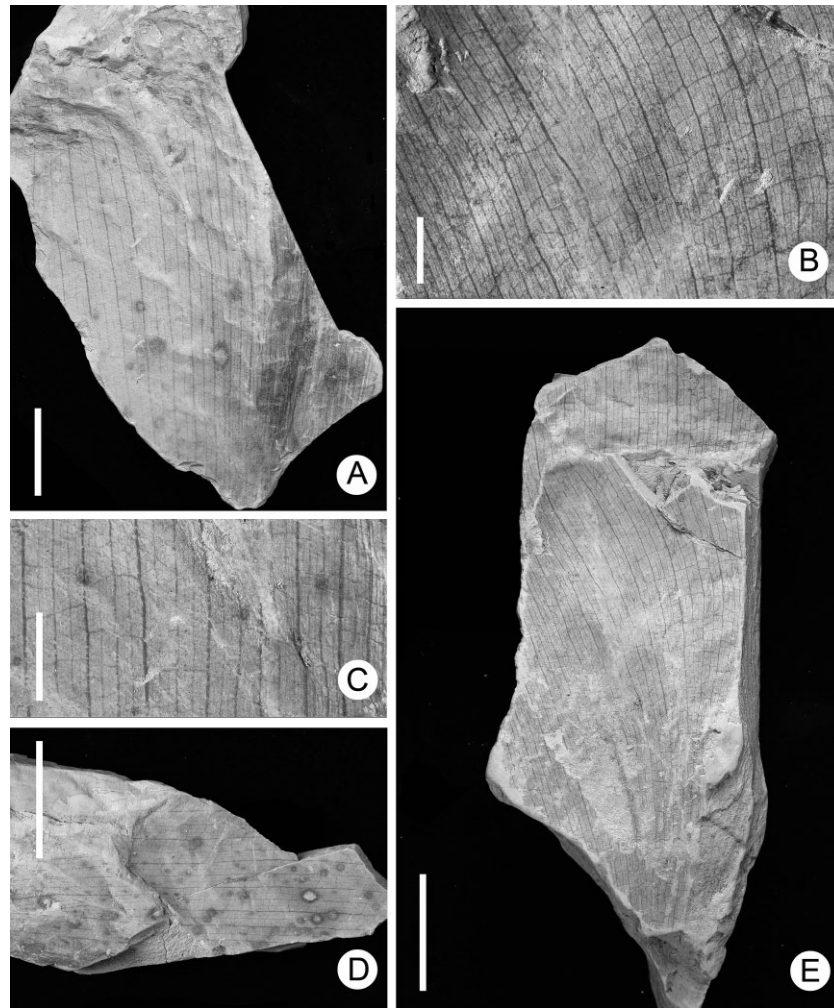
Figure 2. *Orontiophyllum austriacum* (J. Kvaček & Herman) J. Kvaček & S.Y.Smith **comb. nov.** Holotype NHMW 1999B0057/0183. A, Detail of venation. B, Detail of venation near the leaf margin. C, Detail of venation in line drawing. Scale bars: A, B, 5 mm; C, 10 mm.

0.03 mm); they seem to fall into two orders, 0.08–0.06 mm and 0.05–0.02 mm ($N = 20$). The first set frequently connects two adjacent C-level veins and sometimes also the highest order (B-level) veins, whereas the second set of transverse veins connects d-level veins. Both transverse vein orders are straight or curved, sigmoidal or S-shaped, spaced 0.5–2.8 mm apart. They are perpendicularly or obliquely oriented to the primary laterals forming areolae (Fig. 2A). A marginal part of the leaf shows similar areolation, but the areolae are narrow (Fig. 1E, 2B).

Discussion
This taxon was originally described under the name *Araciphyllites* (J.Kvaček & Herman, 2005). Later,

based on similarity of venation, it was assigned to the extant genus *Lysichiton* (Bogner *et al.*, 2007). For the reasons mentioned above, we assign it here to an independent fossil genus.

ORONTIOPHYLLUM RIGGAUENSE (KNOBLOCH) J.KVAČEK & S.Y.SMITH **COMB. NOV.**
(FIGS 3, 4)

Basionym: *Zingiberopsis riggauensis* Knobloch (1979) *Zingiberopsis riggauensis* sp. n. – eine interessante Monokotyledone aus der Kreide Bayerns, Věstník Ústředního ústavu geologického, 54, p. 297, text-figs 1, 2; pl. 1, figs 1–3, pl. 2, figs 1–6, text-figs 1, 2.

Figure 3. *Orontiophyllum riggauense* (Knobloch) J.Kvaček & S.Y.Smith **comb. nov.** A, Specimen showing costa, MMG BaK 5. B, Detail of the holotype showing five orders of venation, MMG BaK 4. C, Detail of MMG BaK 5. D, MMG BaK 6 showing insect-damaged fragment of leaf. E, Holotype MMG BaK 4. Scale bars: A, 20 mm; B, C, 5 mm; D, E, 30 mm.

Holotype: No. MMG BaK 4 defined by Knobloch (1979) (text-figs 1, 2, pl. 1, fig. 3); refigured here as Figure 3A–E.

Type locality: Riggau near Pressath, Oberpfalz, Germany.

Type horizon: Turonian, Late Cretaceous.

Other material: No. MMG BaK 5, MMG BaK 6, MMG BaK 7.

Etymology: From the type locality Riggau.

Emended diagnosis
Leaf entire-margined, midrib multistranded, venation simple pinnate, eucamptodromous. Primary lateral veins simple, forming five well-defined orders. Primary lateral veins leaving costa at sharp angles. Higher order transverse veins oriented perpendicularly (rarely obliquely) to primary lateral veins. Transverse veins always connecting all four lower orders of vein subsets.

Description
The holotype is a fragment of a leaf impression showing a 135×65 mm^2 portion of the lamina (Fig. 3A). The leaf fragment exhibits the central part of the leaf lamina with primary lateral veins comprising six orders. Although the costa is not preserved, they appear to be diverging at angles of < 10°. Each order has veins of specific width: B, 0.5 mm; C, 0.3 mm; d, 0.2 mm; e, 0.1 mm; f, 0.05 mm; g, 0.02 mm ($N = 25$). They are regularly arranged (Figs 3B, 4) with a constant spacing between the veins: B–B, 10–11 mm; C–C, 5–7 mm; d–d, 2–3 mm; e–e, 1.5 mm;
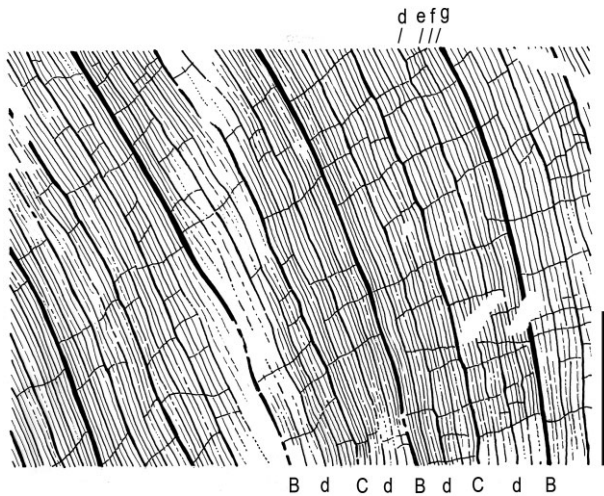
Figure 4. *Orontiophyllum riggauense* (Knobloch) J.Kvaček & S.Y.Smith **comb. nov.** Detail of vein pattern. Scale bar, 5 mm.

f–f, 0.8 mm; g–g, 0.3 mm ($N = 25$). Transverse veins fall into two orders, 0.1 mm and 0.05 mm wide, running perpendicularly or obliquely to the laterals. The lower order transverse veins join the primary lateral veins of higher orders d–g, forming more or less square patterns to the overall vein architecture. The higher order transverse veins connect to primary lateral veins of both low orders (d–g) and high orders (C–B), but they never connect the highest order veins (B–B).

The specimen No. MMG BaK 5 (Fig. 3A) preserves a fragment of a leaf including a multistranded costa. The fragment is 107×82 mm², showing regular venation consisting of six orders of veins and two orders of cross-veins (Fig. 3C). Its costa is at least 30 mm broad (Fig. 3A), suggesting that the original leaf was quite large. The size of the costa could be even larger, because it is not clear whether the costa is preserved in total width. This specimen is particularly important and illustrative, because it shows the multistranded costa and the laterals leaving the costa gradually at sharp angles of *c.* 1–5° (Fig. 3A). The angle is low near to the costa and then gradually increases towards the margins. In areas close to the costa, veins run nearly parallel to the costa (Fig. 3A). There are two other specimens in the type collection of E. Knobloch, which are quite fragmentary, showing only parallel venation with areolae. However, they are of interest because they show circular shapes demarcated by dark margins that could be interpreted as insect damage (Fig. 3D).

Modern comparative material
Zingiberales: As *O. riggauense* was originally placed in *Zingiberopsis*, we must evaluate how its leaf archi-

tecture compares to the Zingiberales. One of us (S. Y. Smith, pers. observ.) has been investigating the leaf architecture of Zingiberales, using cleared leaves from > 100 species of all eight zingiberalean families. Three major vein architectures are recognized (Fig. 5). One pattern is restricted to Lowiaceae (*Orchidantha* N.E.Br.), and is defined by long, gently undulating transverse veins that cross multiple longitudinal veins and are sometimes free ending (Fig. 5A). The second pattern, found in Musaceae, Heliconiaceae, Stretlitziaceae and Zingiberaceae, has short transverse veins connecting only adjacent longitudinal veins at right angles. These generally form square to rectangular areolae, with the long axis of the areolae oriented parallel to the longitudinal veins (Fig. 5B–E). The third pattern, found in Marantaceae, Cannaceae and Costaceae, has transverse veins that connect only adjacent longitudinal veins, and form rectangular areolae with the longitudinal axis perpendicular to the longitudinal veins (Fig. 5F–H). These transverse veins may dichotomize, undulate and/or be at oblique angles.

Araceae: It is clear from a survey of the previous literature (Ertl, 1932; Mayo *et al.*, 1997; Bogner *et al.*, 2007; Herrera *et al.*, 2008) that there is a wide variety of venation patterns in Araceae, but certain clades are recognizable by their venation. Orontioideae is one such clade (Bogner *et al.*, 2007). We examined leaves of all three genera of Orontioideae (Fig. 6; Table 1). *Orontium*, unlike *Lysichiton* and *Symplocarpus*, does not have a well-defined costa. All three genera show at least three sizes of longitudinal veins and two sizes of transverse veins. In *Orontium*, the transverse veins occur at an oblique angle crossing several sets of primary lateral veins (Fig. 6A, B). *Symplocarpus* has the least well-organized venation in the subfamily (Fig. 6C, D). In *Lysichiton*, the larger veins form clear more or less square patterns that enclose higher order veins forming a reticulum (Fig. 6E, F).

DISCUSSION

A new genus, *Orontiophyllum*, is erected to accommodate fragmentary leaf material that shows entire-margined oblong-elliptic leaves with parallel-pinnate venation, transverse veins crossing multiple primary lateral veins and higher order reticulate venation, typical for foliage of Orontioideae. Although the three genera within Orontioideae clearly differ from each other in terms of the prominence of the costa and some of the details of higher order venation, they are nevertheless recognizable compared with other Araceae in having entire-margined oblong-elliptic blades, parallel-pinnate venation, transverse veins crossing multiple primary lateral veins and reticulate
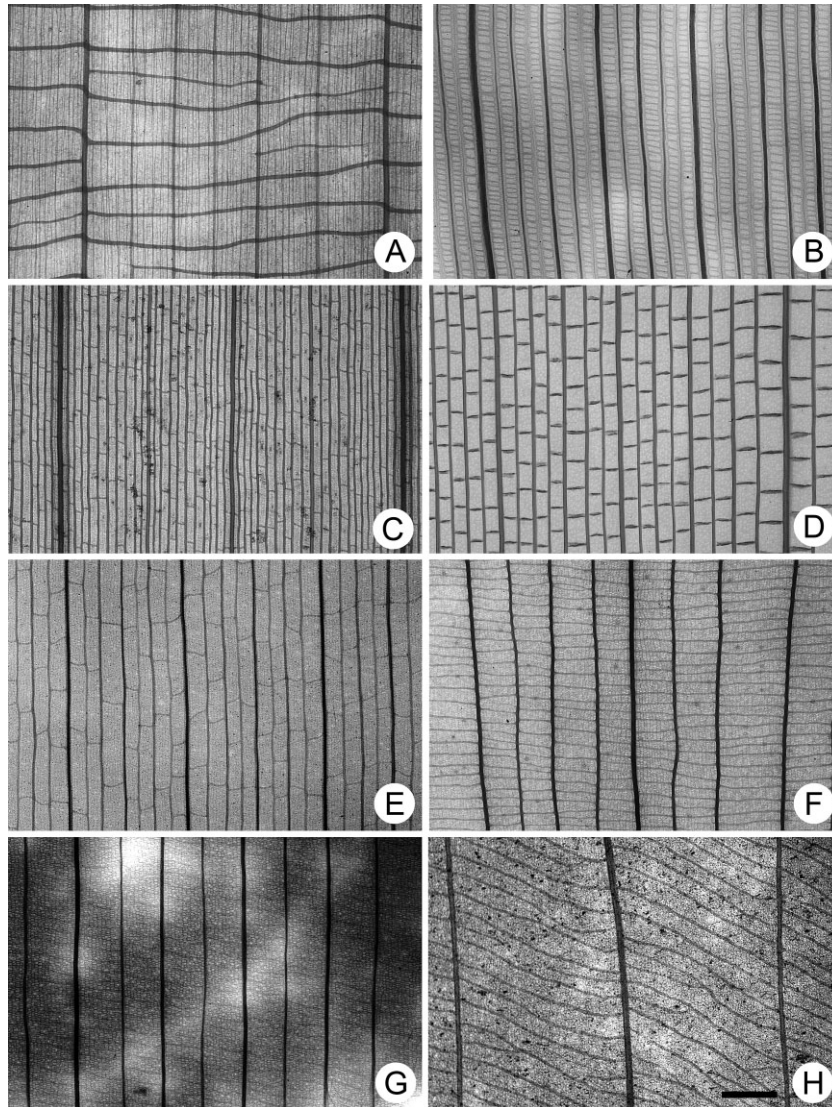
Figure 5. Major vein patterns in extant Zingiberales. A, *Orchidantha fimbriata* Holttum (MCL 55). B, *Ensete lasiocarpum* (Franch.) Cheeseman (MCL 94). C, *Heliconia chartacea* Lane ex Barreiros (MCL 54). D, *Strelitzia reginae* Banks (MCL 93). E, *Zingiber ottensii* Valeton (MCL 47). F, *Trachyphrynium braunianum* Baker (MCL 56). G, *Canna indica* L. (MCL 48b). H, *Cheilocostus globosus* (Blume) C.D.Specht (MCL 52). Scale bar, 1 mm.

higher order venation (Ertl, 1932; Mayo *et al*., 1997; Bogner *et al*., 2007). However, because there is no associated reproductive material that can confirm with more diagnostic characters that the various fossils fit within the diagnosis of modern genera, a more conservative approach is warranted. Two species are recognized: *O. riggauense*, originally described as *Zingiberopsis riggauensis* (Knobloch, 1979), but is clearly not a member of Zingiberales, and *O. austriacum*, which is transferred from *Lysichiton* (J.Kvaček & Herman, 2005; Bogner *et al*., 2007) because there is insufficient evidence to confirm that it fits in this modern genus.

Orontiophyllum riggauense differs from *O. austriacum* in several ways (Table 1). The lateral veins leave the multistranded costa at higher angles in *O. austriacum* than in *O. riggauense*. *Orontiophyllum austriacum* differs from *O. riggauense* in having a less regular arrangement of lateral vein subsets. *Orontiophyllum riggauense* shows five orders of laterals that are better distinguished and more regularly arranged compared with the three orders of laterals in *O. austriacum*. The distances between the different vein orders are also more or less constant in *O. riggauense* and variable in *O. austriacum*. Transverse veins of *O. riggauense* are arranged more regularly.
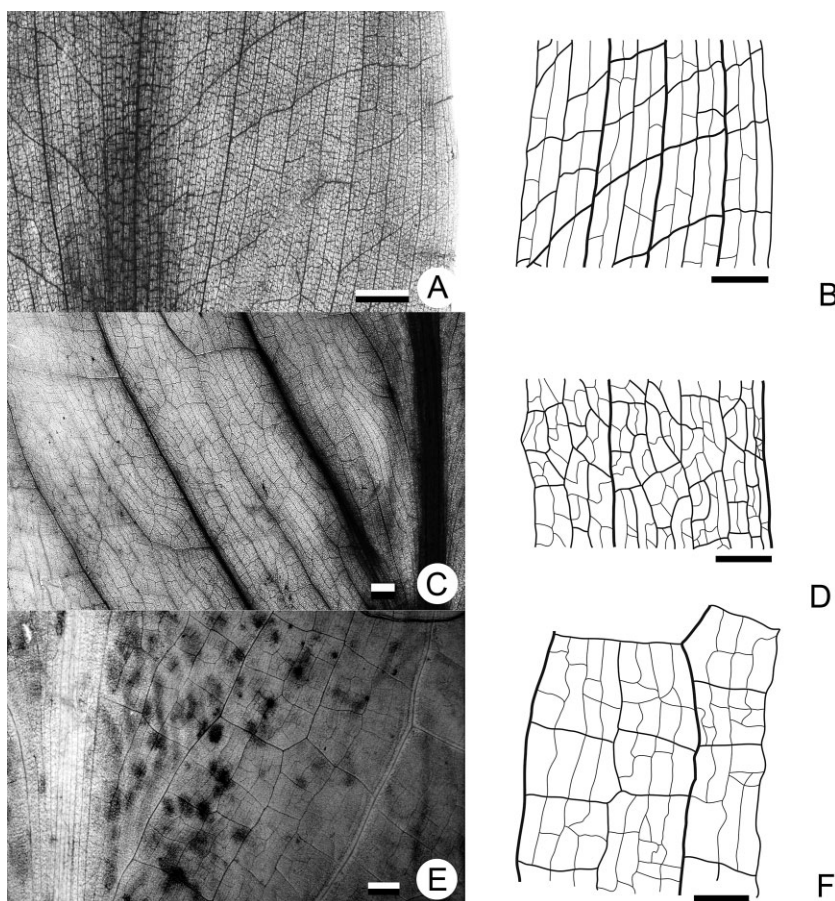
Figure 6. Venation in leaves of Orontioideae. A, B, *Orontium aquaticum* L. C, D, *Symplocarpus foetidus* (L.) Salisb. E, F, *Lysichiton americanus* Hultén & H.St.John (Ehlers & Erlanson 181: MICH). Scale bar, 5 mm.

Transverse veins of *O. austriacum* connect all veins of all orders, including the highest order, whereas, in *O. riggauense*, transverse veins never connect the veins of the highest order. As the marginal parts of *O. riggauense* are not preserved, a comparison of leaf margins is impossible.

Subfamily Orontioideae has been recognized previously based on fossil foliage and one record of a fruit. The fruit *Albertarum* Bogner, G.L.Hoffman & Aulenback from the late Campanian of Alberta, Canada, was closely compared with Orontioideae (Bogner, Hoffman & Aulenback, 2005), but it has a few features that are inconsistent with that subfamily, such as the ribbed testa on the seeds. The earliest records of orontioid leaves are from the Campanian of Austria (J.Kvaček & Herman, 2004a, 2005; Bogner *et al.*, 2007; this paper). Other representatives come from the latest Cretaceous and Palaeogene: *Orontium mackii* Bogner, K.R.Johnson, Z.Kvaček & Upchurch from the Maastrichtian of New Mexico, *O. wolfei* Bogner, K.R.Johnson, Z.Kvaček & Upchurch from the Eocene of the Okanagan region in the western USA,

and *Symplocarpus hoffmaniae* Bogner, K.R.Johnson, Z.Kvaček & Upchurch from the Maastrichtian of North Dakota and Colorado (Bogner *et al.*, 2007). However, the venation of *Orontium mackii* could also be compared with some Arecaceae and Cyclanthaceae, and the closely spaced, regular longitudinal parallel veins are unlike the more irregular courses that veins usually take in Araceae (S. Y. Smith, pers. observ.). Thus, there is some doubt about the affinities of this species.

Members of Orontioideae today are found in North America and East Asia, where they occur in temperate wetlands (Mayo *et al.*, 1997). Several fossil taxa assignable to this subfamily are found in Europe, which points to a wider past distribution. Gymnostachyoideae and Orontioideae represent the two earliest diverging lineages; Gymnostachyoideae is sister to all other Araceae, monogeneric and found today in eastern Australia (Mayo *et al.*, 1997). These two subfamilies were both reconstructed by Nauheimer, Metzler & Renner (2012) as having a centre of origin in North America. More recently, Coiffard *et al.* (2013)

Table 1. Features of fossil and extant orontioid leaf architecture

Species	Venation	Angle between costa and laterals (deg)	Transverse veins	Intramarginal vein	Number of primary lateral vein orders	Transverse veins connecting	Costa	Costa reaching apex
Orontium aquaticum	Parallel-pinnate to parallelodromous	10–15	Oblique; reticulate	Absent	3	Lower orders of laterals	Subtle	No
Lysichiton americanum	Parallel-pinnate	20–30	Perpendicular; reticulate	Present	3	All orders of laterals	Robust	Yes
Symplocarpus foetidus	Parallel-pinnate	20–30	Perpendicular to oblique; reticulate	Present	3	Lower orders of laterals	Robust	Yes
Orontiophyllum austriacum	Parallel-pinnate	10	Perpendicular to oblique; reticulate	Unknown	3	All orders of laterals	Robust	Unknown
Orontiophyllum riggauense	Parallel-pinnate	≤10	Perpendicular to oblique	Unknown	6	Lower orders of laterals	Robust	Unknown

described *Spixiarum* from the Early Cretaceous Crato Formation in Brazil and compared it closely with Orontioideae, suggesting that it may represent a sister lineage to, or be within, the subfamily. However, the venation they illustrate does not fully match that of Orontioideae. The finer parallel veins are more disorganized, and the largest transverse veins occur at a different angle compared with *Orontium* (in *Orontium*, they occur at an acute angle to the central leaf axis, whereas they are at an oblique angle in *Spixiarum*). Also, Coiffard *et al.* (2013) illustrated the thickest parallel veins of *Spixiarum* dichotomizing into veins of equal thickness (their fig. 2), which is not seen in orontioids (S. Y. Smith, pers. observ.; Fig. 6). *Symplocarpus* is the only orontioid with dichotomizing parallel veins, but the splits are unequal, unlike those in *Spixiarum*. For these reasons, the affinities of *Spixiarum* remain uncertain. *Orontiophyllum riggauense* now represents the oldest secure record of Orontioideae, being Turonian in age (89.9–93.9 Mya) compared with the Campanian–Maastrichtian (83.6–66.0 Mya) records from both Europe and North America. This suggests that Araceae had an early centre of diversity in Laurasia, which is also supported by the potential Early Cretaceous araceous remains from Portugal (Friis *et al.*, 2010, 2011).

PALAEOECOLOGICAL REMARKS

The palaeoecology of the Grünbach locality is well understood (J.Kvaček & Herman, 2004b). Here, *O. austriacum* is preserved in a coal-rich sediment that is interpreted as being formed in a lacustrine/lagoonal environment. In association with *Pandanites trinervis* (Ettinghausen) J.Kvaček & Herman and several other fossil plants [*Marseliaceaephyllum campanicum* J.Kvaček & Herman, *Brasenites krasseri* Herman & J.Kvaček, *Sabalites longirhachis* (Unger) J.Kvaček & Herman and *Quereuxia angulata* (Lesquereux) Kryshtofovich], it is interpreted as a plant of a swamp/semiaquatic community (J. Kvaček & Herman, 2004b; Herman & J.Kvaček, 2010). This indicates that *Orontiophyllum* was growing in wet conditions, just as the living members of Orontioideae do today (Mayo *et al.*, 1997). Sedimentological evidence from the locality of Riggau, where *O. riggauense* occurs, is less well studied, but is also interpreted as a more fluvial palaeoenvironment. This suggests that a wetland ecology for *O. riggauense* is probable. Thus, members of Orontioideae have probably had a persistent wetland ecology since their origin.

CONCLUSIONS

Two occurrences of aroid foliage are assigned to the genus *Orontiophyllum* J.Kvaček & S.Y.Smith gen.

nov., which accommodates foliage assignable to Oron-tioideae, but lacking reproductive structures that could confirm placement in an extant genus, and which takes into consideration that fossil taxa often display a mosaic of features that prevents their inclusion in an extant genus. The oldest record, *O. riggauense*, is of Turonian age and was previously described as *Zingiberopsis* (Zingiberales), but clearly does not belong to that order. *Orontiophyllum austriacum* represents another Campanian occurrence of Araceae in Europe. Together, these fossils confirm that early orontioids inhabited wetland areas as they do today, and show that there was a relatively high diversity of orontioids in Laurasia in the Cretaceous.

ACKNOWLEDGEMENTS

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