

ARAUCARIAN CONIFER FROM LATE ALBIAN AMBER OF NORTHERN SPAIN

by JIŘÍ KVAČEK¹ , EDUARDO BARRÓN², ZUZANA HEŘMANOVÁ¹, MÁRIO MIGUEL MENDES³, JAKUB KARCH⁴, JAN ŽEMLIČKA⁴ and JAN DUDÁK^{4,5}

¹National Museum Prague, Václavské nám. 68, 115 79, Praha, Czechia; jiri.kvacek@nm.cz

²Instituto Geológico y Minero de España – IGME, Ríos Rosas 23, 28003, Madrid, Spain

³CIMA – Centre for Marine & Environmental Research, Universidade do Algarve, Campus Universitário de Gambelas, 8005-139, Faro, Portugal

⁴Institute of Experimental & Applied Physics, Czech Technical University in Prague, Horská 3a/22, 128 00, Praha, Czechia

⁵Faculty of Biomedical Engineering, Czech Technical University in Prague, nám. Sítná 3105, 272 00, Kladno, Czechia

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Abstract: Araucarian pollen cones *Rabagostrobus hispanicus* gen. et sp. nov. and their associated foliage *Brachyphyllum obesum* Heer are described from Lower Cretaceous (Albian) strata of northern Spain. Male cones consist of helically arranged microsporophylls bearing 5–8 elongate pollen sacs with *in situ* inaperturate *Araucariacites*-type pollen. The new taxon is compared to material described previously from the Early Cretaceous of North and South Americas. Sterile twigs of *B. obesum* bear helically arranged leaves with wrinkled margins. Its cuticle has files of predominantly transversely oriented stomata. Both twigs and

pollen cones occur as inclusions in amber from the Peñacerrada 1 outcrop (Álava Province), and as compressions are recorded from the amber-bearing strata sediments of the Rábago/El Soplao outcrop. Inclusions of araucariacean plant remains and the co-occurrence of amber and male cone and twig compressions suggest that the amber in these two localities, or at least some of it, was produced by araucariacean plants.

Key words: Araucariaceae, male cones, amber, Early Cretaceous, Spain.

AMBER has been known in Spain from antiquity. The first reference to it was published by Casál (1762) in his *Natural and Medical History of the Principality of Asturias*. The presence of bioinclusions in Spanish amber was indicated by Boscá (1910) at the beginning of the last century, after the study of some fragments from Linares de Mora (Teruel Province). The most significant occurrences of amber from Spain are associated with mid-Cretaceous sedimentary deposits (Alonso *et al.* 2000). Several localities have been cited in stratigraphic surveys (e.g. Ramírez del Pozo & Aguilar 1969; Aguilar *et al.* 1971; Cherchi & Schroeder 1982; Wilmsen 1997), but the amber was generally found in small amounts, and without fossil inclusions.

Plant remains have been found frequently in Cretaceous amber, but those that could be determined taxonomically are scarcer. Cretaceous amber provides excellently preserved plant remains in the form of fragments of bryophytes (Hentschel *et al.* 2009; Ignatov *et al.* 2016), ferns (Poinar & Buckley 2008; Schneider *et al.* 2016), conifers (Moreau *et al.* 2015, 2017) and flowers of angiosperms (Crepet *et al.* 2016; Poinar *et al.* 2016). Coniferous remains are relatively common in amber

(Koller *et al.* 2005; Dörfelt & Schmidt, 2007; Poinar *et al.* 2007; Moreau *et al.* 2017) and are surprisingly well preserved (Koller *et al.* 2005; Moreau *et al.* 2017). Plant remains preserved in amber provide an opportunity to study plants in particular detail. Every amber outcrop is therefore invaluable.

Mid-Cretaceous ambers with a large number of bioinclusions were discovered near the village of Peñacerrada (Álava Province, Sierra de Cantabria, Basque Country) in the 1990s. This amber was extracted in huge quantities for scientific research and is housed in the collections of the Natural Science Museum of Álava (Vitoria/Gasteiz city, Basque Country). The biological inclusions found in the amber from Peñacerrada, which are mainly arthropods belonging to more than 20 orders, exceed 2300 specimens (Delclòs *et al.* 2007). Only three amber specimens of this collection contain conifer remains. Here we describe these first bioinclusions of plant remains preserved in Spanish amber. It is very probable that the producer of some part of this amber could be represented in these bioinclusions.

More recently, mid-Cretaceous amber was also found near El Soplao (Rábago village, Cantabria). This site

shows a remarkable accumulation of amber, with abundant biological inclusions (Najarro *et al.* 2009). As in the case of the Peñacerrada amber, most belong to arthropods. El Soplao amber has provided more than 200 inclusions, including plants (Najarro *et al.* 2010), but to date no conifer remains have been found. However, coniferous fossils are preserved as compressions in the sediment hosting amber and wood fragments at the outcrop.

The significance of conifers found in amber-bearing outcrops in Spain is that three specimens of the same conifer type were found in three amber fragments, together with several shoots and male cones in the associated sediments. This repeated association helps us to resolve the identification of the amber source plant. Studies of amber chemistry, cuticle anatomy and pollen analysis support our arguments. The principal aim of this work is to discuss the taxonomic value of the araucarian bioinclusions and compressions.

GEOLOGICAL SETTING

The study area is located in the latitudinally oriented Cantabrian mountain range that constitutes the western extension of the southern Pyrenees. The strata of the two outcrops hosting amber were deposited in the Basque–Cantabrian Basin, which developed on thinned continental crust between the European and Iberian plates during the Cretaceous (Martín-Chivelet *et al.* 2002).

The Peñacerrada 1 outcrop is located near the southern margin of the Basque–Cantabrian Basin, *c.* 30 km south

of the city of Vitoria/Gasteiz, near the village of Peñacerrada (Álava Province). It incorporates a narrow band of Cretaceous sediments about 5 km long by 2 km wide, extending meridionally (Fig. 1). The sediments of this outcrop belong to the Utrillas Group, which is late Albian in age (Barrón *et al.* 2015). This outcrop is now covered and inaccessible and comprises three stratigraphic intervals (Martínez-Torres *et al.* 2003): (1) interbedded mudstones, sandstones and coal; (2) coarse-grained sandstones; and (3) fine-grained sandstones covered by a heterolithic interval of mudstones. Amber usually occurs associated with the first interval, together with lignified wood fragments.

The Rábago/El Soplao outcrop is located also in the Basque–Cantabrian Basin, near its north-western margin (Fig. 1). The outcrop exposes the Las Peñasas Formation, which is an Albian unit of continental to transitional marine siliciclastic deposits (Najarro *et al.* 2010). The Las Peñasas Formation can be split informally into three units. The amber deposit is located in the top of unit P2, in a deltaic plain facies association at the so-called Rábago Section (Najarro *et al.* 2009). The Rábago/El Soplao outcrop, which contains remarkable accumulations of plant remains and fragments of amber, consists of dark, carbonaceous, pyritiferous shales, with subordinate laminated siltstone and sandstone, and cross-laminated subtle sandstones layers (Najarro *et al.* 2009, 2010). The plant material derives from the taphocoenose dominated by *Frenelopsis turolensis* Gomez (Daviero-Gomez *et al.* 2001; Gomez *et al.* 2002a) and *Mirovia gothanii* Gomez, 2002.

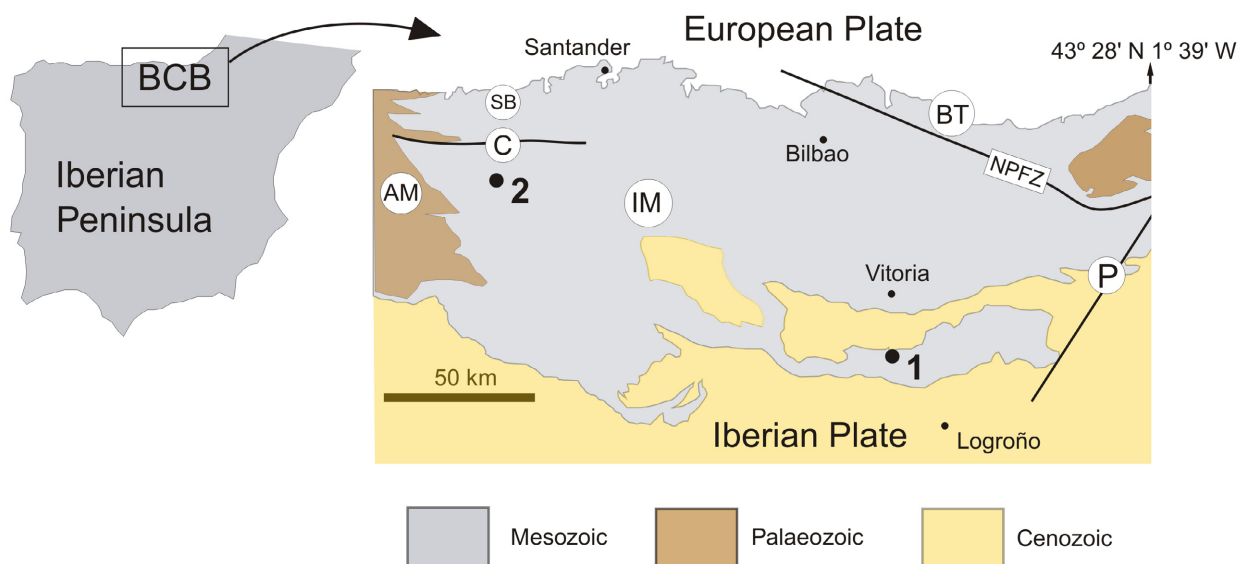


FIG. 1. Map of the studied area. 1, Peñacerrada, 2, Rábago/El Soplao. AM, Asturian Massif; BCB, Basque–Cantabrian Basin; BT, Basque Trough; C, Cabuérniga Fault; IM, Iberian Massif; NPFZ, North Pyrenean Zone; P, Pamplona Fault; SB, Santander coastal domain. Colour online.

MATERIAL AND METHOD

The three amber specimens were hand-collected directly from the sediments in which they were fossilized. According to the techniques proposed by Schlee & Dietrich (1970) and Corral *et al.* (1999) and carried out in the laboratory of Palaeontology of the Natural Science Museum of Álava, two of these (MCNA 13684, MCNA 13926) were embedded in an epoxy resin (Epotek 301) and polished to allow study of the specimens using light microscopy. The conifer specimen MCNA 12736 occurs together with an insect inclusion (Hymenoptera, Platygasteridae). This third amber piece was cut off to segregate it as a fragment. After that, it was also polished, to facilitate the study of the specimen.

The Rábago/El Soplao outcrop was sampled in June 2016 by JaK, EB and MM. The studied samples are housed in the National Museum Prague (NMP). Sediment samples were bulk macerated. Lignified mesofossils were gathered from the sediment by soaking in water and sieving through a 0.125 mm sieve. The material was washed and transferred to glycerine, from where it was picked by brush. Selected lignified mesofossils were cleaned by treatment in HF. After careful washing in water, the material was dried. Mesofossils and amber specimens were studied using an Olympus SZX 12 binocular, and a Keyence digital microscope. The selected material was documented by SEM, then treated for cuticle and pollen *in situ*. The bleaching procedure included maceration with Schulze's reagent: HNO₃ + KClO₃, neutralization in water, and treatment in a low concentration solution of KOH, which was used for washing out the oxidized coal matter. The time for oxidation was about 30–45 min. After chemical treatment, the cuticles were washed in distilled water in Petri dishes. For light microscopy, cuticles were embedded in glycerine and sealed with nail polish. Cuticle preparations were studied in visible light using the Olympus BX50 microscope with a Nomarski DIC. For SEM studies, mesofossils were mounted on aluminium stubs using nail polish, and observed in a Hitachi S-3700N SEM. Amber specimens were also documented using a Sky-scanner 1172 microCT, and analysed using N-Recon and Avizo 9.1.1. software (<http://bruker-microct.com/products/downloads.htm>; <https://www.fei.com/software/amira-avizo/>).

SYSTEMATIC PALAEONTOLOGY

By Jiří Kvaček, Eduardo Barrón, Zuzana Heřmanová and Mário Miguel Mendes

Order PINALES Gorzhankin, 1904

Family ARAUCARIACEAE Henkel & W. Hochstetter, 1865

Genus BRACHYPHYLLUM Brongniart, 1828

Remarks. The genus *Brachyphyllum* was revised by Harris (1979) as conifer foliage, having free parts of leaves shorter than the width of their leaf cushions. On the basis of the scale-like, rhomboid, imbricate and helically disposed leaves, we assign our material to this genus.

Brachyphyllum obesum Heer, 1881

Figure 2

1881 *Brachyphyllum obesum* Heer, p. 20, pl. 17, figs 1–4.

Diagnosis. Branches alternate, numerous, aggregated, thick, short, with obtuse apex, rhombic leaves, densely overlapping, dorsally lightly striated (*sensu* Heer 1881).

Type locality. Almargem, Portugal.

Occurrence. Peñacerrada 1 (amber bioinclusions), Rábago/El Soplao (compressions), Spain.

Material. Peñacerrada 1: MCNA 12736, MCNA 13926; Rábago/El Soplao: NMP K 2893a–c, K 2894, K 2897.

Description. The specimens preserved in amber are two fragments of twigs from Peñacerrada 1. The leafy branches are small, 2.4–6 mm in length and 1.1–2.5 mm in diameter, bearing helically arranged leaves (Fig. 2F). Leaves are small, imbricate, appressed and delicately striated. They are 1–2.3 mm long and 1–2 mm broad. Each leaf is slightly keeled, ribbed in the marginal part, forming an indistinct frill. The leaf margin is typically wrinkled, but in some cases wrinkles are fused to form a nearly entire margin. The smaller specimen (MNCNA 12736) preserves a fragment of a cuticle pattern. The stomata occur in short rows (two or three are visible), and are orientated perpendicularly and obliquely to the leaf margin (Fig. 2L).

Lignified and charcoaled mesofossils come from the Rábago/El Soplao outcrop. Several larger fragments of twigs (NMP K 2893a–c, K 2894) and isolated leaves (e.g. NMP K 2897) from the latter site are 8–13 mm long and 3–3.5 mm broad, bearing helically arranged leaves (Fig. 2A–C, E). The abaxial surfaces of the leaves are delicately ribbed (Fig. 2C, D). The marginal parts of the leaves are wrinkled and pale, forming a weak frill (Fig. 2E, K). Leaves (2–2.5 × 2 mm) are hypostomatic. The adaxial cuticle is confined to a narrow area of the free leaf tip, consisting of narrow ordinary cells 5–15 × 20–35 µm (Fig. 2K). The abaxial cuticle consists of longitudinal interchanging stomatal and non-stomatal rows that cover the entire surface, and converge in the leaf apex (Fig. 2K). The ordinary cells are quadrangular (7–15 × 25–40 µm). Stomata in parallel rows show transverse or oblique orientation to the direction of rows (Fig. 2H, I, M). They are closely set together,

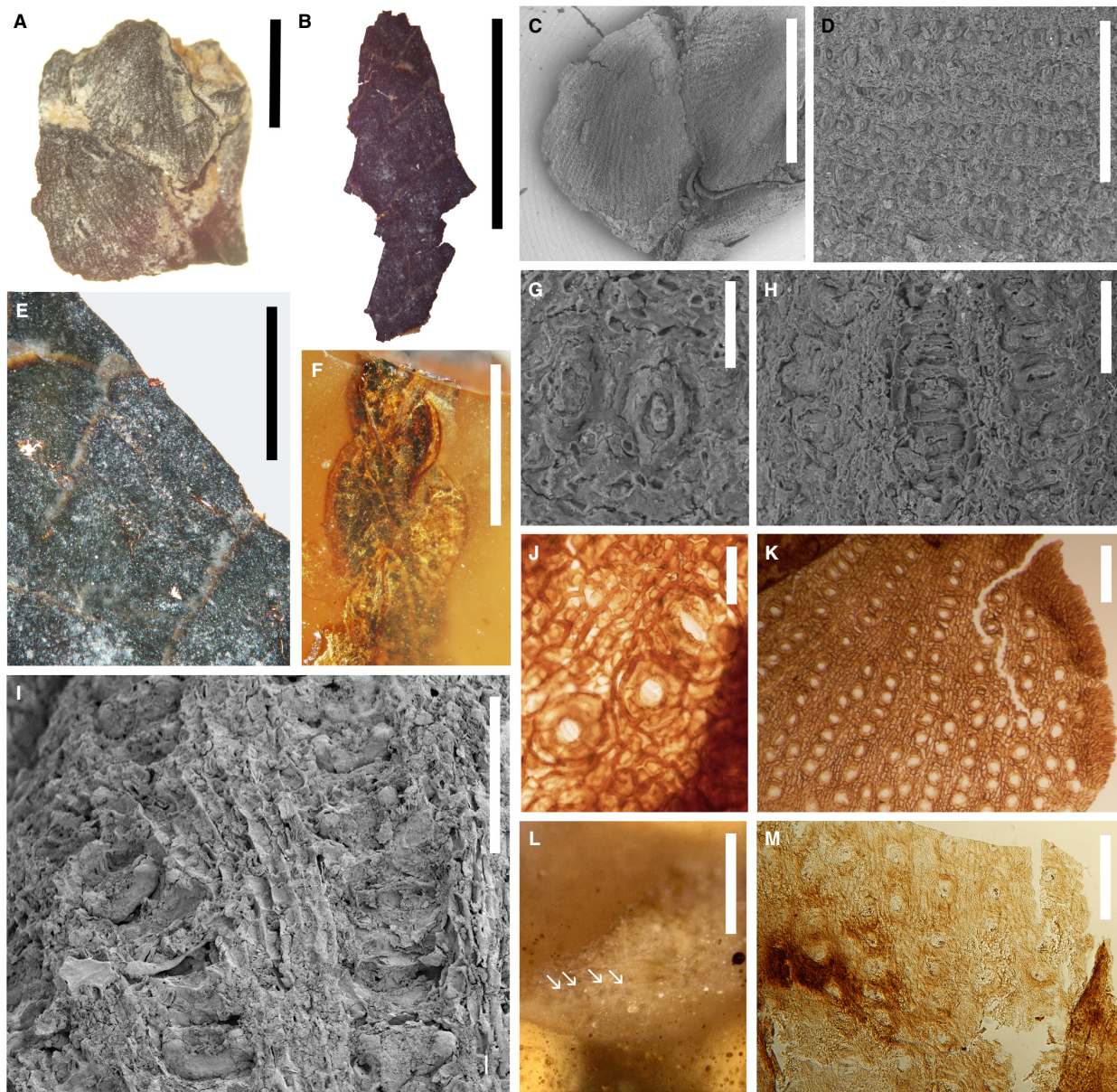


FIG. 2. *Brachyphyllum obesum* Heer, Early Cretaceous (Albian). A, C–E, G–I, M, NMP K 2894, Rábago/El Soplao: A, charcoalfied twig showing leaves with fine striation; C, detail of A, leaf with fine striation representing stomatal rows; D, abaxial cuticle showing rows of stomata, SEM; E, detail of helically arranged leaves (SEM); G, stoma showing Florin ring on abaxial cuticle (SEM); H–I, abaxial cuticle showing rows of stomata (SEM); M, abaxial cuticle showing rows of stomata (SEM). B, NMP K 2893a, Rábago/El Soplao, terminal part of compressed twig. F, MCNA 13926, Peñacerrada 1, detail of helically arranged leaves preserved in amber. J–K, NMP K 2897, Rábago/El Soplao: J, detail of amphicyclic stomata surrounded by 5–6 subsidiary cells; K, leaf margin showing abaxial cuticle with rows of stomata and narrow strip of adaxial cuticle (in marginal part) formed by narrow cells. L, MNCNA 12736, Peñacerrada 1, abaxial cuticle showing rows of stomata (arrows). Scale bars represent: 2 mm (A, C, E); 10 mm (B); 400 µm (D, L); 5 mm (F); 50 µm (G, J); 100 µm (H, I, M); 200 µm (K). Colour online.

adjoining or sharing lateral encircling or even subsidiary cells (Fig. 2H–J). The stomatal rows are separated by areas of ordinary cells, typically 3–6 cells broad. Stomata are completely or incompletely amphicyclic, broadly elliptical ($40 \times 60 \mu\text{m}$) with delicate remains of sunken guard cells (Fig. 2J). Each stomatal chamber is surrounded by four, typically five but up to six

subsidiary cells ($5\text{--}12 \times 10\text{--}25 \mu\text{m}$, Fig. 2J). Stomatal pits are externally surrounded by Florin rings (Fig. 2G).

Remarks. *Brachyphyllum obesum* has been described from various parts of the globe, particularly in Europe (Heer 1881; Saporta 1894), Japan (Yabe & Kubota 2004; Yabe &

Shibata 2011), China (Cao 1994) and Brazil (Kunzmann *et al.* 2004; Batista *et al.* 2017), and accommodates twigs possessing few characters, particularly if only impressions of twigs are available. Our specimens are important for their association with araucariacean male cones, whereas a specimen described by Batista *et al.* (2017) from the Early Cretaceous of Brazil preserves the anatomy of its wood, in addition to the epidermal characters. Several species described from the mid-Cretaceous of Europe and North America are similar to *B. obesum*. The most similar is *Brachyphyllum squamosum* (Velenovský) Palibin, described from the Cenomanian of Czechia (Kvaček 2007). The latter differs in having less pronounced nodulous polar extensions in the stomata (cf. Němejc & Kvaček 1975). *Brachyphyllum crassum* (Lesquereux) Lesquereux from the Cenomanian of the Dakota Formation, USA (Kvaček & Dilcher 2000) is also similar to *B. obesum* but lacks information about the epidermis. *Brachyphyllum patens* (Miquel) van der Ham & van Konijnenburg-van Cittert *in* van der Ham *et al.*, 2003 from the Maastrichtian of the Netherlands differs from *B. obesum* in having larger leaves, with randomly arranged and orientated stomata (not forming rows).

Araucaria vulgaris (Stopes & Fuji) Ohsawa *et al.*, 1995 from the Late Cretaceous of Japan has the same type of twigs: imbricate, appressed and fused to the surface of the stem. The main difference is in the stomata. *Araucaria vulgaris* has only 4–5 subsidiary cells, whereas *B. obesum* has typically 5–6 subsidiary cells. Ohsawa *et al.* (1995) introduced a new subgenus *Yezonia* for this conifer, characterized by *Brachyphyllum*-like foliage and a *Eutacta*-like ovuliferous cone. This model could be quite close to the interpretation of our material, although we do not have a female cone available.

Comparing leaves of *B. obesum* with extant *Araucaria*, there are similarities in micromorphology. Both taxa have stomata in rows, and microscopic marginal projections forming a frill; also, perpendicular orientation of the stomata is typical for Araucariaceae (e.g. *Araucaria laubenfelsii* Corbasson or *A. muelleri* Carrière Brongn. and Gris; see Stockey & Ko 1986). Leaves of *Araucaria nathorstii* Dusén described from the Eocene of Chile (Ohsawa *et al.* 2016) differ from *B. obesum* in having longitudinally orientated stomata, which are in all cases surrounded by only four subsidiary cells.

Genus RABAGOSTROBUS nov.

Type species (by monotypy). *Rabagostrobus hispanicus* sp. nov. described herein.

Derivation of name. From the locality of Rábago.

Diagnosis. Pollen cones with helically arranged microsporophylls. Each microsporophyll peltate, bearing abaxially numerous (at least six) elongate pollen sacs containing pollen of *Araucariacites*-type.

Remarks. The genus *Masculostrobus* Seward is generally used for male cones of conifers of uncertain affinity. However, its last emendation, published by Grauvogel-Stamm & Schaarschmidt (1979) narrowed the scope of the genus, specifying pollen sacs as spherical. Moreover, the type (*M. zeilleri* Seward) is a compound male inflorescence with microsporophylls, having only two pollen sacs per microsporophyll, and pollen possessing a distinct papilla, which indicates its systematic affinity to Cupressaceae (van Konijnenburg-van Cittert & van der Burgh 1989). The material in hand, although not perfectly preserved, shows all characters of Araucariaceae, particularly numerous elongate pollen sacs attached abaxially to peltate microsporophylls, and *Araucariacites* pollen *in situ*. On this basis, we decided to introduce a genus for araucariacean pollen cones that are in most characters similar to extant *Araucaria*, except for their size and associated foliage. *Rabagostrobus* gen. nov. differs from *Nothopheuen* Del Fueyo from the Early Cretaceous of Argentina in having more than four pollen sacs (Del Fueyo 1991), and from *Upatoia* Leslie, Herendeen & Crane from the Santonian of Georgia, USA in having more than three pollen sacs (Leslie *et al.* 2009). *Alkastrobus* Del Fueyo & Archangelsky, 2005, which is also assigned to Araucariaceae, differs from *Rabagostrobus* in having *Cyclusphaera* Elsie pollen *in situ*.

Rabagostrobus hispanicus sp. nov.

Figures 3–5

Derivation of name. The epithet *hispanicus* is derived from Spain, the country where the specimens were collected.

Type specimens. Holotype: NMP K 2794a–e (Fig. 3A, B, G, I, K, L). Paratype: MCNA 13684 (Fig. 3C, D).

Type locality. Rábago/El Soplao outcrop, Spain.

Type unit. Las Peñasas Formation, Rábago Section.

Age. Late Albian, Early Cretaceous.

Diagnosis. Pollen cone with numerous microsporophylls arranged helically on delicate axis. Each peltate microsporophyll consists of narrow and well-developed triangular distal lamina. Epidermis consists of elongate

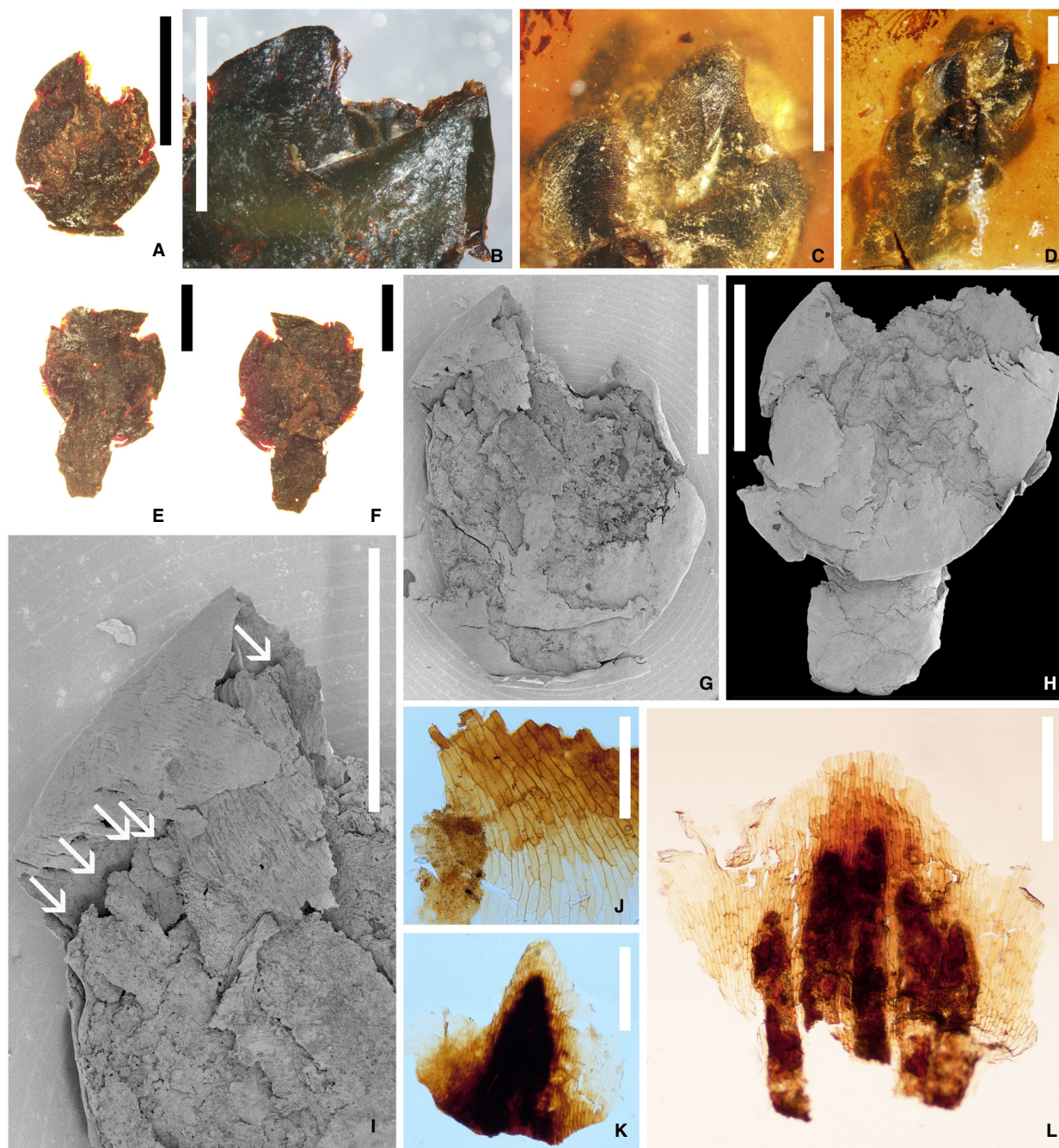


FIG. 3. *Rabagostrobus hispanicus* gen. et sp. nov., Early Cretaceous (Albian). A–B, G, I, NMP K 2794, (holotype) Rábago/El Soplao: A, pollen cone showing helically arranged sporophylls; B, detail of apical part showing details of sporophylls; G, SEM image; I, SEM image showing portion of pollen sacs (arrows). C–D, MCNA 13684 (paratype), Peñacerrada 1: C, detail of sporophylls; D, pollen cone showing helically arranged sporophylls. E–F, NMP K 2895, Rábago/El Soplao; pollen cone showing helically arranged sporophylls. H, NMP K 2895, Rábago/El Soplao; SEM image of pollen cone. J, NMP K 2895c, Rábago/El Soplao; sporophyll cuticle. K, NMP K 2794c, Rábago/El Soplao; sporophyll from holotype, notice dark interior formed by mass of pollen sacs. L, NMP K 2794e, Rábago/El Soplao; sporophyll from holotype showing 5–6 pollen sacs. Scale bars represent: 4 mm (A); 3 mm (B, G, H); 2 mm (C–F); 1 mm (D, I); 60 μm (J); 0.5 mm (K, L). Colour online.

cells. Pollen sacs numerous (about 5–8), very elongate containing nonsaccate pollen of *Araucariacites*-type. Pollen sacs free for most of their length, partially fused in

basal parts at the place of attachment to the microsporophyll. Inaperturate pollen grains with psilate to slightly scabrid ornamentation.

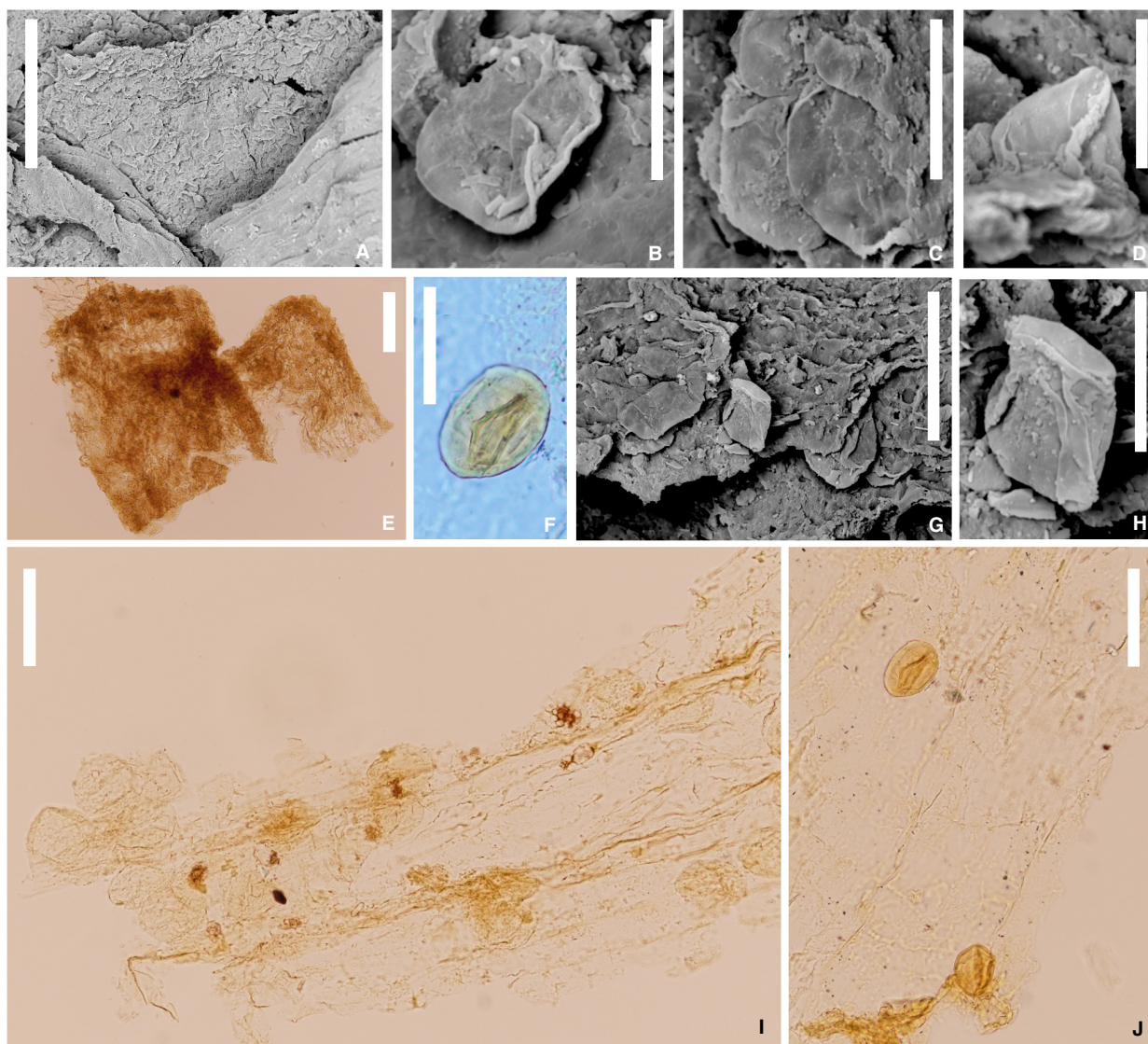


FIG. 4. *Rabagostrobus hispanicus* gen. et sp. nov., Early Cretaceous (Albian), SEM images. A–D, G–H, NMP K 2794b, Rábago/El Soplao: A, detail of pollen sac; B–D, *Araucariacites* sp. pollen from holotype; G, group of pollen *Araucariacites* sp. from holotype; H, *Araucariacites* sp. pollen from holotype. E–F, I–J, NMP K 2895b, Rábago/El Soplao: E, detail of macerated pollen sac; F, *Araucariacites* sp. pollen, detail of J; I, cuticle of pollen sac with *in situ* pollen; J, pollen sac with *in situ* pollen. Scale bars represent: 200 μm (A); 20 μm (B–D, H); 100 μm (E); 30 μm (F); 50 μm (G, I, J). Colour online.

Description. The holotype (NMP K 2794) is an isolated complete ovoid pollen cone (4×5 mm). The pollen cone is broadly ovate, consisting of about 18 helically arranged deltoid microsporophylls. Each microsporophyll has a peltate triangular lamina ($1\text{--}1.2 \times 1.5\text{--}2.2$ mm, Fig. 3K), with fragments of five or six pollen sacs (0.8 mm long, 0.2 mm wide) attached to the distal lamina of the microsporophyll (Fig. 3I, L). The pollen sacs are elongate and attached to the microsporophyll lamina (Fig. 3L). There are about eight pollen sacs on larger microsporophylls (based on exposed parts, Fig. 3I). The pollen sacs partly adhere to the microsporophylls (Fig. 3L). The distal side of the microsporophyll lamina is formed by elongate cells ($10\text{--}25 \times 55\text{--}105$ μm ; Fig. 3J). Surfaces of the pollen sacs are

wrinkled (Fig. 4A, E), and covered by thin cuticle. The paratype (MCNA 13684), the pollen cone from amber (2.8×6.3 mm) has helically arranged peltate microsporophylls (Fig. 3D). The cone is incomplete: its apical part is missing. The fragment consists of about 18 helically arranged peltate microsporophylls, each is about 1.5×1.8 mm. Marginal parts of the microsporophylls are irregularly formed by variously shaped and sized emergences. MicroCT studies of the paratype revealed well-preserved peltate microsporophylls (Fig. 5A). A 3D reconstruction of the cone shows a clear helical arrangement of the microsporophylls and a deltoid, slightly lobate shape (Fig. 5B, C). Specimen NMP K 2895 is a well-preserved compressed pollen cone, born on a twig 2 mm long and 1.8 mm broad. It consists of more

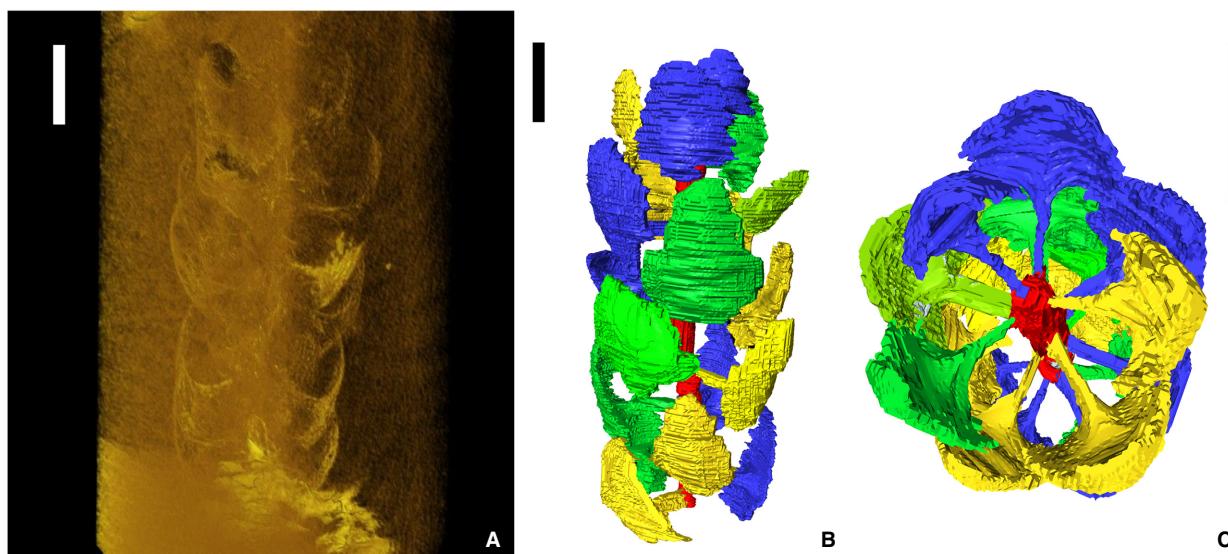


FIG. 5. *Rabagostrobus hispanicus* gen. et sp. nov., Early Cretaceous (Albian), paratype, pollen cone MCNA 13684, Peñacerrada 1. A, longitudinal section, microCT. B–C, reconstruction of pollen cone: B, lateral; C, apical view. All scale bars represent 1 mm. Colour online.

than 18 helically arranged sporophylls. Pollen sacs show delicate cuticle consisting of elongate cells (Fig. 4I).

The pollen grains found *in situ* in the holotype are assigned to *Araucariacites australis* Cookson. This taxon usually occurs as dispersed pollen in the sediments at the Rábago/El Soplao and Peñacerrada 1 outcrops (Najarro *et al.* 2010; Barrón *et al.* 2015). The studied specimens of *A. australis* are inaperturate, and roughly spherical to elliptical. They usually bear folds formed by sediment compressions (Fig. 4B–D, F–H). Their average diameter is 35.58 μm (range 27.8–40.62 μm). The exine is about 2–3 μm thick. The exine surface is psilate to slightly scabrate, granulate, and seemingly columellate in only few cases. The immature pollen grains found in the holotype are smaller, about 22–23 μm ; their psilate ornamentation could be related to the immaturity of these grains.

Remarks. The pollen cones, *Nothopheuen brevis* Del Fueyo, from the Baqueró Formation, Santa Cruz, Argentina (Del Fueyo 1991) are most similar to the described taxon. They contain similar pollen of *Araucariacites*-type, and have vegetative characters similar to *Brachyphyllum* (bearing around eight male cones with *Araucariacites*-type pollen; Del Fueyo 1991). These male cones differ from *Rabagostrobus hispanicus* in their smaller size and the presence of only four pollen sacs per microsporophyll. *Masculostrobus graiterensis* Allenbach & van Konijnenburg-van Cittert, 1997 has a very similar arrangement of cone-scales, cuticle pattern and partly pollen. However, *M. graiterensis* differs from *R. hispanicus* in the larger size of the cones, and the *in situ* pollen being represented not only by *Araucariacites* but also *Callialasporites*. In contrast to *R. hispanicus*, it is associated with *Pagiophyllum* type foliage. Closer comparison is difficult, because the number of pollen sacs of *M. graiterensis* and

other structural details are not known. Pollen cones associated with *B. mamillare* Brongniart from the Jurassic of Yorkshire (van Konijnenburg-van Cittert 1971; Harris 1979) are of similar shape and size as those of *R. hispanicus* but differ from the latter in having only three pollen sacs per microsporophyll. The presence of male araucariacean cones and *Brachyphyllum* twigs has been reported from the Crato Formation, Brazil, but with no details (Martill *et al.* 2005). Pollen grains related to Araucariaceae have been found in male cones associated with *Brachyphyllum mirandai* Archangelsky and *B. irregulare* Archangelsky from the Early Cretaceous of Patagonia (Archangelsky 1963; Archangelsky & Gamero, 1967). Pollen grains found in male cones of *B. irregulare* were attributed to *Balmeiopsis*, which is characterized by spheroidal pollen grains with thick exine and a polar hilum (Archangelsky 1977). However, this pollen type has not been found *in situ*, nor in dispersed form in the Peñacerrada 1, nor the Rábago/El Soplao outcrops. Its presence as dispersed pollen is known in Albian sediments from the Iberian Range (Villanueva-Amadoz 2009). Comparing pollen of extant genera *Agathis*, *Wollemia* and *Araucaria*, our material, particularly due to its smooth exine most resembles the genus *Araucaria*, and several species of *Agathis*, such as *A. australis* Salisb. (see e.g. Pocknall 1981; Del Fueyo *et al.* 2008).

DISCUSSION

Araucariaceae is an ancient family of conifers, today restricted to the southern hemisphere, being represented by three genera: *Agathis*, *Araucaria* and *Wollemia*,

containing 41 species (Anderson *et al.* 2007). The presence of Araucariaceae throughout the northern hemisphere during the Mesozoic is demonstrated not only by plant remains (e.g. Wilde & Goth 1987; Kunzmann 2007; van der Ham *et al.* 2010) but also by the occurrence of fossilized resins (Lambert *et al.* 1993; Lambert & Poinar 2002; Poinar *et al.* 2007). Representatives of this family were common in the Albian ecosystems of Iberia. Pollen grains and shoot fragments of *Brachyphyllum* occur commonly in Spanish outcrops (Gomez *et al.* 1999; Sender *et al.* 2008; Najarro *et al.* 2009, 2010; Villanueva-Amadoz 2009; Barrón *et al.* 2015; Peñalver *et al.* 2015). Association of amber and *Brachyphyllum* has also been reported in Gondwana (Early Cretaceous, South Africa; Gomez *et al.* 2002b). The only coniferous remains found in the amber from Peñacerrada 1 are those described herein, and assigned to Araucariaceae. This fact suggests that at least some of the amber in this locality was produced by plants bearing foliage of *Brachyphyllum obesum* and male cones of *Rabagostrobus hispanicus*.

Both the occurrence of sparse bioinclusions and the results of infrared and nuclear magnetic resonance spectra on Lebanese ambers allowed Poinar & Milki (2001) to interpret the amber as having been produced by Araucariaceae. More specifically, Poinar & Milki (2001) designated the species *Agathis levantensis* Poinar & Milki as the producer of the Lebanese amber, although they did not provide any direct evidence. The appearance of wood fibre inclusions, and spectroscopic studies also point to plants of Araucariaceae as sources of the Myanmar amber (Poinar *et al.* 2007).

Araucariacean pollen occurs in conspicuous quantities in the Peñacerrada 1 and Rábago/El Soplao outcrops. *Araucariacites australis* Cookson and *Callialasporites dampieri* (Balme) Dev emend. Norris are the pollen-species represented (Barrón *et al.* 2015). These are inaperturate, monosaccate and cavate species respectively, and could have been produced by different species, or by the same taxon (Chambers *et al.* 1998); the extant *Araucaria excelsa* R. Brown produces these two types of pollen grains in the same cone, with the inaperturate *Araucariacites*-type much more abundant than the monosaccate *Callialasporites* one (Courtinat 1986). Pollen of *Araucariacites*/*Callialasporites*-type also occurs in male cones attached or associated with two Jurassic species of *Brachyphyllum*: *B. lorchii* Raab, Horowitz & Conway and *B. mamillare* Brongniart (van Konijnenburg-van Cittert 1971; Raab *et al.* 1986). With regard to the Peñacerrada 1 record, *A. australis* is abundant in all the studied levels, whereas *C. dampieri*, although common in several levels, is less frequent (Barrón *et al.* 2015). Likewise, *A. australis* is better represented than *C. dampieri* in the Rábago/El Soplao area (Najarro *et al.* 2010), although the quantity of all araucariacean pollen is lower than at Peñacerrada

1 (Peñalver *et al.* 2015). Comparable quantitative representation of these pollen species were inferred from the *in situ* pollen assemblages of the mentioned *Brachyphyllum* species. The first has most grains belonging to *Araucariacites*, and only about 10% to *Callialasporites*, whereas in the second species, 60% of the grains were related to *Araucariacites* and 40% to *Callialasporites* (Balme 1995). *Callialasporites* has also been found in pollen cones of the podocarp *Apterocladus* from the Lower Cretaceous of Patagonia (Gamerro 1965; Archangelsky 1966). Thus, this pollen type could also be produced by podocarp conifers.

Cretaceous fossil remains from the southern hemisphere indicate that *Araucariacites* and *Balmeiopsis* are pollen grains of Araucariaceae. Both were produced in male cones attached to *Brachyphyllum* twigs (Archangelsky & Gamerro 1967; Archangelsky 1994). Other araucariacean pollen grains were initially found dispersed in Campanian sediments, and later observed *in situ*, in araucariacean male cones from the Early Cretaceous of Argentina (Elsik 1966; Del Fueyo & Archangelsky 2005). However, *Cyclusphaera* is geographically restricted to Gondwana (Jaramillo *et al.* 2013).

The genus *Dilwynites* was established by Harris (1965) for Cenozoic dispersed pollen grains with similar morphology to *Araucariacites*, but with more variable sculptural elements (presence of bacula, gemmae and/or clavae), and thicker exines (Chambers *et al.* 1998). These grains are indistinguishable from those in the pollen of two extant species of New Caledonian *Agathis* (*A. morei* Mast. and *A. ovata* (Vieill.) Warb.) and the Australian 'living fossil' *Wollemia nobilis* Jones, Hill & Allen (Chambers *et al.* 1998; Macphail & Carpenter 2013). As *Cyclusphaera*, this pollen type only has been recorded in Gondwana. However, similarly to *Dilwynites*, dispersed scabrate to granulate inaperturate pollen grains of the genus *Uesuguipollenites* (Dino 1994) have been identified in the Spanish mid-Cretaceous (Villanueva-Amadoz 2009). The pollen grains present in *Rabagostrobus hispanicus* and the dispersed ones in the Spanish ambarigenos Albian sediments differ substantially from *Dilwynites* and *Uesuguipollenites* in having psilate to slightly ornamented exine surfaces.

Chemical analysis of amber from the Peñacerrada 1 outcrop indicates the presence of the compounds *ent*-beyerane, *ent*-16 β (H)-kaurane and *ent*-16 α (H)-kaurane (Alonso *et al.* 2000). Significantly, kauranes are very abundant in *Agathis*. Other possible coniferous origins may be discarded, owing to the absence of some compounds: the lack of tetracyclic diterpenoids, such as phyllocladanes precludes their origin in Podocarpaceae, and the absence of α -cedrene and cuparene excludes an association with the Cupressaceae (Chaler & Grimalt 2005).

Additional amber from the Rábago/El Soplao outcrop was analysed (Menor-Salvan *et al.* 2010; Najarro *et al.* 2010). Two types of amber were found, termed A and B.

Type A contains phenolic terpenoids: ferruginol, totarol and hinokiol. These compounds indicate the conifer families Cupressaceae and Podocarpaceae as possible producers of type A amber, and simultaneously, the presence of these terpenoids precludes Araucariaceae as a biological precursor. Importantly, Cupressaceae are proven sources of ambers from the Cenomanian of Czechia, based on *in situ* finds of fossilized resin in cones of the cupressoid conifer *Sphenolepis pecinovens* J. Kvaček (Kvaček 1997; Otto *et al.* 2000). Other co-occurrences of amber and cupressoid remains have been found from the Turonian of north-western France (Néraudeau *et al.* 2017) as well as from the Eocene of the Baltic Sea (Koller *et al.* 2005). Type B amber has shown only the biomarkers pimaric/isopimaric acids. Menor-Salván *et al.* (2010) claimed that the lack of phyllocladane/kaurane-type terpenoids and the absence of macrofossil plant remains exclude the possibility of Araucariaceae as a source for type B amber, leaving Cheirolepidiaceae as the only possible source. However, we dispute this claim, for several reasons:

1. Published arguments identifying amber of Cheirolepidiaceae are based solely on co-occurrence (Roghi *et al.* 2006; Bray & Anderson 2008; Dal Corso *et al.* 2013; Nohra *et al.* 2015).
2. We have several specimens of Araucariaceae co-located with these ambers.
3. Most importantly, mature Cheirolepidiaceae wood (e.g. *Protocupressinoxylon purbeckensis* Francis) completely lacks resin canals (Francis 1983; Barale & Doludenko 1985; Philippe *et al.* 2010), and foliage of *Pseudofrenelopsis*, *Hirmeriella*, *Frenelopsis* and its male (*Clasostrobos*) and female (*Alvinia*) cones do not contain fossil resin (Alvin 1983; Francis 1983; Kvaček 2000).

All of this would seem to preclude Cheirolepidiaceae as a possible source of resin.

The presence of araucariacean remains of *Brachyphyllum obesum* and *Rabagostrobos hispanicus* as bioinclusions in the amber of Peñacerrada 1, together with the geochemical data, seem to favour Araucariaceae as the source of the resin. On the other hand, the lack of plant bioinclusions in the amber from the Rábago/El Soplao outcrop, and the geochemical analysis of only a few amber pieces from Peñacerrada 1 prevent us from reliably relating this amber to Araucariaceae. Nevertheless, the occurrence of the foliage and cones described here in the amber-bearing strata is another important argument for an araucariacean origin for at least part of this amber.

CONCLUSIONS

1. As indicated by palynological and macrofloristic studies, conifers are common in the Albian of the northern Iberian Peninsula.

2. Araucariaceae are represented in amber inclusions from the Peñacerrada 1 outcrop (Álava) as pollen cones and sterile foliage.
3. The occurrence of male cones with 5–8 pollen sacs provide adequate grounds for establishing the new genus *Rabagostrobos*.
4. The male cones *Rabagostrobos hispanicus* and sterile foliage, *Brachyphyllum obesum*, also occur as compressions in the amber-bearing sediments of the Rábago/El Soplao outcrop.
5. Pollen of *Araucariacites* was found *in situ* in *Rabagostrobos hispanicus*, underpinning the occurrence of extinct northern hemisphere species of Araucariaceae in Spain.
6. Regarding origins of the amber in the Peñacerrada 1 outcrop, the presence of bioinclusions of *Brachyphyllum* and *Rabagostrobos* (Araucariaceae) suggests that these conifers could have been producers of the fossil resins at this locality.

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