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First record of the mangrove palm *Nypa* from the northeastern Ebro Basin, Spain: with taphonomic criteria to evaluate the drifting duration

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┤ A B S T R A C T ├

Fossil fruits pertaining to the mangrove palm genus *Nypa* STECK, (Arecaceae, Arecales) were collected from a new plant-bearing assemblage in the Arguis Formation (Fm.), northeastern Ebro Basin (Arguis, Huesca Province, Spain). This formation is Bartonian to early Priabonian in age and comprises pro-delta and carbonate platform deposits. The new assemblage consists of nine specimens of fossil *Nypa* fruits and one monocotyledon leaf fragment. Over half of these fossil fruits are nearly-complete (*i.e.* with preserved mesocarps) while the other represent endocarps. From the point of view of morphology and size they resemble other European records of this genus. The type of remain preserved (fruits or endocarps), presence of abrasion, *Teredo* borings and sedimentary facies provide criteria to infer contrasting lengths of transport (drifting). However, they indicate in all cases that these fossil fruits were afloat in seawater for a considerable time. The discovery of *Nypa* fruits suggests a tropical-subtropical climate in the area, as well as the presence of a coastal environment and littoral forests during deposition. This interpretation corroborates previous findings from the nearby Eocene outcrops of the Catalan Central Depression (Eastern Pyrenees range).

KEYWORDS | Mangrove. South-Pyrenees External Sierras. Palm. Iberian Peninsula. Arecaceae.

INTRODUCTION

Fossil occurrences of the mangrove palm genus *Nypa* STECK (Harley, 2006) have deep significance for paleoecological, paleoclimatic and paleogeographical reconstructions, and play an important role in regional correlations (*e.g.*, Gee, 1990). The fossil remains of *Nypa* have been well documented at many localities worldwide, in Europe (Tralau, 1964; Biosca and Via, 1988); in Asian-

Pacific regions (Tralau, 1964; Pole and Macphail, 1996; Mehrotra *et al.*, 2007); in Africa (Tralau, 1964; El-Soughier *et al.*, 2011); and on the American continents (Tralau, 1964; Westgate and Gee, 1990; Gee, 2001; Gómez-Navarro *et al.*, 2009). The oldest fossil evidence of *Nypa* genus consists of pollen, originating from the Campanian (Late Cretaceous), discovered in what is presently Egypt (Gee, 2001). This genus diversified at the global level during the early-middle Eocene (Krutzsch,

1989). However, at present, this genus is represented by just a single species: *Nypa fruticans* Wurmberg. The living species exists across a range of environments in the tropical Indo-West Pacific region; from India, through Asia to northern Australia and the western Pacific Islands (Teo *et al.*, 2010).

In Spain, the fossil record of *Nypa* is only well documented in the Eocene. The first specimens attributed to *Nypa* fruits were described by Álvarez-Ramis (1982). These fossil remains appeared in the Bartonian of Catalonia (Catalan Central Depression, northeastern Spain) and were described as *Nipadites burtini* (Álvarez-Ramis, 1982). Five years later, Biosca and Via (1988) carried out an additional study on *Nypa* plant remains from the same area and age. In both cases, the authors argued for the past presence of paleomangroves based mainly on this fossil evidence. Later Cavagnetto and Anadón (1995) provided evidence of *Nypa* pollen along with pollen from other mangrove plants from these localities. However, the oldest Spanish records of *Nypa* pollen come from the Maastrichtian in the Eastern Pyrenees (Villalba-Breva *et al.*, 2012).

Here, we describe new material identifiable as the fossil fruits of the genus *Nypa*, family Arecaceae, from the Arguis Fm. (Mangin, 1959-60), Prepyrenean External Sierras. This paper aims to extend the present knowledge on the fossil remains of *Nypa* from the Iberian Peninsula. It also contributes to a more comprehensive understanding of the taphonomic processes that affected them, helping in the reconstruction of the coastal plant communities in the Pyrenees during the mid-Paleogene.

LOCATION AND STRATIGRAPHICAL SETTING

The fossil plant-bearing locality is near the town of Arguis, in the northern part of the Huesca Province (Figs.1; 2). This mountainous area forms a natural boundary between the Jaca Basin and the Ebro Basin (Fig. 1). The stratigraphic record of the External Sierras consists of a Mesozoic sequence covered by a thick Paleogene/Neogene sequence (Vidal-Royo *et al.*, 2013); the outcrop is located within the thick Paleogene sequence (Fig. 3). The Paleogene/Neogene sequence is composed of continental sandstones, siltstones, and lacustrine limestones of the Cretaceous-Paleocene transition (Tremp Fm.), shallow marine platform limestones (Guara Fm. of Lutetian age), shallow marine and transitional marls, limestones, and deltaic sandstones of the Arguis and Belsué-Atarés fms. (Bartonian to middle Priabonian), as well as the fluvial clays, sandstones, and conglomerates of the Campodarbe Fm. (middle Priabonian to middle

Oligocene) (see Vidal-Royo *et al.*, 2013, and references therein; Cohen *et al.*, 2013).

The Arguis Fm. consists mainly of bluish-grey marls and interbedded limestones. Thickness is variable (100-1200m), around 1000m in the Arguis syncline (Arguis area) and represents the Bartonian-early Priabonian time interval based on biostratigraphic and magnetostratigraphic data (Millán *et al.*, 1994; Canudo *et al.*, 1991; Pueyo *et al.*, 2002; Cohen *et al.*, 2013). This formation has been described as a shallow-marine, mixed siliciclastic-carbonate setting; nevertheless, a deltaic component can also be detected and the facies also show significant fluvial influence, including the effects of storms and tides (Castelltort *et al.*, 2003).

Millán *et al.* (1994) distinguished three depositional sequences (DS I to DS III) in the Arguis Fm. (Figs. 2; 3). Each depositional sequence, as a whole, consists of two stacked units: the lower unit is formed by marls, whereas the upper unit mainly comprises shallow siliciclastic and carbonate deposits. According to Millán *et al.* (1994), in the Arguis syncline, the DS II in its lower part, consists mainly of marls bearing rare fossils and bioturbation. Interlayers of bioclastic and siliciclastic graded beds occur in the upper part of the sequence which form thick carbonate successions associated with wackestones with burrows. The depositional setting of this sequence is interpreted as a low-angle carbonate ramp. The marls were deposited in a relatively deep marine environment, in the outer part of the ramp below storm wave base level. The carbonate units are interpreted as storm deposits which were deposited in the middle and inner parts of the ramp (Millán *et al.*, 1994). The DS II defined by Millán *et al.* (1994) corresponds to the Facies Association 2 (FA2) of Castelltort *et al.* (2003). The paleoenvironment of FA2 is interpreted by the latter authors as prodelta to distal delta front-lower to distal/median upper offshore, and its paleobathymetry has been estimated at 30-80m.

The fossil plant remains were found in the middle part of DS II, within the shallow-marine siliciclastic and carbonate-marly deposits, very close to a unit that was dated as 39.30Myr (*i.e.* Bartonian) based on paleomagnetic data by Pueyo *et al.* (2002).

MATERIAL AND METHODS

The fossil remains of nine fruits and one leaf fragment are studied and described below. Observations are based on the external morphological characteristics of the fossils. Each item was cleaned with the help of a fine chisel and hammer and then examined with a Nikon SMZ-2 stereomicroscope. A calliper and a ruler
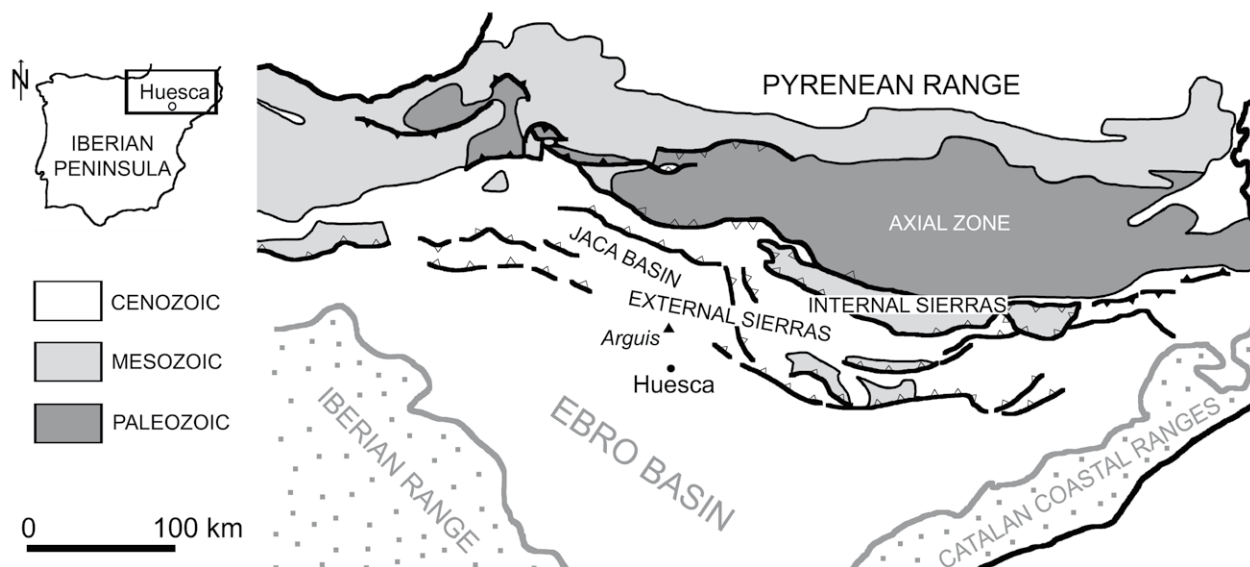
FIGURE 1. Map of the general geological setting of the Arguis Casa Migalón site (arrow) in the Huesca Province in northeastern Spain. Modified from Luzón (2005).

were used to measure the dimensions of the fossils. All specimens are housed in the Museo Aragonés de Paleontología (Teruel, Spain). Photographs were taken with a Nikon D-90 camera and an AF-S Micro Nikon 60mm macro lens.

RESULTS

Systematic paleobotany

Angiosperms

Order Arecales BROMHEAD
Family Arecaceae BERCHTOLD & J. PRESL
Subfamily Nypoideae GRIFFITH
GENUS ***Nypa*** STECK
Nypa burtinii (BRONGNIART, 1828) Ettingshausen, 1879 (Fig. 4A–G, I)
Synonymy
1982 *Nipadites burtini* Brongniart - Álvarez-Ramis, p.7, figs.1–3.
1988 *Nypa burtini* (BRONGNIART, 1828) - Biosca and Via, p.17, pl. I, figs.1–6, p. 19, pl. II, figs.1-3, p. 21, pl. III, figs.1–3.

Material studied. ARCM-1-1; ARCM-2-1; ARCM-3-1; ARCM-4-1; ARCM-5-1; ARCM-6-1; ARCM-7-1; ARCM-8-1A; ARCM-8-1B; ARCM-8-1C; ARCM-8-2; ARCM-9-1.

Description. Fruits partly preserved, laterally compressed; ovoid to planoconvex in shape; maximum preserved length 90–140mm, width 45–90mm, and thickness 20–45mm; exocarp and mesocarp poorly visible or not preserved; the upper part of the fruit is convex, or ends in an umbo of triangular shape, which is somewhat truncated and compressed, with a hollow centre (Fig. 4I); ridges up to three or not visible (Fig. 4I). Endocarps-entirely or partly preserved, compressed, generally with a truncated base; ovoid, globular, oblong, planoconvex or flattened in shape; maximum preserved length 86–112mm, width 76–100mm, and thickness 30–65mm; basal aperture preserved or not visible, elliptical in cross section, maximum diameter 22–40mm (Fig. 4A, B, C); sulcus not visible; the surfaces of the endocarps are smooth or with deep longitudinal furrows running from the base to the apex (Fig. 4C, D); some of the endocarps display very fine longitudinal parallel striations (Fig. 4A).

Remarks. Five of the *Nypa* megafossil remains from the Casa Migalón site are endocarps, and four are near-complete fruits (*i.e.* with husks partly preserved): ARCM-3-1 (Fig. 4F), ARCM-7-1 (Fig. 4I), ARCM-8-1 (Fig. 4D) and ARCM-9-1 (Fig. 4G). The smallest fruit (ARCM-9-1) is plano-convex in shape, 90mm long and 45mm wide, and its cross section is roughly triangular. Based on its size and shape, it could correspond to an immature, abortive or young fruit (Reid and Chandler, 1933; Tralau, 1964). We observe a small variance in size between samples, and there is a dominance of endocarps over complete fruits (Fig. 5). The structure and morphological characteristics of all fruits and endocarps are similar to those described by Biosca and Via (1988): p.17, pl. I, fig. 2 (ARCM-9-1); p.17, pl. I, fig. 3 (ARCM-2-1); p.17, pl. I, fig. 4 (ARCM-
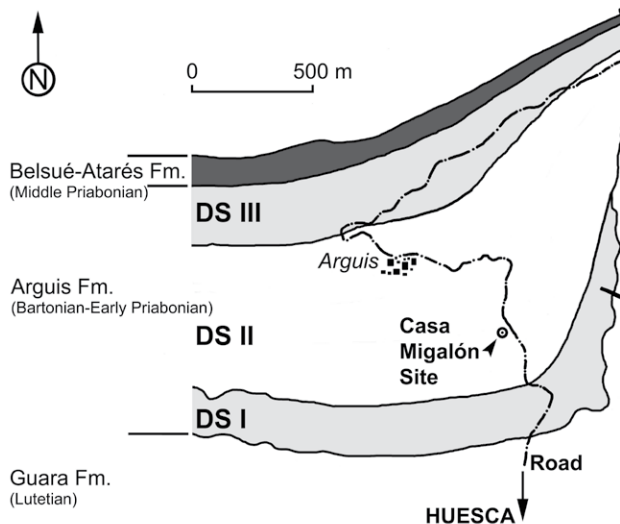
FIGURE 2. Detail of the geological formations surrounding the Casa Migalón site (arrowhead). Modified from Pueyo *et al.* (2002).

3-1; ARCM-4-1; ARCM-6-1); p.19, pl. II, fig. 3 (ARCM-3-1; ARCM-6-1). Evidence suggests one type of animal borings. Such damage is distributed over the surface of the remains: the presence of borings on the endocarps is very scarce or absent, but in the case of the fruits practically the entire specimens are affected. The damage to the fruits consists predominantly of elongate borings nearly-straight or subparallel (*e.g.*, ARCM-8-1, ARCM-3-1); while, on the endocarps these borings are sinuous and contorted, and much shorter than in the fruits (*e.g.*, ARCM-2-1). These endocarps almost always show small-sized borings (*e.g.*, ARCM-2-1; 0.4-0.65mm in diameter) while in the case of the fruits the borings are mainly large-sized (*e.g.*, ARCM-3-1; 0.67-3.8mm in diameter). The damages are consistent with *Teredo* borings which are formed by marine bivalves of family Teredinidae (Kumar *et al.*, 2011) (*e.g.*, ARCM-3-1, ARCM-7-1, ARCM-9-1). When compared to the specimens of Biosca and Via (1988), the remains of the Casa Migalón site are slightly larger and bear numerous *Teredo* borings on their surface. Álvarez-Ramis (1982) and Biosca and Via (1988) commented on the similarity of their specimens with those from other Eocene sites in Europe. In the best known *Nypa* fossil sites in Europe, the remains of *Nypa* have the same structure though they may vary in size and shape (Collinson, 1993). Tralau (1964) stated that, in general, it should be remembered that the size and form may vary significantly depending on the degree of development, former position in the fruiting head and the state of preservation; however, the structure of the fruit remains unchanged.

Occurrence. *Nypa burtinii* is found in Eocene deposits from the Catalan Central Depression (Comarca del Bages), and at the quarry of Balçamuller (Castellgalí) and Can Font Els Comtals (Mal Balç trackway, Manresa) (Álvarez-Ramis, 1982). It also occurs in the Monistrol and Vacarisses area (upper Lutetian/lower Bartonian), North of the Manresa area and near the town of Sant Fruitós de Bages (upper Bartonian/lower Priabonian), the area of Castellterçol and Monistrol de Calders area (Bartonian), and at the Vallbona quarry (lower Bartonian), which are all located in the Catalan Central Depression (Biosca and Via, 1988).

MONOCOTYLEDON LEAF (Fig. 4H)

Material studied. ARCM-12-1.

Description. Laminar size microphyll. Laminar shape linear and symmetrical, 90mm in length and 15mm in preserved width. Margin entire. Apex and base not preserved. Primary venation parallelodromous or campylodromous, other orders of veins and areolation not visible.

Remarks. According to Mehrotra *et al.* (2003) the occurrence of a leaf fragment within the endocarps of *Nypa*, suggests that it might correspond to a fragment of a *Nypa* palm frond; however, the same authors also stated that the fossil records of *Nypa* leaves are very sparse because they cannot be easily differentiated from other palm foliage. This study follows Read and Hickey (1972) who state that the partial preservation of a parallel venation in a leaf formed by just one order of parallel veins will allow us only to assign this fragment as coming from a monocotyledon leaf.

DISCUSSION

Taphonomic considerations

Through the presence of abrasion, *Teredo* borings and sedimentary facies, the specimens from the Casa Migalón site are considered as an allochthonous fossil assemblage. Their sedimentological setting reflects a significant distance between the origin and deposition places of the fossil fruits.

Currently, several authors agree that those disseminules (fruits and seeds) which show signs of erosion are clearly of drift origin (*e.g.*, Nakanishi, 1987; Smith, 1992; Quigley *et al.*, 2014). The angles of living fruits which have drifted in the sea become worn, or may even be obliterated (Reid and Chandler, 1933). In this regard, Nakanishi (1987)

observed that most of the disseminules washed ashore on beaches of the Japanese mainland typically have their exocarp decomposed and the fibrous mesocarp exposed. Occasionally endocarps have been found on the beach, however, they are very rare. On the one hand, this fact implies that endocarps sink soon after becoming separated from the fruit during prolonged drift (Smith, 1992). On the other hand, the intact and uneroded disseminules may have fallen on to the beach directly from overhanging plants (Smith, 1990), or they may have drifted in seawater only for a short time (*e.g.*, Nelson, 1978; Nakanishi, 1987; Brochard and Cadée, 2003). Thus, the absence of facets in many of the fossil *Nypa* fruits suggests a common cause (Reid and Chandler, 1933). Many authors have cited the presence of abrasion in the *Nypa* fossils: for instance, Reid and Chandler (1933), Tralau (1964), Gregor and Hagn (1982), Collinson (1993), Mehrotra *et al.* (2003). According to these authors, the abrasion would point to some drifting of the fossil *Nypa* fruits in seawater.

Over half of the specimens in the fossil assemblage described herein are endocarps, while the rest of the *Nypa* fossils are fruits which show evidence of abrasion that has worn off the exocarp and its ribs on the fossil fruits but preserved the mesocarp. This evidence suggests that the specimens have been drifting in the sea, with floating times that were shorter for near-complete fruits than for endocarps, but the exact relative durations cannot be known. For example, Nakanishi (1987) suggests that most living fruits or seeds have been drifting in the ocean for many months, and sometimes for years (Gunn and Dennis, 1976), while endocarps can come from fruits which have been drifting for even more time (Smith, 1992).

Cocos nucifera (coconut) is a well-known drift palm fruit. This fruit can be used as a model to explain the main floatation processes and causes of sinking which may have affected the fossil *Nypa* fruits studied. Thus, for instance, according to Bobrov *et al.* (2012), the structure of the peripheral zone of the mesocarp of *Cocos nucifera* is generally similar to *Nypa fruticans* (nipa), and this zone secures the buoyancy in the seawater of *Cocos* and *Nypa*.

A whole coconut mainly consists of a husk (exocarp-mesocarp), a nut (endocarp-endosperm), and an aqueous milky sap inside the cavity of this nut (Armstrong, 2007). The husk is fibrous, and the endosperm has the same specific gravity as seawater (Hewitt, 2005a). Essentially, when a husk is in prolonged contact with seawater it becomes saturated with seawater and heavy (Harries and Baker, 2005). Then, seawater slowly begins to penetrate the area of the coconut "eyes" (the three pores of the endocarp), causing microorganisms to start the rotting process (Cadée, 2008). According to Hewitt (2005a), the endosperm is gradually consumed by microorganisms and
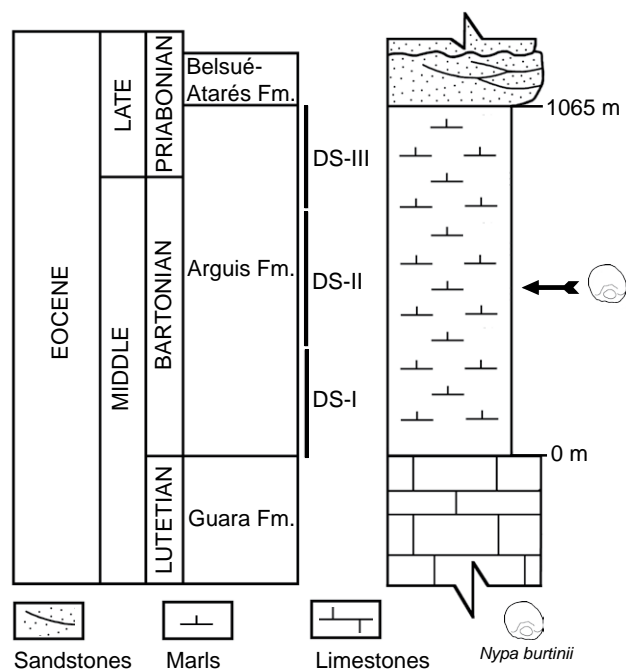
FIGURE 3. A schematic stratigraphic section in the Arguis syncline (central part of the External Sierras), showing the horizon from which the fossil *Nypa* specimens were collected. Modified from Vidal-Royo *et al.* (2013), and with data from Pueyo *et al.* (2002) and Cohen *et al.* (2013).

replaced by air or an obnoxious decomposition gas. In a rough sea the coconut would soon be sunk by effusive loss of this air pocket. When no such decay takes place the specific gravity stays more or less unchanged, although it will subsequently, then, start increasing as seawater reaches beyond the initially soaked endocarp. In this case the coconut becomes negatively buoyant and sinks.

Because both nipa and coconut fruits have a similar structure, it is logical to expect that the extant nipa fruits may have suffered the same processes as coconuts when floating at sea. In contact with seawater, the fibrous mesocarp of nipa or coconut becomes saturated and heavy, and in the case that the mesocarp breaks, the exposed fibres of husk saturate quickly (Hewitt, 2009). The mesocarp cannot remain intact due to the effect of the different mechanisms in action: the buffeting by waves, the exposure to light, the temperature variations, the penetration by water and the action of marine borers (Thiel and Gutow, 2005a). All these processes could erode and break the mesocarp, and separate the mesocarp from the endocarp. Thus, the abrasion of the exocarp and mesocarp down to the endocarp would be enough to start the sinking of the endocarp to the seafloor (Gee, personal communication). Also, when a whole *Nypa* fruit is completely saturated with seawater, it may have a specific gravity greater than the seawater

FIGURE 4. *Nypa burtinii* (Brongniart, 1828) Ettingshausen, 1879. Fruits. A) ARCM-1-1, lateral and basal vision; B) ARCM-6-1, basal vision; C) ARCM-2-1, lateral vision; D) ARCM-8-1, lateral vision; E) ARCM-4-1, basal and lateral vision; F) ARCM-3-1, lateral vision; G) ARCM-9-1, lateral vision; I. ARCM-7-1, apical vision; H: ARCM-12-1, fragment of a monocotyledon leaf with badly preserved parallel venation. t: *Teredo*-borings; ba: basal aperture; f: furrows; a: apex. All scale bars equal 1cm.

and therefore, may sink. However, the increase in growth of the fouling community (*e.g.*, *Teredo*) also can augment the specific gravity of the fruit, which results in sinking (Thiel and Gutow, 2005a).

How long does it take for such a drifting fruit to sink? On one hand, Nakanishi (1987) and Smith (1999) have suggested that current *Nypa* fruits may drift in seawater for a few months before they sink. On the other hand, in the case of *C. nucifera* the maximum known floatation time is 34 years (Hewitt, 2005b). Such a long time difference is probably due to the dynamic balance between the decay of endosperm just under the pores of the endocarp tending to sink coconuts by admitting water, and general internal decay in which the endosperm is changed into gas which cannot escape (Hewitt, 2005b). The fossil *Nypa* fruits studied may have suffered the same processes and similar time periods of floatation as extant nipa and coconut fruits.

While the presence of *Teredo* borings is very common in many fossil *Nypa* fruits, their presence is unknown in recent *Nypa* (*e.g.*, Gregor and Hagn, 1982). Nevertheless, the bathyal crustacean *Onesmoides chelatus* and the mytilid bivalve *Adipicola longissima* are reported in association with living *Nypa*; from deep sea dredge samples from the Caribbean Sea, the Gulf of Guinea and Celebes Sea (Barnard, 1961; Cadée, 1996).

It is well-known that *Teredo* and other marine epizoa are scarce in living disseminules. This fact can suggest some antifouling activity of the seed or fruit coat (Cadée, 1996). For example, Quigley *et al.* (2014) stated that the presence of specified chemical compounds demonstrating anti-fouling properties that have been isolated from a number of *Barringtonia* species, may naturally inhibit the settlement of marine bio-fouling organisms on drifting *Barringtonia* fruits. This implies the existence of chemical differences between fossil and living seed and fruit coats that would explain the absence of *Teredo* in living fruits.

Teredo excavates burrows in floating and submerged wood and wooden materials and lives in them, feeding on wood and nutrients scraped of water (Kumar *et al.*, 2011). Harries and Baker (2005) found one specimen of *Teredo navalis* in a coconut fruit (*C. nucifera*) from a beach on one of the Western Isles in Scotland. This shipworm had penetrated and damaged the husk (exocarp-mesocarp) but once within it only damaged the kernel (endocarp-endosperm), not causing the endosperm to rot. These authors suggested that the high oil content of the endosperm was probably not to the "*shipworm's taste*"; in other words, in edible for these shipworms. Nelson (1978) also reported the presence of a number of marine bivalve *Psiloteredo megotera* in a husk of

Cocos nucifera from Irish beaches, and that they had bored into the fruit as far as the bony endocarp. Thus, it seems that *Teredo* only perforates and lives in the exocarp-mesocarp. We believe that it is for this reason that, in the fossil fruits studied show many *Teredo* borings while their presence in the endocarps is very scarce or non-existent.

Recent drift disseminules may have marine algae, bryozoa, small borers, barnacles or echinoderms attached to them (Nelson, 1978; Nakanishi, 1987; Thiel and Gutow, 2005a). The absence of these rafting organisms suggests a short time at sea (Ebbesmeyer, 2012), while their presence implies a long time in the ocean (Nelson, 1987; Nakanishi, 1987; Harries and Baker, 2005; Ebbesmeyer, 2012). The evidence of *Teredo* borings in fossil *Nypa* also suggests a long floating time (Gregor and Hagn, 1982; Collinson, 1993). Thus, the presence of *Teredo* borings in the studied fossils indicates a long floating time, being however shorter than when only endocarps without *Teredo* are preserved.

Overall, it is difficult to do a precise calculation of the longevity of floating objects on the sea surface, but an approximate idea can be done via some indirect measures (Thiel and Gutow, 2005a). Each shipworm eliminates a column of wood or wooden material of the same dimension as its largest size (Balakrishnan and Saraswathy, 1971). From this, the approximate floating time can be estimated by measuring the length of these burrows and comparing it to their growth rates. Several authors (*e.g.*, Balakrishnan and Saraswathy, 1971; Thiel and Gutow, 2005b and references therein for details) have reported mean growth rates between 0.24mm and 4.06mm per day for current teredinid bivalves. Balakrishnan and Saraswathy (1971) and Thiel and Gutow (2005b) highlighted that such variations in the growth rates may be explained mainly by changes of temperature, substratum characteristics and by the effect of crowding. Interestingly, it has been documented a growth rate of 0.59mm per day in average for teredinid molluscs (Thiel and Gutow, 2005b), which it makes possible an indirect estimation of floating longevity.

In the fossil assemblage from the Casa Migalón site, it seems that the nearly-complete borings in the endocarps are 13-18mm in length (Fig. 4C). So, considering an average growth rate of 0.59mm per day, this length may represent between 22 and 30 days-old specimens. Moreover, it also appears that the fruits (Figs. 4D, F) show incomplete burrows with maximum preserved length between 28-51mm. These lengths would represent growth periods between 47-87 days according to the same principle.

Then again, following principles of Kumar *et al.* (2011), we interpret that the long and large borings belong to adult specimens (Figs. 4D, F), while short, sinuous or contorted and smaller borings belong to
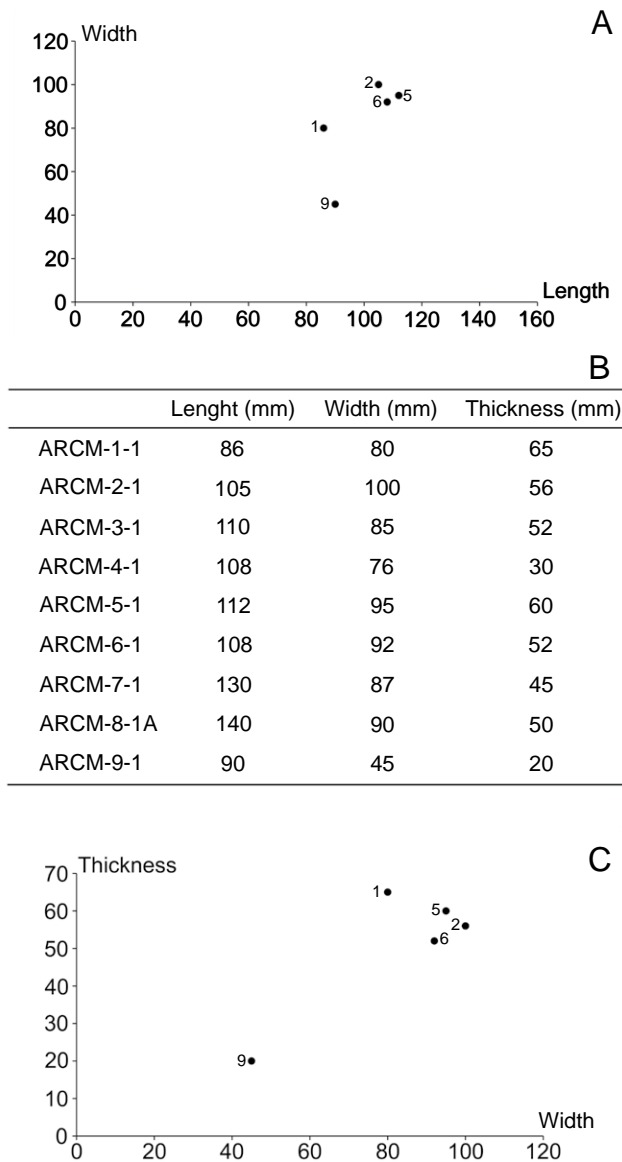
FIGURE 5. A) Scatter diagram of the measurements of width and length of the *Nypa* fossil remains from the Casa Migalón site. B) Measurements of the samples from the Casa Migalón site. Endocarps: 1,2,5,6; Immature Fruits: 9. C) Scatter diagram of the measurements of thickness and width of the *Nypa* fossil remains from the Casa Migalón site. Only specimens with well-preserved dimensions are represented. Measurements expressed in mm.

	Lenght (mm)	Width (mm)	Thickness (mm)
ARCM-1-1	86	80	65
ARCM-2-1	105	100	56
ARCM-3-1	110	85	52
ARCM-4-1	108	76	30
ARCM-5-1	112	95	60
ARCM-6-1	108	92	52
ARCM-7-1	130	87	45
ARCM-8-1A	140	90	50
ARCM-9-1	90	45	20

to the seafloor started after upon separation of mesocarp from the endocarp. The evidence suggests that the total floatation time of the endocarps after separation could have lasted between 20-30 days. Conversely, evidence suggests that the fruits were floating three times more than endocarps (*i.e.*, three months approx.). This time interval is similar to the Nakanishi's (1987) proposal for the current nipa. If accepted, this scenario would imply that the buoyancy of the fossil endocarps would be much less that of fruits.

Paleoecology and Paleoclimate

Currently, the mangrove palm *Nypa* is confined within the Indo-West-Pacific region (Teo *et al.*, 2010). In this region the climate is tropical, with mean temperatures above 18ºC all year round (Kottek *et al.*, 2006) and seasonal variations of precipitation. This palm grows in quiet estuaries or shallow lagoons collecting fresh water steams (Tomlinson, 1986), and it often develops forming vast natural stands. It seems to favour brackish waters, often forming a wide border beyond the fringe of adjacent mangroves or swamp forest. However, it does not appear on shores exposed to too much wave action or in hypersaline conditions (Tomlinson, 1986).

Current climatic preferences and the characteristic morphology of the *Nypa* palm may be good indicators of past vegetation and climate when found in the fossil record (El-Soughier *et al.*, 2011). Assuming that the genus grew under similar conditions in the past as it does now, information about the paleoenvironment in the areas where its fossils are found can be extracted for paleoecological reconstructions (*e.g.*, Tralau, 1964; Collinson, 1993; Gee, 2001; Plaziat *et al.*, 2001; El-Soughier *et al.*, 2011).

The first published record of fossil *Nypa* was provided by Parsons (1757-58). From the middle of the eighteenth century, these fossils were referred to as species of "*eastern mango*", "*almond*" or as some species of "*coconut*" or even as belonging to the genus *Cocos* Linnaeus (Brongniart, 1828). However, it was not until 1840 that Bowerbank (1840) identified the close affinity of these fossils with *Nypa* (Reid and Chandler, 1933). From that time onwards, all authors have accepted the close similarity between the fossil and living populations of *Nypa* (Tralau, 1964).

Using this premise, many authors have reconstructed the paleoecological conditions of the fossil *Nypa* during the Eocene (*e.g.*, Reid and Chandler, 1933; Arnold, 1952; Tralau, 1964; Collinson, 1983; Plaziat, 1970, 1975; Plaziat *et al.*, 1983, 2001; Bhattacharyya, 1983; Biosca and Via, 1988; Krutzsch, 1989; Westgate and Gee, 1990; Pole and Macphail, 1996). For instance, Westgate and Gee (1990) described pure dense stands of *Nypa* flourishing along

juvenile specimens (Figs. 4C, I). Furthermore, according to Balakrishnan and Saraswathy (1971), shipworms attain sexual maturity between 20-60 days after settling upon a piece of wood or wooden material. Thus, evidence suggests that the specimens are very young and not mature in the endocarps, while the specimens are mainly mature and adults in the fruits.

Data reveal that the endocarps had a floating time much shorter than the fruits. The sinking of the endocarps

low-energy coastlines and in estuaries and shallow lagoons in the middle Eocene of Texas, and they speculate that *Nypa* probably dominated the intertidal area, in tropical to subtropical conditions.

Thus, the presence of *Nypa* in the fossil assemblage studied suggests the existence of mangroves, in surrounding areas during the Eocene. The climatic conditions that have been interpreted for occurrences of fossil *Nypa* remains have been tropical-subtropical and characterized by low seasonal variation. We conclude that the climatic conditions of fossil *Nypa* in the Eocene Arguis Fm. (northeastern Spain) were identical to those of *Nypa* occurrences at other Eocene sites.

CONCLUSIONS

We report herein new fossil evidence of fruits of the mangrove palm *Nypa*, which increases its fossil record in Spain. Near-complete fruits (including part of the husk) and endocarps were collected from a new plant-bearing assemblage in the Arguis Fm. (Bartonian to lower Priabonian) sited at the Prepyrenean External Sierras (Arguis, Huesca Province, northeastern Spain). The new occurrence consists of nine specimens of *Nypa* fossil fruits and one monocotyledon leaf fragment. This fossil assemblage is interpreted as allochthonous, considering its sedimentary setting, *Teredo* borings and presence of abrasion. Evidence suggests that different transport lengths can be inferred from the preservation of mixed assemblages of endocarps and fruits with husks partly preserved, the latter indicating shorter drifting times. Also, fruits with different extent of boring by *Teredo* provide additional biostratinomic criteria. The taphonomic analysis suggests the existence of mangroves, in the northeastern Ebro Basin during the Bartonian. The climatic and paleoecological conditions were determined by the "nearest living relatives" method, and we conclude that the climatic conditions were tropical-subtropical and characterized by low seasonality contrasts.

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