



Research papers

A reconstruction of the fossil palm *Sabalites longirhachis* (Unger) J. Kvaček et Herman from the Maastrichtian of Pyrenees

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ABSTRACT

Fragmented leaf laminas were the only organ known of the fossil palms *Sabalites longirhachis* (Unger) J. Kvaček et Herman. Recently, isolated leaves of *S. longirhachis*, palm logs and rooting systems have been found associated in Fumanya, a new Maastrichtian locality from the Southern Pyrenees. This has allowed proposing a taphonomy-based hypothesis of the habit and paleoecology of these extinct palms.

Fossil leaves are represented by complete laminas bearing petioles attached. Leaves and logs are parautochthonous at the base of the first coal seam of the stratigraphic succession. Rooting systems provide evidence for autochthony in coal layers formed at the top of lacustrine limestones. The tree bearing *S. longirhachis* leaves is reconstructed as relatively slender, of up to 14 m high, showing a smooth trunk with adventitious roots at the base and a crown keeping the marcescent leaves attached. The rooting system consisted of straight radial rootlets of about 1.5 m in total diameter. Taphonomic and facies analyses carried out in Fumanya suggest that the habitats colonized by this species were small peat mires at the lakeshores of freshwater alkaline lakes.

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1. Introduction

The fossil record of plants is mainly composed of fragmentary remains, with organs detached one from each other or even fragmented, making whole plant reconstructions a difficult task for paleobotanists. Since the very beginning of paleobotany, hypotheses were proposed to understand the complete body of fossil plants, mainly based on exceptionally well-preserved fossils showing anatomical connections or on repeated taphonomic associations of the different organs. Although misleading interpretations were proposed by the past, whole plant reconstructions continue to be one of the main goals of paleobotanical research. They contribute to a more complete understanding of plant evolution, help to correct mistakes in systematic paleobotany and are the basis for paleoecological and paleobiogeographical studies (Kvaček, 2008).

Some groups of fossil plants are more prone to be found with their organs attached, since they were living in the very same depositional setting in which they were later buried, such as in peat mires. However, land plants showing anatomically connected organs are extremely rare in most depositional settings and whole plant reconstructions can be only carried out hence based on taphonomic hypotheses. This is the case of most palms, which normally grow

outside but sometimes not far from areas with a high sedimentation rate.

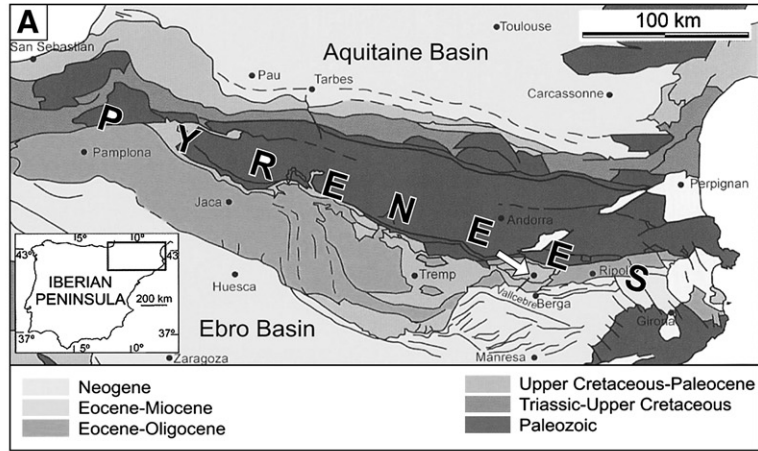
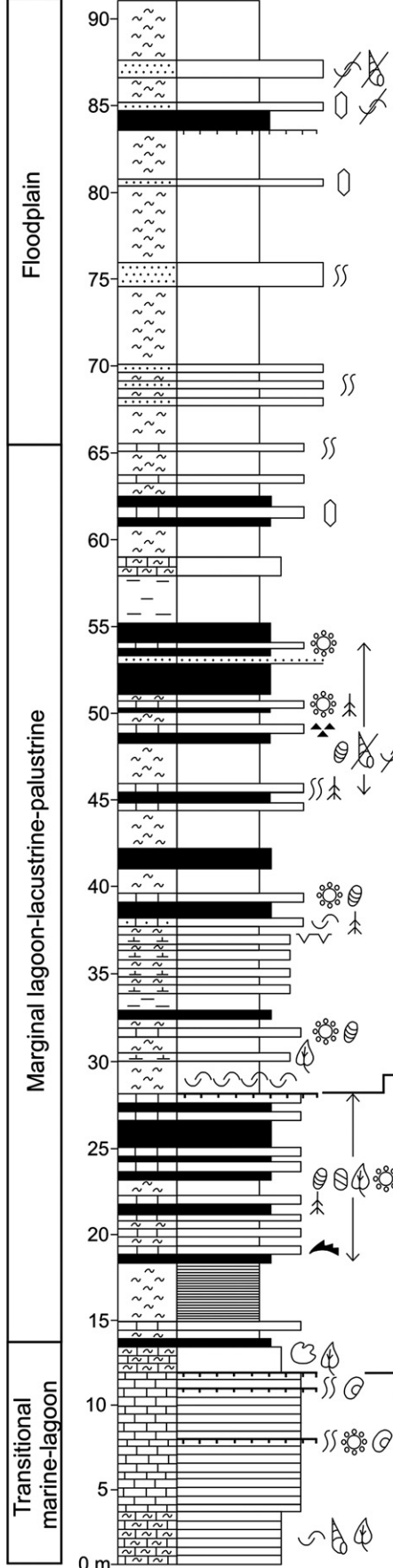
The evolutionary history of Arecaceae probably began in the Early Cretaceous, according to molecular data (Janssen and Bremer, 2004). The earliest unequivocal palm fossils are from the lower Upper Cretaceous (Harley, 2006). During the latest Cretaceous, palms were widely present in the Pantropical and part of the North Temperate Realms (Horrell, 1991). By this time, there is a range of variation within each organ category indicating that the family was already a well established lineage (Harley, 2006). Palm pollen grains, leaves and stems are particularly abundant in the fossil record. Records of fruits, rhizomes and roots are scarcer and rachillae, inflorescences or individual flowers are rare (Harley, 2006). Among the earliest megafossil palm remains there are leaves with long petiole bearing costapalmate lamina of *Sabalites longirhachis* (Unger) J. Kvaček et Herman. *Sabalites longirhachis* is known from the upper Santonian–Maastrichtian of southwestern, central and eastern Europe (Saporta and Marion, 1885; Tuzson, 1908, 1914; Kvaček and Herman, 2004; Marmi et al., 2008). The gross morphology and cuticular features of *S. longirhachis* were described by Kvaček and Herman (2004) and Marmi et al. (2008). However, other vegetative organs (e.g. stems and roots) as well as reproductive structures (e.g. flowers, seeds and fruits) of this fossil palm species were completely unknown so far.

In the Iberian Peninsula, Schulp and Brox (1999) mentioned for the first time “well-preserved palm leaves” at the “titanosaur megatrack” localities from the Early Maastrichtian of Fumanya

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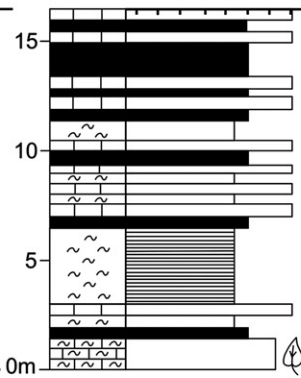
E-mail address: josep.marmi@icp.cat (J. Marmi).

B Composite synthetic section

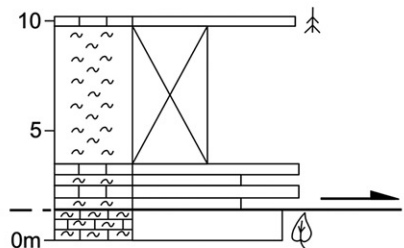


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|--|-------------------------|--|------------------------|--|------------------|
| | Sandstones | | Ostracodes | | Dinosaur icnites |
| | Calcarenitic limestones | | Oysters | | Bioturbation |
| | Limestones | | Bivalves | | Rootlet marks |
| | Marlstones | | Gastropods | | Mud crack |
| | Siltstones | | Charophyte thalli | | Black pebbles |
| | Lignite | | Brackish gyrogonites | | Pyrite nodules |
| | Marls | | Freshwater gyrogonites | | Hardground |
| | Claystones | | Plant remains | | Fault |
| | Covered (opencast mine) | | | | |

Fumanya Sud



Mina Esquirol



(Eastern Pyrenees). In the last years, prospections on the Fumanya localities have allowed for documenting tens of *Sabalites longirhachis* leaf adpressions, more than one hundred log casts, many of them attributed to palms, and probable palm stumps with adventitious rooting systems. Although organs are unattached, they co-occur in the same bedding surface or in directly overlying and sedimentologically related horizons. This allows us to propose, for the first time, a hypothesis for the reconstruction of a Mesozoic palm habit based on a taphonomic approach and, on the same basis, to provide evidence for the habitat of *S. longirhachis*.

2. Geological setting

The studied plant fossils are contained in the Tremp Formation (Mey et al., 1968), regionally called “Garumnian” (Leymerie, 1862), which is formed by transitional to non-marine rocks deposited in the South Pyrenean Basin mainly during the Maastrichtian–Paleocene, when the sea gradually retreated westwards (Mey et al., 1968). The initial stage of the evolution of the South Pyrenean foreland basin in the Late Cretaceous, resulted in the development of successive thrusts-sheets. As a consequence, the basin was segmented into uplift-bounded depocenters or synclines, which are, from East to West, Vallcebre, Coll de Nargó, Tremp and Ager (Oms et al., 2007). Although Garumnian palm megafossil remains occur in almost all these areas, they have been found better preserved in the Vallcebre syncline.

The Tremp Formation or Garumnian in the Vallcebre depocenter is up to 850 m thick (Vergés et al., 1994) and was divided by Rosell et al. (2001) into four lithological units, of which the transitional basal unit (Grey Garumnian) was the subject of our study. It is formed by a heterolithic succession, up to 100 m thick containing grey lutites and marls with intercalations of lignite, charophyte limestones and sandstones (Fig. 1). Micritic marlstones comprise the dominating lithology at the base and contain frequent dinosaur trackways at the top. These trackways are close to the Campanian–Maastrichtian boundary and fall within the C32n.1n magnetochron (ca. 71 Mya) as indicated by paleomagnetic data (Oms et al., 2007). Marlstones are covered by a succession of alternating organic marl, lignite and charophyte limestones that correspond to the base of the C31r magnetochron. Thus, the age of this part of the transitional basal unit is early Maastrichtian, according to Oms et al. (2007). Coquinas may be associated with these materials. A succession of variegated siltstone with dinosaur eggshell fragments represents the top of the Grey Garumnian. These materials were deposited in peritidal to supratidal environments, including brackish lagoons at the base, followed by well-developed wetlands with brackish marshes and freshwater lakes and ending with floodplains to the top.

3. Materials and methods

In the Vallcebre syncline, the fossil localities studied occur near the Fumanya Pass, close to the villages of Figols and Vallcebre and not far from the town of Berga, northern Catalonia (Fig. 1). A large structural surface, ca. 16,000 m² in size, containing most of the plant remains studied herein corresponds to the base of a relatively thick coal seam which was exploited in the opencast coal mines during the second third of the last century (Fig. 2).

Seventy-six partial to complete impressions and compressions of palm leaves have been observed at the base of the first coal seam from the Fumanya Sud (N42°10′50″ E01°47′42″) and Mina Esquirol (N42°11′8″ E01°47′51″) opencast mines (Figs. 1 and 2). They have been recorded by means of drawings and photographs. Thirty-three speci-

mens consist of fragments of leaf laminas with a few fused segments and in some cases are very damaged by surface weathering. Among the best preserved specimens, there are nineteen leaves with complete or almost complete laminas, of which twelve maintain their petioles in anatomic connection. One hundred and thirty casts of logs have been documented by means of pictures on the same palm-leaf bearing surface (Fig. 2). Three casts preserve details of cortical structures. Some brush-like rooting systems appear at the top of a freshwater charophyte limestone bed, about 9 m above the marly limestone surface with palm leaves and logs of Mina Esquirol (Figs. 1 and 3). Resin replicas of leaves are stored in the collection of the Institut Català de Paleontologia under the codes IPS-41681 and IPS-41682.

4. Description of fossil organs related to the *Sabalites longirhachis*-bearing palm

4.1. Leaves

Leaves are costapalmate and ovalo-lanceolate symmetrical megaphylls (Plate 1). They were highly variable in size and measured up to 125 cm long (Table 1). The most complete leaf laminas (Plate 1, 1, 2) are 43–75 cm long and 10–41 cm wide. Laminas are longer than wider, having a length/width ratio from 1:1 to 4:1. The base angle of leaf lamina is acute (lower than 90°, see Table 1). The base and the apex shapes are convex. The leaf lamina is composed of approximately 25–30 pairs of opposite, induplicate and fused segments that are nearly linear and generally become wider in their apical part. Segment lengths range 16–41 cm, while basal widths are 0.15–1.6 cm. The segments merge into the costa at acute angles (11.3°–53.4°, see Table 1). The basal borders of segments are slightly decurrent on the costa. The costa is long and thick, and penetrates up to roughly the middle of lamina. In the best preserved specimens, narrow longitudinal grooves are observed on surfaces of costas and petioles (Plate 1, 3). For each segment, the mid-vein and four parallel lower-order veins can be distinguished (Plate 1, 4, 5). The smallest vein widths range 0.02–0.2 mm. The petioles are 44–53 cm long. The ratio between the lamina and petiole lengths is 0.8 for the most complete leaf (IPS-41682). Some petioles preserve circular to elliptic marks of 0.5–0.7 cm in their surface (Plate 1, 3). These marks are interpreted as bases of spines.

Leaves studied herein show all macroscopic characters reported by Kvaček and Herman (2004) in the diagnosis of *Sabalites longirhachis* from the lower Campanian of the Grünbach Formation (Austria) (i.e. leaves costapalmate, induplicate, lanceolate; thick long costa; leaf segments fused, nearly linear, slightly wider towards the apex, each of them V-shaped in transversal section and emerging at an acute angle from the costa). Kvaček and Herman (2004) introduced venation pattern and cuticle characters in the diagnosis of *S. longirhachis* leaves. However, cuticle characters were not preserved in the available Fumanya specimens, which led Marmi et al. (2008) to assign them to *Sabalites* cf. *longirhachis*. In the present study, the venation is reported for leaves from Fumanya showing a pattern similar to *S. longirhachis* from Austria (i.e. mid-vein and four parallel vein orders for each segment). According to Read and Hickey (1972), the genus *Sabalites* Saporta includes costapalmate palm leaves. *Sabalites* spp. from the Late Cretaceous and Paleogene of North America—*S. carolinensis* Berry, *S. tenuirhachis* (Lesquereux) Read et Hickey, *S. ungeri* (Lesquereux) Dorf, *S. rugosa* (Knowlton) Read et Hickey, *S. powellii* (Newberry) Berry, *S. leei* (Knowlton) Read et Hickey, *S. inquerenda* (Knowlton) Read et Hickey, *S. grandifolia* (Newberry) Read et Hickey, and *S. grayanus* Lesquereux—showed clear differences in costa lengths and shapes and segment dissection compared to *S. longirhachis* (Read and Hickey, 1972; Kvaček and Herman, 2004 for a review). Thus, palm leaves from the lower



Fig. 2. Fumanya Sud open cast mine showing the ca. 10,000 m² surface bearing *S. longirhachis* leaves and logs and titanosaur trackways, which corresponds to the base of the first coal seam. Palm logs are indicated as black lines and leaves as racket-like shapes showing their original orientations.

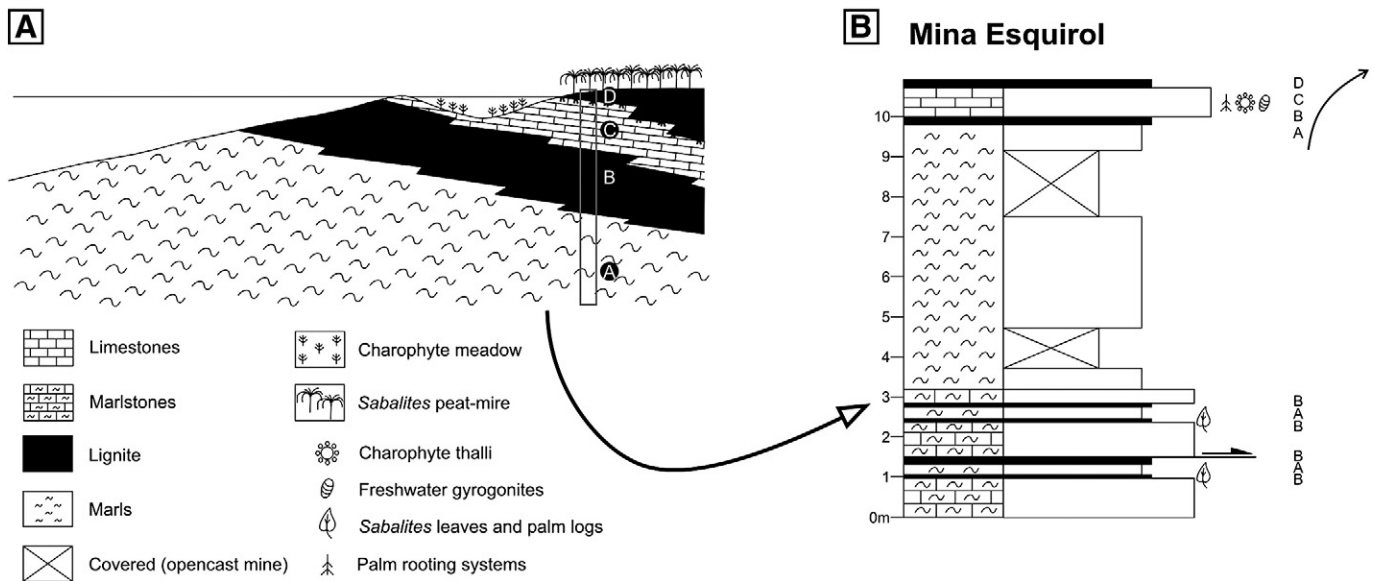


Fig. 3. Facies analysis and paleoenvironmental reconstruction of the Mina Esquirol locality showing that the different layers with palm remains belong to laterally equivalent facies. (A) Paleoenvironmental diagram showing vertical development of a sedimentary cycle. (B) Detailed stratigraphic section of Mina Esquirol, with indication of facies represented in (A).

Maastrichtian of Fumanya are identified as *S. longirhachis* based on gross morphology and venation features.

4.2. Stems

Logs are preserved as non-branched cylindrical impressions lacking internal anatomical details (Plate II). Dimensions of nine logs range 2.5–13.8 m long and 16–22 cm in maximum width. A few logs consist of casts showing structures on their surfaces (Plate II, 1, 3, 4). These external structures are ellipsoidal reliefs of 1.0–1.8 cm long and 0.3–0.6 cm wide arranged in parallel, longitudinal rows compared to the log axis. Narrow, longitudinal grooves and circular to elliptic holes are also observable (Plate II, 3, 4). In some cases, these structures are covered by a 1–2 cm thick coaly lamina, sometimes also showing narrow longitudinal grooves.

Palm stems with internal anatomy preserved are included in the genus *Palmoxydon* Schenk and they are abundant in the fossil record (Harley, 2006). The diagnoses of this genus and its species are based on characteristics of fibrous and fibrovascular bundles, presence or absence of stigmata and presence of leaf traces (e.g. Trivedi and Verma, 1971; Nambudiri and Tidwell, 1998). Unfortunately, these structures are not preserved in logs from Fumanya Sud and Mina Esquirol. Nevertheless, even lacking the preservation palm synapo-

morphies, these logs show external features typical of living palms (i.e. they are straight, slender and of nearly uniform width, or tapered upwards). There is no evidence of spines or persistent bases of leaves suggesting that the original stems were smooth with only narrow grooves (Plate II, 3). The log surfaces showing ellipsoidal structures and holes are attributed to basal parts of the palm stems bearing adventitious roots (see Plate II, 4; Plate IV). This feature can be observed in some living palms (e.g. *Phoenix* spp.) in which adventitious roots may be visible at the base of the tree trunk above the soil surface (see Plate IV, 1 and Jones, 2007).

4.3. Stumps and roots

Rooting systems were only found in the Mina Esquirol outcrop (Plate III). The most complete specimen consists of an internal cast of a brush-like rooting system with a central circular mark of about 19 cm in diameter from which about sixteen rectilinear or slightly curved rays of 0.9–1.3 cm in diameter emerge, forming a conical structure (Plate III, 3, 4). The maximum diameter of the whole structure is almost 140 cm. A number of additional stumps are preserved in the same layer as adpressions. They measure between 20 and 21 cm in diameter and show remains of coaly adventitious roots radiating from a central depression (Plate III, 1, 2).

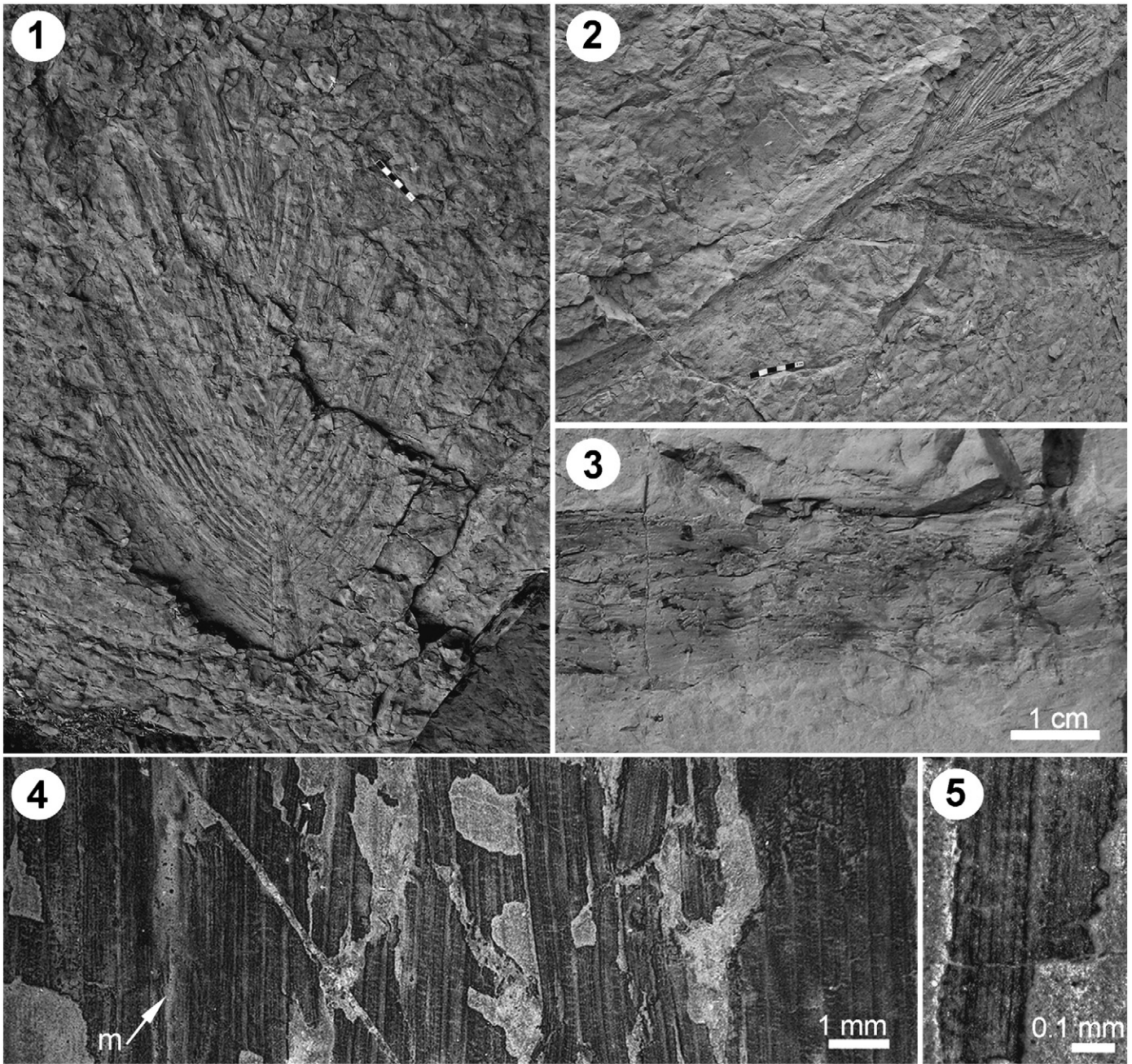


Plate I. *Sabalites longirhachis* leaves from the Fumanya opencast mines.

1. Complete lamina. Scale bar = 5 cm.
2. Complete leaf bearing a long petiole. Scale bar = 5 cm.
3. Detail of a petiole with circular marks that might be spine bases.
4. Detail of general pattern of venation (m = mid-vein).
5. Detail of thinnest veins.

These fossils are preserved as adpressions and internal casts without anatomical details. However, they can be interpreted as palm rooting systems based on their great similarity in shape and size to those of living palms (see Plate IV). The circular central mark may correspond to the palm stump and falls within the diameter range of logs reported from the Fumanya localities. Radiating structures are related to palm roots (see Plate III, 3, 4; Plate IV, 3). Adventitious roots at the bases of logs and preserved rooting systems range 0.3–1.3 cm wide, which fall within the ranges of root widths measured in living tree palms: *Phoenix canariensis* Chabaud (0.5–1 cm), *Phoenix dactylifera* Linnaeus (0.4–0.9 cm), and *Washingtonia* sp. (0.5–1.3 cm).

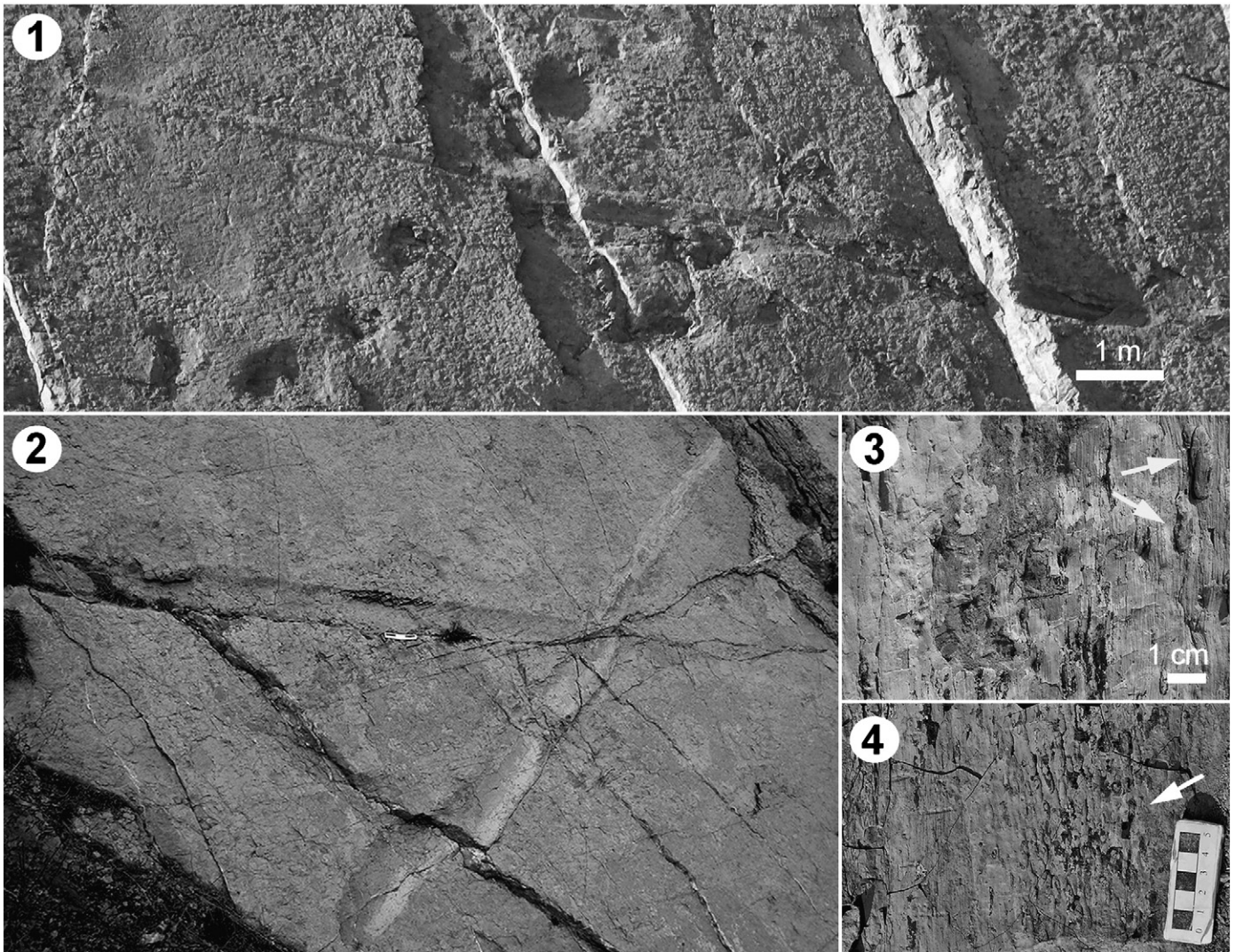
Other vascular plants identified in the Fumanya opencast mines are large amounts of conifer leafy axes attributed to *Frenelopsis* (Schenk) Watson, a fragment of pandan-like leaf (Pandanaceae) and a probable cycadalean leaf along with large number of angiosperm seeds (Villalba-Breva et al., submitted for publication). Rooting systems of these plants are different to palms in many features. Conifers and most angiosperms usually have axonomorph rooting systems. Cycadalean roots consist of a taproot with small, branched lateral roots arranged in two rows and reaching great depths (Singh, 2006). Pandanaceous trees like living *Pandanus* Parkinson produce many thick stilt roots near the trunk base to provide support (Dahlgren et al., 1985).

Table 1

Measures, in centimetres, of costapalmate leaves from the Maastrichtian of Fumanya.

	IPS-41681	IPS-41682	V-FUM27	VFUM40	VFUM86	VFUM137
Total length	125.5 ^a	96.0	?	?	77.2 ^a	99.8
Laminar size ^b	2126.5	281.2	?	?	400.1	486.5
Lamina length	75.0	43.0	?	?	26.7	51.5
Lamina width	41.0	10.0	?	?	20.3	11.6
Base angle ^c	84.4	50.9	?	?	?	?
Costa length	30.0	15.0	14.6	8.4	11.8	29.6
Costa width	3.6	2.0	2.2	2.3	?	1.8
Number segments	56	47	?	?	?	?
Segment length ^d	39.2	18.7	?	?	20.1	34.8
Segment width range	0.53–1.56	0.21–0.63	0.16–0.96	0.15–0.66	0.30–0.77	0.17–0.80
Cos-seg angle range	30.5–53.4	14.7–33.4	22.9–34.6	37.3–47.0	24.4–43.4	11.3–24.1
Petiole length	?	53.0	?	44.0	?	48.2

? Missing data.

^a Inferred values.^b Measures in square centimeters (cm²).^c Base angle is the angle from the vertex to the points where a line perpendicular to the costa (at 0.25 lamina length from the base) intersects the margin. The vertex of the angle lies in the centre of the base of costa at the point where the basal most laminar tissue touches the petiole.^d Mean value.**Plate II.** Logs attributed to *Sabalites longirhachis* palms from the Fumanya opencast mines.

1. Large sized log of c. 14 m.
2. Two crossed impressions of logs. Scale bar = 15 cm.
3. Detail of the surface of the basal part of (1) showing narrow longitudinal grooves and some adventitious roots (arrows). Scale bar = 1 cm.
4. Detail of the surface of a log cast showing marks of adventitious roots (arrows). Scale bar = 5 cm.

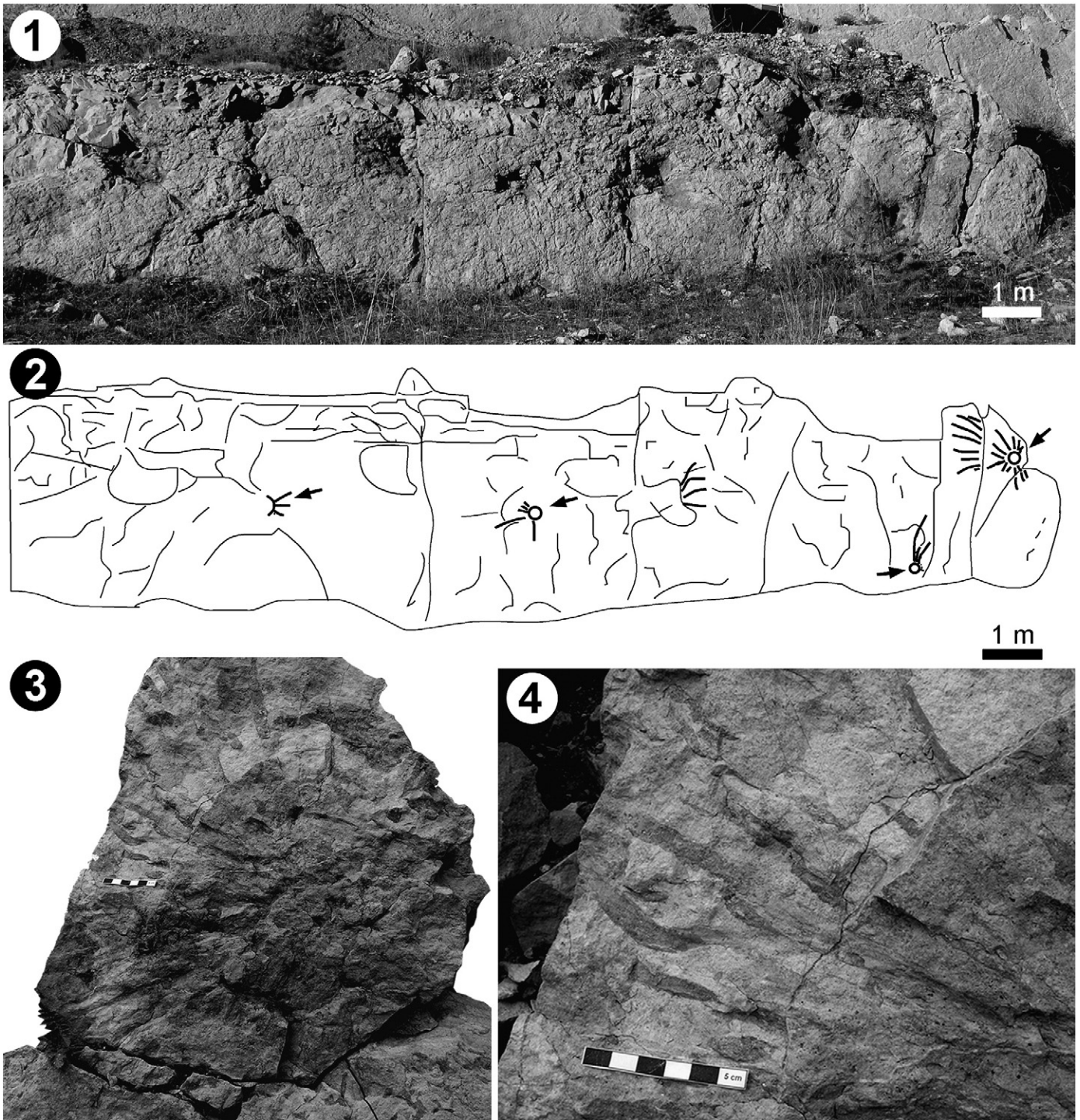


Plate III. Stumps attributed to *Sabalites longirhachis* palms from the Mina Esquirol locality.

1. Charophyte limestone surface with several palm stumps.
2. Scheme of the rock surface with stumps indicated by arrows.
3. Stem base with adventitious rooting system. Scale bar = 5 cm.
4. Detail of adventitious roots. Scale bar = 5 cm.

5. Sedimentology and taphonomy

From the sedimentological point of view the succession with palm remains at Fumanya is composed of alternating organic marlstones, coal and charophyte limestones. Facies analysis suggests that these lithologies are organized in small sedimentary cycles (Villalba-Breva et al., submitted for publication), representing a gradual shift from brackish to freshwater depositional environments. Thus, a basal

brackish term formed by the marls is succeeded by coals resulting from the parautochthonous accumulation of plant remains, which is finally overtopped by a freshwater term with charophyte limestones and autochthonous coals with rootlet casts representing limnic peat mires around a lake.

Casts and adpressions of palm leaves and associated logs are randomly distributed and oriented on the bedding surface of the first coal seam (Figs. 2 and 3). Most leaves include entire laminas bearing

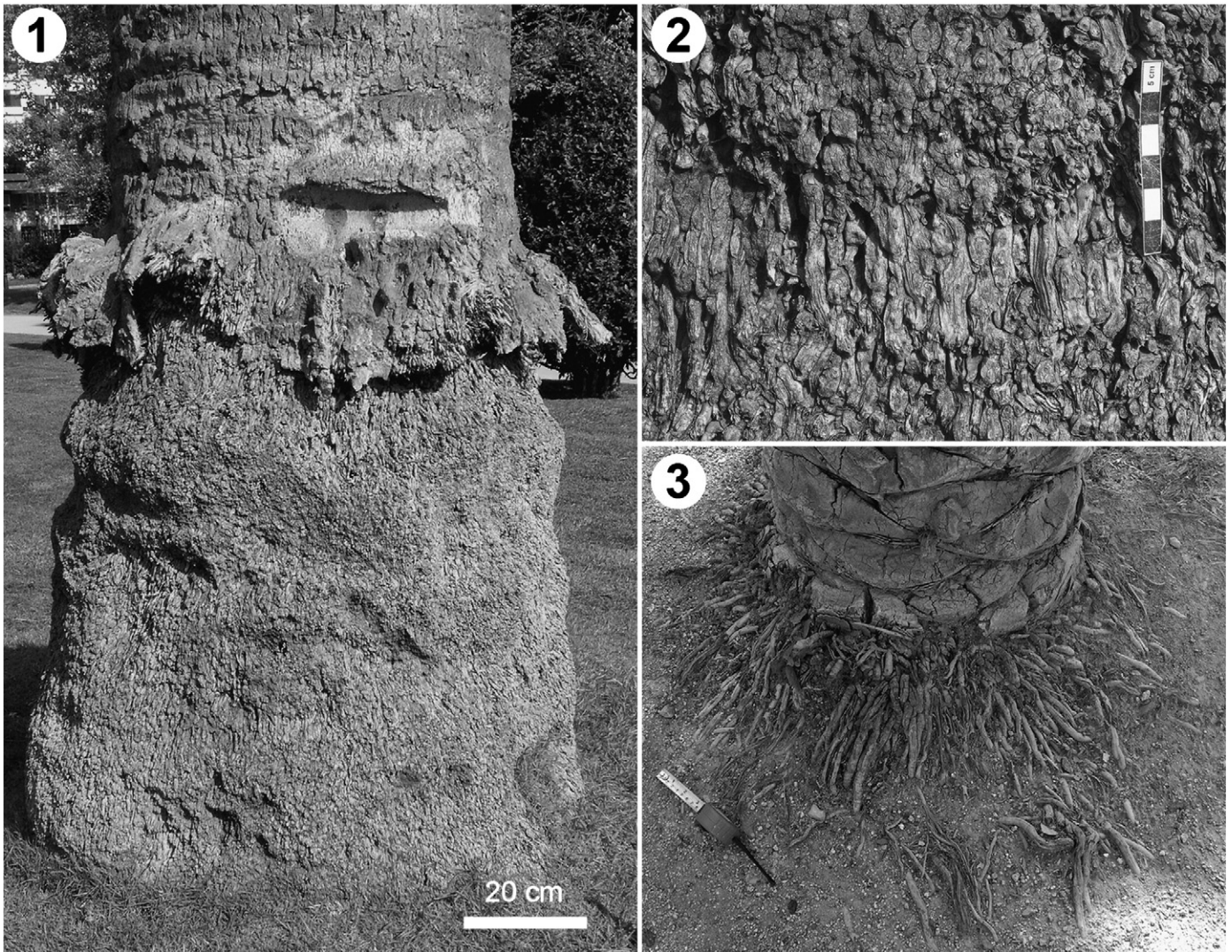


Plate IV. Tree bases of living palms.

1. Base of the stem of living *Phoenix canariensis* bearing adventitious roots.
2. Detail of adventitious roots of *Phoenix canariensis*. Scale bar = 5 cm.
3. Stump and roots of a living *Phoenix* sp. Scale bar = 10 cm.

almost complete petioles, which suggest a traumatic production and short transport before deposition at the bottom of the water table (Martín-Closas and Gomez, 2004). Also, laminas show fans opened out or folded down, suggesting that leaves were torn from the parental plants at different ontogenetic stages, i.e. when still green or being already marcescent respectively. All these data, along with the lack of rootlet marks at the base of the coal suggest that leaves accumulated as parautochthonous remains.

Logs are relatively long and do not show evidence of rounding at the ends. Some superficial characters, such as the marks of adventitious roots, have been preserved in the adpressions available, indicating short transport and absence of decay before deposition in the mudflat-edge bottom. However, the absence of rooting marks at the base of the first coal seam in Fumanya indicates that logs, like the leaves, were also parautochthonous.

Evidence of in situ palm growth comes from the top of an overlying charophyte limestone layer. The detailed stratigraphic succession shows the lignite layer with palm leaves and logs at its base, covered by up to 8 m of brackish marls and 1 m of the freshwater charophyte limestones with the palm rooting systems at the top (Fig. 3). These rooting systems

depart from a thin coal layer covering the charophyte limestones. Facies analysis suggests that this coal represents small peat mire formed at the lakeshores of the charophyte lake. Also, according to sedimentological evidence, the palm rooting systems found at the top of the charophyte limestones and the coal layer bearing the palm leaves and logs in its base, may represent two laterally equivalent facies of the same sedimentary environment as shown diagrammatically in Fig. 3A.

The whole dataset obtained from Fumanya indicates that *S. longirhachis* palms were growing autochthonous in small peat mires at the lakeshores of freshwater alkaline lakes, where lime mud was accumulated by important meadows of charophytes. The aerial remains of these palms, including complete leaves and logs, were episodically torn out or uprooted by storms or strong winds and transported by flotation across the freshwater wetland, seawards. Finally they were deposited and preserved at the bottom of the mudflat edge, where a thick layer of parautochthonous peat was being accumulated in an anoxic bottom, thus preventing the decay. The detached palm organs may also have deposited into the freshwater lake but the oxic conditions and the active growth of charophyte meadows hindered their preservation there.

Although the three available organs attributed to palms (i.e. leaves, logs and rooting systems) found at Fumanya, were detached from each other, both morphological and taphonomic evidence suggest that they belong to the same plant species. From a morphological point of view, the three organs are in the same order of size and both logs and rooting systems are compatible in showing adventitious rootlets. Taphonomic evidence suggests that the three organs were deposited in laterally equivalent facies and came from a single site of growth. These conclusions lead us to propose a reconstruction of the habit of the plant on the basis of the remains described. We propose to use the term '*Sabalites longirhachis*-bearing plant' for the plant reconstructed here.

6. Discussion

6.1. Reconstruction of *Sabalites longirhachis*-bearing palm and systematic implications

According to the taphonomic hypothesis presented above, we suggest that *Sabalites longirhachis* were slender palm trees of up to ca. 14 m tall. Measurements of logs and leaves suggest that the *S. longirhachis*-bearing plant probably displayed heights similar to the living cabbage palm *Sabal palmetto* (Walter) Loddiges. Stems of the *S. longirhachis*-bearing plant were straight, a few decimetres thick, and tapered upwards (Plate V). Their surfaces were probably smooth, without marks of persistent bases of leaves. Adventitious roots covered the basal part of the tree trunk. The stumps were up to ca. 22 cm wide and straight roots emerged radially from their surfaces making a cone of up to ca. 150 cm in diameter. Leaves up to ca. 130 cm long, costapalmate and with long and probably armed petioles were borne at the top of the tree trunk in a crown, like in most living palms (Plate V). The presence of folded leaves, considered here as marcescent, suggests that the parental palm retained the leaves in the crown bottom, partially covering the upper part of the tree trunk. Tuzson (1914, pl. XVIII) reported a reconstruction of the fossil palm *Juranyia hemiflabellata* Tuzson from the Maastrichtian of Rusca Montana (Romania). Recently, Kvaček and Herman (2004) considered this species a synonym of *S. longirhachis*. However, in the Tuzson's paper only a fragment of a large costapalmate leaf, a probable palm fruit and a partial inflorescence were represented (Tuzson, 1914, pl. XVII).

Field recognitions of living palm taxa are based on leaf morphology and inflorescence, flower and fruit features (Sitte et al., 2003; Dransfield et al., 2008). Fossil leaves are the most abundant organ of *Sabalites longirhachis* available. However, palm leaves show a high degree of homoplasy in gross morphology and anatomy, especially among major clades (Horn et al., 2009). This and the absence of reproductive characters in *S. longirhachis* fossil remains collected make difficult to infer any phylogenetic relationships with living palm subfamilies. Kvaček and Herman (2004) suggested that *S. longirhachis* represents the basal form from which both pinnate and palmate leaves evolved. The earliest costapalmate leaves are reported from the late Coniacian–Santonian of South Carolina and New Jersey (North America), while the earliest pinnate leaves are reported from the lower Campanian of northern Montana (North America) (see review by Harley, 2006 and references therein). In contrast, molecular phylogenies suggest the subfamilies Calamoideae and Nypoideae with pinnate or bipinnate leaves as basal groups within the Arecaceae, while palmate palms (many of them belonging to Coryphoideae) may be derived (Asmussen et al., 2006). Hence, Cretaceous palms bearing costapalmate leaves, such as *S. longirhachis*, may represent an extinct, intermediate lineage between palms with pinnate and palmate leaves.

6.2. Paleocology of the *Sabalites longirhachis*-bearing plant

Combined taphonomic and sedimentological analyses suggest that *Sabalites longirhachis* palms from Fumanya were growing in the

lakeshores of freshwater charophyte lakes, where small peat mires occurred. The outcropping structural surface of charophyte limestones with palm rooting systems is of 61.7 m². This area contains at least four well-preserved rooting systems, with a couple of other possible stump marks being present but difficult to document with precision. This gives a minimum density of one palm individual per



Plate V. Hypothetic reconstruction of *Sabalites longirhachis* palm trees based on taphonomic data from Fumanya.

15.4 m² and up to one plant each 10 m² as a maximum density. Accordingly, *S. longirhachis* palms might grow at very high densities, similar to densities of living palms in swampy areas, such as the *Nypa* Steck mangroves, where monotypic stands of palms completely cover the ground surface. However, the palm stands described were not similar to extant *Nypa* swamps since they were growing in a freshwater habitat; also they did not form monotypic stands. Villalba-Breva et al. (submitted for publication) and Riera et al. (2010) reported abundant parautochthonous remains of *Frenelopsis* sp. associated with the *S. longirhachis* organ remains described in detail herein. The inferred *Frenelopsis* peat mire vegetation was surely much more dense and significant in term of biomass than the palm stands. Isolated leaf fragments probably belonging to a cycadalean and a pandan-like plant and monotonous assemblages of unidentified angiosperm seeds were found in the same horizon bearing *Sabalites* and *Frenelopsis* remains. However, these plant remains probably were transported from large distances and their source plants grew far away from the habitat of *S. longirhachis* (Villalba-Breva et al., submitted for publication).

Fossil data indicate that palms first occurred in swamps, apparently starting a progressive replacement of conifers that inhabited these environments (Coiffard and Gomez, 2010). Lower energy cost for stem development might allow for a faster growth or better seed production in palms than conifers. Moreover, large palm leaves may shade out woody seedlings preventing their regeneration, as it has been observed in living palms (Denslow et al., 1991). The results documented here indicate that *S. longirhachis* might inhabit wetlands close to the cheirolepidiaceus conifer *Frenelopsis* during the Maastrichtian. Accordingly, the turnover of conifers by palms in swampy environments was still in course at the earliest Maastrichtian at least in the Iberian Peninsula. *Sabalites longirhachis* palms probably occupied during the Late Cretaceous a larger range of habitats. Hence, data from the Campanian Grünbach flora (Austria) suggest that *S. longirhachis* also dominated juglandaceous and palm wetland forests and probably lived in swamp/semiaquatic communities of *Pandanites trinervis* (Ettingshausen) J. Kvaček and Herman (Pandanaeae) in a large deltaic lowland (Herman and Kvaček, 2007, 2010). However, *S. longirhachis* is a morphotaxon and might be represented by more than one natural species. Thus, ecological inferences at a regional level should be taken with caution.

7. Conclusions

Although leaves, stems, inflorescences, flowers, fruits, seeds and pollen grains of palms are unequivocally present since the Late Cretaceous (Harley, 2006), a few examples of association of palm organs in the same assemblage were reported in the literature. Palm fruits and fronds from the upper lower Eocene of Tasmania were attributed to *Nypa* based on the presence of these organs and pollen grains intermixed in the same horizon (Pole and Macphail, 1996). *Nypa* fruits with remains of spathes were documented in the Eocene of the Ebro Basin (northeastern Iberian Peninsula) by Biosca and Via (1987) and the isolated fruits were recorded also from the Eocene London Clay (Collinson, 1983). Other noteworthy examples are five stems attached with petiole bases and roots and associated with isolated petioles and laminas from the middle Eocene Princeton chert (British Columbia, Canada) (Erwin and Stockey, 1991), and leaves connected to petioles and stems from the Miocene of the Lower Rhenish Plain (Germany) (Van der Burgh, 1984). The association of organs described herein is older than these examples. Moreover, it provides for the first time taphonomic evidence to reconstruct a palm tree habit in the earliest stage of the evolution of the family Arecaceae.

Data from Fumanya localities also provide evidence for physiological, anatomical and ecological adaptations of fossil palms in the earliest evolutionary history of this family. There is indirect evidence for keeping marcescent leaves at the top of stems, as suggests laminas with fans folded down. Whole leaf persisting attached on the stem after death is a typical pattern of some living species such as *Washingtonia filifera* (Lindley) Wendland. Also, fossil palms such as *Sabalites longirhachis* had already presented adventitious roots. These types of roots have high capacity to absorb water and minerals and allow adaptation to unstable substrates in habitats frequently subject to flooding such as wetlands (Kozłowski, 1984). More than two-thirds of living palms inhabit rainforests, many different species coexisting together in small areas. In open habitats, they form extensive colonies usually of a single species (Jones, 2007). Some species inhabiting open habitats prefer wetlands such as marshes, swamps, permanent stream margins, lakes and lagoons, growing in dense colonies or thickets (Jones, 2007). During the Maastrichtian palms were well represented in the tropical everwet and tropical seasonal biomes (Horrell, 1991; Willis and McElwain, 2002). This suggests that early palms already

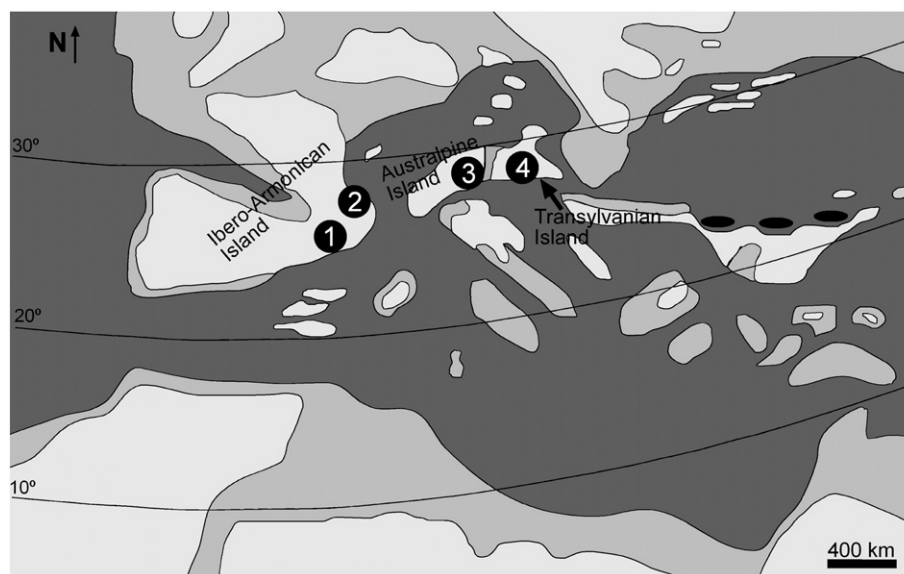


Fig. 4. Paleogeographic map of the Western Tethys during the latest Cretaceous based on Dercourt et al. (2000) and Benton et al. (2010). Numbers indicate the localities known with *S. longirhachis* leaf remains: 1, Southern Pyrenees (Maastrichtian); 2, Fuveau (upper Santonian–Campanian) and Barjols (Campanian–Maastrichtian) (both in the Ibero-Armonian island); 3, Grünbach (lower Campanian) (in the Australpinae island); 4, Rusca Montana (Maastrichtian) (in the Transylvanian island). Light colour indicates emerged lands, light grey is shallow marine, dark grey is oceanic basins and black means volcanics.

inhabited rainforests as well as open habitats. *Sabalites* palms from Fumanya fit well with the open habitat ecological pattern of living palms.

Sabalites longirhachis was probably widespread through low to moderate diversity plant communities of wetlands from the Late Cretaceous of southwestern, central and eastern Europe (Fig. 4). Emerged lands corresponding to the present-day northeastern Spain and southern France margins were far and isolated by the Tethys Sea from those corresponding to Austria and Romania (Tyson and Funnell, 1987; Dercourt et al., 2000). The fruit type of *S. longirhachis* is unknown, as is its dispersal mechanism. Nowadays, palm fruits are usually fleshy and dispersed by flotation in sea water or, more frequently, by a wide variety of birds and mammals.

Sabalites species from the Late Cretaceous and Paleogene of North America clearly differ in gross morphology from *S. longirhachis*. Leaves of these species have partially dissected segments and/or shorter costas than *S. longirhachis* (reviewed in Kvaček and Herman, 2004). This suggests that the geographical range of *S. longirhachis* was restricted to the south European Cretaceous archipelago and that it became extinct at or just before the K/T boundary.

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