ECOLOGICAL AND PALYNOLOGICAL NOTES ON PELLICIERA RHIZOPHORAE

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SUMMARY

Pelliciera rhizophorae is now found almost exclusively along the Colombian Pacific Coast, but its pollen is found in the Oligo/Miocene of Nigeria, Mexico, and Northern South America, Differentiation between the pollen of *Pelliciera rhizophorae* and the genus *Hura* which often have been lumped together, may permit a finer paleoecological interpretation.

Relatively high percentages of huroid pollen alone may point to deposition outside a mangrove belt and to a climate with a rather pronounced dry season. Pellicieroid pollen without huroid pollen but frequently associated with rhizophoroid pollen may indicate deposition near a pronounced mangrove belt and a humid climate without pronounced seasonal changes. Huroid pollen associated with pellicieroid and rhizophoroid pollen may point to transport of the former from areas with a relatively dry season into a depositional area in the neighbourhood of a mangrove belt.

During the sampling of Recent sediments in the area of the Lower Baudó on the Pacific Coast of Colombia in connection with a project on transport and deposition of sporomorphs in a Recent river system[1], an extremely unusual plant association within the mangrove belt was recognised in several places (*fig. 4*).

This almost monotypical association consists of *Pelliciera rhizophorae* Planchon & Triana (Theaceae), a tree measuring between 6 and 15 m, with a well developed, simple, erect trunk and a narrow, elongate crown. The lower part of the trunk, up to about 1.5–2 m above soil level (average high-tide line) is conical, owing to the presence of pronounced buttresses. The diameter of the trunk including the plank buttresses at soil level may measure up to 1.5 m, but measures only 15–20 cm above the average high-tide mark (*figs. 1* and *2*).

The sharply pointed, oblanceolate (12–15 cm long/2.5–4 cm broad), leathery, asymmetric leaves with rather obscure veins and midribs are clustered at the ends of the twigs (*fig. 3*). The white flowers, 8–10 cm across, are sessile in the leaf clusters, have very narrow, elongate petals and drop off very easily (*figs. 2* and *3*). The distinctive fruit is beaked, blackish to dark grey, biconvex, strongly corrugated on the sides, at maturity about 10 cm long, 8 cm broad and 3–4 cm thick, with a cordate body, orbicular or broadly ovate, abruptly contracted and prolonged at the apex into a stout beak 1.5–2.5 cm long (*fig. 3*). The fruits do not, however, fall with their pointed apex down to the surface, but, having their heavy end on the side opposite to the pointed end, fall either on one face, or more frequently on their broad end.

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[1] Initiated by Koninklijke/Shell Exploratie en Produktie Laboratorium.

Fig. 1. Pure stand of *Pelliciera* on the left bank of the Rio Baudó embayment. Note the solid, sandy ground and the pronounced marks of Spring high-tide coinciding with the upper end of the pronounced plank buttresses.

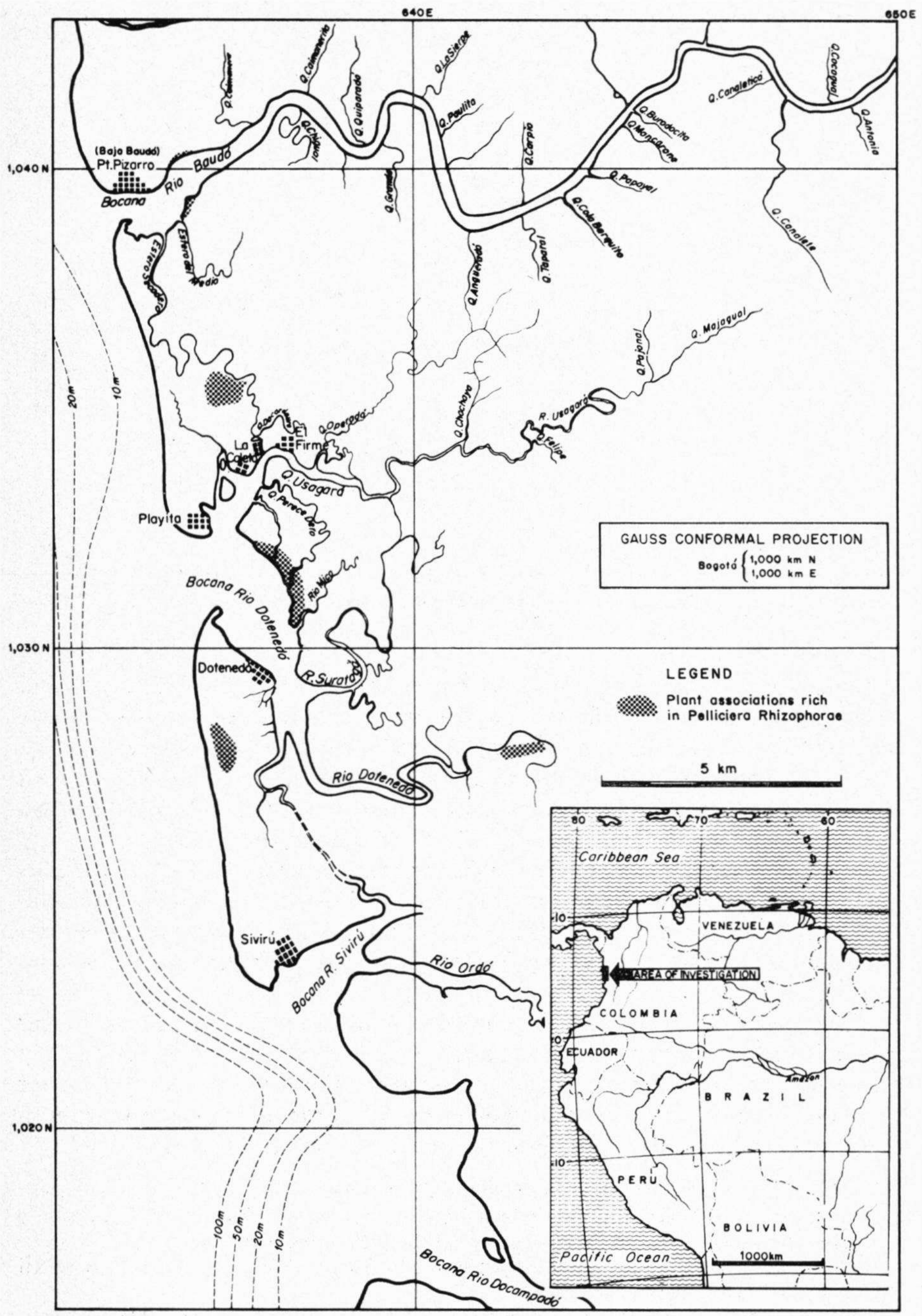
Fig. 2. View from the *Pelliciera* stand across the River Baudó. Note flowers in upper centre of photograph and seedlings in front of old trees.

Fig. 3. Flowers and fruits of *Pelliciera.* Note the pronounced beak of fruits.

The fruits float with their beaked end downwards and at low tide may settle in this position into the soil where they soon start to germinate (*fig. 2*). Fruit growth and flowering seem to have been observed throughout the year, but the main fruit crop seems to occur towards the end of the rainy season (October–November) and is shed from mid-November to mid-December.

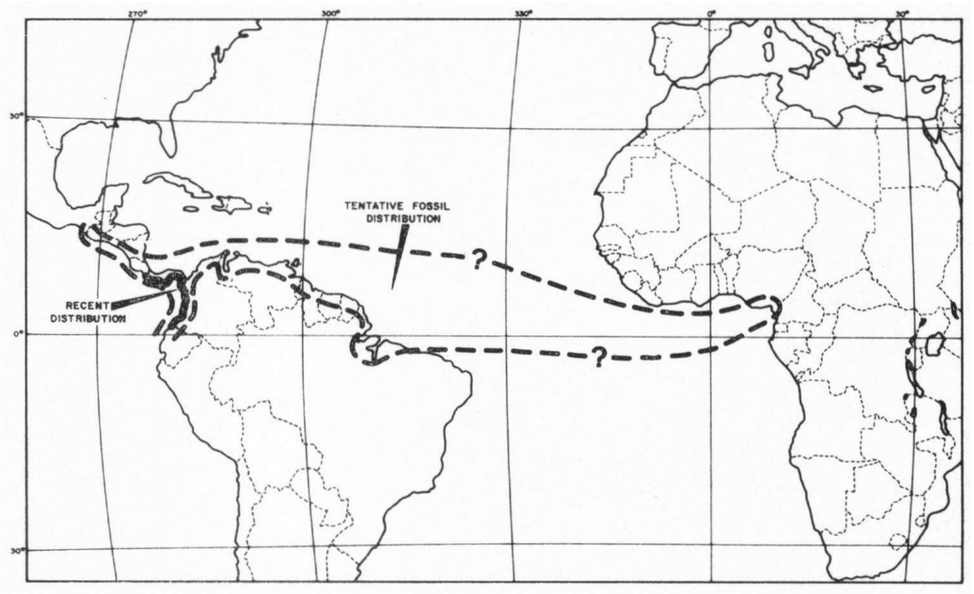
The protection of the seed by the fruit wall is extremely poor, and the seeds are quickly killed by mechanical destruction if battered against hard objects or by drying out when tossed upon sun-exposed beaches. Therefore, although the fruits are relatively well equipped for floating and can thus obviously be dispersed by tidal movements or transported over longer distances by ocean currents, their germinating power is believed to be preserved during a short time only, and effective disperal only to be possible across a relatively short distance from their place of origin.

This poor propagative power may be responsible in the first instance for the



DISTRIBUTION OF PELLICIERETUM RHIZOPHORAE IN THE LOWER BAUDÓ AREA

Fig. 4



RECENT (TREE) AND TENTATIVE FOSSIL (POLLEN) DISTRIBUTION OF PELLICIERA RHIZOPHORAE

Fig. 5

extremely restricted geographical distribution in recent times (*fig. 5*)[1]. *Pelliciera rhizophorae*[2], found for the first time at the embayment of Buenaventura (TRIANA & PLANCHON 1862:38), seems nowadays to be restricted to the coastal area of the Pacific between northernmost Ecuador and southernmost Costa Rica, with a wider distribution and higher frequencies along the Pacific coast of Colombia between Tumaco in the South and Cabo Corrientes in the North.

Another restricting factor seems to be the rather peculiar ecological demands of this mangrove representative. It appears, at least in the Baudó-Dotenedó area, that the most flourishing trees of *Pelliciera* occur in rather restricted but pure stands of widely spaced trees forming an open-type forest with virtually no undergrowth.[3]

These pure stands of *Pelliciera* are found on firm, sandy, slightly higher grounds of low salinity covered with a very thin (5–10 mm) layer of recently deposited mud. On lower, soft mud ground with a thicker mud layer and greater salinity, *Pelliciera* may be associated with *Rhizophora*, in which case both *Pelliciera* and *Rhizophora* are developed as only small-sized trees.

[1] The fossil distribution reconstructed from the pollen-occurences in the Tertiary of northern South America and Nigeria can be explained only by continental drift, unless one assumes a marked difference in the propagative power of the pellicieroid ancestor.

[2] Local names: Piñuelo (Baudó-area); Igaunero (area South of Buenaventura); Palo de Sal (Panamá); Mangle pinuela (Costa Rica).

[3] But with an herb (*Tuberostyles rhizophorae*) climbing along the *Pelliciera* trunks, frequent epiphytic orchids (*Epidendrum nocturnum*) and scattered individuals of the bromeliad family growing in the axils of the twigs of *Pelliciera*.

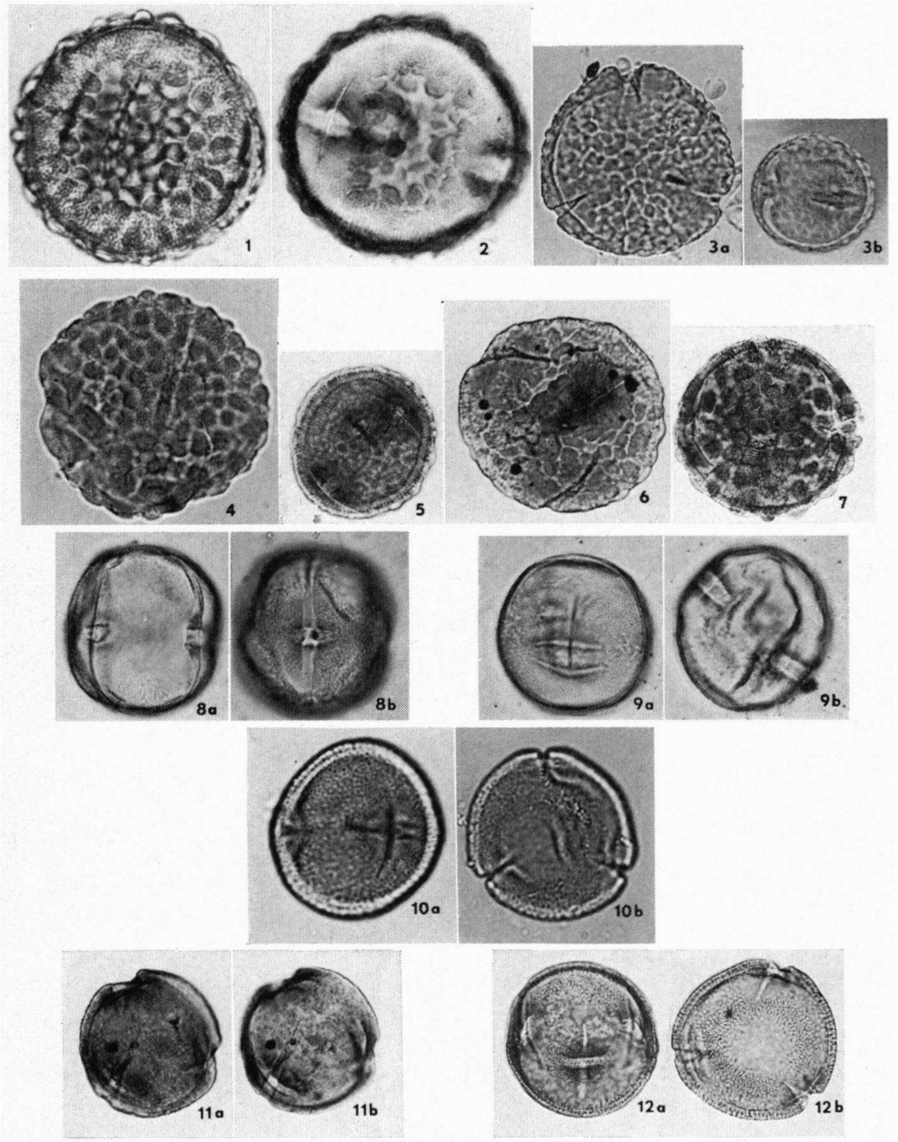
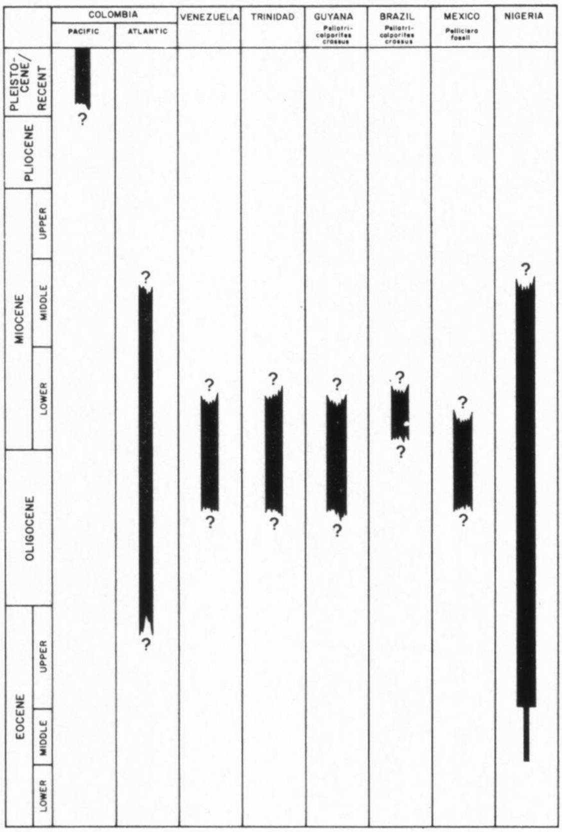


Plate I, 2. *Pelliciera rhizophorae*, Recent; 3a, 3b. *Verrutricolporites crassus*, Colombia Baudó, sub-Recent; 4. *Verrutricolporites crassus*, Colombia Atlantic, Oligo/Miocene; 5. *Verrutricolporites crassus*, Venezuela, Oligo/Miocene; 6. *Verrutricolporites, crassus* Trinidad, Oligo/Miocene; 7. *Verrutricolporites crassus*, Nigeria, Eocene-Miocene; 8a, 8b. *Hura crepitans*, Recent; 9a, 9b. *Hura polyandra*, Recent; 10a, 10b. *Foveotricolporites ementitus*, Colombia, Eocene-? Recent; 11a, 11b. *Foveotricolporites ementitus*, Venezuela, Eocene-? Recent; 12a, 12b. *Foveotricolporites ementitus*, Nigeria.

Occasionally *Pelliciera* is associated with *Mora oleifera* and *Euterpe cuatrecasana*, plants considered to be typical fresh-water swamp representatives. It then forms a transitional zone over short distances between the mangrove and the fresh-water swamp. A third vegetation type in which *Pelliciera* is seen in the form of dwarfed, widely spaced shrubby trees, is found in fairly widespread swamp areas in the interior of the high mangrove-belt between the small, meandering rivers (quebradas) and natural water channels (esteros). The vegetation in these brackish-water swamps that are flooded by spring tides is only four to six feet high and composed mainly of sedges and *Acrostichum aureum* (back swamp fern) (*fig. 6*). WEST (1956:111) ascribed this vegetation type "to the slow rise of land through decay of mangrove vegetation" and thought that "owing, perhaps, to acidity and lack of fine muddy sediment rich in organic matter, tall mangrove forests fail to regenerate themselves in the inner channel areas".

The pollen of this unusual mangrove representative has long been known to palynologists studying Tertiary sediments, but has been lumped with pollen with close affinities to the recent representatives of the genus *Hura* L. (*e.g.*



TENTATIVE STRATIGRAPHIC DISTRIBUTION OF VERRUTRICOLPORITES CRASSUS

(VAN DER HAMMEN & WIJMSTRA) COMB. NOVA

Fig. 7

GERMERAAD *et al.* 1968: 330–332/t. 16, ff. 1, 2). Although the pollen of *Pelliciera* and *Hura* have many features in common, there is – at least among grains of recent pollen – a clear difference in sculpture which appears to separate them (see comparative description and *plate 1*).

According to the literature (*e.g.* BEARD 1946: passim; LINDEMAN 1953: 80–81/105–106) *Hura,* in contrast to *Pelliciera,* seems to be a locally important accessory species in marginal marsh forests in the peneplain and hill areas along ridge margins, sometimes extending into the fresh-water back swamp area.

It seems that *Hura* is confined to areas in southern Central and northern South America (from Honduras to Bolivia and Peru) with rather pronounced dry seasons. However, judging from personal observations and according to literature (WEST 1957; CUATRECASAS 1958a; 1958b), it appears to be absent from the typical, tropical low-land, marshy rain forests such as those found along the Pacific coast between Panamá and the Tumaco in Colombia.

Reconstruction of the paleophytogeographical distribution (*fig. 5*) and the stratigraphical range (*fig. 7*) of the fossil pollen resembling the pollen of *Pelliciera rhizophorae* described in the comparative description on page 892 is considerably hampered because its pollen has been lumped together with pollen resembling that of the genus *Hura.*

The two pollen types seem to have been combined within one paleopalynotype not only by GERMERAAD *et al.* (1968: 330–332/t. 16, ff. 1, 2), but also by the authors who described *Psilatricolporites crassus* VAN DER HAMMEN & WYMSTRA (1964: 237)[1]. This latter palynomorph was recently interpreted by WYMSTRA

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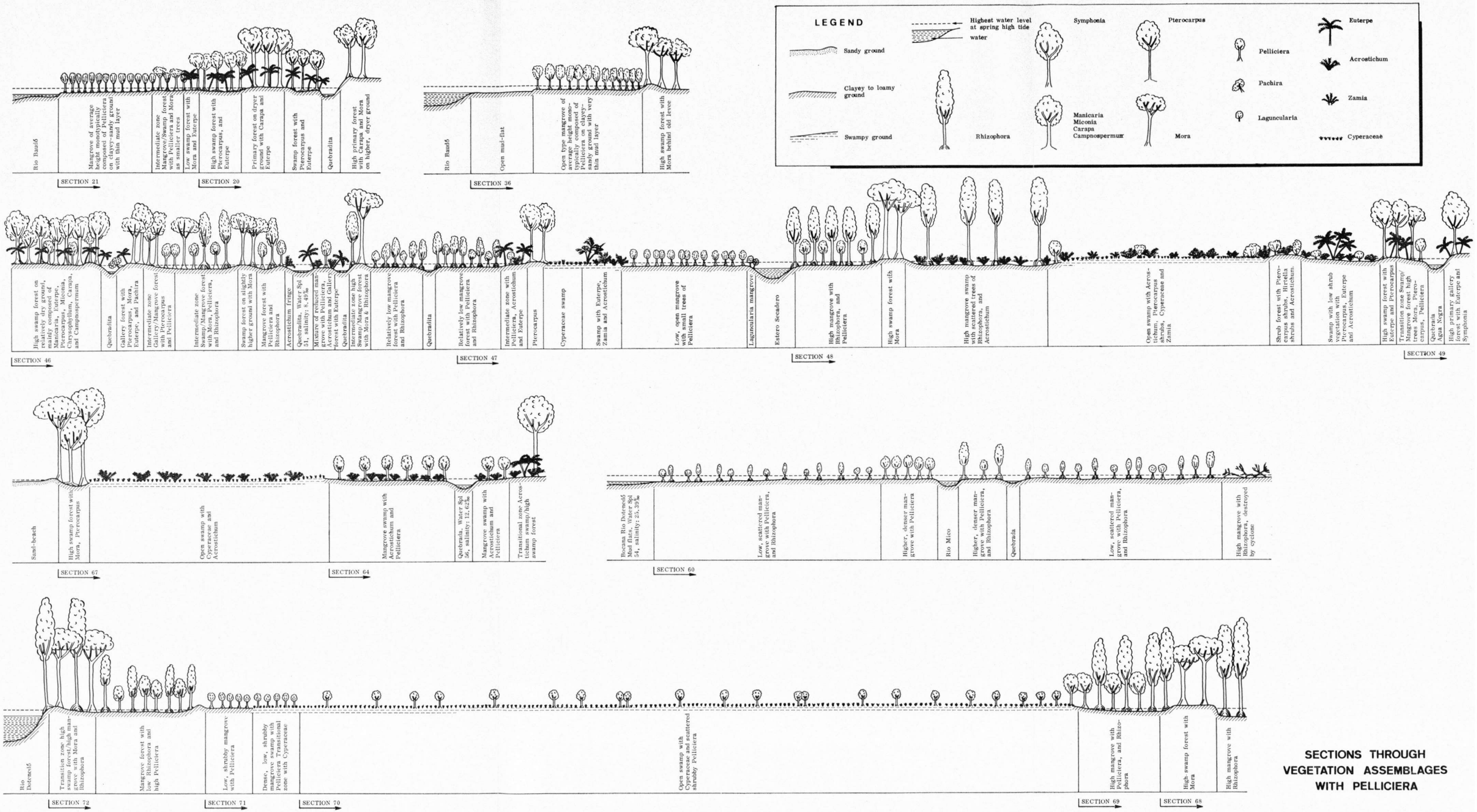
[1] A remark on the nomenclature of *Psilatricolporites crassus* may be added here. The name *Psilatricolporites* was originally proposed by van der Hammen (1956: 91) for a form-subgenus within the genus *Tricolporites,* with the subgenotype *Tricolporites* (*Psilatricolporites*) *inornatus,* the pollen of the recent taxon *Clethra bicolor* [Bonpland, ex] Kunth [adjuv. Humboldt]. The fact that the name *Psilatricolporites* was originally proposed for a form-subgenus gives rise to the discussion of whether a form-genus may be typified by a part of a Recent plant (see Potonié 1960: 50 and the reply by van der Hammen & Wijmstra 1964: 236). The taxon *Psilatricolporites* was raised to generic rank by Pierce (1961: 53) and typified by *Psilatricolporites prolatus* from Upper Cretaceous sediments and with close resemblance to the Recent pollen of *Lithocarpus densiflora* Rehder (Fagaceae-Castaneoideae). This renders superfluous the later publication of the name *Psilatricolporites,* invalidly typified by the typus eventualis *Psilatricolporites operculatus,* with close resemblance to species of the genus *Alchornea* (Euphorbiaceae). As to the nomenclature of the fossil pellicieroid and the fossil huroid pollen, following the nomenclatural principles outlined by van der Hammen (1956: 71–77), embracing as they do palaeopalynotypes with a psilate sculpture as is found actually with *Clethra* as well as with *Lithocarpus* and *Alchornea,* neither palaeopalynotype pertains to the form genus *Psilatricolporites* (van der Hammen) Pierce. From the descriptions of the pollen of *Pelliciera* and *Hura* it is evident that they are not psilate, and they should therefore be placed in other form-genera:
pellicieroid pollen:
Verrutricolporites crassus (Van der Hammen & Wijmstra) H. P. Fuchs, *comb. nova* = *Psilatricolporites crassus* Van der Hammen & Wijmstra (1964: 237/t.1, ff.1–2, *pro parte*)
huroid pollen:
Foveotricolporites ementitus H. P. Fuchs, *formaspec. nova* = *Psilatricolporites crassus* Van der Hammen & Wijmstra (1964: 237/t.1, f. 3–4 *pro parte*)

Comparative Palynomorphological Descriptions

	Pelliciera rhizophorae TRIANA & PLANCHON (Theaceae)	*Hura crepitans* LINNAEUS *Hura polyandra* H. BAILLON[1] (Euphorbiaceae)
Shape	Length of polar axis approximately equal to equatorial axis, around 80 micron (77–82); grain in polar and equatorial view practically round.	Length of polar axis approximately equal to equatorial axis, around 50 micron (48–55); grain in polar and equatorial view practically round.
Apertures	Three, arranged in radial symmetry, grain isopolar.	Three, arranged in radial symmetry, grain isopolar.
Ektexinous	Elongated, fairly long, up to 40 micron, with straight to slightly convex sides and indistinct terminations.	Elongated, fairly long, up to 40 micron, narrow with straight sides and indistinct terminations (short, around 10 micron with straight sides and ± pointed 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.	Perpendicular to ektexinous apertures, equatorially elongated to ovally shaped, ± 12 micron wide with rounded terminations (± 20 micron long, ± 4 micron wide); endexine thickened along endexinous apertures.
Structure	Exine clearly differentiated, 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 micron.	Exine clearly differentiated, up to 2–2.5 micron (up to 1.5 micron). *Endexine* up to 1 micron or less (about 0.5 micron); *pillars* smaller than 1 micron, of equal length and slightly varying diameter (fairly uniform diameter), densely spaced, unbranched, irregularly arranged; *tegillum* of equal thickness over the entire surface of the grain, generally 1 micron or less (around 0.5 micron).
Sculpture	Macropositive elements with rounded to irregular or undulating base, convex shaft and rounded top, up to 2 micron high, of practically uniform height, placed uniformly or 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 micron.	Micronegative, often fairly indistinct, consisting of very small, ± round, widely spaced and regularly placed perforations.

[1] Features of *Hura polyandra* which differ from those of *Hura crepitans* are placed between brackets.



SECTIONS THROUGH VEGETATION ASSEMBLAGES WITH PELLICIERA

(1968: 114–116) as being most probably conspecific with the Recent pollen of *Pelliciera rhizophorae.*

Fortunately, however, the fossil pollen of *Pelliciera-* and *Hura*-affinities have originally been kept and counted separately by Shell palynologists; this permits at least some general conclusions as to the paleophytogeographical distribution and the stratigraphical range (see tentative range chart).

In Colombia, where *Pelliciera* still occurs today, pellicieroid pollen has been found in cutting samples from a well in the central area of the Rio Atrato as well as in surface samples from the Lower Valley of the Magdalena River, both river systems belonging to the Caribbean drainage area. The stratigraphical range in Colombia seems to cover periods from Uppermost Eocene to Middle Miocene (WYMSTRA 1968: 114–116), but should theoretically cover the entire range from the Uppermost Eocene to Recent.

In Venezuela, Trinidad, the Guianas, and the Brazilian Amazonas area, pellicieroid pollen has been reported mainly from Miocene sediments. LANGENHEIM *et al.* (1967: 314) found pellicieroid pollen in amber of Oligo/Miocene age in the Chiapas-province of Mexico, and Company records from Nigeria indicate the same type of pellicieroid pollen in Oligo–Miocene sediments of the Niger delta (*fig. 5*).

As may be expected in view of the ecological demands of *Pelliciera* nowadays, and assuming that these demands have not changed since Oligo/Miocene times, pellicieroid pollen is found mainly in small quantities associated with rhizophoroid pollen, but may become fairly abundant in certain samples.

Separation of the palaeopalynotype with pellicieroid affinities from the huroid type may provide a possible indication as to the environment of deposition, assuming that the palynomorphological characters are fair indicators of the taxonomical affinities of the fossil plants and that the ecological demands of these plants have not changed since Middle Tertiary times. In this case, the occurrence of huroid pollen alone and in relatively large percentages may point to deposition in areas outside a typical mangrove belt, and possibly in a climate with a relatively pronounced dry season. Pellicieroid pollen, nearly always found associated with high percentages of rhizophoroid pollen, indicate deposition within a pronounced mangrove belt at relatively short distance and possibly in a humid climate with no pronounced changes between wet and dry seasons. Huroid pollen associated with pellicieroid and rhizophoroid pollen may point to transport of the former from areas with a pronounced dry season over some distance to a depositional area close to a pronounced mangrove belt.

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