A critical evaluation of fossil pollen records from the mangrove tree *Pelliciera* beyond the Neotropics: biogeographical and evolutionary implications

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Abstract

Pelliciera is a Neotropical mangrove tree restricted to a small region around the Panama Isthmus. In the past, this taxon was distributed across much of the Neotropics, reaching its maximum extent during the Oligo-Miocene. The occurrence of *Pelliciera* outside the Neotropics had been debated based on a few fossil pollen records from Africa and Europe, though many of these records have been questioned. However, the recent proliferation of fossil pollen records identified as the fossil representatives of *Pelliciera* pollen, warrants reconsideration. This paper provides a detailed review of the morphological features of extra-Neotropical records published to date, comparing them with extant *Pelliciera* pollen. Over 80 records from Africa, Europe, the Middle East, and North America were retrieved for this review. Only those published in Scopus-indexed journals are considered to avoid issues related to gray literature and predatory journals. Records mentioning purported *Pelliciera* fossils without providing material suitable for morphological comparison were also excluded, as were those featuring poor-quality images impossible to resolve. Among the records that met these criteria, only a subset of African fossil pollen types are compatible with *Pelliciera*: three with high reliability and another three with medium-high reliability, ranging from the Eocene to the Plio-Pleistocene. With these data, the occurrence of *Pelliciera* fossil pollen outside the Neotropics cannot be dismissed. However, the evidence remains insufficient to construct a transcontinental biogeographical and evolutionary framework for *Pelliciera* over time. Continued research in this direction is recommended, and suggestions for advancing this task are provided.

Keywords: *Pelliciera*, fossil pollen, pollen morphology, botanical affinity, Neotropics, biogeography

1. Introduction

Currently, *Pelliciera* (*Tetrameristaceae*) is restricted to a relatively small region of tropical America surrounding the Panama Isthmus (Fig. 1). It is a minor component of mangrove ecosystems, which are typically dominated by *Rhizophora* (Rhizophoraceae). The canopy of *Rhizophora* provides a suitable microhabitat that allows *Pelliciera* to withstand environmental stressors, such as excessive light and salinity (Dangremond et al., 2015). *Pelliciera* is listed as "Vulnerable" on the IUCN Red List of Threatened Species (Polidoro et al., 2010), with habitat loss and severe fragmentation caused by urban expansion identified as the main threats (Blanco-Libreros & Ramírez-Ruiz, 2021). Historically, *Pelliciera* has been considered a monotypic genus represented by *P. rhizophorae* Planch. & Triana, alongside a variety known as *P. rhizophorae* var. *benthamii* Planch. & Triana (Triana & Planchon, 1862). However, Duke (2020) recently distinguished two species: *P. rhizophorae* and *P. benthamii* (Planch. & Triana) N.C. Duke. These species are closely related, and some degree of hybridization has been suggested. Initially, the genus was named "*Pelliceria*" (Triana & Planchon, 1862) but was later corrected to *Pelliciera* (Hemsley, 1879; Kobuski, 1951). While some authors still use the original generic name (e.g., Frederiksen, 1985, 1988; Graham, 1995), *Pelliciera* is the accepted term in the International Plant Name Index (IPNI; https://www.ipni.org/).

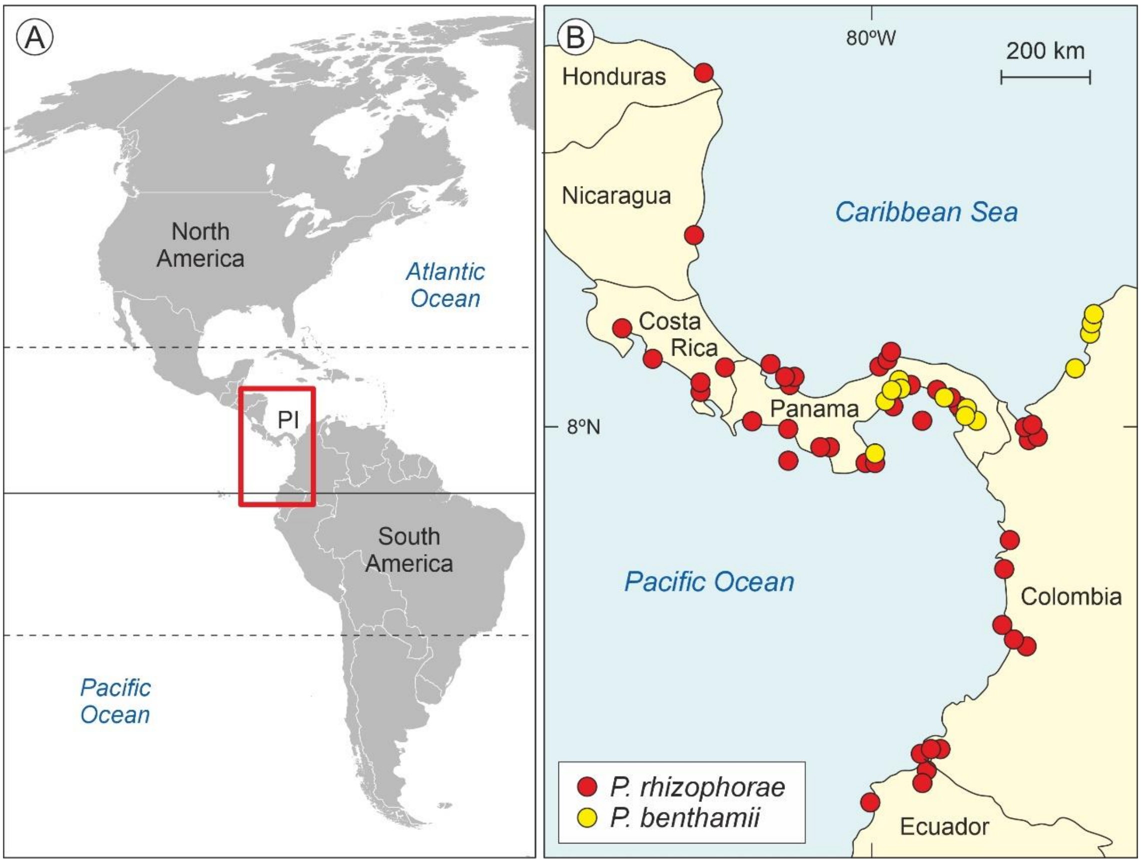

Figure 1. Distribution map of extant *Pelliciera*. A) General map of the American continent indicating the Equator (solid lines), the northern and southern tropics (dotted lines) and the area of distribution of *Pelliciera* (red box) around the Panama isthmus (PI). B) Close up of the PI region where extant *Pelliciera* species have been documented (Duke, 2020). Modified from Rull (2023a).

Since its Eocene origin, the distribution of *Pelliciera* has varied across the Neotropics, characterized by successive expansions and contractions consistent with the concept of the taxon cycle, as defined by Wilson (1961). The genus reached its maximum extent during the Oligo-Miocene, when *Pelliciera* was distributed throughout the entire northern and part of the southern Neotropical region (Fig. 2). Its current distribution is similar, though not identical, to that of the Middle Eocene, an epoch when *Pelliciera* was the sole mangrove-forming genus in the American tropics, dominating these ecosystems. During this time, *Nypa* and *Acrostichum* were present in the understory and back-mangrove swamps, respectively (Rull, 2022). The biogeographical history of Neotropical *Pelliciera* has been reconstructed using fossil pollen evidence. These data are compiled in a comprehensive database called CARMA (*CARibbean MAngroves*), which includes published Paleogene and Neogene records of pollen from Neotropical mangrove-forming trees. The database covers *Pelliciera*, *Rhizophora*, *Avicennia* (*Acanthaceae*), and *Laguncularia* (*Combretaceae*) from nearly 90 localities (Rull, 2023d). The full story—including Quaternary records and modern analog studies based on surface sediments, comprising a total of 160 records—can be found in more detail in Rull (2024).

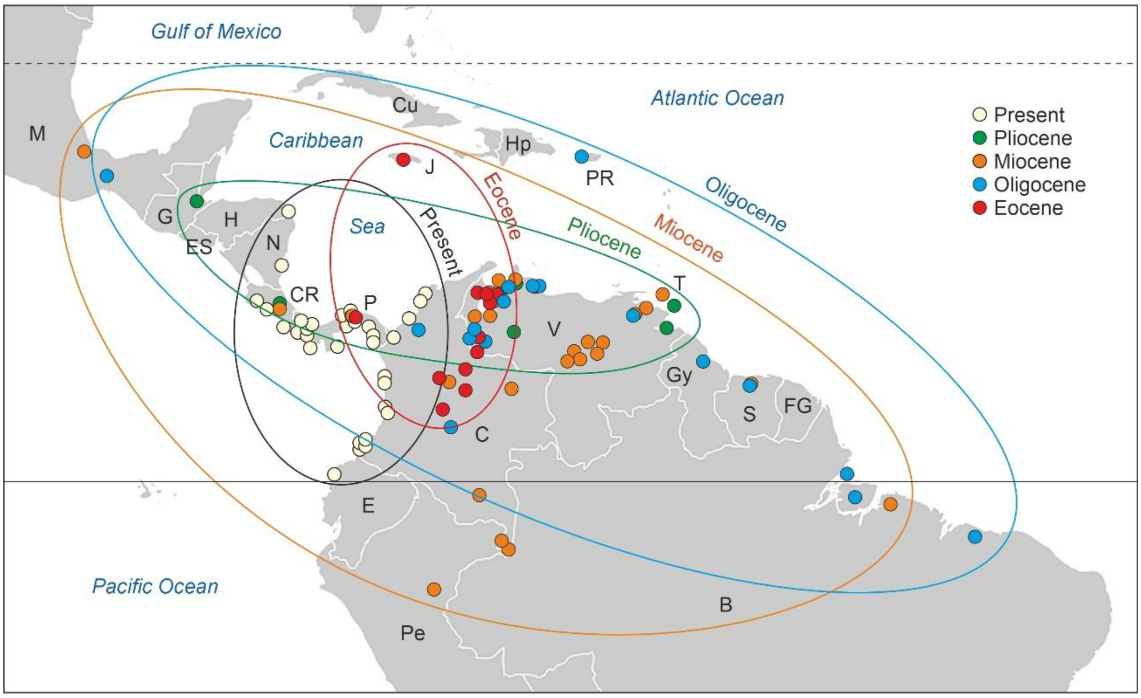

Figure 2. Sketch-map showing the range shifts of *Pelliciera* fossil pollen across the Neotropics from the Eocene to the present. B, Brazil; Bz, Belize; C, Colombia; CR, Costa Rica; Cu, Cuba; E, Ecuador; ES, El Salvador; FG, French Guiana; G, Guatemala; Gy, Guyana; H, Honduras; Hp, Hispaniola (Haiti and Santo Domingo); J, Jamacia; M, Mexico; N, Nicaragua; P, Panama; Pe, Peru; PR, Puerto Rico; S, Surinam; T, Trinidad and Tobago; V, Venezuela. Simplified from Rull (2023a).

This exclusively Neotropical paleobiogeographical perspective has been challenged by several potential records of fossil *Pelliciera* from North America, Europe, Africa, and the Middle East. Until the late 20th century, these records were considered doubtful or in need of revision. For example, Muller (1981) noted that the African records reported by Germeraad et al. (1968) – in which Muller was a co-author – and Fuchs (1970) required confirmation. Similarly, Frederiksen (1985) acknowledged that the high morphological variability of *P. crassus* made identifying *Pelliciera* somewhat uncertain, particularly for European specimens. However, the increasing number of recent records from Africa and the Middle East over the last few decades warrants special attention. If confirmed, these records would necessitate a reconsideration of *Pelliciera*'s evolutionary and biogeographical trends over time. Unfortunately, the raw data for many of these records are not publicly accessible and remain confidential within oil companies. The only available information comes from scientific publications that include morphological descriptions and/or pollen images, which are useful for morphological comparison.

This paper reviews the available descriptions and images of extant *Pelliciera* pollen and its potential fossil analogs to analyze the morphological correspondence among them and evaluate the proposed botanical affinities. The information gathered is then used to examine the published extra-Neotropical fossil occurrences and their potential correspondence with *Pelliciera*. Finally, the results of these investigations are utilized to assess whether the new findings warrant a reconsideration of the current Paleogene and Neogene biogeographical and evolutionary trends for *Pelliciera*.

2. Pollen morphology

The morphological details of extant (Section 2.1) and fossil (Section 2.2) pollen provided in this section correspond to the current distribution area of this genus (Fig. 1) and the Neotropical region (Fig. 2), respectively, where *Pelliciera* and its putative fossil form-species have been described. These descriptions retain the original terminology used in the referenced studies to preserve the objectivity of the raw data. However, pollen terminology has varied over time and across authors. Therefore, Section 2.3 compares modern and fossil pollen using the updated and standardized terminology proposed by Punt et al. (2007) and Halbritter et al. (2018) to facilitate comparative analysis (Appendix 1).

2.1. Modern pollen

The first illustrations of modern *P. rhizophorae* pollen, in reference to its potential fossil representatives, were published by Langenheim et al. (1967) and Wijmstra (1968). However, no detailed morphological descriptions were provided at the time. The pollen of extant *P. rhizophorae* was first described by Fuchs (1970) using plant material from the Colombian Pacific coast, with the following description:

"<u>Shape</u>: Length of polar axis approximately equal to equatorial axis, around 80 micron (77-82); grain in polar view practically round.
<u>Apertures</u>: Three, arranged in radial symmetry, grain isopolar. Ektexinous: Elongated, fairly long, up to 40 micron, with straight to slightly convex and distinct terminations. Endexinous: Perpendicular to ektexinous apertures, equatorially elongated, with straight to sometimes slightly convex sides, ± 15 micron long, 4-5 micron wide, with indistinct terminations; endexine thickened along endexinous apertures.
<u>Structure</u>: Exine clearly differentiate, up to 3.5 micron (not taking into account sculptural elements). Endexine up to 2 micron; pillars practically 1 micron; of ± equal length and fairly uniform diameter, densely spaced, unbranched, irregularly arranged; tegillum between sculptural elements slightly more than 0.5 microns.
<u>Sculpture</u>: Macropositive elements with rounded to irregular or undulated base, convex shaft and rounded top, up to 2 micron high, of practically uniform height, placed uniformly sometimes with varying distances. Tegillum present between elements, sometimes with fine and very indistinct perforations, consisting of very small, round, wide and regularly spaced lumina of a diameter less than 0.5 microns."

This description aligns closely with the pollen morphology of extant *P. rhizophorae* from the Colombian coasts, recently published by the author (Rull, 2022) using photographs provided by Ligia E. Urrego from the Universidad Nacional de Colombia in Medellín (Fig. 3). Thanikaimoni (1978), studying *P. rhizophorae* pollen from Panama, described its sculpture as foveolate-fossulate, sometimes verrucate-rugulate. Thus, a wide range of sculptural types appears to be present in the pollen of this genus.

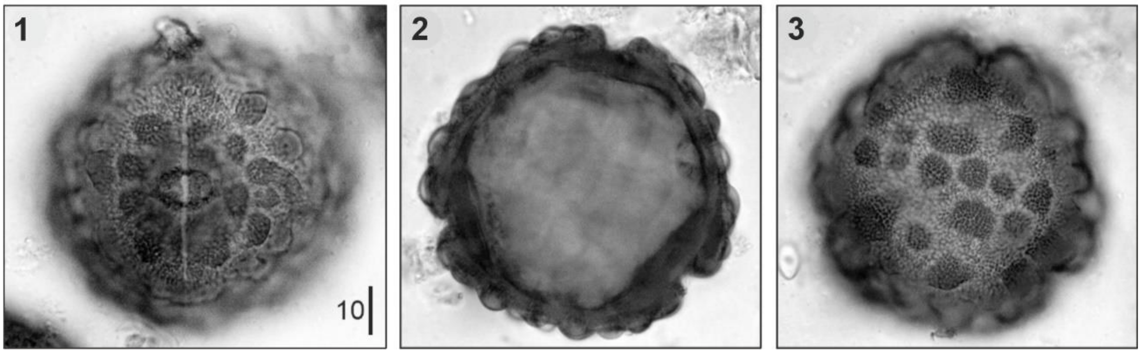

Figure 3. Pollen grain of extant *Pelliciera rhizophorae* from The Pacific Colombian coasts. A) Equatorial view showing the characteristic apertures (colpori). B) Polar view showing the thick exine in optical section and the endexine thickening in the apertures (costae). C) Polar view of the same grain with focus on the characteristic sculpture elements (verrucae). This pollen fits well with the description and the illustrations provided by Fuchs (1970). Photos courtesy of Ligia E. Urrego, from the Universidad Nacional de Colombia at Medellín.

Fuchs (1970) noted that *Pelliciera* pollen shares many features with *Hura* (*Euphorbiaceae*), particularly *H. crepitans* L. and *H. polyandra* Baill. However, the sculpture—also referred to as ornamentation in pollen morphology—clearly distinguishes these two genera, as *Hura* is psilate with "*… very small ± round, widely spaced, and regularly placed perforations*." Graham (1977) highlighted the high morphological variability of *Pelliciera* pollen, particularly in size and ornamentation. According to this author, size ranges from 40 µm to 90 µm, with moderate percentages of smaller abortive grains. Regarding sculpture, some specimens display conspicuous mound-like scabrae—likely referring to the verrucae described by Fuchs (1970) and depicted in Fig. 3, as the term "scabra" technically refers to a different sculptural pattern (Appendix 1). In other specimens, the scabrae are less prominent, and the grains exhibit a distinctly reticulate pattern. According to Graham (1977), This variability in size and ornamentation is characteristic of *Pelliciera* pollen and can even occur among grains from the same flower.

The morphological study of *Pelliciera* pollen was recently revisited by Castillo-Cárdenas et al. (2015), who identified two distinct morphological types corresponding to two *P. rhizophorae* variants (A and B) previously differentiated using molecular markers. The primary differences between the pollen of these variants were observed in ornamentation and exine thickness, while shape and dimensions remained relatively consistent. Specifically, no significant differences were found in the polar diameters—58.65 ± 4.13 µm (Variant A) and 55.24 ± 3.74 µm (Variant B)—or in the equatorial diameters—61.22 ± 4.13 µm (Variant A) and 57.96 ± 3.59 µm (Variant B). However, the exine was significantly thicker in Variant B (3.19 ± 0.50 µm) compared to Variant A (2.40 ± 0.67 µm). Additionally, Variant A exhibited a perforate-verrucate sculpture, whereas Variant B was smoother and punctate (perforations <1 µm). These palynological features, together with the molecular differentiation mentioned above, led the authors to propose incipient diversification, potentially driven by adaptation to differing environmental conditions. Variant A thrives in wetter climates, whereas Variant B occurs in relatively drier environments.

Similar results—namely, size and shape homogeneity (~60 µm, oblate-spheroidal, and tricolporate) with sculptural differences—were reported by Duke (2020) in *P. rhizophorae* and *P. benthamii*. This author identified three sculpture categories, which he termed "smooth" (punctate), "rough" (perforate to verrucate), and "between" (finely perforate-verrucate). However, none of these pollen types were exclusive to either species. The "between" category predominated in *P. rhizophorae* (~53%), while the "smooth" type was more abundant in *P. benthamii* (~84%). A significant proportion of collapsed grains (~72%) was observed in plants intermediate between *P. rhizophorae* and *P. benthamii*, with most (~76%) belonging to the "between" category. Duke (2020) interpreted this as evidence of reproductive isolation, characteristic of hybrid forms between these two species. A visual comparison of SEM images provided by Castillo-Cárdenas et al. (2015) and Duke (2020) suggests that the "smooth" pollen type corresponds to Variant B, while Variant A exhibits a more "rough" sculpture. However, no clear relationship has been established between the *Pelliciera* species and the molecular variants described by these authors.

2.2. Fossil pollen

The fossil *Pelliciera* pollen corresponds to the form-species *Psilatricolporites crassus* Van der Hammen & Wijmstra, also referred to as *Lanagiopollis crassa* (Van der Hammen & Wijmstra) Frederiksen. Initially, *P. crassus* was associated with the extant euphorbiaceous genus *Hura* (Germeraad et al., 1968; Fuchs, 1970), but its most widely accepted botanical affinity is with *Pelliciera* (Wijmstra, 1968; Regali et al., 1974; Muller, 1981; Frederiksen, 1985; Lorente, 1986). *L. crassa* has also been linked to *Alangium* (*Alangiaceae*) (Frederiksen, 1988), though this potential affinity is rarely discussed in the literature. *P. crassus* was first described by van der Hammen & Wijmstra (1964) as follows:

"Pollen grain tricolporate, furrow Cα1, Cβ2a, Cγ2, pore Pαc, Pβ1, Pγ2, sculpture type ± psilate, perforate tectum, with a maximum diameter of the lumina of 1 μ. The polar area is rather large. The thickness of the exine is 2.5-4.5 μ; the endexine is ≥ the ectexine. The columellae are clearly visible and have a diameter from 0.5-1 μ. The pollen grain has clearly marked costae transversales which do not fuse at the ends. Some grains are completely tectate, in that case the exine shows more clearly a ± polygonal pattern. The size of the holotype is 55 μ. Variation of size from 40-65 μ, index pollinis 1.2, index polaris 0.4, index exinae 0.08."

These authors did not specifie a particular botanical affinity with any extant species. The subsequent description by Germeraad et al. (1968) reaffirmed the psilate-perforate sculpture and expanded the size range:

"Single grain, radially symmetrical, isopolar, spherical to subpolate; outline in polar view circular. Tricolporate; colpi medium long, ectexinous, straight with pointed ends; pores endexinous, equatorially elongated, oval or slit-shaped, 15-19 μ long, distinctinctly costate, costae 5 μ wide and up to 4½ m thick, parallel to the pores. Endexine 1½ m thick, columellae ½ μ thick and 1 m long, tectum psilate to finely perforate-foveolate, 1-1½ thick. Dimensions: 41-70 m."

These authors highlighted the significant variability in size, exine thickness and width of perforations. They also emphasized that *P. crassus*:

"…is susceptible to corrosion of the tectum, which may lead to pseudo-ornamentations such as areolate scultpture with widely spaced irregular groves, gemmate sculpture with deep groves, verrucate sculpture, densely intersected by grooves or scabrate sculpture with the columellae protruding through membrane-thin remnants of the tectum."

However, as noted in the previous section on extant pollen, variability in sculpture is also evident in fresh material from living *Pelliciera* (Graham, 1977). Germeraad et al. (1968) emphasized the close resemblance between *P. crassus* and the pollen of extant *Hura*, particularly *H. crepitans*, which inhabits Caribbean coastal environments. However, while *H. crepitans* pollen is psilate, *P. crassus* is perforate-foveolate. Germeraad et al. (1968) also referenced the discovery of fossil

Pelliciera-like pollen by Langenheim et al. (1967), although those authors had not mentioned the fossil form-species *P. crassus* previously described by Van der Hammen & Wijmstra (1964).

Wijmstra (1968) established the identity between *P. crassus* and *Pelliciera*. This author did not re-describe *P. crassus* but based its botanical affinity with *Pelliciera* on structural elements of the exine: "*…they both have a perforate tectum and possess* coastae transversales *parallel to the longitudinal axis of the transverse furrows.*" Wijmstra (1968) also noted that fossil samples containing *P. crassus* often exhibit high percentages of *Rhizophora* and frequent occurrences of *Verrutricolporites rotundiporus*, indicative of mangrove environments. This argument for reinforcing the botanical affinity of *P. crassus* with a mangrove element like *Pelliciera* was also employed by Langenheim et al. (1967), who found *Pelliciera*-like fossil pollen in a *Rhizophora*-dominated assemblage, interpreted as evidence of in situ mangrove communities.

According to Fuchs (1970), paleobiogeographical and stratigraphical reconstructions based on fossil *Pelliciera* are *"…considerably hampered because its pollen has been lumped together with pollen resembling that of the genus* Hura*."* The author emphasized that these two pollen types had been combined into a single morphotype, *P. crassus*, by Germeraad et al. (1968) and Wijmstra (1968), which may lead to confusion. In addition to biogeographical and stratigraphical challenges, treating these two pollen types as a single morphotype could impact paleoenvironmental reconstructions. Pellicieroid pollen is typically found alongside *Rhizophora* pollen and is therefore a reliable indicator of mangrove environments. In contrast, huroid pollen suggests deposition outside the mangrove belt, likely in humid climates with a relatively pronounced dry season (Fuchs, 1970).

This author also noted that *Pelliciera* pollen is not psilate (see his description in Section 2.1 and Fig. 3); therefore, its fossil representative cannot be classified under the genus *Psilatricolporites*. Consequently, Fuchs (1970) proposed new combinations: *Verrutricolporites crassus* (Van der Hammen & Wijmstra) H. P. Fuchs for pellicieroid pollen with verrucate sculpture, and *Foveotricolporites ementitus* H. P. Fuchs for huroid pollen with foveolate/perforate sculpture. However, these two form-species have rarely been adopted, and *P. crassus* has remained the most widely used designation regardless of its sculptural features. Muller (1981) regarded *V. crassus* as the verrucate-areolate variety of *P. crassus*. Castillo-Cárdenas et al. (2015) suggested that *V. crassus* and *F. ementitus* could correspond to Variants A and B of extant *Pelliciera*, respectively.

The genus *Pellicieroipollis* Sah & Kar, originally described in the Eocene of India (Sah & Kar, 1970), was considered by Tomasini-Ortiz and Martínez-Hernández (1984) to be similar to *P. crassus*, with minor differences in size—40–50 µm for the former and 35–40 µm for the latter—and sculpture, which is scabrate in *Pellicieroipollis* and psilate-perforate or reticulate in *P. crassus*. These authors associated *Pellicieroipollis* with extant Theaceae and *P. crassus* with extant Clethraceae. However, Muller (1981) did not accept this distinction, considering *Pellicieroipollis* almost certainly a pollen grain of *Alangium*. This was further confirmed by Morley (1982).

Frederiksen (1985) emphasized that identifying *Pelliciera* from *P. crassus* is somewhat uncertain due to the significant morphological variability observed in both extant and fossil taxa. This is especially true for extra-Neotropical records (North America, Africa, Europe). Later, Frederiksen (1988) highlighted that the most distinctive characteristics of *Pelliciera* pollen are the broad and thick endannuli, or the prominent tumescence surrounding the endoapertures, which is clearly visible in polar view (Fig. 3). In the same paper, the author included the fossil *Pelliciera* pollen in the newly established species *Lanagiopollis crassa* (Van der Hammen & Wijmstra) Frederiksen, considering *P. crassus* as the basionym for *L. crassa*. Frederiksen (1988) did not formally describe

L. crassa, as he believed that the specimens used in his study, referred to as the *L. crassa* type, did not correspond to *L. crassa* sensu stricto – i.e., the *P. crassus* of Germeraad et al. (1968).

Although Frederiksen (1988) based his definition of *L. crassa* and the inclusion of *P. crassus* in this form-species on samples from North American sites outside the Neotropics (Gulf Coast), this concept was later adopted by Jaramillo & Dilcher (2001) for the Neotropical region. These authors described *L. crassa* as follows:

"Monad, radial, isopolar, spherical, amb circular; tricolporate, occasionally tricolpate, ectocolpi simple, CEi 0.5, mid-sized, borders straight, ends pointed, endopores costate, lalongate, 10 μm wide, 1 μm long, shaped alit-like, costae 2-3 μm wide, 2-3 μm thick; tectate, exine 2.5-3.0 μm thick, nexine 1 μm thick columellae 0.5-1.0 μm thick, tectum 0.5-1.0 μm thick, columellae 0.5 μm thick, tectum easily corroded; sculpture psilate, extremely variable pseudosculpture produced by degree of tectum corrosion, from psilate to scabrate, micropitted, foveolate, reticulate, and rugulate. Dimensions: Equatorial diameter 33 (43) 55 μm, SD 6.2; equatorial diameter length/width 1.05, μm: 30; polar diameter 40 (47) 50 μm, polar/equatorial diam. 1.1, μm: 3; no: 319."

These authors identified the following as the most diagnostic characters for the form-species: *"Psilatricolporate, mid-sized (33–50 μm), pore lalongate costate, tectum thick with columellae clearly distinct, sculpturing and thickness of the wall extremely variable."* They also supported the botanical affinity with *P. rhizophorae*.

Finally, it is important to note that the practice of identifying fossil *Pelliciera* pollen without referencing their potential fossil form-species, as in Langenheim et al. (1967), is not uncommon in the Neotropics. This approach is particularly evident in the numerous and influential works of Graham (1995, 2000, and literature therein). Using material from the same locality as Langenheim et al. (1967), Graham (19779) described the *Pelliciera* fossil pollen as follows:

"Oblate, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, 22–26 μm long, inner margin entire, pore circular, 3–4 μm in diameter, situated at midpoint of colpus, inner margin entire; sculpture variable from finely to coarsely verrucate; tectate, wall 4 μm thick, columellae evident (400x magnification); size variable (45–65 μm)."

This description is very similar to those provided by the author for other Neotropical records (Graham, 1985, 1989; Graham & Jarzen, 1969; Graham & Dilcher, 1998), with minor variations depending on the age and geographical location.

2.3. Comparisons

This section compares modern *Pelliciera* pollen with its potential fossil representatives: fossil *Pelliciera* not associated with any form-species (*sensu* Langenheim et al., 1967), *P. crassus*, and *L. crassa*, using the information reviewed in Sections 2.1 and 2.2, summarized in Table 1. All fossil representatives differ from the extant pollen type in certain features. In fossil *Pelliciera*, the main differences lie in the shape and size of the os—most notably, the characteristic costae bordering the endoaperture are not mentioned—although other characteristics fit well with modern *Pelliciera*.

For *P. crassus* and *L. crassa*, the primary differences are in the shape of the pollen grain (*P. crassus* exhibits subprolate forms) and the psilate-perforate sculpture, as other ornamentation types are considered to result from exine corrosion. Additionally, *L. crassa* is comparatively smaller (up to 50 µm) than other modern and fossil representatives.

As previously noted, sculptural features are highly variable and merit special attention. The pollen of extant *Pelliciera* exhibits a wide range of ornamentation, from perforate to verrucate, as well as combinations and intermediate forms. Moreover, these sculptural types are not restricted to specific species (*P. rhizophorae*, *P. benthamii*) or genetic variants (A, B) (Castillo-Cárdenas et al., 2015; Duke, 2020). Therefore, pollen morphology in *Pelliciera* shows high variability, and ornamentation appears to be an unreliable taxonomic character.

The same may hold true for fossil species, and the proposal to create two new fossil form-species to differentiate verrucate (*V. crassus*) and foveolate (*F. ementitus*) forms (Fuchs, 1970) may have limited usefulness in modern taxonomy. However, Fuchs (1970) correctly argued that *Pelliciera* pollen is not exclusively psilate, and therefore its fossils should not be included in the genus *Psilatricolporites*. This inconsistency traces back to the initial definition of *P. crassus*, which was based on a psilate holotype (Van der Hammen & Wijmstra, 1964) and later associated with *Pelliciera* (Wijmstra, 1968) in a flawed manner that has surprisingly gone largely unnoticed. The same photograph used by Van der Hammen & Wijmstra (1964) to describe *P. crassus* was reused by Wijmstra (1968) to illustrate modern *Pelliciera* pollen and establish their identity. Naturally, they appeared identical! In the interim, Langenheim et al. (1967) had already noted that *Pelliciera* pollen was verrucate, not psilate. Nevertheless, *P. crassus* continued to be used as the fossil representative of *Pelliciera*, expanding the sculptural range to include verrucate and perforate types (Table 1).

It is also noteworthy that Germeraad et al. (1968) considered *P. crassus* to be psilate, attributing other ornamentations to exine corrosion. The same assumption applied to *L. crassa*, as described by Jaramillo & Dilcher (2001). Graham (1977) and Thanikaimoni (1987) recognized the great variability in the ornamentation of modern *Pelliciera*, though they did not conduct detailed palynological studies of the genus. Recent works by Castillo-Cárdenas (2014) and Duke (2020) have confirmed this high intrageneric variability. However, these studies primarily used pollen to support hypotheses on plant morphology and genetics for *Pelliciera* species and variants. A systematic study focusing on pollen morphology and its potential taxonomic implications remains to be undertaken.

3. Fossil pollen records outside the Neotropics

In total, over 80 published fossil pollen records attributed to *Pelliciera* from outside the Neotropics—most from West Africa—were identified for this review. Of these, only records published in journals indexed in Scopus (https://www.scopus.com/) were considered, to minimize potential issues associated with so-called gray literature and predatory journals (Schöpfel, 2011; Beall, 2012). These records constitute the majority (40%), and the list is probably incomplete due to the recent proliferation of open-access journals of this type (Table 2). Among the remaining records, only those containing pollen descriptions, images, and/or morphological details useful for comparison with *Pelliciera* were selected. Records that merely document the occurrence of fossil *Pelliciera*, *P. crassus*, or *L. crassa* in the text or tables have been excluded. Additionally, papers providing low-quality images insufficient for morphological comparison were not considered. These images are often poor-quality photographs that lack resolution or depict damaged or deformed pollen grains. It is worth noting that most reports failing the Scopus filter also belong to the mention-only category, with only a few providing undiagnostic pollen images. Therefore, none of these records would qualify for the final selection anyway. This three-step selection process does not imply that the excluded records are dismissed outright but rather that they cannot be evaluated as potential *Pelliciera* fossils on

Table 1. Main pollen morphological features of extant *Pelliciera* species and the fossil form-species attributed to *Pelliciera*. The terminology has been updated and homogenized following Punt et al. (2007) and Halbritter et al. (2018). Although not specified in many descriptions, all pollen grains are monads, zonotricolporate, radially symmetric and isopolar. Se the Appendix 1 for these and other pollen morphological terms used in the table.

Taxa	**Shape**	**Grain size**	**Ectoapertures (colpi)**	**Endoapertures (ora)**	**Exine**	**Sculpture**	**References**
Extant *Pelliciera*	Spherical to suboblate, amb circular	40-90 μm	Thin, straight and long (up to 40 μm), distinct terminations	Lalongate (15x5 μm), costate	2.5-3.5 μm thick (excluding sculpture), tectate, columellate	Verrucate, rugulate (supratectal), perforate, foveolate, fossulate	Fuchs (1970), Graham (1977), Thanikaimoni (1987); Castillo-Cárdenas et al. (2015), Duke (2020)
Fossil *Pelliciera*	Oblate, amb circular (occasionally oval-triangular)	50-90 μm	Narrow, strait, 20-30 μm long	Circular (3-4 μm diameter) or oval (lalongated)	3-4 μm thick, tectate, columellae evident (400x)	Finely to coarsely verrucate (occasionally scabrate), perforate	Graham (1985, 1989, 1999), Graham & Jarzen (1969), Graham & Dilcher (1998)
P. crassus	Suboblate to subprolate, amb circular	40-70 μm	Long, strait, pointed ends	Oval or slit-shaped, lalongate (15-19 μm), costate	2.5-4.5 μm thick, columellae evident	Psilate to perforate/foveolate, pseudosculpture (after corrosion) variable (areolate, gemmate, verrucate, scabrate)	Van der Hammen & Wijmstra (1964), Germeraad et al. (1968)
L. crassa	Spherical, amb circular	40-50 μm	Simple, mid-sized, borders stratight, ends pointed	Lalongate (10x1 μm), costate	2.5-3.0 μm thick, tectate, columellate	Psilate, pseudosculpture (after corrosion) extremely variable (scabrate, perforate, foveolate, reticulate, rugulate)	Frederiksen (1988), Jaramillo & Dilcher (2001)

Table 2. References mentioning or depicting fossil pollen types attributed to *Pelliciera* or its fossil form-species which fall within the three categories not considered in this work.

Region	**Country**	**Journals not indexed in Scopus**	**Mention only**	**Unsuitable images**
West Africa	Nigeria	Adebayo & Olajide (2012); Uzodimma (2013); Ola & Adewale (2014); Adebayo & Ojo (2014); Adebayo et al. (2015); Adeniran (2015); Ilhunda et al. (2017); Behi et al. (2018); Chiadikobi et al. (2018); Ogbahon (2019); Ogbahon et al. (2019); Onema et al. (2019); Bié et al. (2020); Onuigbo et al. (2020); Ekwere & Osokpor (2020); Efemena et al. (2021); Igbinigie & Ogbamikhumi (2021); Owoeye et al. (2022); Yao et al. (2022); Olatunji (2023); Alla et al. (2023); Asadu & Onowaro (2023); Aturamu (2023); Aigbadon & Igbinigie (2024); Ekom et al. (2024) Nosa & Godwin (2024); Okeke et al. (2024)	Jan du Chêne & Salami (1978); Jan du Chêne et al. (1978a); Morley & Richards (1993); Bankole et al. (2007); Umeji & Nwajide (2014); Adeonipekun et al. (2016, 2019); Bolaji et al. (2020); Ikegwuonu et al. (2020); Chukwuma-Orji et al. (2021); Olayiwola et al. (2022a); Ocheli et al. (2023)	Umeji (2003); Adebayo et al. (2016); Ikegwuonu & Umeji (2016); Essien et al. (2017); Olatunji et al. (2020); Chukwuma-Orji (2022); Aigbadon et al. (2024)
	Cameroun		Salard-Cheboldaeff (1981)	
	Senegal	Pokryshkin & Prokof'Yev (1974)		
	Republic of Guinea	Zaklinskaya & Prokof'Yev (1971)		
Middle East	Turkey		Akgün et al. (2013); Toker et al. (2013)	
Europe	France	Gruas-Cavagnetto (1987); Olivier-Pierre et al. (1987); Gruas-Cavagnetto et al. (1988); Plaziat & Cavagnetto (1996)	Schuler (1990); Plaziat et al. (2021)	Popescu et al. (2021)
	Hungary		Bignot et al. (1985)	
	Spain		Cavagnetto & Anadón (1996)	
North America	USA		Oboh & Reeves Morris (1994)	

the basis of the available information. It should also be clarified that this procedure does not question the expertise of the involved palynologists, but relies solely on the information provided for comparison.

The locations and main features of the remaining selected records are summarized in Table 3 and Fig. 4. Morphological comparisons of the selected fossil records with extant *Pelliciera* pollen are conducted using the diagnostic characters listed in Table 1, including size, shape, aperture features, exine structure, and sculpture. The results of this analysis are also presented in Table 3 and Fig. 4, where six categories have been established to indicate the reliability of the reported pollen types as potential *Pelliciera* fossils:

- High reliability indicates a perfect match with the diagnostic characters of extant *Pelliciera*.
- Medium-high reliability refers to fossil pollen with minor differences but still consistent with *Pelliciera* morphology.
- Medium and low reliability indicate increasing degrees of significant differences that prevent the attribution of the involved pollen types to *Pelliciera*.
- Null reliability signifies a complete lack of similarity with *Pelliciera*.
- Doubtful includes acceptable images that do not clearly resolve the diagnostic characters necessary to evaluate their similarity with *Pelliciera*.

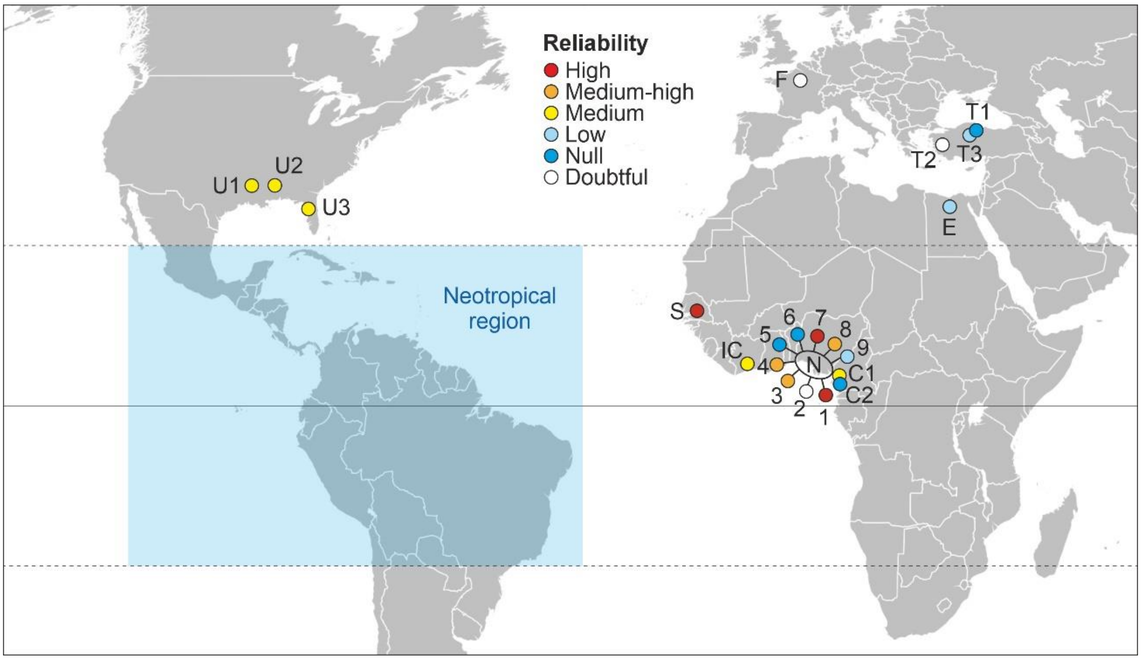

Figure 4. Published records of *Pelliciera* fossil pollen and associated form-species outside the Neotropical region after filtering for the three criteria specified in the text. Reliability refers to the degree of botanical affinity with extant *Pelliciera* pollen, see Table 3 for details. Neotropical records are shown in Fig. 2.

3.1. West Africa

The Nigerian records remain the most numerous and are concentrated in the Niger Delta and its surroundings. The first of these records, published by Shell palynologists Germeraad et al. (1968), corresponds to *P. crassus*, with the pollen descriptions and images provided aligning well with this form-species. Surprisingly, Muller (1981), one of the authors of that seminal paper, argued that this record required further confirmation, although he did not specify the reason. It is likely that Muller had access to additional information for such assessment. *P. crassus* was consistently abundant in numerous samples from four localities, ranging from the Middle Eocene to the Pilo-Pleistocene. Therefore, issues of scarcity can likely be ruled out.

Regarding identification, we should reference Fuchs (1970), another palynologist from the same company, who emphasized that pellicieroid and huroid forms—designated by the author as *V. crassus* and *F. ementitus*, respectively—of *P. crassus* were counted separately by Shell palynologists. However, this distinction was not made by Germeraad et al. (1968), who considered *P. crassus* to be very similar to *Hura*, although they also noted its resemblance to the fossil *Pelliciera* form described by Langenheim (1967). With this information, along with the doubts expressed by Muller (1981), it is not possible to determine whether the *P. crassus* of Germeraad et al. (1968) corresponds to *Hura* or *Pelliciera* fossils, or a mixture of both. Nevertheless, the information provided match well with the psilate-perforate form of *Pelliciera*.

Fuchs (1970) provided a Nigerian image of *P. crassus* corresponding to his pellicieroid form (*V. crassus*), characterized by conspicuous verrucae, as seen in his description of extant *Pelliciera* (see also Fig. 3). However, the grain is shown in polar view, making it impossible to distinguish aperture details. Furthermore, the author did not provide specific information regarding the location, abundance, or chronostratigraphic range of the sample. This record was also questioned by Muller (1981), again without explanation. The record by Jan du Chêne et al. (1978b) is similar to *Pelliciera* but deviates due to its reticulate sculpture and the absence of a tectum.

Table 3. Published records of potential fossil pollen records of *Pelliciera* outside the Neotropics containing descriptions, morphological hints and/or images useful for comparison. See Appendix 1 for terminology. Reliability refers to the degree of botanical affinity with extant *Pelliciera* pollen (Table 1), based on the material provided in the references listed. Diagnostic characters: GS, falling within the grain size interval; SS, spherical to suboblate shape; AC, amb circular; ET, falling within the range of exine thickness; TP, tectum present; CV, columellae visible; CLTS, colpi long, thin and stratight; OL, ora lalongate; OC, ora costate. Presence/absence: 1, yes; 0, no; ?, indistinguishable or more than one possibility in different grains; PVO, polar view only; EVO, equatorial view only. All these localities and their corresponding reliability as potential *Pelliciera* fossils are depicted in Fig. 4. Three of these records have been published in journals now discontinued or occasional but of international recognition in the field of palynology. These are indicated by uppercase number after the references and explained at the base of the table.

Map	**Location**	**Identification**	**Age**	**Reference**	**GS**	**SS**	**AC**	**ET**	**TP**	**CV**	**CLTS**	**OL**	**OC**	**Sculpture**	**Remarks**	**Reliability**
N1	Niger Delta (Nigeria)	*P. crassus*	Middle Eocene-Pleistocene	Germeraad et al. (1968)	1	1	1	1	1	1	1	1	1	Psilate to finely perfortae	Questioned by Muller (1981)	High
N2	Niger Delta (Nigeria)	*V. crassus*	Oligo-Miocene	Fuchs (1970)	1	?	1	1	?	0	?	?	?	Verrucate	PVO. Questioned by Muller (1981)	Doubtful
N3	Niger Delta (Nigeria)	*P. crassus*	Late Eocene	Jan du Chêne et al. (1978b)^1	1	?	1	1	0	1	1	1	1	Microreticulate	PVO. Unusual sculpture	Medium-high
N4	Niger Delta (Nigeria)	*P. crassus*	Miocene	Bankole et al. (2014)	0	?	1	1	1	1	1	1	1	Psilate-perforate	PVO. Grain very small (<30 μm)	Medium-high
N5	Niger Delta, offshore (Nigeria)	*P. crassus*	Late Miocene-Pleistocene	Olayiwola & Bamford (2016a)	0	0	0	0	0	0	?	?	?	Psilate	Prolate?	Null
N6	Niger Delta, offshore (Nigeria)	*P. crassus*	Plio-Pleistocene	Olayiwola & Bamford (2016b)	0	?	1	0	0	0	0	1	0	Psilate	PVO. Colpi costate	Null
N7	Niger Delta (Nigeria)	*P. crassus*	Middle Miocene	Durugbo & Olayiwola (2017)	1	1	1	1	1	1	0	1	1	Psilate-perforate	Colpi short	High
N8	Niger Delta (Nigeria)	*L. crassa*	Late Paleocene-Early Eocene	Mander et al. (2023)	1	1	1	1	1	1	1	1	0	Psilate	Colpi may be short and wide	Medium-high
N9	Dahomey Basin (Nigeria)	*P. crassus*	Late Eocene-Early Oligocene	Olayiwola et al. (2021, 2022b)	?	?	?	1	?	0	1	1	1	Verrucate	Grain small (<30 μm)	Low
C1	Littoral (Cameroon)	*P. crassus*	Late Eocene	Salard-Cheboldaeff (1976, 1979)	1	?	0	1	1	1	1	?	?	Psilate-perforate	PVO. Amb subtriangular	Medium
C2	Douala Basin (Cameroon)	*P. crassus?*	Paleocene-Early Eocene	Kwetche et al. (2018)	1	0	?	0	0	0	1	0	0	Psilate	EVO. Prolate, colpi marginate, os lolongate	Null

IC	Littoral (Ivory Coast)	*P. crassus*	Early Miocene	Bacchiana et al. (1982)	?	?	0	1	?	?	1	1	?	Rugulate	PVO. Colpi marginate	Low
S	Southern Senegal	*P. crassus*	Miocene	Médus (1975)[2]	1	1	1	1	1	1	1	1	1	Psilate to verrucate, perforate	Very similar to *P. crassus* of Germeraad et al. (1968)	High
E	Abu El Gharadig Basin (Egypt)	*P. crassus*	Oligocene	El Atfy et al. (2022)	0	?	0	1	1	1	?	?	?	Psilate	Grain small (<30 μm)	Low
T1	Çankiri-Çorum Basin (Turkey)	*P. crassus*	Eocene	Akgün (2002)	?	0	0	1	0	0	1	0	0	Reticulate	Prolate, amb subtriangular, colpi marginate	Null
T2	Çardak-Tokça Basin (Turkey)	*P. crassus*	Mid-Late Eocene	Akkiraz et al. (2006)	?	?	1	?	?	?	1	?	0	Psilate	PVO. Different forms in the same type	Doubtful
T3	Çankiri Basin (Turkey)	*P. crassus*	Mid-Late Eocene	Akkiraz et al. (2008)	1	?	?	1	0	0	1	1	?	Reticulate	Amb subtriangular	Low
F	Paris Basin (France)	*Pelliciera*	Late Eocene-Oligocene	Châteauneuf (1980)	0	?	?	?	?	?	1	1	1	Psilate-scabrate	Different forms in the same type	Doubtful
U1	Mississippi embayment (USA)	*Pelliciera?*	Eocene	Elsik (1974)	1	?	1	1	1	1	1	?	0	Foveolate	VPO	Medium
U2	N Gulf coast (USA)	*L. crassa*	Eocene-Early Oligocene	Frederiksen (1988)[3]	1	?	?	1	1	1	?	1	1	Perforate	Different forms in the same type	Medium
U3	NE Gulf coast (USA)	*L. crassa*	Middle Eocene	Jarzen & Dilcher (2006)	1	?	0	1	1	1	1	?	?	Psilate to verrucate, perforate	Amb subtriangular	Medium

[1] Revista Española de Micropaleontología (published until 2012)

[2] Pollen et Spores (published until 1994)

[3] American Association of Stratigraphic Palynologists Contributions Series (occasional papers)

The remaining Nigerian records of *P. crassus* meeting the aforementioned criteria for reliable comparisons are from the last decade (2014 onward) and primarily consist of images. In only one instance (Mander et al., 2023), *L. crassa* is used instead of *P. crassus* to refer to fossil *Pelliciera* pollen, with both images and a formal description of the fossil available. Among these records, only one (Durugbo & Olayiwola, 2017) reliably matches *Pelliciera* pollen. Two others differ in key diagnostic features, such as smaller grain size (Bankole et al., 2014) and the absence of endoapertural costae (Mander et al., 2023). Other records show some partial similarities but cannot be confidently ascribed to the *Pelliciera*-type, while certain images bear no resemblance to *Pelliciera* pollen. Other West African records come from Cameroon, Ivory Coast, and Senegal. The records from Cameroon and Ivory Coast show low or no similarity with *Pelliciera*. In contrast, the Senegal record (Médus, 1975) is highly reliable as a potential *Pelliciera* fossil.

In summary, three West African pollen records (N1, N7, and S) are compatible with *Pelliciera*, and three others (N3, N4, and N8) are sufficiently similar to qualify as potential fossils of this genus. These records range from the Eocene to the Plio-Pleistocene. At these localities—especially N1, N4, N7, N8, and S—*P. crassus*/*L. crassa* frequently co-occurs with mangrove representatives such as *Zonocostites ramonae* (*Rhizophora*), *Spinizonocolpites echinatus*/*S. baculatus*/*S. prominatus* (*Nypa*), *Deltoidospora adriennis* (*Acrostichum*), and *Verutricolporites rotundiporus* (*Crenea*), among others (Germeraad et al., 1968; Médus, 1975; Bankole et al., 2014; Durugbo & Olayiwola, 2017; Mander et al., 2023). This provides indirect evidence for fossil pollen types as mangrove components, although primary evidence for *Pelliciera* fossils should rely on morphological similarity. As in the Neotropical region (Rull, 2022, 2023b, c), the association of *Pelliciera* with *Nypa* occurred during the Eocene, while its co-occurrence with *Rhizophora* extended from the Oligocene onward, when *Nypa* disappeared, and *Rhizophora* began to dominate mangroves in both regions.

3.2. Europe

A single record from Europe, corresponding to France, is available. Although the images are clear, key diagnostic features such as grain size, shape, and exine structure are difficult to discern or differ from *Pelliciera*, placing this record in the doubtful category. To address issues related to size, Châteauneuf (1980) proposed a new subspecies, *Psilatricolporites crassus* subsp. *minor*, to encompass smaller pollen types (20–30 µm). The proposed botanical affinity was tentatively linked to the Theaceae family, which at the time included *Pelliciera*. However, the pollen illustration provided by Châteauneuf depicts a very thin exine, with columellae not visible and linear ora rather than oval or fusiform. This subspecies has only been cited in local and relatively contemporaneous literature (Schuler et al., 1990). In addition, different morphologies are included in the same pollen type, which complicates identification. These records correspond to the Late Eocene and Oligocene, and in some Eocene intervals, *P. crassus* appears alongside *Nypa* and other mangrove elements such as *Bruguiera* and *Avicennia* (Châteauneuf, 1980).

3.3. Middle East

All the images provided for the Middle East (Egypt and Turkey) differ significantly from *Pelliciera*. The primary differences are observed in grain shape, exine structure and aperture features, which are highly diagnostic characteristics (Table 2). The inclusion of more than one morphological type within *P. crassus* makes identification uncertain. The Turkish records date to the Middle to Late Eocene and occur alongside other mangrove and back-mangrove components, such as *Nypa*-like and *Avicennia*-type pollen (Ağkün, 2002; Akkiraz et al., 2006, 2008).

3.4. North America

North American fossil records – all of them situated near the N-NE Gulf coasts – fall within the medium-reliability category as they exhibit some similarity to *Pelliciera*. However, the images provided either differ from or lack information on diagnostic characters such as grain shape in equatorial and polar views and apertures (e.g., os lalongate, costate). Additionally, in some cases, different pollen morphologies are grouped under the same type—most notably in *L. crassa* (Frederiksen, 1988)—which complicates the clear definition of certain morphological features. Gulf Coast records correspond mostly to the Eocene and *L. crassa* occurs together other mangrove components such as *Nypa* and *Crenea* (Jarzen & Dilcher, 2006).

North American fossil records, all located near the N-NE Gulf coasts, fall into the medium-reliability category as they exhibit some similarity to *Pelliciera*. However, the images provided either differ from or lack important diagnostic details, such as grain shape in equatorial and polar views, and apertures (e.g., os lalongate, costate). Moreover, in some cases, different pollen morphologies are grouped under the same type—most notably in *L. crassa* (Frederiksen, 1988)—which complicates the clear definition of certain morphological features. Gulf Coast records are primarily from the Eocene, and *L. crassa* occurs alongside other mangrove components, such as the fossil representatives of *Nypa* and *Crenea* (Jarzen & Dilcher, 2006).

4. Conclusions

Based on the above analysis of fossil palynological evidence, the only region outside the Neotropics where *Pelliciera* might have occurred is tropical West Africa. While the possibility of *Pelliciera* being present in other regions cannot be ruled out, it also cannot be confirmed with the currently available fossil evidence. In several cases, the co-occurrence of potential *Pelliciera* fossils with other mangrove elements—particularly *Nypa* in the Eocene and *Rhizophora* from the Oligocene onward, as is typical in the Neotropics (Graham, 1995; Gee, 2001)—supports their mangrove affinity. However, pollen morphological features should remain the primary evidence for establishing a reliable botanical affinity between *Pelliciera* and their putative fossil representatives.

The available evidence remains insufficient to propose a new global paleobiogeographical and evolutionary framework for *Pelliciera* from the Eocene to the present, as has been done for the Neotropical region (Rull, 2023a). Nevertheless, the potential past presence of this mangrove tree on both sides of the Atlantic opens new avenues for understanding the origins and evolution of mangroves since the Eocene, a time when *Rhizophora* was still absent or scarce in both the Americas and Africa. Such a broad investigation requires a more comprehensive and accurate dataset, with a particular focus on reliable taxonomic identification—a significant challenge in the existing records, likely due to the considerable morphological variability of *Pelliciera* pollen and its purported fossil representatives.

Efforts to address this issue are worthwhile, not only for *Pelliciera* but also for other taxa. It would be valuable to determine whether current palynological databases could withstand a rigorous taxonomic review like the one attempted here and to assess how the results of such an analysis might necessitate evolutionary and paleobiogeographical reconsiderations.

5. Further research

A thorough and detailed study of extant *Pelliciera* pollen using standard palynological methods and terminology remains to be undertaken and is urgently needed. This initiative should be relatively straightforward, given the limited geographical range of the genus and the accessibility of field and herbarium specimens. Such a study could provide essential reference information to account for the high morphological variability of extant species, facilitating meaningful comparisons with fossil material.

Ideally, studies on potential fossil *Pelliciera* representatives should include detailed morphological descriptions and high-quality illustrations of pollen morphology, enabling direct comparisons with modern *Pelliciera* pollen. Palynologists working with confidential materials are especially encouraged to include this type of information in their publications. As a former biostratigrapher with over 12 years of experience in an oil company, the author is aware that this information can be shared without breaching confidentiality (e.g., Germeraad et al.; Regali et al., 1974; Lorente, 1986; Muller et al., 1987; Rull, 2024).

Publishing in internationally recognized journals with rigorous peer-review standards is also crucial. Publishing in gray literature of local or institutional scope – usually in languages other than English – or in journals with questionable review practices, can hinder the dissemination of reliable information and compromise the credibility of potentially valuable data. Gray literature is often difficult, if not impossible, to access and, over time, becomes increasingly useless. Conversely, journals prioritizing pay-to-publish business models over scientific rigor may offer wide accessibility but can undermine the integrity of academic progress (Schöpfel, 2011; Beall, 2012).

Many records of *Pelliciera* and other pollen fossils are primarily focused on their chronostratigraphic and paleoenvironmental utility, especially in the context of hydrocarbon exploration and exploitation in specific sedimentary basins. However, broader global and regional biogeographical considerations should not be overlooked. Palynologists must recognize that, with the advent of large-scale databases, their fossil records may be used to reconstruct the historical biogeography of specific taxa and communities. It is not uncommon for such databases to incorporate bulk records without verifying the taxonomic accuracy or botanical affinities of individual entries. Therefore, palynologists must not only be rigorous in their identifications but also provide comprehensive information to validate their raw data. Without such diligence, data may be lost, misinterpreted, or rendered useless, potentially leading to flawed biogeographical and evolutionary conclusions.

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Appendix 1

Updated and homogenized pollen morphological terminology used in Table 1 following Punt et al. (2007) and Halbritter et al. (2018).

Amb. Outline in polar view.

Areolate. With the ectexine forming a negative reticulum of polygonal areas separated by grooves.

Colpus (pl. colpi). Meridionally elongated aperture with a length/breadth ratio greater than 2.

Columella (pl. columellae). Rod-like element of the ectexine supporting a tectum.

Costate. With costae (thickening of the endexine bordering an enoaperture).

Ectoaperture. Aperture in the outer layer of the grain (ectexine).

Endoaperture. aperture in the inner layer of the grain (endexine).

Fossulate. With fossulae (elongated, irregular grooves in the surface).

Foveolate. With fovelolae (more or less rounded depressions or lumina >1 μm in diameter, the distance between foveolae is greater than their breadth).

Gemmate. With gemmae (an ectexine element >1 μm constricted at its base).

Isopolar. With identical proximal and distant faces or poles.

Lalongate. Shape of a transversely elongated endoaperture (os).

Margo (pl. margines). Area of exine around the ectocolpus that differentiate either in ornamentation or in thickness.

Monads. Single grains.

Oblate. Polar axis (P) shorter than equatorial diameter (E), P/E <1.

Os (pl. ora). Synonym of endoaperture.

Perforate. Pollen wall with holes less than 1 μm diameter.

Prolate. Polar axis (P) longer than equatorial diameter (E), P/E >1.

Psilate. Pollen wall with a smooth surface.

Radially symmetric. With two or more planes of symmetry (three, in this case).

Rugulate. With rugulae (elongated ectexine elements > 1μm long arranged in an irregular pattern).

Scabrate. With scabrae (elements of the ornamentation of any shape <1 μm in all directions, close to the resolution of the light microscope).

Spherical. Polar axis (P) and equatorial diameter (E) of equal size, P/E =1.

Supratectal. Situated on the top of the tectum.

Syncolporate. With the colpi end anastomosed at the poles.

Tectate. With tectum (the layer of the extexine that forms a roof over the columellae).

Verruca (pl. verrucae). Wart-like ectexine element >1 μm wide broader than high and not constricted in the base.

Vestibulum. Separation between exine layers forming a cavity between the inner and outer apertures.

Zonotricolporate. With tree colpori (colpus + os) regularly distributed along the equator.